Size-related Mating and Reproductive Success in a Drosophilid: *Phorticella striata*

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Sarat C. Yenisetti and Sreedhara N. Hegde (2003) Size-related mating and reproductive success in a drosphilid: *Phorticella striata*. *Zoological Studies* **42**(1): 203-210. Influence of male and female body size on mating preference in *Phorticella striata* is studied with the help of male and female choice experiments. In female preferential mating (female choice), males with long wings were observed to be successful mating with both large and small females, indicating the success of large over small males in male rivalry, which may also be due to selection by females. In male preferential mating (male choice) both large and small males preferred mating with large females. These results prove that size-assortative mating exists in the drosophilid *P. striata*. Courtship latency, mating latency, copulation duration, fecundity, and fertility were studied using 4 different crosses (large male x large female; large male x small female; small male x large female; small male x small female). Courtship latency and mating latency were shorter for crosses in which 1 or both sexes were large. In the small male x small female cross the longest courtship and mating latencies were observed. Lower fecundity was noticed in the cross small male x large female cross, and differences in fecundity with the other 3 crosses were statistically insignificant. The large male x large female cross showed the highest fertility, and differences between the other 3 crosses were statistically insignificant. Correlations among longer copulation duration, higher fecundity, and the highest fertility exist only for the cross involving both sexes of the large size. This reveals that higher fertility depends on both duration of copulation and body size of both sexes involved. The number of ovarioles present in larger and smaller *Phorticella* was studied. As body size increases, the ovariole number also increases. In the light of results obtained in *Phorticella striata*, the authors support the hypothesis of ⸢bigger the better⸥ proposed by Hegde and Krishna (1997).
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Body size in *Drosophila*, and in many other organisms, is closely linked to life history traits such as fecundity, dispersal ability, and mating success (Robertson 1957, Roff 1977 1981 1986, Atkinson 1979, Partridge 1988, Prout and Barker 1989, Ruiz et al. 1991). The adaptive nature of body size in *Drosophila* has also been demonstrated by many workers both in natural populations (Prevosti 1955, David and Bocquet 1975, Parsons 1983, Coyne and Beecham 1987) and in laboratory populations (Anderson 1966 1973, Powell 1974, Lande 1977).

Size has been an important theme in many investigations of *Drosophila* mating systems (Partridge and Farquhar 1983, Markow 1985 1988, Hoffmann 1987, Wilkinson 1987, Santos et al. 1988). Partridge et al. (1987a) and Santos et al. (1988) showed the influence of body size on mating success. Body size also influences mating latency, fecundity, and other fitness components (Aplatov 1929, Ewing 1961, Monclus and Prevosti 1971, Partridge and Farquhar 1981 1983, Partridge et al. 1987b, Santos et al. 1988 1992, Taylor and Kekic 1988, Ruiz and Santos 1989, Hegde and Krishna 1997 1999a b, Krishna and Hegde 1997a b). Very few studies of *Drosophila*

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male mating success have been conducted in the field, but they also support the importance of male size (Partridge et al. 1987a, Markow 1988, Santos et al. 1988 1992, James and Jaenike 1992). It was also observed that fitness characters like starvation tolerance and dessication tolerance are significantly higher for *D. repleta* and *Zaprionus indianus* which are characterized by large body size in comparison with other sophophoran species (Parkash and Munjal 1999).

Partridge et al. (1987a b) demonstrated that large males have a mating advantage over small males, while in females, size imparts no mating advantage. Contrary to this, Hedge and Krishna (1997) proved with their size-assortative mating experiments in *D. malerkotliana* that large males pair with large females, and small males with small females; and that large females mate with large males and small females with large males. Apart from male competition, pheromones influencing female choice was also reported in *D. grimshawi* (David and Benjamin 1988). Correlations between copulation duration and fertility, and variation in mating propensity have also been studied in *D. bipectinata* (Singh and Sisodia 1995, Sisodia and Singh 1996).

