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irtsvögeln, die den  
eis. Jene Arten, die  
könnte die Verhal-  
eise funktionieren.

## SEXUAL COMPETITION IN *SCATOPHAGA STERCORARIA*: SIZE- AND DENSITY-RELATED CHANGES IN MALE ABILITY TO CAPTURE FEMALES

by

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(With 11 Figures)  
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### INTRODUCTION

In resource-based mating systems male success in aggression with conspecific males is a primary determinant of male mating success (VERNER, 1964; BROWN, 1964; ALEXANDER, 1975; BORGIA, 1979). The mating system of the fly, *Scatophaga stercoraria* (Diptera: Scatophagidae), has offered an opportunity to test one aspect of this theory; that changes in patterns of resource structure influence individual male success in obtaining matings (BORGIA, 1980a). Results of these experiments showed that large males reproduce at a higher rate than small males under conditions of limited availability of resources. This result is consistent with models of mate choice developed for systems in which females choose mates. However, *Scatophaga* males capture females and this leads to different predictions for the effect of male size on individual mating success. Specifically, that at low resource availability large males should be no more successful than small males (BORGIA, 1979).

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In this paper I explore how changes in resource structure and male density affect male agonistic and mate-searching behavior. This is done to document the effect of changes in resource availability on male behavior, and to help interpret results from resource manipulation experiments.

Males of *Scatophaga* commonly aggregate around droppings or pats of fresh cow dung to capture females that visit pats to oviposit. Males copulate with females immediately after capture and then guard the females as they oviposit (see HAMMER, 1941; FOSTER, 1967a, b, c; PARKER, 1970a, b, d, e, 1974c; BORGIA, 1979, 1981a). Single males also attack other individuals that are amplexing with females, attempting to separate the pair and take the female. Males successful in takeovers copulate with the female and fertilize most of the eggs she carries (PARKER, 1970e). Sexually mature male *Scatophaga* vary greatly in size (5.2-11.5 mm wing length), and size differences are largely a product of varying larval growth conditions (BORGIA, 1980c).

PARKER (1970d) made an extensive study of male behavior around the oviposition site of *Scatophaga* in England. He described males around the site as in "turmoil", moving rapidly about with frequent attacks on one another. He provides a detailed analysis of behavior sequences and rates of attack by males on other unpaired males and males engaged with females. PARKER's emphasis, however, is largely typological, and although valuable in understanding generalized behavior patterns common within a species, tends to mask patterns of intrasexual variation in aggressive ability and mating success. This is best illustrated by his assertion that "... all males searching for females achieve an approximately equal fertilisation rate..." (PARKER, 1970d) that conflicts with results of my work in Michigan that shows that male mating success is strongly size dependent (BORGIA, 1981a).

The study of intrasexual variation in patterns of mate-searching forms the focus of this report. Male-male interactions are analyzed with special reference to how size differences among males influence individual success in the capture and control of females. Specific behaviors considered include analysis of 1) attacks on individuals of different size in the vicinity of the oviposition site, 2) territorial behavior by males on low male density pats, 3) non-territorial behavior with searching behavior common at high male density, and 4) influence of male size on the ability to win and resist replacement or "takeover" attempts.

Observations of male behavior were made in Michigan in the Fall of 1977. Several continuous records of fly activity described specific sounds into a tape recorder. Noting counts on the footage meter and duration of each type of behavior to

Extremely short duration behavior with a Bolex camera and a Macro-lens markings could be recognized. The Analyser which allows slow-motion which a particular behavior occurs. Relatively long duration events were recorded. Cumulative time stopwatches were used.

For experiments requiring paired males presented with gravid females that were the most successful method for capturing the female inside. Flies that had been captured by gentle tapping of the vial.

Another method which proved successful was presenting her to a hemostat, and then presenting her to a male. He accepted such females, but small males were more likely to attack them toward them. Once the male made contact, he chased the flies from natural and synthesized behavioral differences.

Flies were measured in two ways. One was measuring with dial calipers. Wing length of captured flies were made with calipers. The projection as the wing is folded over the body. In some experimental results, size measurements were made. A complete discussion of these methods is given in BORGIA (1981a).

Statistical analyses include: simple correlation, Wilcoxon test (W), Spearman's  $r_s$  (S), and NAGOTT (1972). Means are designated by  $\bar{x}$ .

## MALE-MALE INTERACTIONS

On pats with 10 or more males, there is unrestricted movement over the pat. Males reach peak numbers on a pat at the same time. Activity is greatest while the pat is fresh or much more rapidly at high density.

Collisions are common among males searching for mates. Females generally are captured immediately after oviposition is complete. This is usually other species, capture of *Scatophaga* is relatively rare, in part because of the high density of *Scatophaga* on a pat.

## METHODS

Observations of male behavior were carried out in a pasture 5 km S.W. of Ann Arbor Michigan in the Fall of 1977. Several methods were used to quantify male behavior. For a continuous record of fly activity descriptions of behavior were made by uttering behavior-specific sounds into a tape recorder for the length of time each type of behavior occurred. Noting counts on the footage meter during replay of tapes allowed both frequency and duration of each type of behavior to be computed.

Extremely short duration behavior was timed by means of 16 mm movie pictures taken with a Bolex camera and a Macro-Switar lens. Color film was used so that individual markings could be recognized. The processed film was viewed on a Vanguard Motion Analyser which allows slow-motion and single frame analysis. By counting frames in which a particular behavior occurred the duration of events could be determined. Relatively long duration events were tracked by noting time of beginning and end. Cumulative time stopwatches were also used for some repetitive behavior.

For experiments requiring paired males of specific size, males of the desired size were presented with gravid females that were detached from their initial partner. For small males the most successful method for establishing pairs involved placing the female in a glass vial. The mouth of the vial was placed over a searching male on a pat who then captured the female inside. Flies that had paired in the vial could be coaxed out and onto the pat by gentle tapping of the vial.

Another method which proved successful involved clamping the leg of a female in a long hemostat, and then presenting her to males. Large and medium size males readily accepted such females, but small males flew off when the female plus hemostat was moved toward them. Once the male made contact with the female she was released. Amplexing flies from natural and synthesized pairings were observed and showed no obvious behavioral differences.

Flies were measured in two ways. The first method involved the capture of flies and measuring with dial calipers. Wing length was used to estimate fly size. Measurements on captured flies were made with calipers from the front end of the left wing to the most distal projection as the wing is folded over the fly's abdomen. When capture of flies would likely bias experimental results, size measurements were made from photographs. For a more complete discussion of these methods see BORGIA (1981a).

Statistical analyses include: simple linear regression — DRAPER & SMITH (1966); Wilcoxon test (W), Spearman's  $r$  — CONOVER (1971); t-test — WONNACOTT & WONNACOTT (1972). Means are designated by 95 percent confidence intervals.

