

Size-dependent alternative male mating tactics in the yellow dung fly, *Scathophaga stercoraria*

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Whenever males can monopolize females and/or resources used by females, the opportunity for sexual selection will be great. The greater the variation among males in reproductive success, the greater the intensity of selection on less competitive males to gain matings through alternative tactics. In the yellow dung fly, *Scathophaga stercoraria*, males aggressively compete for access to receptive, gravid females on fresh dung. Larger males are better able to acquire mates and to complete copulation successfully and guard the female throughout oviposition. Here we demonstrate that when an alternative resource is present where females aggregate (i.e. apple pomace, where both sexes come to feed), smaller males will redirect their searching for females from dung to the new substrate. In addition, we identify a class of particularly small males on the alternative substrate that appears never to be present searching for females on or around dung. Smaller males were found to have a mating 'advantage' on pomace, in striking contrast to the pattern observed on dung, providing further support for the existence of an alternative male reproductive tactic in this species.

Keywords: sexual selection; sperm competition; body size; reproductive strategy; *Scathophaga stercoraria*

1. INTRODUCTION

Whenever sexual selection is particularly intense, with great fitness disparity between the most and least successful males, alternative male reproductive strategies and tactics are predicted to arise (Wade & Shuster 2004). Some of the most dramatic examples of alternative male strategies are the few known examples of genetic polymorphisms that are evolutionarily maintained owing to their equal fitnesses provided by frequency-dependent selection (reviewed by Gross 1996; Shuster & Wade 2003; Oliveira *et al.* 2008). Much more common, as illustrated by a myriad of examples in diverse taxa (Oliveira *et al.* 2008), are alternative male reproductive phenotypes constituting a conditional strategy. In this case, males 'decide' which tactics to employ based on their individual status and the competitive environment (Gross 1996). There is considerable debate over the underlying genetics and evolutionary dynamics required for the maintenance of such phenotypic variation (Shuster & Wade 2003; Tomkins & Hazel 2007). Irrespective of these controversies, there are intuitive predictions regarding the evolutionary origin and maintenance of conditional male reproductive tactics (Shuster & Wade 2003): (i) variation in the spatial and/or temporal distribution of females presents the opportunity for the invasion of alternative tactics and (ii) males that are disadvantaged in 'traditional' competition for mates will be the ones to

employ the alternative tactic. Here we test these predictions with the yellow dung fly, *Scat(h)ophaga stercoraria*.

Cow dung is the larval substrate for *S. stercoraria*, and adult males aggregate on fresh dung pats in order to mate with females coming to the dung to oviposit (Hammer 1941). The reliability of encounters with gravid and receptive females on this concentrated resource provides conditions of strong sexual selection on male traits involved in both pre- and post-copulatory male–male competition. Intense male–male competition for females has given rise to male-biased sexual size dimorphism (Jann *et al.* 2000; Blanckenhorn 2009) and sperm competition adaptations, contributing to last male sperm precedence (Parker 1978a; Simmons *et al.* 1999). This easily observable and frequently intense reproductive competition among males has made *S. stercoraria* instrumental in theoretical advances relating to mate searching (Parker 1978b), male combat (Parker 1974a), mate guarding (Parker 1974b; Alcock 1994), sperm competition (Parker 1970a,b) and sexual conflict (Parker 1979). Owing to these and a multitude of additional investigations of this species, we have accumulated a robust and nuanced understanding of male and female reproductive strategies in this species.

Depending on the availability of fresh dung and the density of flies, the mating system of *S. stercoraria* varies between resource defence and scramble competition polygyny (Emlen & Oring 1977; Thornhill & Alcock 1983). When population density is low, males may exhibit territorial behaviour (e.g. some males aggressively exclude

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others from the dung), and when density is high, they tend to move about the dung more searching for females (Parker 1970*c,d*, 1974*c*; Borgia 1980, 1982). There is no courtship; when females arrive at a pat, they tend to copulate immediately, often with the first male encountered. It is common for multiple males to attempt to copulate with a given female, and aggressive struggles among males occasionally result in female injury or death (Borgia 1981). Following copulation, which typically lasts approximately 36 min (e.g. Parker & Simmons 1991), the male continues to guard the female by standing over her while she oviposits (Parker 1970*d,e*). The last male to mate with the female sires on average approximately 80 per cent of her subsequent progeny (e.g. Parker 1970*b*). During both copulatory and guarding phases, other males commonly attempt to aggressively 'take over' the female, copulating with her when successful. Females depart from the dung following oviposition. Despite fresh dung being a potentially valuable food resource for females, they are believed to avoid dung unless they are gravid and receptive owing to male harassment. There are (mostly anecdotal) reports of female *S. stercoraria* mating off of dung (e.g. on flowers), but the life history of females between their numerous clutches remains largely unknown (Parker 1970*f*, 1971, 1992; Gibbons 1987).