Reproductive success of large and small flies of *D. malerkotliana* and *D. bipectinata* was studied using a no-choice method by Krishna and Hegde (1997a b). Results indicate that large males have higher remating ability and longevity than do small males. They further observed that large females also have higher reproductive success because they have a greater number of ovarioles, lay more eggs, and produce more fertile offspring than do small females and also mate with more males in their lifetime than do small females through their greater longevity. These findings suggest that large flies have higher reproductive success than small flies. On the basis of a size-assortative study in *D. malerkotliana*, Hedge and Krishna (1997) hypothesized that ʻbigger is betterʼ.

Different species have adopted different evolutionary strategies, and hence whether this hypothesis is applicable to other species or not has to be verified. Therefore the authors studied size-related mating and reproductive success in *Phorticella striata* (Nirmala and Krishnamurthy 1975). The present investigation aims to understand whether: a) there is any size-assortative mating in *Phorticella striata*; b) large flies of *Phorticella striata* have higher reproductive success; and c) the hypothesis ʻbigger is betterʼ is applicable to *Phorticella striata*.

MATERIALS AND METHODS

Fifty naturally inseminated female flies collected from Brindavan Gardens, Mysore, Karnataka formed the material for the study. Flies were placed in 10 bottles and inbred for 10 generations. After each generation flies were mixed together and then redistributed to 10 bottles. Eggs were collected from stock drawn from the above following the procedure of Delcour (1969).

One hundred eggs were seeded in fresh culture bottles with 25 ml of soji-jaggery-agar medium and maintained at a temperature of 22 ± 1°C in order to reduce environmental variation in size due to changes in temperature and larval competition. When adults emerged, virgin females and bachelor males were separated within 3 h of eclosion and maintained separately at 22 ± 1°C. Since wing length exhibits a continuous variation, large and small flies were determined as follows. Wing lengths of males and females emerging in a culture bottle were measured, and mean wing lengths of both sexes were calculated. Flies with a wing length greater than the mean were considered to be large (the mean for males was 2.1 mm and for females 2.2 mm), while flies with a wing length less than or equal to the mean were considered to be small.

Size-related mating

Virgin females and bachelor males at 11 to 12 d old were used to study whether there is any difference in mating (mating preference) between long-winged (selected males with a wing size ranging from 2.1 to 2.4 mm, and females with a wing size ranging from 2.2 to 2.4 mm) and short-winged (males with a wing size range of from 1.6 to 2.1 mm, and females with a wing size range of from 1.9 to 2.2 mm) flies.

In the male pairing experiment (male choice experiment), a male with long wings was introduced into a mating chamber (5 x 5-cm circular glass chamber with a lid) together with a female with long wings and another with short wings. A reciprocal pairing was made with a male with short wings and 2 females, one with long wings and another with short wings. Similarly in the female pairing experiment (female choice experiment) a female with long wings was introduced into a mating chamber together with long- and short- winged males. Reciprocal pairing was made here too. Experiments for each combination (LM x SF-LF; SM x SF-LF; SF x SM-LM; LF x SM-LM) (LM, large

male; SM, small male; LF, large female; SF, small female) were conducted in triplicate, and each set consisted of 25 trials. Observations were made for 1 h. Flies that did not mate within 1 h were considered as unmated. For each mating, mate preference was observed.

The fly (male or female) with long wings was identified by marking it with Indian ink on the scutellum in each of the above pairings. Whether the Indian ink mark had any effect on mating choice was tested by painting small-winged flies. Results clearly indicate that painting had no influence on the performance of these flies.

Size-associated reproductive success

The same stock used for the study of size-related mating was used here also. When adults emerged, virgin females and bachelor males were isolated within 3 h of their eclosion and maintained separately at 22 ± 1°C. The left wing length of male and female flies was measured (from the humeral cross vein to the tip of the wing was measured with an ocular micrometer at x 40 magnification); (Fig. 1) separately when they reached the required age. After measuring wing length, each fly was placed separately in fresh food vials to study their fitness characters.

Virgin females and bachelor males at 11 to 12 d old with a chosen range of wing size (as mentioned above in the size-related mating experiment) were taken, and 4 different crosses were made: 1) large male x large female; 2) large male x small female; 3) small male x large female; and 4) small male x small female. In the matings, courtship latency, mating latency, and mating duration were recorded.