## MALE-MALE INTERACTION AT MEDIUM DENSITY

On pats with 10 or more males the behavior of most males involves unrestricted movement over the pat in their search for females. Males reach peak numbers on a pat approximately 15 minutes after deposition. Activity is greatest while the pat is fresh, but slows within several hours, or much more rapidly at high temperature or wind conditions.

Collisions are common among males on the pat surface as they search for mates. Females generally avoid the pat unless gravid and leave immediately after oviposition is complete. Males may feed on other flies, usually other species, captured on the pat surface. But such feeding is relatively rare, in part because most other species avoid pats heavily populated with *Scatophaga*. Movement on and around pats allows males to

increase the area over which they can capture females. Such searching activities are likely to be profitable if males can increase the area they survey without appreciably lessening their ability to sight females within those areas. In fact, these movements appear not only to increase the area males search, but also to enhance male ability to survey an area. Movements allow males to check behind obstructions, such as tufts of grass and crevices, and approach and investigate objects resembling females in the vicinity of the pat. Males of *Scatophaga* also appear to use movement of other males as cues for the location of females; the ability to move rapidly and utilize these cues has obvious advantages.

Under all conditions tested large males are more successful in obtaining matings with females, but their greatest success occurs at medium and high numbers of flies per pat (BORGIA, 1979, 1981a). The lower success rate among small males results from their relative scarcity on pats with large males and lower relative copulation rate relative to larger males on the same pat (BORGIA, 1979, 1981a). When large males are removed from pats, they are rapidly replaced by small males (Fig. 1). Results of these removal experiments and comparisons of the size of males on and off pats (BORGIA, 1979, 1981a) suggests that small males are excluded or intimidated by larger conspecifics who occupy pats.

A problem arises in explaining the relative scarcity of small males on pats with numerous flies. At high male density there are frequent collisions among males, but there is no obvious attempt by males to be overtly aggressive, or exhibit territorial behavior. Moreover, with a large number

of males on a pat, individual males may be excluded or intimidated, and perhaps suffer a net loss for females. So why are small males?

One likely answer is that for small males, the cost of searching for females may be costly to them, especially to the more passive or less active searching male. If male movement is costly, one might expect that small males should be inclined to show the differences in behavior might be due to mate capture strategies chosen by small males that reduce their potential harm.

If small males are attacked by large males, then avoidance of these attacks, then avoidance of collisions for survival and maximum longevity may be only one of a set of strategies chosen by small males over other males. PARKER (1970d) has shown that small males mate more frequently than recently large males. This may be related to the level of male activity. If large males cause attacks by being less active. If large males causes small males to be less active, then the hypothesis suppose that it is expensive for small males to be on a pat populated by large males is a reasonable one.

The behavior of male *Scatophaga* during pat activities important in the capture of females can be used to estimate the relative success of searching for individual females.

*Flyup*: short stylized flights by males which are 1-2 cm but commonly moves less than 5 cm to the left. Flight is slow, males often descend to the pat after an epigamic display. This behavior does not result in attack (see below).

*Walk*: a male begins to walk on or off the pat, a common form of movement on the pat.

*Turn*: movements in which the male turns around.

*Transitions*: the movements by which males change from one activity to another. This is a measure of gross movement.

*Attacks*: encounters with another fly which result in forceful strikes on other flies which result in a fly of interest, relatively mild touches by other flies intermediate between these extreme behaviors.

A fly is attacked when touched or

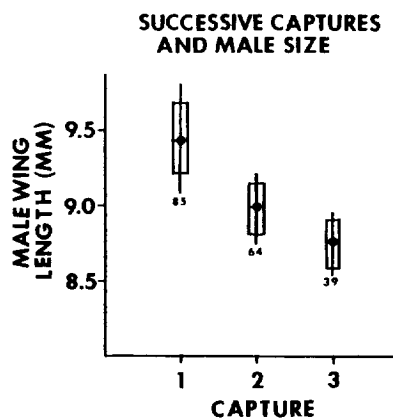


Fig. 1. Successive captures from a high male density pat vs male size. Captures were made at 10 minute intervals with captured flies held until the end of the experiment.  $\bar{X} \pm 95$  and  $\pm 99$  percent confidence intervals.

of males on a pat, individuals should gain very little from overt aggression, and perhaps suffer a net loss of time that could be spent searching for females. So why are small males rare on pats heavily populated with males?

One likely answer is that frequent collisions among males searching for females may be costly to both flies involved in the encounter, and especially to the more passive individual who is often grabbed by the searching male. If male movement activities are critical in mate capture one might expect that small males, barring any physiological disabilities, should be inclined to show the same activity patterns as large males. Differences in behavior might be interpreted either as separate size-related mate capture strategies chosen by males, or a result of intimidation of small males that reduce their searching movements in order to avoid potential harm.

If small males are attacked more frequently or suffer more harm from these attacks, then avoidance of heavily populated pats may be important for survival and maximum long-term reproduction. Avoidance should be only one of a set of strategies to minimize harm from encounters with other males. PARKER (1970d) has shown that moving males are attacked more frequently than recently killed males. This implies that attack rate is related to the level of male activity, and that small males might avoid attacks by being less active. If it can be shown that the presence of large males causes small males to become less active then there is reason to suppose that it is expensive to be attacked and avoidance of pats populated by large males is a response to this cost.

The behavior of male *Scatophaga* was surveyed and classified in terms of activities important in the capture of females. These behavioral activities can be used to estimate the relative effort individual males make in searching for individual females. The behaviors are as follows:

*Flyup*: short stylized flights by males as they move around the pat. A male rises 10-20 cm but commonly moves less than 5 cm horizontally, often landing on the same perch that he left. Flight is slow, males often descending with legs outstretched in what appears to be an epigamic display. This behavior differs from the rapid flight which is often part of an attack (see below).

*Walk*: a male begins to walk on or around the pat after standing still. This is the most common form of movement on the pat surface.

*Turn*: movements in which the male changes orientation without walking or flying.

*Transitions*: the movements by which a male moves between marked quadrats of a pat. This is a measure of gross movement by flies as they search different areas of the pat.

*Attacks*: encounters with another fly initiated by the observed male. These include forceful strikes on other flies which result from rapid running and flying toward the object of interest, relatively mild touches by males passing one another, and forms of approach intermediate between these extreme levels of intensity.

A fly is attacked when touched or struck by another male.

All of the activities described above showed a positive and statistically meaningful relationship with male size (Figs. 2-5): large males showing greater activity than their smaller counterparts. Significant differences in the transition rate show that large males are able to search a greater area on and around the pat.

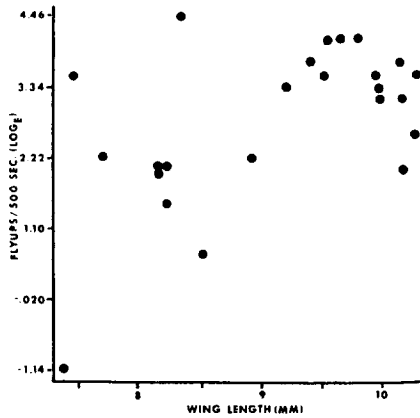


Fig. 2.