Larger males have numerous demonstrated advantages over smaller males in both pre-mating and post-copulatory reproductive competition. At low densities, larger males are better at establishing territories (Borgia 1980), and at higher densities, they are more active and have higher encounter rates with females. They attack other males more frequently, and smaller males are preferential targets and suffer more harm from these attacks (Borgia 1980). Larger males are also more successful at aggressively interrupting and displacing other copulating and guarding males, and they are better at resisting takeovers themselves (Parker 1970*d*; Borgia 1980, 1982; Parker & Thompson 1980; Sigurjónsdóttir & Parker 1981). Finally, although intrasexual competition is paramount in this mating system, there is evidence that, when provided the opportunity, females on dung preferentially approach larger males and exhibit other behaviours that would bias mating in favour of larger males (Borgia 1981). Considering the risk of physical injury and time costs suffered by females as a consequence of intense male–male competition, such a female preference when mating on dung makes sense. Female benefits from mating with larger males may include shorter copulation duration (resulting from faster sperm transfer rate; Parker & Simmons 2000) and additional time savings and lowered risk of injury associated with a lower probability of takeover (Borgia 1980, 1981).

Within this system characterized by large-male mating advantages, it has been suggested that *S. stercoraria* exhibits size-dependent alternative male mating tactics (Brockmann 2008). Specifically, smaller males are less likely to exhibit aggressive and territorial behaviour. They are also more likely than larger males to search for females in the grass surrounding the dung rather than on the pat itself (Parker 1970*g*, 1974*c*; Borgia 1980). Although the size distributions of males in grass and on dung are biased towards small and large males, respectively, they are far from discrete (Parker 1970*f*;

Sigurjónsdóttir & Snorrason 1995). Moreover, because they are attacked more frequently and probably suffer more harm from these attacks, small males are being physically displaced from the dung pats. Indeed, when male densities on dung are naturally lower, and when males were experimentally removed from pats, smaller males were then found to occupy them (Borgia 1980). It is thus questionable whether this specific suite of continuous behavioural variation constitutes 'alternative reproductive tactics' (Taborsky *et al.* 2008).

Here, we report the discovery of large numbers of female *S. stercoraria* regularly frequenting an alternative resource: composting pressed apple (or 'pomace'). We observed dramatic differences between dung and pomace in the availability and spatial distribution of *S. stercoraria* females: (i) numerous females were continuously present on pomace and (ii) the distribution of flies was highly dispersed on pomace relative to dung. The pomace resource also differs from dung pats in its economic defensibility. Given these differences, we tested the predictions that (i) alternative male mating tactics would be used to secure matings on pomace and (ii) the alternative tactic would involve smaller males (i.e. those disadvantaged in competing for mates on dung).

2. MATERIAL AND METHODS

(a) *Sex-specific size distributions and mating success on different resources*

All research was conducted on a natural population of *S. stercoraria* at Toad Hollow Farms, Nedrow, New York, USA in 2007 and 2008. In 2007, we initially observed numerous copulating pairs of *S. stercoraria* on a large pile (approx. 4 m in diameter and 1 m high) of composting apple pomace (the pressed pulp remaining after juicing). This compost pile was located approximately 7 m from the edge of a cattle pasture and was continuously available to the flies throughout the summer and autumn with fresh pomace regularly added. A pilot study was conducted with 33 copulating fly pairs collected and transferred to vials using large aspirators. Immediately after collecting each pair, the nearest (typically within 100 cm of the pair) 'single' *S. stercoraria* male was collected, with each 'trio' receiving unique identification for paired statistical analyses. At the same time, single males ($n = 44$) were collected from fresh dung pats in the adjacent pasture. Shortly after collection, all vials were placed on ice until arrival in the laboratory. Flies were then killed by freezing, and body size was estimated by measuring hind tibia length (HTL) to the nearest 0.02 mm using the ocular reticule of a stereomicroscope at 250 \times magnification. HTL is a standard and reliable index of body size variation in this species (e.g. Simmons & Ward 1991).

In 2008, the size of copulating flies ($n = 58$ pairs), as well as single males ($n = 59$) and single females ($n = 55$), on pomace was again examined, albeit not using a paired design. Flies were again contemporaneously collected from dung pats in the pasture adjacent to the pomace resource ($n = 34$ copulating pairs; $n = 89$ single males; $n = 29$ additional females from mass collections), as well as from dung pats in a more distant pasture ($n = 101$ copulating pairs; $n = 190$ single males; $n = 20$ additional females from mass collections), located approximately 200 m from the pomace resource.

Flies were collected from dung by gently lowering a large insect net over the dung pat and then shaking the bag while

holding the end upright. Other techniques such as blowing through the netting onto the surface of the dung helped to flush flies up into the net. This method proved successful in the capture of nearly all flies on dung pats and the grass immediately adjacent to pats. As the goal was to compare the size of males searching for females on and around dung in pastures with that of males searching for females on pomace, no attempt was made to separate males occupying the dung pat proper from those occupying the grass immediately surrounding a pat. Flies were transferred from the nets to vials by aspiration, then transferred to the laboratory for measurement of HTL as described earlier.