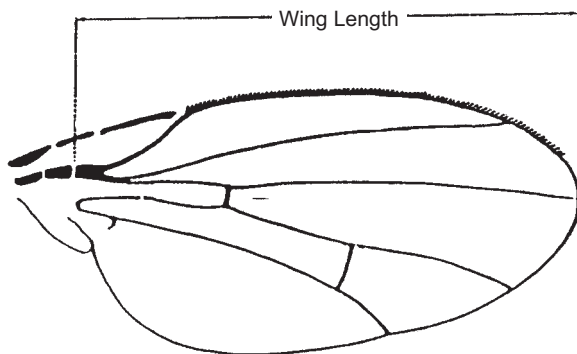Soon after mating, females were transferred into fresh food vials every 24 h without etheriza-tion. The total number of eggs laid in each vial (fecundity) and the total number of adults which appeared (fertility) were counted over a period of 15 d. Experiments for each cross were conducted in triplicate, and 25 trials comprised 1 set. Mean courtship latency (time elapsed between introduction of a male and female until performing the 1st act of courtship in seconds), mating latency (time elapsed between introduction of a male and female until initiation of copulation in seconds), mating duration (copulation duration in seconds), fecundity, and fertility were obtained.

Wing size and number of ovarioles

Twenty-two flies (11 to 12 d old) of different sizes were taken, and the length of the left wing was measured with an ocular micrometer at a magnification of x 40. Individual females were dissected separately in a drop of invertebrate physiological saline (0.7% NaCl) under a binocular stereomicroscope. Ovarioles of each ovary were separated from each other with a fine needle and counted.

RESULTS

Size-related mating

Table 1 depicts the results obtained in the choice experiments (pairing experiments). In the female pairing experiment, short-winged females usually mated with long-winged males (46 of 60 trials; χ^2 calculated on the basis of the 1:1 null

Table 1. Mating success of large and small *Phorticella striata* flies along with χ^2 values

a) Female-choice method

	LM	SM	Total	χ^2
SF	46	14	60	17.07***
LF	50	16	66	17.52***

b) Male-choice method

	LF	SF	Total	χ^2
SM	38	14	52	10.24**
LM	46	20	66	11.07**

***$p < 0.0001$; **$p < 0.001$.
LM:large male (2.1-2.4mm); SM:small male (1.6-2.1mm);
LF:large female (2.2-2.4mm); SF:small female (1.9-2.2mm).

Fig. 1. Measurement of wing length.

hypothesis, 17.07; $p < 0.0001$). In the reciprocal pairing, 50 of 66 long-winged females were also mated by long-winged males ($\chi^2 = 17.52$; $p < 0.0001$). In the male pairing experiment, 38 of 52 short-winged males mated with long-winged females ($\chi^2 = 11.07$; $p < 0.001$). In the reciprocal pairing 46 of 66 long-winged males mated with long-winged females ($\chi^2 = 10.24$; $p < 0.001$).

Size-associated reproductive success

Summaries of the mean courtship latency, mating latency, copulation duration, fecundity, and fertility of the 4 different crosses, namely, LM x LF, LM x SF, SM x LF, and SM x SF, are tabulated in Table 2. To identify whether any difference exists between different crosses in the studied fitness characters, and if a difference exists, to identify the extent of significance, one-way analysis of variance (ANOVA) followed by Duncans' multiple range test (DMRT) was applied.