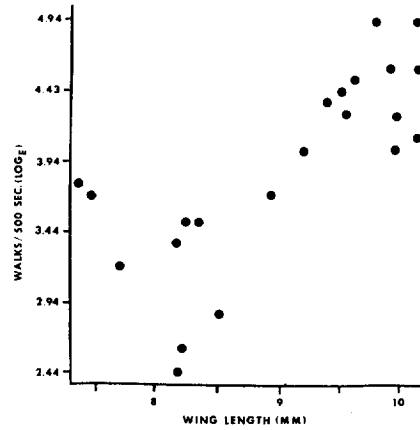


Fig. 3.

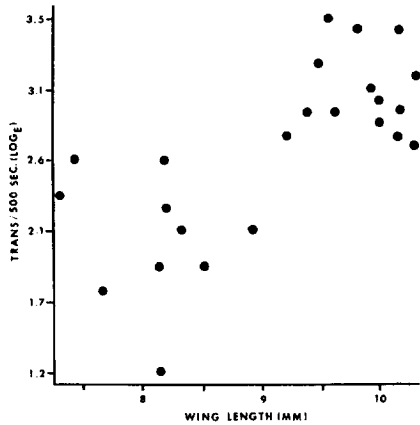


Fig. 4.

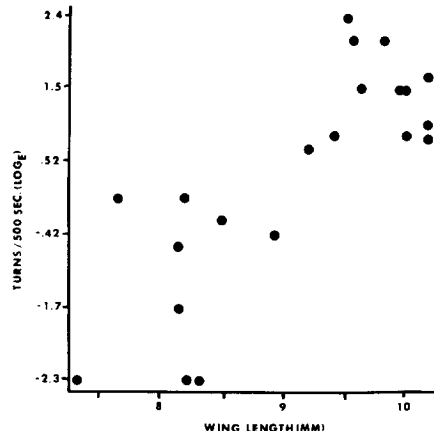


Fig. 5.

- Fig. 2. Number of flyups vs male wing length. Regression equation is  $Y = .70X - 3.60$ ,  $r^2 = .3022$ ,  $P = .005$ ,  $SE = 1.089$ .
- Fig. 3. Number of walks vs male wing length. Regression equation is  $Y = .52X - .770$ ,  $r^2 = .5571$ ,  $P < .001$ ,  $SE = .4699$ .
- Fig. 4. Number of transitions vs male wing length. Regression equation is  $Y = .41X - 1.08$ ,  $r^2 = .4902$ ,  $P < .001$ ,  $SE = .4239$ .
- Fig. 5. Number of turns vs male wing length. Regression equation is  $X = .86Y - 7.49$ ,  $r^2 = .3766$ ,  $P = .001$ ,  $SE = 1.129$ .

Size-related attack behavior. Large males than do smaller males (1 then the tendency by sr portunities for these ma Small males may si Presumably the reduce likelihood of capturing frequency of attack leading between male size and th tacks (Fig. 7) shows that

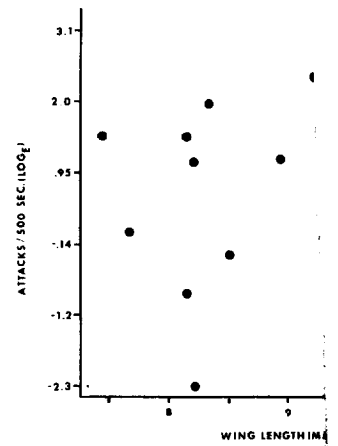


Fig. 6.

- Fig. 6. Number of attacks vs male wing length.  $r^2 = .4902$ ,  $P < .001$ ,  $SE = .4239$ .
- Fig. 7. Times attacked vs male wing length.  $r^2 = .3766$ ,  $P = .001$ ,  $SE = 1.129$ .

parent opportunities to ca larger individuals. Thus, males does not occur. Two tempts to avoid being attac movement rates among sr lower attack rates, but bec is no obvious size-related di tacked.

Relative susceptibility of sidering the ratio of times

Size-related attack rates parallel other size-related differences in behavior. Large males attack other males consistently more frequently than do smaller males (Fig. 6). If attacks are important in female capture then the tendency by small males to initiate fewer attacks may limit opportunities for these males to capture females.

Small males may suffer some real cost when they are attacked. Presumably the reduced rates of movement and the resulting lower likelihood of capturing females are repaid as reduced intensity and frequency of attack leading to physical damage. However, the relationship between male size and the frequency with which an individual receive attacks (Fig. 7) shows that small males, even with less movement and ap-

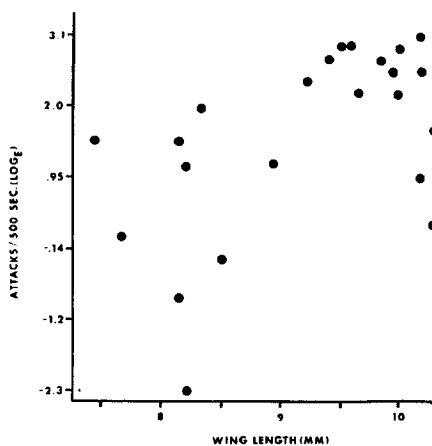


Fig. 6.

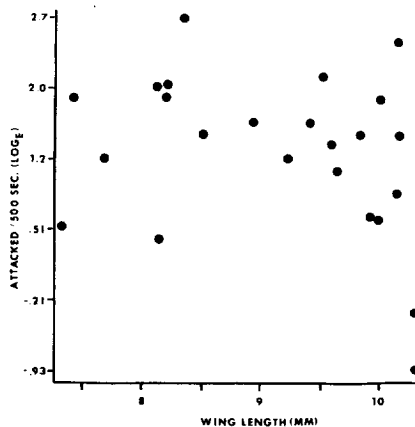


Fig. 7.

Fig. 6. Number of attacks *vs* male wing length. Regression equation is  $Y = .99X - 7.64$ ,  $r^2 = .3921$ ,  $P = .001$ ,  $SE = 1.261$ .

Fig. 7. Times attacked *vs* male wing length. Regression equation is  $Y = -.22X + 3.27$ ,  $r^2 = .0682$ ,  $P = .22$ ,  $SE = .8248$ .

parent opportunities to capture females, are attacked at rates similar to larger individuals. Thus, the expected lowering of attack rate on small males does not occur. Two possible explanations for this result are: 1) attempts to avoid being attacked by other males are not the cause of lower movement rates among small males, or 2) small males' behavior does lower attack rates, but because they are more susceptible to attack, there is no obvious size-related difference in the frequency at which they are attacked.