(b) Size of 'floater' males waiting to occupy dung

We conducted an experiment similar to that performed by Borgia (1980) to determine whether smaller males similar to those observed on pomace are present in the pastures as floater males—aggressively displaced from dung by larger males but searching for opportunities to occupy pats. Pats ($n = 10$ for each pasture) were chosen as those with considerable fly activity. All flies were collected, in the same manner as described earlier, at 10 min intervals for 30 min; thus, there were four cohorts collected per pat, with the first cohort designated 'time 0'. HTL of all flies was then measured to determine whether body size decreased in later cohorts.

(c) Resources and reproductive competition: attempted takeovers of copulating females

Behavioural interactions between copulating pairs of flies and single males were examined in 2008 for comparison between the two different substrates: pomace and dung. Specifically, we quantified the number of (i) 'encounters' between copulating pairs and single males and (ii) 'takeover attempts'. Encounters were functionally defined as an approach of the copulating pair by a single male to within a distance of one body length (approx. 2 cm), without proceeding to a takeover attempt. Takeover attempts were defined as any overt physical interaction between a single male and a copulating pair. These almost invariably took the form of the single male climbing or flying on top of the copulating pair and frequently escalated into grappling and wrestling bouts. On pomace, copulating pairs ($n = 23$; different from those collected for size determination, as described earlier) were continuously observed from the time of their discovery (pair formation was never observed) until the end of copulation, from a distance of 1.5–2 m. Observation start time, copulation end time and the number of encounters and takeover attempts were recorded. Contemporaneously, video cameras (Samsung Hi-8 SCL 860) on tripods, positioned 1 m distant, recorded continuous behaviour of flies on dung pats for 1 h per pat ($n = 5$ pats in each of the 'adjacent' and 'distant' pastures). These tapes were then viewed in slow motion using a Sony Video Hi-8 player with a Sony LCD multi-function display (MFM-HT75W), and the start time, end time and all encounters and takeover attempts were recorded for focal-watched pairs. Again, complete copulations were rarely observed, mostly owing to copulating pairs walking or flying off the dung pat or otherwise out of view of the camera. Owing to variation in movie quality, data came from $n = 4$ and 3 pats from the adjacent and distant pastures, respectively. From these data, encounter and takeover attempt rates were calculated for both substrates.

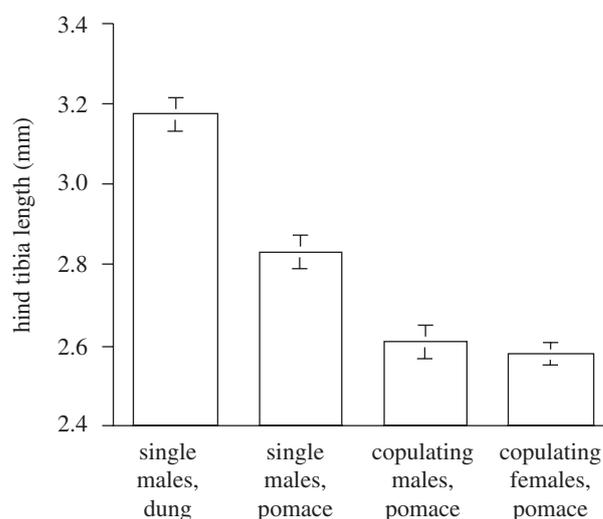


Figure 1. Mean HTL of single and copulating males on pomace, copulating females on pomace and single males on dung in the adjacent pasture in 2007. Bars, 1 s.e.

(d) Pomace as an alternative oviposition substrate

To investigate whether pomace provides an alternative substrate for oviposition and larval development, we collected 20 copulating pairs of *S. stercoraria* on pomace and transported these to the laboratory where they were placed in eight-dram shell vials containing approximately 6 cm of autoclaved pomace. These pairs were observed to copulate in the laboratory, and males were removed the following morning. Several days later, all vials were examined for eggs and larvae. In addition, a large bucket of pomace, collected from the surface of the pile (approx. top 10 cm), was transported to the laboratory, where it was spread out in a large shallow pan to a depth of approx. 10 cm. The pan was covered with a mesh screen and placed in a greenhouse where it was kept moist and then examined for pupae and adult *S. stercoraria* after several weeks.

3. RESULTS

(a) Sex-specific size distributions and mating success on different resources

The experiment conducted in 2007 revealed that single *S. stercoraria* males resident on pomace were significantly smaller (10.77% on average) than single males resident on dung in the adjacent pasture (figure 1; ANOVA $F_{1,75} = 27.20$, $p < 0.0001$). Further, males found in copula on pomace were significantly smaller (7.98% on average) than single males on pomace (figure 1; paired $t = 3.78$, d.f. = 32, $p < 0.001$).