One-way ANOVA revealed a significant difference between mean courtship latency ($F = 10.84$; df = 3 and 96; $p < 0.001$), mean mating latency ($F = 10.74$; df = 3 and 96; $p < 0.001$), mean copulation duration ($F = 6.74$; df = 3 and 96; $p < 0.001$), mean fecundity ($F = 3.75$; df = 3 and 96; $p < 0.01$), and mean fertility ($F = 12.76$; df =3 and 96; $p < 0.001$) of different crosses. Furthermore, Duncans' multiple range test (DMRT) estimated for courtship latency showed that the courtship latencies of LM x LF and LM x SF, and SM x SF and SM x LF were statistically the same. However, the courtship latency of SM x SF was found to be highest and to differ from that of all other crosses. In case of mating latency, DMRT clarified that the difference in mating latency of LM x LF and LM x SF was statistically non-significant, and that of LM x SF and SM x LF was also non-significant. However, mating latency of SM x SF was identified to be the highest and to differ from that of all other crosses. DMRT values of copulation duration show that differences in copulation durations of LM x LF, SM x LF, and SM x SF were statistically non-significant. However, the copulation duration of LM x SF was found to be the shortest and to differ from that of all other crosses. DMRT results of fecundity proved that differences in fecundity of SM x SF, LM x SF, and LM x LF were non-significant, and fecundities of SM x LF and SM x SF were also statistically the same. However, the fecundity of SM x LF was found to be the lowest and to differ from that of all other crosses. DMRT applied to fertility clarified that differences in the mean fertility of the crosses, SM x SF, SM x LF, and LM x SF, were statistically non-significant. However, the fertility of cross LM x LF was observed to be the highest and to differ from that of all other crosses.

Wing size and number of ovarioles

In *Phorticella*, ovariole number is dependent on body size (Fig. 2). Twenty-two females of varying wing lengths from 1.9 mm (minimum) to 2.4 mm (maximum) with a mean wing length of 2.1 ± 0.1 mm showed variation in the number of ovarioles of from 8 (minimum) to 27 (maximum), with a mean ovariole number of 16.3 ± 1.3. A significant positive correlation was observed between wing length and ovariole number ($F = 0.948$; $p < 0.001$).

DISCUSSION

According to Santos et al. (1988) males or females can enhance their reproductive success if they are able to preferentially choose their mates by means of "male choice" (male preferential mating): If males choose from a variety of females and

Table 2. Fitness characters of different crosses in *Phorticella striata* (values are the mean ± S.E.)

Parameter	Different Crosses				*F* value
	Large male x large female	Large male x small female	Small male x large female	Small male x small female	
Courtship latency	332.76 ± 85.06	493.44 ± 107.85	821.12 ± 164.42	1494.76 ± 227.72	10.84**
Mating latency	349.60 ± 90.69	501.36 ± 107.22	842.24 ± 161.7	1501.64 ± 227.44	10.74**
Copulation duration	170.80 ± 4.04	145.92 ± 2.7	175.24 ± 11.77	190.40 ± 6.35	6.74**
Fecundity	70.04 ± 4.87	65.6 ± 7.14	46.48 ± 4.37	55.64 ± 4.94	3.75*
Fertility	22.92 ± 1.19	14.92 ± 1.39	13.64 ± 1.39	13.56 ± 1.02	12.76**

* $p < 0.01$; **$p < 0.001$
Large male (2.1-2.4 mm); Large female (2.2-2.4 mm); Small male(1.6-2.1mm); Small female (1.9-2.2mm).

mate with those which are large and consequently have higher fecundity; or "female choice" (female preferential mating): If females choose from a variety of males and mate with those which confer higher quality to the offspring. Further, the male or female choice tests will also indicate the role of the male or female in sexual selection.

In female choice experiments, large males were successful on both occasions. This is in agreement with the work of Krebs and Barker (1991) who while studying male size difference and mating success in *D. buzzatii* showed that when 2 males that differ in thorax length by at least 100 units (approximately 0.04 mm) were placed in a mating vial with a single virgin female, the larger of the 2 would mate with the female. Dow and Von Schilcher (1975), while studying aggression and mating success in *D. melanogaster*, showed that large males successfully mated with females. In the present studies, large males won out over small males in mating competition. At the same time, this also supports the existence of female choice in *Phorticella*. However, in male choice experiments (Table 1) where there was no competition between different types of males, and females of both sizes were available, large females were mated by large males, and small males also preferred large females. Thus it is clear that both large and small males prefer to mate with large females.