Relative susceptibility of small males to attack can be tested by considering the ratio of times attacked over total encounters (attack + at-

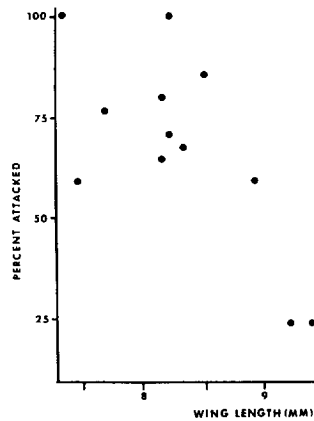


Fig. 8. Percent attacked (times attacked/attacks times attacked) vs male wing length. Regression equation is  $Y = -.24X + 2.67$ ,  $r^2 = .7170$ ,  $P < .001$ ,  $SE = .1556$ .

tacked) in relation to male body size (Fig. 8). This comparison generates a highly significant regression. Small males are either involved in few attacks, or if active in attacks, suffer higher rates of attack than they inflict on flies around them. Large males show a lower proportional attack/encounter ratio suggesting that they attract fewer attacks for every attack they deliver.

The lower attack/encounter ratio for small males supports the hypothesis that small males are more susceptible to attack. This suggests that lower rates of movement by small males may be especially important in reducing the likelihood, and hence, the total cost of being attacked. However, a lack of significant correlation between male size and frequency at which a fly is attacked is shown in Fig. 7. But this result may be due to two factors acting in opposite directions. Small males are more likely to be attacked in a given situation; yet by restricting themselves and their movements to the downwind side of the pat, away from the majority of large males who are likely to attack them ( $t = 9.6$ ,  $n = 257$ ,  $P < 0.001$ ), they are able to reduce the rate at which they are attacked. The net effect is the absence of any demonstrable difference in attack rate among male size classes.

Additional evidence for intimidation of small males by larger counterparts comes from several sources. If small males ( $\bar{X} = 8.02 \pm 0.21$  mm; wing length) and large males ( $\bar{X} = 9.88 \pm 0.34$  mm; wing length) are compared, small males appear to leave the pat more often after attack (12/677 vs 9/209,  $\chi^2 = 12.71$ ,  $df = 1$ ,  $P < 0.001$ ).

Reaction of attacking males to the sample of large and small males involved grasping the attacked fly suitable for attempted copulation were attacked (17/69) than with ( $\bar{X} = 33.45$ ,  $df = 1$ ,  $P < 0.001$ ) for females. Such mistakes by males sometimes because attacking males of this appears to reduce resistance suggested below that these strong opponents, especially when delivered

#### MALE TERRITORIALITY LOW

At conditions of low male density *Scatophaga* males changes dramatic when males are present. Males maintain dung pats, or at least from certain areas appear to meet most copulations (BROWN & ORIANS, 1970). At a great majority of cases (54/57) than any other male in the vicinity to patrol the pat and attacks central portions. Typically the subordinate males standing on the pats by the dominant male subordinate to 1) visit defecation vicinity of the pat.

Behavior of males seemed to defend dung pat. Pats of a standard shape could be obtained. Pats conical in shape, with a small diameter cm above the substrate. A dominance relationships among a percent of the occupied pats. The closest male to the center of the pat (in minute intervals) of the time spent more than twice as long as the male (24.3% vs 7.4%;  $t = 12.71$ ,  $df = 1$ ,  $P < 0.001$ ) dominants on subdominant



Reaction of attacking males to the fly they attack is also size-related. In the sample of large and small males, orientation by attackers, which involved grasping the attacked fly and changing orientation to a position suitable for attempted copulation, was more common when small flies were attacked (17/69) than when large males were attacked (1/209) ( $\bar{X} = 33.45$ ,  $df = 1$ ,  $P < 0.001$ ). Small males may be more often mistaken for females. Such mistakes by attackers may be costly to their male victims because attacking males often stroke their legs on a captured female; this appears to reduce resistance by her as they insert their genitalia. It is suggested below that these strokes are potentially harmful to their recipients, especially when delivered by large males.

#### MALE TERRITORIALITY AND SEXUAL COMPETITION AT LOW MALE DENSITY

At conditions of low male density per pat (2-8 males) the behavior of *Scatophaga* males changes dramatically from what is common when more males are present. Males may actively exclude conspecific males from dung pats, or at least from certain portions of a pat. These defended areas appear to meet most common requirements to be called territories (BROWN & ORIANS, 1970). At most there is one territory per pat and in the great majority of cases (54/57), the male controlling the territory is larger than any other male in the vicinity of the pat. The dominant male tends to patrol the pat and attacks males which land on its windward and central portions. Typically the territory involves the whole pat with subordinate males standing on the perimeter or in the surrounding grass. Attacks by the dominant male on other males apparently discourage the subordinate to 1) visit defended areas on the pat, and 2) move in the vicinity of the pat.

Behavior of males seemed to be strongly dependent on the shape of the dung pat. Pats of a standard shape were constructed so that consistent results could be obtained. These pats were 18 cm in diameter, roughly conical in shape, with a smooth surface reaching to a central pinnacle 10 cm above the substrate. At low male density in the late spring clear dominance relationships among males were established on about 75 percent of the occupied pats. On these pats the dominant male was the closest male to the center of the pat 78.4 percent (data from 20 five-minute intervals) of the time on pats with 3-7 males. Dominant males spent more than twice as much time moving as the average subordinate male (24.3% vs 7.4%;  $t = 8.4$ ,  $P < 0.001$ ). The ratio of attacks by dominants on subdominants was strongly biased (21.7:1).

Effects of intimidation by dominant males were most evident when one dominant male was superceded by another colonizing male. In one case a male (8.4 mm) occupied the center of the pat, moved about patrolling its surface, and attacked two smaller peripheral males as they ventured onto the pat. A larger male (9.1 mm) arrived 8.3 minutes later and with one attack caused the former dominant to move to a peripheral position on the pat perimeter and significantly reduce his activity. The new male occupied the pat center and patrolled the pat surface. Another, still larger male (9.85 mm) arrived 6.1 minutes later and the replacement process was repeated. Not long after the last dominant male arrived (4.8 min) he was able to capture a gravid female. Replacement of one male by another was common, and I observed three sequences involving successive replacement of three males.

This process of male succession to dominance is of special interest since it shows that when suitable opportunities are available small males engage in active searching and territorial behavior. Such activities by small males show they are not disabled because of small size or a poor growth environment, a possible alternative explanation for the activity patterns discussed above. The tendency for males to change behavior after being attacked by a larger male, sometimes attacking him then moving to the edge of the pat or even moving to the periphery without an attack, leaves little doubt that intimidation due to the prospects of harm from further attacks strongly influences male distributions on pats at low density.

Intimidation by dominant males is apparently associated with attempts to control areas where females are likely to be captured. At low density females fly to a point 10-15 cm from the edge of a pat and then move slowly to the pat edge. In the case of pats with central pinnacles described above, females walk onto the pat up to the highest point, moving most often when no males are nearby. Near the top they are usually discovered by a dominant male who "captures" them. In five cases females displayed toward the dominant male which apparently facilitated their capture by him.