More extensive sampling of single and copulating flies on pomace and dung in 2008 replicated the mating advantage of smaller males on pomace and revealed that it was unique to the pomace substrate. Again, copulating males were significantly smaller than single males on pomace (figure 2; ANOVA $F_{1,115} = 18.17$, $p < 0.0001$). In contrast, and consistent with numerous previous studies (§1), copulating males were larger than single males (though not significantly so) on dung in both the adjacent (figure 2; ANOVA $F_{1,121} = 1.94$, $p = 0.17$) and distant pastures (figure 2; ANOVA $F_{1,289} = 3.61$, $p = 0.058$). Copulating males on pomace had HTLs that were 18.37 per cent shorter on average than those

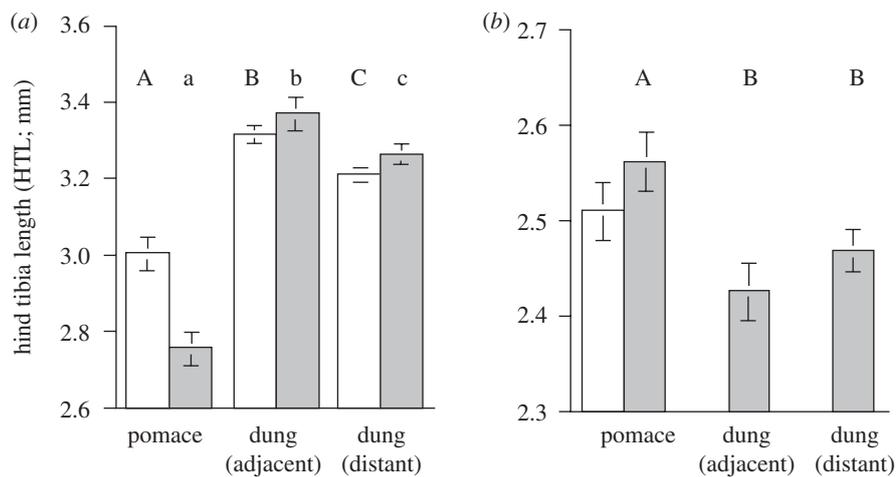


Figure 2. Mean size of single (white bars) and copulating (grey bars) male (a) and female (b) *Scathophaga stercoraria* on pomace and on dung (both adjacent and distant pastures, relative to the location of pomace) in 2008. Bars with different letters above them are significantly different (see text). Error bars, 1 s.e.

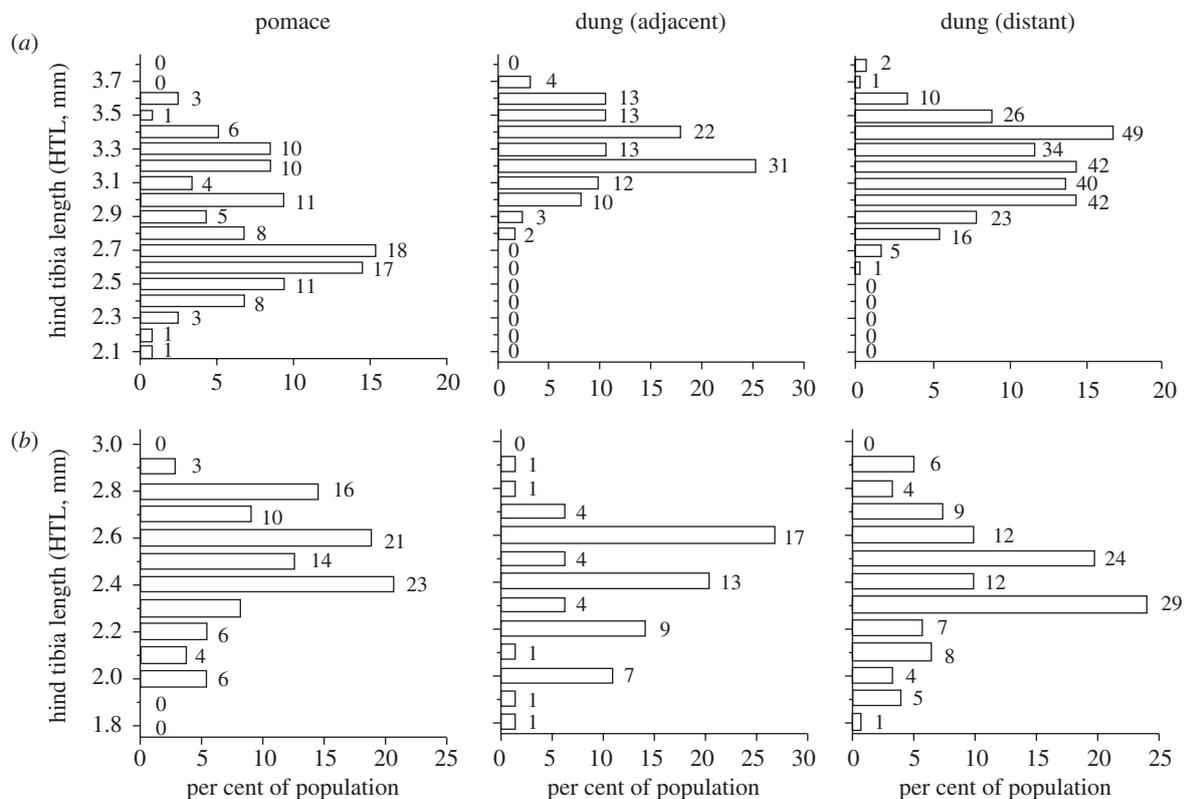


Figure 3. Frequency distributions of (a) male and (b) female body size for all flies collected from each substrate and location in 2008. The number of flies comprised by each size class is indicated above bars.

of copulating males on dung in the adjacent pasture (figure 2). In contrast to males, there was no size difference between copulating and single females on pomace (figure 2; ANOVA $F_{1,110} = 1.45$, $p = 0.23$).