This kind of assortative mating of *Phorticella* indicates that females can discriminate between males during sexual selection. This agrees with the finding of Singh and Chatterjee (1992) who, while studying intraspecific sexual isolation in *Drosophila*, found that females are more important in sexual selection than males. In *D. malerkotliana*, Hegde and Krishna (1997) showed that

mating is size-assortative; large mates with large, small with small. However, they further declared that whether the mate choice or intrasexual competition causes this mating pattern remains to be investigated. Edvardsson and Arnqvist (2000) reported cryptic female choice in the red flour beetle *Tribolium castaneum*. David and Benjamin (1998) demonstrated that female choice was influenced by pheromones in the Hawaiian fruitfly *D. grimshawi*. They observed that female choice has resulted in the evolution of elaborate male courtship signals. Based on their work, they said that "male mating success is found to be non-random and males that court females intensely and deposit many pheromone-containing streaks on the substrate are more successful". In *D. buzzatii* (Norry et al. 1995) in contrast to males, there is no indication of selection in females, nor is there any evidence of size-assortative mating. A comparison of results with respect to size-related mating indicates that there are interspecific and intergeneric variations.

Vigor is an important factor in male mating success (Maynard 1956), and larger *Drosophila* males seem to have higher vigor than do smaller ones. In *Phorticella*, larger males by virtue of their higher vigor will be successful in obtaining mates. This agrees with the work of Butlin et al. (1982) who, while studying the effect of chromosomal inversion on adult size and male mating speed in the seeweed fly (*Coelopa frigida*), showed that when the data are grouped in terms of size difference between 2 competing males, mating is random if the difference in size is less than 0.2 units; otherwise the mating is non-random.

Contrary to the observations of Partridge et al. (1987a), Hegde and Krishna (1997) showed in their study that both large males and large females have an advantage. They further stressed that "large males perform different courtship acts more quickly and more often than small males. Through these courtship acts the males not only convey sexual signals but also stimulate the females (Spieth 1968). Large males can transmit sexual signals to, and stimulate, the courting females more quickly. Large females, on the other hand, show more rejection responses than small females. Because they are more active, however, large males can repeatedly and quickly stimulate the females to reach the threshold for copulation". On the basis of their experiment, Hegde and Krishna (1997) hypothesized that 'bigger is better'. *Phorticella* is a true representative of this well-acknowledged hypothesis. Here even small
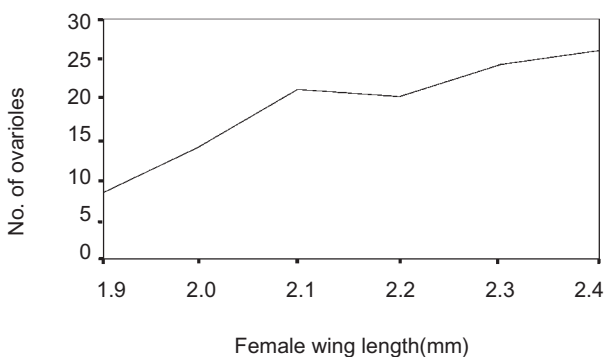
Fig. 2. Relationship between female wing length and number of ovarioles in *Phorticella striata.*

males prefer to mate with large females. It is true that 'bigger is better'.

Higher mating success alone does not qualify an individual for higher reproductive success. The reproductive success of males depends on the number of sperm that take part in fertilization, while in females it depends on the number of eggs produced and fertilized. Data on fecundity and fertility of different crosses involving large and small flies of both sexes in *P. striata* (Table 2) show that both copulation duration and body size of individuals involved in the cross determined the fertility, not just copulation duration alone. Krishna and Hegde (1997a b) showed the advantage of large size in both *D. malerkotliana* and *D. bipectinata*. They showed that fecundity and fertility are lowest in crosses involving both sexes with short wings and higher in all other crosses (LM x LF, LM x SF, and SM x LF), even if one of the 2 sexes is larger. Singh and Mathew (1996 1997) reported in *D. ananassae* that flies possessing a greater number of sternopleural bristles are larger in size, exhibit greater mating success, and produce more progeny than those with a low number of bristles. Sisodia and Singh (1996) observed significant positive correlations between duration of copulation and number of progeny produced in different strains of *D. bipectinata*.