Virgin females move to high points near the center of pats. Control of this area by a dominant male allows him the opportunity for a significantly higher than expected rate of female capture (BORGIA, 1980). Thus the success of dominant males results not only from the effects of intimidation but also from female movement toward positions where large/dominant males are common (BORGIA, 1980).

Territoriality is not an autom pat. For instance, territoriality males on the pat are very near attacks males will commonly ta pat surface and only infrequentl they are typically of the short d ty. Attacks on smaller males wh occasionally venture onto the pat involve leg thrusts. The high lil females may explain this differ

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## CONTRASTS IN MALE M

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After observing flies, five vari intensity of male aggression at c Straddles—a behavior in which male and reaches around the a volve reaches in which right a which front legs are on one side on the other. This behavior diff (1970d) which involves only wa tacked fly. Straddles appear mor with leg strokes. ii) Behavior af attacker after the attack. The fly stays on the pat or makes ar perimeter after an attack. iii) L times an attacking male, which the body of the victim. Male l

Territoriality is not an automatic consequence of low male density per pat. For instance, territoriality is unlikely if two or more of the largest males on the pat are very near the same size. After initial long duration attacks males will commonly take up positions at various points on the pat surface and only infrequently attack one another. When attacks occur they are typically of the short duration characteristic of high male density. Attacks on smaller males who often remain near the pat edge but occasionally venture onto the pat commonly may be of long duration and involve leg thrusts. The high likelihood of confusion of small males with females may explain this difference in patterns of attack.

PARKER (1964c) specifically states that no territoriality occurs in *Scatophaga*. This may be true in the populations he observed in which there is less size variation (see BORGIA, 1981b) and hence the likelihood of male profit from this sort of behavior is reduced.

#### CONTRASTS IN MALE BEHAVIOR AT LOW AND HIGH DENSITY

The descriptions above make it clear that males behave differently at low and high male density. Characterization of these differences and then correlation with particular needs of males provides another test for the adaptive nature of male behavior. Such tests are especially important for insects because they show that individual behavior is highly situation specific and less rigid than is often suggested for insects (see ALCOCK, 1979).

After observing flies, five variables were chosen to measure the relative intensity of male aggression at different density conditions. These are: i) Straddles—a behavior in which an attacking male moves atop another male and reaches around the attackee with his legs. A straddle may involve reaches in which right and left legs are on opposite sides, or in which front legs are on one side and middle, hind or both pairs of legs are on the other. This behavior differs from a mount as described by PARKER (1970d) which involves only walking over or touching the back of the attacked fly. Straddles appear more aggressive in nature and are associated with leg strokes. ii) Behavior after attack—deals with the reaction of the attacker after the attack. The fly's reaction is categorized as to whether it stays on the pat or makes an obvious move off or toward the pat perimeter after an attack. iii) Leg strokes are a count of the number of times an attacking male, which has straddled a fly, moves his legs over the body of the victim. Male legs carry stout tarsal bristles and hairs.

This fact plus the context in which strokes are delivered, the behavior of recipients of attacks involving strokes, and the intensity with which strokes are applied all suggest that leg strokes inflict damage on the recipient. iv) Attack duration is the time the attacking male is in physical contact with the attackee. v) Attacks/encounter represents the total number of attacks divided by attacks + times attacked.

Preliminary observations suggested that each of these variables might be important both in being different under each of the conditions considered and in showing relevant differences in tactics related to the capture of females. Some difficulty exists in these comparisons because they take place at different densities and on pats on which the size of interacting males is not constant. To remove some bias, large males on high density pats were chosen to compare against similarly-sized territorial males.

Comparison of male attack behavior under the two density conditions is shown in Table 1. Statistically meaningful differences in behavior exist for all of the chosen behavioral categories. This supports the hypothesis that behaviors at different density conditions are qualitatively different and that attacks at low density are more severe.

Long duration attacks with numerous leg strokes are of special interest when dominant males attack subordinate males who have recently attacked them or not moved after an initial attack. For example, at low density dominant males are infrequently attacked (this is shown by the encounter rate), but occasionally after an attack on a male who has been subordinate the subordinate returns the attack on the dominant. The

dominant then re-strokes are much more frequent than the earlier attack. In the case of the dominant male, the time between attacks by the dominant male is shorter ( $\bar{X} = 51.6$  sec; with unreciprocated attacks) than the time between second attack left the subordinate.

Attacks on the dominant male are much more frequent than these interacting males. The size of the pat is much smaller than the size of the pat of the subordinate, even though they are of the same size ( $P < 0.001$ ). Large differences in pat size lead to situations in which the subordinate response except that the subordinate may be able to escape.

The pattern of behavior of the subordinate during the colonization of a pat is of interest. Initial attacks by other males on the pat, this behavior becomes more frequent on pats of high male density. These colonizing males are of the same size as the subordinate. The relationship between the subordinate and the pat is interesting. The relationship between the subordinate and the pat is interesting.

TABLE 1  
*Attack behavior at high and low density*

Behavior	High male density	Low male density	Significance
Straddles / Attacks	14/108 (13.0)	38/46 (82.6)	$p < .001$ ( $t = 11.78$ )
Attacked male leaves/ Attacks	21/303 (6.9)	281/455 (61.8)	$p < .001$ ( $t = 14.9$ )
Leg strokes / Attack	0 $n = 104$	$6.42 \pm 1.76$ $n = 43$	$p < .001$ ( $W = 0$ )
Attack duration (seconds)	$479 \pm .39$ $n = 108$	$1.61 \pm .84$ $n = 46$	$p < .001$ ( $t = 7.01$ )
Attacks / Encounters	191/328 (58.2)	827/866 (95.5)	$p < .001$ ( $t = 10.88$ )

Parentheses indicate percents.

Fig. 9. Typical pattern of a

dominant then re-attacks the subordinate. In this return attack leg strokes are much more vigorous, and the attack lasts much longer than the earlier attack. Data are available for only six cases of second attacks by the dominant male, but they show significantly increased attack duration ( $\bar{X} = 51.6$  sec;  $W = 47$ ,  $m = 45$ ,  $n = 6$ ,  $P < 0.001$ ) when compared with unreciprocated attacks, and a tendency toward an increased number of leg strokes ( $P = 0.064$ ). In all six cases the male receiving the second attack left the center of the pat.

Attacks on the dominant male by subordinates are most common when these interacting males are nearly the same sizes. Males more than one mm smaller than the dominant male accounted for only 9/38 of the attacks even though they made up 18/26 of the males present ( $\chi^2 = 13.38$ ,  $P < 0.001$ ). Large differences between dominant and subordinate males lead to situations in which dominants are attacked and there is no response except that the small attacker moves to a peripheral location. The small fly may orient toward a large fly and then fly off.