Examination of the size distribution of all measured males (single and copulating combined) across both substrates and locations (i.e. comparing among pomace, dung (adjacent pasture) and dung (distant pasture)) revealed significant differences between the three sites (figure 3; ANOVA $F_{2,528} = 109.24$, $p < 0.0001$). A Tukey–Kramer honestly significant differences (HSD) test indicated significant differences between all three locations,

with males smallest on average on pomace (as in 2007) and largest on average on dung in the adjacent pasture (figure 3). Females similarly differed in size between the three locations, comparing either all females (figure 3; ANOVA $F_{2,293} = 4.78$, $p < 0.01$) or perhaps more legitimately as single females are only found on pomace, when comparing only copulating females (figure 2; ANOVA $F_{2,238} = 4.86$, $p < 0.01$). However, the pattern was of the opposite direction to that of males, with the largest females found on pomace (and no significant difference between pastures), as indicated by a Tukey–Kramer HSD test (figure 3).

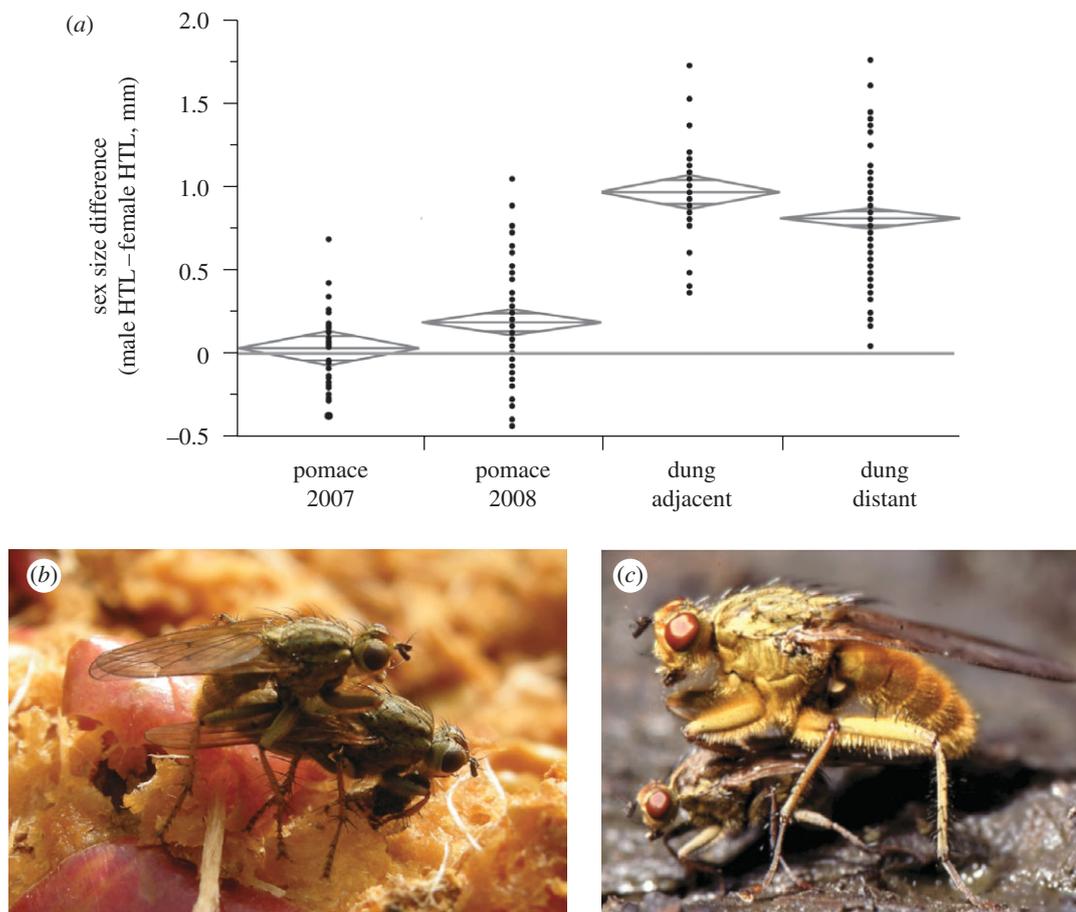


Figure 4. (a) Size difference between males and females within copulating pairs on pomace and on dung in each of the two pastures. Each point represents an individual copulating pair; diamonds illustrate the mean and 95 per cent confidence intervals for each group. The horizontal grey line indicates the point at which males and females are of equal size; points below this line indicate that females were larger than their mates. (b) Photo of a relatively small male copulating with a larger female on pomace. (c) Photo of a male guarding a female on dung.