Kaul and Parsons (1965) found a negative correlation between mating latency and copulation duration for different inversion kayotypes in males of *D. pseudoobscura*. Parsons (1973) suggested that the individual completing mating and copulation rapidly will most readily leave genes in subsequent generations, and thus there is some selective advantage in completing mating and copulation rapidly. A positive correlation between male mating activity and fertility was found in *D. subobscura* and *D. ananassae* (Maynard 1956, Singh and Chatterjee 1987). Fulker (1966) investigated the relations between time to beginning mating, duration of copulation, the number of copulations resulting in fertilization, and the number of progeny produced in *D. melanogaster*. All 4 measures appeared to be general characteristics of male mating behavior and males that mated more quickly also copulated successfully and left more progeny. Gilbert and Richmond (1982) reported that at 16°C, *D. melanogaster* males with active esterase-6 mated sooner, copulated for a shorter duration, and produced more progeny per mating than did males without esterase-6. Ringo et al. (1986) found that there was a negative correlation between male mating success and post-mating fitness in *D. simulans*

as the males of certain strains had higher mating propensity, greater virility, and lower production. The lower productivity of the males might have been caused in part by exhaustion of rapidly synthesized components of the ejaculate (Fowler 1973). Hay (1976) found a negative correlation between male mating speed and female fertility in certain laboratory strains of *D. melanogaster*. The line with faster males had females with lower fertility, which resulted in a smaller number of progeny for that line. Thus it is not necessarily true that the fastest male genotypes also have greater reproductive fitness.

Thus contradictory results have been obtained by different workers. The aims of the experiments of these workers differed, and hence they might have overlooked the relationship of many of these characteristics with size. For example, Krebs and Barker (1991), while studying inter- and intraspecific competition between *D. aldrichi* and *D. buzzatii*, showed that large males are successful because of their ability to outweigh smaller ones. Similarly Norry et al. (1995) demonstrated that large males are successful not because of female selection but just because of their capability to win out over smaller ones. Comparisons of results with respect to the relationship among mating activity, duration of copulation, and fertility reported for *D. melanogaster*, *D. pseudoobscura*, *D. subobscura*, *D. robusta D. ananassae*, *D. simulans*, *D. bipectinata*, and *D. malerkotliana* clearly indicate that there are intra- and interspecific variations.

The current investigation of *Phorticella* includes certain aspects of sexual behavior and post-mating fitness of 4 different crosses (LM x LF, LM x SF, SM x LF, and SM x SF). The LM x LF cross showed the highest fertility, higher fecundity, longer copulation duration, and shorter courtship latency and mating latency. A comparison of results reveals that the highest fertility was obtained after a longer copulation duration in the cross LM x LF. If one of the partners was small, although copulation lasted for a longer duration, lower fertility was observed. In the LM x SF cross, a shorter copulation duration and lower fertility were observed. This indicates that *Phorticella* fertility is dependent on the size of both sexes and on the duration of copulation. Therefore various species of *Drosophila* and different genera in the family Drosophilidae differ in certain aspects of sexual behavior and reproductive success.

The difference between the fecundities of LM x SF and SM x SF was also non-significant. However the authors do not simply accept that

fecundity differences indicate that large males are better than small males. It is interesting to note that the difference in the fecundities of SM x LF and SM x SF was also non-significant. Fecundity simply indicates the number of eggs laid without giving any information on whether they were fertilized or not. We are of the opinion that physical force of the mating activity (being greater in the case of larger males) supplements the fecundity of LM x LF. In this context, the study of Gruwez et al. (1971) is worth mentioning. According to them, higher fecundity of a female is correlated with the number of ovarioles it bears. The present data on body size and the number of ovarioles (Fig. 2) show that large females have a greater number of ovarioles than do small ones. This means that body size has a telling effect on the number of ovarioles. These observations agree with the findings of Montague (1985) who demonstrated that larger females carry more ovarioles and have higher potential fecundity. Santos et al. (1992) also found a positive correlation between thorax length and the number of ovarioles in *D. buzzatii*.

Thus it is evident that large males have higher reproductive success as they being highly vigorous can move faster, encounter females more quickly, and mate faster. Large females also have higher reproductive success, as they have more ovarioles and are able to produce a greater number of fertile eggs when mated with large males.

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