The pattern of bouts shifting from long to short duration is common in the colonization of medium density pats away from areas of high male concentration. Initial colonists may show typical territorial behavior but, after attacks by other males of similar or larger size which come onto the pat, this behavior begins to change (Fig. 9). Placement of fresh pats near pats of high male density leads to rapid colonization from nearby pats. These colonizing males rarely participate in long duration encounters. The relationship between numbers of males on a pat and behavior suggesting exclusion is shown in Fig. 10.

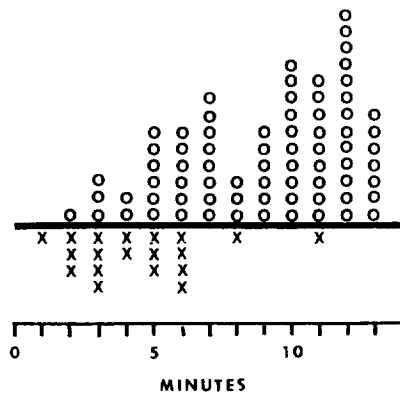


Fig. 9. Typical pattern of attack on newly colonized pat. X's represent attacks > 1 sec; O attacks < 1 sec.

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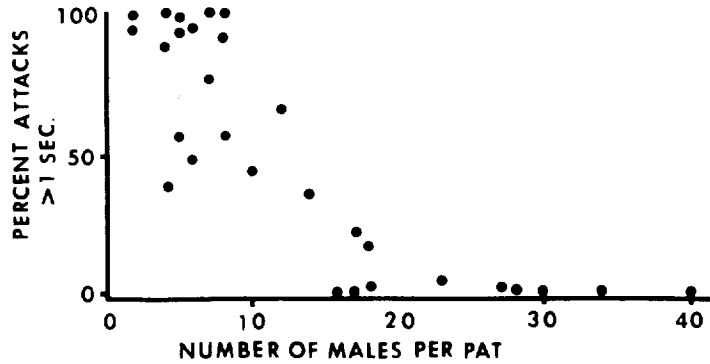


Fig. 10. Percent long-duration attacks *vs* the number of males on a pat 15 minutes after it is dropped. Spearman's  $r = .79$ ,  $P < .01$ .

Occasionally a very large male on a medium density pat will engage in straddling and repeated long duration attacks on other males. Individuals showing this kind of behavior were extremely rare, but their behavior may be significant in helping them to takeover females from other males (see below).

#### TAKEOVERS

Although male success in capturing mates is determined largely by the ability to find unpaired females, male ability to takeover a female from another male provides an alternative route for gaining females. PARKER (1970d) pointed out that an amplexed male's ability to cover a female is a key element in determining whether or not an initial touch by an unpaired male will lead to a takeover attempt. The amount of cover a male offers a female and, therefore his ability to prevent her detection by other males, depends on his size. Small males may not even cover the abdomen of their females while large males may totally envelop their mates. Male ability to achieve takeovers when initially unpaired is also strongly size-dependent. Large males are much stronger and more able to avoid potentially damaging stroking than their smaller counterparts.

Bouts that lead to takeovers commonly occur when males controlling females lose their balance. This especially common on steep pats when a pair is attacked by another male. Such tilts are, however, not necessary for takeover. Especially with large males attacking small males paired to females, the attacker may simply pry apart the pair. The attacking male breaks the paired male's foreleg hold on the female with the initial shock of his attack. Then he lifts the paired male away from the female while

standing above and inserting himself between the pair. The attacker forces himself between the pair, wedging himself between the pair. If the aggressor is the initial consort is displaced by the displaced female only by his genitalia or he may attempt to insert himself. After a split the attacking male uses both middle and rear legs with whom he is attempting to displace the attacker and attacked the legs of his antagonist. Straddling to stroke the abdomen of the displaced male and spines. Although I observed damage, three factors suggest: 1) attacking males invariably attack the displaced male, apparently among males, 2) stroking the attackee's abdomen, a curs seemed more often than no stroking occurred by the

The greater success of this condition is shown in Fig

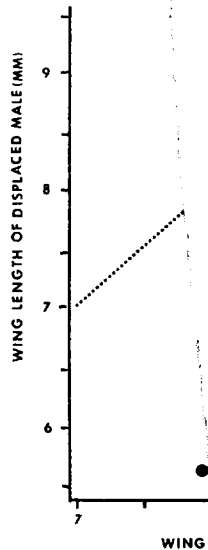


Fig. 11. Takeover, displaced male *vs* attacking male.  $r^2 = .3231$

standing above and inserts his abdomen between them from the side, forcing himself between the pair using his body and hind limbs as a wedge. If the aggressor is successful, the pair is split so that the female's initial consort is displaced, or, more commonly, that male holds the female only by his genitalia. These may be engaged at the time of attack or he may attempt to insert before becoming separated from the female. After a split the attacking male grasps the female with his front legs and uses both middle and rear legs to push against the abdomen of the male whom he is attempting to replace. With large size differences between the attacker and attacked the latter may be forced on his back by the longer legs of his antagonist. Smaller differences in size allow the attacked male to stroke the abdomen of the attacker with its paralobes, tarsal bristles, and spines. Although I could not associate instances of stroking with damage, three factors suggest that it is potentially harmful to recipients: 1) attacking males invariably hold their wings apart and away from the attacked male, apparently to minimize wing damage, which is common among males, 2) stroking occurs whenever the attacked male can reach the attackee's abdomen, and 3) apparent stalemates where stroking occurs seemed more often resolved in favor of the attacker than those where no stroking occurred by the aggressor.

The greater success of large males in takeovers under uncontrolled conditions is shown in Fig. 11. The successful attacking male is larger

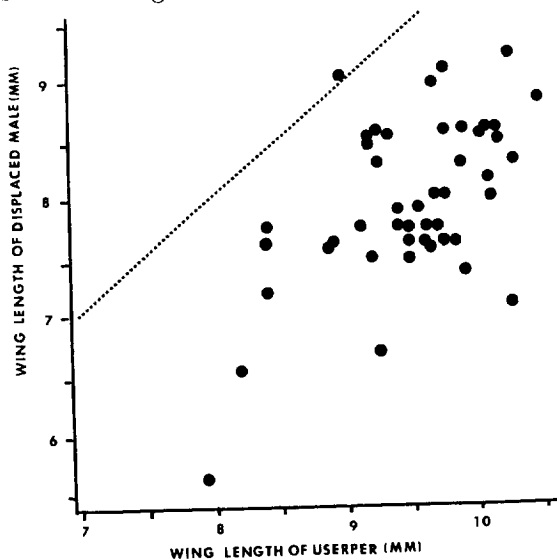


Fig. 11. Takeover, displayed male *vs* userper. Regression equation is  $Y = .73X + 1.00$ ,  $r^2 = .3231$ ,  $P < .001$ ,  $SE = .6065$ .

than the male displaced from his consort in 45 of 46 cases. Winners are, on average,  $1.43 \pm 0.39$  mm larger than males they displace. An interesting but unexpected result is the statistically significant regression of the size of displaced males on winner size. The relatively constant size-difference between winners and losers seems to stem from a minimum size-difference for effective takeover plus the tendency for small males, whose females large males might easily takeover, to be rare where the large males are common.