Differences between sites in sex-specific size distributions were due to both the redistribution of flies in the presence of the alternative resource of pomace and to the presence of particularly small males found uniquely on pomace. Compared with the population of flies on dung in the distant pasture—where the alternative resource of pomace was not available—the population on dung in the pasture adjacent to the pomace had proportionately fewer smaller males and larger females (figures 2 and 3). This difference is presumably due to the smallest males and largest females occupying pomace in lieu of dung. In support of this interpretation of size-dependent redistribution of flies in the presence of pomace, comparison of female sizes between the two geographical locations (i.e. (pomace + dung in the adjacent pasture) versus dung in the distant pasture) reveals no significant difference in the size of females (ANOVA $F_{1,294} = 0.98$, $p < 0.32$). The situation for males was different, however. In addition to size-dependent redistribution of smaller males from dung to pomace, the pomace was occupied by males of extremely small size classes that were not present on dung, even when this alternative resource was unavailable (i.e. the distant pasture; figure 3). As a consequence, males were significantly smaller in the geographical location of the pomace + adjacent pasture relative to the distant pasture (ANOVA $F_{1,529} = 20.86$, $p < 0.0001$).

Owing to male-biased sexual size dimorphism and the mating advantage of larger males, copulating males on dung tend to be considerably larger than their mates (Blanckenhorn 2009). The sex-specific size distributions observed in this study largely explain variation among sites in size differences between a copulating fly and its mate (figure 4; ANOVA $F_{2,184} = 93.76$, $p < 0.0001$). The within-pair size difference is significantly smaller on pomace than it is on dung in either pasture, owing to the relative abundance of smaller males and larger females on pomace, in addition to the mating advantage of smaller males (figure 4). Indeed, in the 2007 sample of copulating pairs on pomace, there was no significant difference in size between copulating males and their mates (figure 1; paired $t = 0.67$, d.f. = 32, $p = 0.506$), a pattern in striking contrast to the direction of sexual size dimorphism in this species. Although copulating males were on average larger than their mates at all locations in 2008 (figure 4; pomace: paired $t = 4.30$, d.f. = 57, $p < 0.0001$; dung (adjacent): paired $t = 18.92$, d.f. = 33, $p < 0.0001$; dung (distant): paired $t = 25.23$, d.f. = 94, $p < 0.0001$), it was only on pomace that any males were smaller than their mates (figure 4). In addition, the within-pair size difference was significantly greater on dung in the adjacent pasture relative to the distant pasture, as indicated by a Tukey–Kramer HSD test. This difference is presumptively attributable to larger

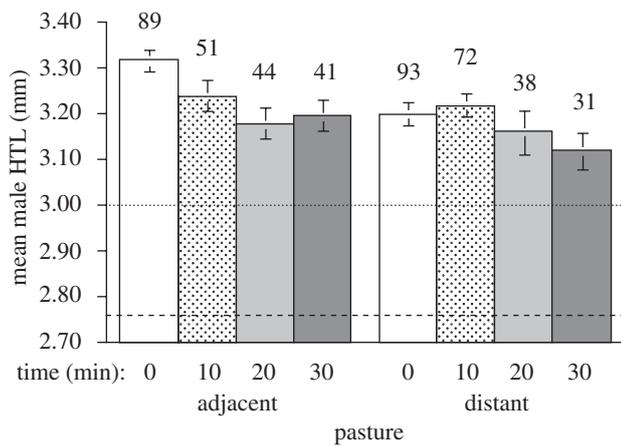


Figure 5. Results of floater experiment, illustrating mean male HTL for cohorts of males collected off dung pats at 10 min intervals (time 0 indicates first collection; males from all experimental pats were combined for each pasture). Horizontal lines indicated mean HTL for single males (dotted line) and copulating males (dashed line) on pomace. Error bars, 1 s.e.; sample sizes indicated above each bar.

females, and smaller males being less abundant in the adjacent pasture owing to their redistribution onto pomace.

In the present study, no attempt was made to rigorously quantify the sex ratio of flies on dung pats. However, the number of male and female flies collected at time 0 in the floater experiment indicates that sex ratios on dung in our study were consistent with previous reports (i.e. male : female ratios varied from 3 to 12 in the adjacent pasture and from 5 to 15 in the distant pasture; e.g. Parker 1970c). Our collection of single flies on pomace in 2008, which did not discriminate by sex, suggests a sex ratio of approximately 1 (60 males : 55 females).

(b) *Size of 'floater' males waiting to occupy dung*

The size of males occupying dung pats over four successive, 10 min time intervals ('cohort') following capture and removal of all flies was analysed by ANOVA, with COHORTS nested within individual dung pats and dung pats nested within pasture (adjacent and distant). There was a general trend for males to get smaller across successive collections, with both cohort[pat] (ANOVA $F_{38,403} = 1.92$, $p < 0.005$) and pat[pasture] (ANOVA $F_{16,403} = 3.25$, $p < 0.0001$) explaining a significant amount of the variation in male size. For illustrative purposes only, figure 5 shows mean values for males from all pats at each of the collection time intervals, sorted by pasture. Notably, the smallest male captured at 'time 30' (figure 5) had an HTL of 2.88 mm in the adjacent pasture and 2.72 mm in the distant pasture. This result suggests that the exceptionally small size classes of males found only on pomace (approx. 2.1–2.7 mm HTL; figure 3) are generally not present in pastures around dung, not even as floater males.

(c) *Resources and reproductive competition: attempted takeovers of copulating females*

There were 62 copulating pairs focal watched (on videotapes) on dung ($n = 18$ and 44 pairs in the adjacent and

distant pastures, respectively), generating a cumulative 395 'pair minutes' of observation. There were no differences between pastures in either the encounter rate (ANOVA $F_{1,60} = 0.014$, $p = 0.91$) or the attempted takeover rate (ANOVA $F_{1,60} = 1.155$, $p = 0.29$). A copulating male on dung (both pastures combined) is encountered by a single male (without it leading to an attempted takeover) once every 3 min on average and is the target of an attempted takeover every 28 s on average.

In striking contrast, for the 23 copulating pairs focal watched on pomace, with a cumulative 621 pair minutes of observation, we observed 14 encounters and 0 attempted takeovers. Therefore, during a typical copulation on pomace, the copulating male is encountered by a single male once every 42 min on average (i.e. roughly once throughout the copulation), and he is never challenged by another male attempting to take over his mate.

(d) *Pomace as an alternative oviposition substrate*

No eggs or larvae were observed in any of the pomace-containing vials that had housed copulating pairs of flies. Similarly, no *S. stercoraria* adults were found in the pan of pomace from the greenhouse, although hundreds of *Drosophila* (*simulans* and/or *melanogaster*) had eclosed from the substrate.

4. DISCUSSION

We provide three kinds of evidence for the presence of size-dependent, alternative male reproductive tactics in *S. stercoraria*. First, males present at the alternative resource occupied by females (i.e. pomace) were significantly smaller than males present on dung. The patterns observed suggest two contributing mechanisms. (i) Comparison of the male size distributions between the adjacent and distant pastures shows that when the alternative resource is nearby, smaller males that would otherwise search for females on dung will leave the pasture for the alternative resource. (ii) Comparison of the male size distributions between pomace and the distant pasture shows that particularly small males are uniquely present on pomace and do not search for females on dung even when this alternative resource is absent (and not even as floater males). Second, males found in copula are significantly smaller than single males on pomace. The mechanism(s) giving rise to this pattern is as yet unknown. Possible explanations include (i) only smaller males seek copulations on pomace (e.g. larger males on pomace are only there to feed), (ii) smaller males are better at searching for females on pomace (Blanckenhorn *et al.* 2008), and/or (iii) females are able to exert mate choice on pomace and have a preference for smaller males. Any combination of these three mechanisms supports the interpretation of an alternative mating tactic. Third, both post-copulatory mate guarding and attempts to aggressively take over the mating partners of other males—two behaviours that are staples of intrasexual competition for mates on dung (Parker 1970d, 1970e, 1971)—are completely absent on pomace, as has also been reported for copulations on flowers (Parker 1971).

It is perhaps unsurprising that alternative mating tactics exist in *S. stercoraria*. When sexual selection is intense, with great variation among males in reproductive success,

there will be strong selection for alternative means of reproducing. Moreover, the greater the variation in reproductive success among males employing traditional tactics, the more easily an alternative tactic can invade (Shuster & Wade 2003; Wade & Shuster 2004). Despite a lack of parental care by either sex, the reproductive potential of males far exceeds that of females in *S. stercoraria*. Although males are predicted to spend time every few days feeding at locations away from dung in lieu of mate searching, the majority of their time is spent trying to mate, and they are capable of inseminating many females in a day (Ward & Simmons 1991; Parker 1992). In contrast, females appear to mate once (with the exception of takeovers) per clutch, and the typical time interval between egg clutches is estimated in the laboratory at 6–7 days (Parker 1970*b*; Gibbons 1987). Consequently, operational sex ratios on dung are highly male biased (e.g. Parker 1970*g*; Jann *et al.* 2000). With gravid and receptive females concentrated in space and time (dung pats are attractive to flies only for about the first 5 h; Parker 1970*g*), higher quality (in this case, larger and more aggressive) males are able to monopolize matings. Indeed, the intensity of sexual selection on male size has been shown to be consistently strong in *S. stercoraria* (Jann *et al.* 2000), and variation among males in reproductive success, owing to contributions of genetic variation in traits other than size, may be much higher than selection gradient estimates based strictly on male size and without regard to individual males (Jann *et al.* 2000).

It is easy to see why different male tactics would be favoured on pomace from on dung (Emlen & Oring 1977). The pomace resource patch is extremely large compared with a dung pat, with both males and females widely dispersed, thus altering the economics of territoriality and male–male competition on dung. In addition, only approximately 5 per cent of females observed on and around dung pats are not paired (i.e. copulating with or guarded by a male). Based on copulation and oviposition time, including consideration of the influence of takeovers, females are thus estimated to spend not more than approximately 2 min unpaired in the vicinity of dung (Parker 1970*g*). In dramatic contrast, the majority of females on pomace at any time are unpaired, although copulations are frequently observed (S. Pitnick 2007/2008, personal observation). In addition, whereas sex ratios are male-biased on dung, they are unbiased on pomace (more information on sex-specific maturity of flies on pomace is needed to estimate operational sex ratios). Finally, the cost–benefit relationship to females as a function of male size, aggression and takeover attempts probably differs substantively between dung and pomace, possibly affecting female mate discrimination and rejection behaviour.