The above results imply an advantage for large males both in attempting and in resisting takeovers. In order to determine size related success in resisting takeovers, pairs with males of known size were observed as they were attacked. Pats were chosen on which there were many males larger than 9.5 mm. Attacks by these males on marked pairs were recorded.

The shape of pats seems to strongly influence the likelihood of takeover. Pairs commonly fall from steep pats when attacked, and up to nine males may become entangled in the ensuing scramble for the female. Pairs often use crevices for oviposition when they occur on pats. Presence of pairs within crevices makes them practically immune to takeover, regardless of the male's size. In order to avoid effects due to pat shape, a flat pat, 6 cm tall and 30 cm in diameter, a type commonly produced when cows eat wet grass, was used to standardize observations.

Results (Table 2) show that small males obviously suffer much higher takeover rates than large males ( $\chi^2 = 59.25$ ,  $df = 3$ ,  $P < 0.001$ ). For paired males of the smallest classes, takeover is virtually assured unless they are able to avoid the full force of attack of large males. For these males all pairs observed except one were taken over. In the next largest size grouping only four of fifteen pairs were able to complete the copulation/oviposition sequence together. In the two larger groups completion of oviposition was the rule, the exception being only four takeovers in 387 attacks.

TABLE 2  
*Size-related takeovers by large males*

	Size of male attacked (mm)			
	8	8-9	9-9.5	9.5
Attacks	52	49	169	218
Splits	27	18	6	0
Takeovers	12	11	4	0

Splits which did not result in takeovers and although they were with the female, the result was that both individuals of the same size class, in which the smaller male was not displaced, fit the model in Table 2 ( $\chi^2 = 96.7$ ,  $df = 3$ ,  $P < 0.001$ ). Small males may, together with many large males, be taken over by large males (see BORGIA 1970).

PARKER's (1970d) results suggest that a male will lead to a takeover if he is larger than the role for takeovers in a pair. However, the above results suggest that a male of different size in dictating the role of the male, takeovers present a threat to the female. Arranging size classes from individuals that are larger than a male of his mate procurement success such as prolonged off-pat oviposition may have a higher rate of takeovers among small males. The takeover threat is not equal for all males may also gain, especially if they are actively pursuing takeover. A male is able to accomplish six takeovers in attacking pairs and increased his fitness far above that of a male searching only for unpaired females. A female fertilizes most of the eggs of a male (PARKER 1970d) has suggested that the time pairs begin to oviposit is difficult to develop a interpretation of this behavior.

Changes in the tendency of conspecifics have been suggested by PARKER (1970d) has also been suggested by PARKER (1970d) has also been suggested by high density. Generally it is difficult to develop a interpretation of this behavior.



Splits which did not lead to male replacement were more common than takeovers and although there may be no change in the male associated with the female, they suggest increased risk of injury and time delay for both individuals of an amplexing pair. Patterns of splits for four size classes, in which the guarding male was wedged away from the female but not displaced, follow the same pattern as takeovers, as shown in Table 2 ( $\chi^2 = 96.7$ ,  $df = 3$ ,  $P < 0.001$ ). The greater costs due to splits for small males may, together with takeovers, cause these males to avoid pats with many large males and perhaps cause females to prefer matings with large males (see BORGIA, 1981b).

PARKER's (1970d) results show only a 1.75% likelihood that an attack will lead to a takeover. Such a low rate suggests a relatively insignificant role for takeovers in influencing reproductive strategies among flies. However, the above results show the importance of takeovers to males of different size in dictating optimal reproductive strategies. For the small male, takeovers present a real threat whenever he is associated with a female. Arranging search strategies to capture and hold females away from individuals that are likely to takeover must be primary determinants of his mate procurement strategies. Special behaviors seen in small males such as prolonged off-pat copulation and failure to guard females during oviposition may have developed as a result of the high frequency of takeovers among small amplexed males. For males of large size the takeover threat is not critical except perhaps on very steep pats. Large males may also gain, especially when associated with small males, from actively pursuing takeovers. In one case a very large male (11.4 mm) was able to accomplish six takeovers in one afternoon. This male was very active in attacking pairs and there is little doubt that these takeovers increased his fitness far above what he might gain from a strategy involving searching only for unpaired females, since the last male to mate with a female fertilizes most of her eggs (PARKER, 1970c; BORGIA, 1981b). PARKER (1970d) has suggested that males may move onto the pat about the time pairs begin to oviposit to engage in takeover attempts. Although it is difficult to develop tests for this hypothesis, it seems likely that his interpretation of this behavior is correct, at least as it applies to large males.

#### DISCUSSION

Changes in the tendency for males to form territories related to density of conspecifics have been shown in grasshoppers (OTTE & JOERN, 1975). It has also been suggested by EMLEN (1976) that male bullfrogs form leks at high density. Generally it is not clearly stated in these models what the

basis for mate choice is, and how male behavior influences these decisions. Elsewhere I have pointed out (BORGIA, 1979) that males must hold territories for mating purposes, independent of size or density of males, as long as females are free to choose mates and as long as territories are important in their mating decisions. Males can only hope to be successful in joining mating leks when the pattern of female choice is altered so that the quality of resources in the area he defends is unimportant in female decisions. The situation is quite different in *Scatophaga* where, commonly, females have only limited opportunities to choose a mate (BORGIA, 1981b). For a male in a mating system in which females are captured as they approach a limited resource, territories may be only important to the degree that they enhance a male's access to incoming females. Thus at low male density, territories result from the exclusion of other males by dominant individuals from sites where females are likely to arrive. Males are expected to abandon a territorial behavior when it compromises their ability to capture females without concern for the "demand" a female may make for territories of a particular quality.

Abandonment of territorial behavior might occur because as male density per pat increases, an individual's ability to exclude conspecifics from a relatively large area is reduced. The advantages to territories for *Scatophaga* rapidly disappear because i) numerous non-territorial searching males are likely to capture females within or before they reach the male's territory, and ii) there is no reason, at least in terms of access to resources, for females to favor males holding territories. Shifts in male behavior should follow this emphasis on searching and reduced gain from territoriality.

Observed differences in male patterns of attack show differences in exclusion and searching behavior by males. Long duration attacks cost a male more energy, and reduce time available to him to capture incoming females. There should be little gain from use of these attacks in exclusion attempts on a high male density pat because i) more large males are present who are less likely to be driven off, and ii) gain from exclusion of some males must be shared with males who remain on the pat, and may not invest energy in attempts at territorial behavior.

The greater expense of long duration attacks in time and/or energy is suggested by long duration of second attacks. If it were not expensive to make these longer attacks which appear to be more effective in excluding males, initial attacks would likely be of similarly long duration.