The reasons for females on pomace being larger than those on dung need to be investigated. Female body size covaries positively with clutch size in *S. stercoraria* (Parker 1970*b*; Borgia 1981; Blanckenhorn 1997), and it may be that larger females need to feed more and/or have longer inter-clutch intervals, thus spending proportionately more of their time at a foraging site such as pomace.

We presume that the variation in mating tactics described is condition dependent, arising through

status-dependent selection (Gross 1996; Tomkins & Hazel 2007). That is, selection has favoured phenotypic plasticity in male mating tactics in *S. stercoraria*, with alternative ‘decisions’ made by individual males based on the assessment of their physical condition and hence mating opportunities. Adaptive phenotypic plasticity in growth rates and body size has been demonstrated for *S. stercoraria* (Blanckenhorn 1998). It is probably the case that the smallest males that were observed to successfully mate with females on pomace have higher fitness than hypothetical males of similar size that only searched for females on dung. There is some debate regarding whether genetic variation underlies the variation among individuals expressing different tactics (Gross 1996; Shuster & Wade 2003; Tomkins & Hazel 2007; Shuster *in press*). Body size is significantly heritable in *S. stercoraria*, with values ($h^2 = 0.3–0.7$; Simmons & Ward 1991; Mühlhäuser *et al.* 1996) consistent with those generally found for morphological traits (Mousseau & Roff 1987). However, the extent of genetic variation underlying the behavioural phenotypes characteristic of the tactics, or of any putative ‘switch point’ determining which tactic to employ, is unknown. If there is a switch point, it is likely to be density dependent given the nature of male–male competition for mates, further complicating the overall nature of sexual selection on male size and behaviour in this system.

It is nevertheless possible that the alternative male tactics of *S. stercoraria* represent a genetic polymorphism maintained by frequency-dependent selection (and hence alternative ‘strategies’; Gross 1996; Shuster & Wade 2003; Oliveira *et al.* 2008). Virtually all females mating on pomace will remate on dung prior to oviposition, with the last male siring on average 80 per cent of the female’s subsequent progeny (Parker 1970*b*). Hence, a successful mating on dung will make roughly four times the contribution to a male’s reproductive success as will a mating on pomace. However, the critical comparison is between the reproductive success of an average male on pomace versus an average male on dung. Given the intense intrasexual competition on dung and consequent high variation in male mating success, average male reproductive success of males employing this tactic may be relatively low. Other considerations when comparing fitness consequences of the two tactics include the following: (i) copulating females on pomace are on average larger than those on dung, so that the reproductive effort of males on pomace is concentrated on the most fecund females; (ii) search times for females off dung may not be as long and energetically demanding as previously presumed (Parker 1971, 1992); (iii) copulating males on pomace never lose their mates through takeovers; (iv) energy savings and reduced risk of injury owing to the lack of aggressive interactions between males should contribute to enhanced male longevity on pomace; and (v) males on pomace can feed while mate searching whereas, owing to the general lack of opportunity to capture prey on dung, these are alternative functions that temporally trade-off for males on dung (Parker 1992; for other considerations of size-dependent energetics in *S. stercoraria*, see Blanckenhorn & Viele 1999; Blanckenhorn *et al.* 2007). Intriguingly, with these same considerations in mind, Parker (1992) has modelled the alternative strategy of males copulating

exclusively away from dung and has concluded that such a tactic might be adaptive and that extra-dung maters would be smaller on average (Parker 1978b).

Irrespective of the differences between models for the evolutionary maintenance of the alternative tactics in *S. stercoraria*, their mere existence will have two evolutionary consequences. First, genetic variation in male body size will be maintained. Studies of male reproductive success on dung indicate strong directional sexual selection on male body size (e.g. Jann *et al.* 2000). Although it has been presumed that such selection is restrained by counterselection through larval or adult viability selection against large body size, evidence for this is generally lacking (Blanckenhorn 1998; Jann *et al.* 2000). Enhanced reproductive success of the smallest males in the population as a consequence of alternative mating tactics would contribute to genetic variation in size through disruptive selection. Second, the extra-dung mating tactic will erode the opportunity for sexual selection in this species, the extent of which is a function of the proportion of males in the population expressing the alternative phenotype (Shuster & Wade 2003; Wade & Shuster 2004).

Finally, it must be considered whether results presented here are artefactual, in that the alternative resource, being such a large quantity of apple pomace, is unusual and not historically part of the selective environment for *S. stercoraria*. Until the behaviour of dung flies across their range is more thoroughly explored to determine where they go and what they do when they are not on dung, this will remain an outstanding question. Nevertheless, we postulate that observations and patterns reported here are diagnostic of a widespread, naturally occurring phenomenon. In particular, the abundance of very small male *S. stercoraria* on pomace—size classes that are completely absent from dung even in a location where pomace was not available—suggests that small males naturally inhabit substrates other than dung. Moreover, the different responses of males and females to the presence of pomace and the smaller-male mating advantage on pomace are consistent with the ‘alternative male mating tactic’ hypothesis and are unexplained by the ‘artefact’ hypothesis.

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