Abandonment of territorial behavior suggests that at high male density size might not be an important determinant of male reproductive success.

However, as my results show, this is not the case at high density. Two types of attacks seem to account for the results on populated pats. These are i) attacks on seeking females, and ii) attacks on the positive correlation of success which has been pointed out in *Scatophaga*, but not in *Scatophaga* males is a pre- and postcopulatory behavior which distinguishes the sex of other males. And, it might have the highest relative

PARKER (1970d) has argued that the ability of males on other males is to distinguish arriving females. He has argued, due to any significant extent, that they would not occur. And, they might have the highest relative ability to discriminate between their target. He based this on the fact that they were attacked at a greater rate than they were able to discriminate between them. They can distinguish males from other males due to errors in sex identification. This should reduce time spent

However, the available data on males in sex-related discrimination between males. Differences in behavior are not good indicators of the sexes. Pairs behave differently in behavior can be used to exclude flies make fewer rapid movements than males. Also, the position of a lone male. This point is further supported by the fact that they show lower attack rates on other males.

More important is the demonstration that females in size and coloration are more active than larger more sexual males. The relationship between size

However, as my results from experimental changes in pat availability show, this is not the case. In fact, size appears to be more important at high density. Two types of costs which are especially high for small males seem to account for the relative scarcity of these males in heavily populated pats. These are i) possible harm from attacks by other males seeking females, and ii) takeovers of smaller males by large males. Thus the positive correlation of male density and high variance in reproductive success which has been predicted for avian systems (ORIAN, 1969) also occurs in *Scatophaga*, but not for the postulated reason: enhanced ability of males to control resources. The higher relative reproductive success of large *Scatophaga* males is an apparent artifact of mate searching, both for pre- and postcopulatory females. Moreover, if males could easily distinguish the sex of other conspecifics, then attacks on small males would not occur. And, except for costs due to takeovers, small males might have the highest relative success on pats with many males.

PARKER (1970d) has argued that the principal function of attacks by males on other males is to steal females from males in the process of capturing arriving females. He said it is "unlikely" that male attacks are due, to any significant extent, to male errors in determining the sex of their target. He based this conclusion on his finding that searching males were attacked at a greater rate than pairs, his argument being that male ability to discriminate between pairs and single males is evidence that they can distinguish males and females. He went on to suggest that attacks due to errors in sex identification should be rare because "... selection should reduce time spent on fruitless encounters..."

However, the available data are not sufficient to deny problems for males in sex-related discrimination as an important cause for encounters between males. Differences in the relative attack rate on pairs and individuals are not good indicators of male ability to discriminate between the sexes. Pairs behave differently from single males and these differences in behavior can be used to explain differences in attack rate. Amplexing flies make fewer rapid movements of the type that attract attacks by males. Also, the position of a male's body in a pair differs from that of a lone male. This point is further supported by PARKER's (1970c) data that show lower attack rates on pairs and recently killed males than live males.

More important is the demonstration that small males, who resemble females in size and coloration, endure more attacks at a given level of activity than larger more sexually distinct males. However, even though the relationship between size and frequency at which a fly is attacked

strongly suggests that these small males are initially perceived as females, this result could also be explained by a tendency for large males to preferentially cue on small males, from whom they are more likely to win females. A clue to the higher rates of attack on small males is gained by observing reactions of large males after attacks on males of different size. The greater tendency for males to mount small males during attacks indicates that some attacks are due to the inability of males to discriminate the sex of flies they attack, even after they touch.

I agree with PARKER's argument that selection should cause males to avoid wasting time on "fruitless encounters". However, I believe this will occur only if avoidance could be done at no added cost. The ability to precisely discriminate males from females, and to make rapid response, is very likely a genetic alternative that has not been available in the evolutionary history of this species. So if there are premiums on rapid response with large numbers of males on pats, time delays for more precise discrimination could lead to severe reductions in a male's fitness. The number of females captured would be very low with savings from precise discrimination leading to only insignificant reduction of costs associated with attacks. Given the available alternatives, high attack rates by males coupled with limited ability to discriminate between sexes may be no less fruitless than cueing on movement by other males for the presence of females, the explanation PARKER favored for the high frequency of male bouts. Therefore it appears that difficulties in discrimination and cueing are both important causes of the high levels of male attacks apparent in *Scatophaga*.

#### SUMMARY

The behavior of males near the oviposition site of *Scatophaga stercoraria* is highly variable, being dependent on male size and on male density conditions. At low density males are often territorial with dominance relationships, the largest male often initiating high intensity attacks. At high densities attacks are much less intense, with more symmetrical interactions among males. Large males are most active under all density conditions. Absence of small males from high density pats, even though there is no apparent attempt to exclude these males, appears to occur for two reasons: Small males may suffer proportionately more harm in interactions than larger males, and success of these males in retaining captured females is extremely low, as shown by extreme differences in takeover rates relative to male size.

My finding (BORGIA, 1980a, 1981) that large males are relatively more successful in capturing females under conditions where there are few pats can be explained in terms of these results. However, unlike predictions from avian mating system models, lower variants in male reproductive success occurs not because more powerful males actively exclude others from a more restricted resource base, but as an indirect effect of large males searching for mates.

Differences in male behavior under varying density conditions, and by males of different size, show the extreme adaptability of male behavior in *Scatophaga*. These findings

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## RÉSUMÉ

Le comportement des mâles près du lieu de ponte varie largement, notamment avec la taille et la densité des mâles. À basse densité, les mâles sont souvent territoriaux et ont des rapports de dominance; les mâles les plus gros entament fréquemment de fortes attaques. À densité élevée, les attaques sont moins fortes, sans rapports de dominance entre les mâles. En toutes conditions de densité, les mâles les plus gros sont les plus actifs.

Sur les mottes d'excréments à hautes densités de mâles, il n'y a qu'une minorité de mâles petits. Pour cela, il y a deux raisons: 1) les mâles petits souffrent relativement plus des interactions que les gros, et 2) le succès des mâles petits à garder les femelles capturées est très insignifiant. La grande différence en fréquences de remplacement reflète aussi l'effet de la taille des mâles.

Ma découverte (BORGIA, 1980a, b) peut être expliquée ainsi: les grands mâles ont relativement plus de succès à capturer des femelles où se trouve peu de mottes d'excréments. Ce résultat ressemble au système d'accouplement des oiseaux. Cependant chez *Scatophaga* cela se produit d'une façon indirecte, parce que les gros mâles recherchent des femelles, et non parce que les mâles les plus forts chasseraient les autres.

La différence d'attitude des mâles en diverses densités et par des mâles de taille différente montrent la faculté d'adaptation effective dans le comportement des mâles chez *Scatophaga*. Ces conclusions s'accordent à la proposition d'ALCOCK (1979) que le comportement des insectes est moins stéréotypé que l'on croit en général.

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P. J. B.

(Ethology & Neurophys

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