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Influence of body size in mating success in three sympatric species of *Drosophila*

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ABSTRACT

Influence of male and female body size in courtship and mating success was studied in three sympatric species of *Drosophila*: *D. rajasekari* (medium-sized flies), *D. bipectinata* (small-sized flies) and *D. nasuta* (large-sized flies) using male choice, female choice and pair-wise matings. In pair-wise mating, in all the above species mating latency was negatively correlated with male and female wing length; long-winged flies performed courtship and mating activities with greater intensity than did short-winged flies. In female choice mating, too, long-winged males had greater mating success than short-winged ones, while in male choice mating, long-winged males mated more selectively with long-winged females, and short-winged males with short-winged females indicating size-assortative mating to be present in all three sympatric species. Thus, this study suggests that in *Drosophila*, irrespective of species size, long-winged flies have greater intensity in courtship activities and mating success, confirming the "bigger is better" hypothesis and that sexual selection favours large size.

KEY WORDS: Wing length - *Drosophila* - Mating success.

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INTRODUCTION

In *Drosophila*, mating is resource independent and males do not show parental care (Hoikkala & Liimatainen, 1992). However, The size of the courting pairs has an important role in courtship and mating (Hegde & Krishna, 1997), when, during courtship activities, the female recognizes potential mate (Hegde & Krishna, 1997). Body size also has been an important theme in many investigations of the *Drosophila* mating system (Markow, 1985). Wing length is an excellent index of body size (Sokoloff, 1966) and studies have shown influence of body size on mating success and sexual behaviour in a number of *Drosophila* species (Ewing, 1961, 1964; Monclus & Prevosti, 1971; Partridge *et al.*, 1987; Santos *et al.*, 1988, 1992; Naseerulla & Hegde, 1992; Hegde & Krishna, 1997; Sisodia & Singh, 2001). Both laboratory and field studies have already suggested that male mating success is related to male size for a number of *Drosophila* species (Markow, 1985, 1988; Partridge *et al.*, 1987; Santos *et al.*, 1988, 1992; Aspi & Hoikkala, 1995; Hegde & Krishna, 1997). However, the influence of female size on mating success has been largely ignored. Further, different reasons have also been suggested for greater mating success of large males (Partridge *et al.*, 1987; Hegde & Krishna, 1997), and it is interesting that in *D. subobscura* small males, too, have courtship advantage (Steele & Partridge, 1988).

In *Drosophila*, studies have also pointed out that the individuals of a population belong to various cohorts such as body size, age-classes, different generations etc. (Capy & Lachaise, 1986). In such a situation, one can expect occurrence of assortative mating among different cohorts. Parsons (1965) who, while working on *D. melanogaster*, found assortative mating for sternopleural chetae number, and suggested that it was similar to that found in man for many physical traits. Recently, using wing length as an index of body size (Hegde & Krishna, 1997), we noticed size-assortative mating in *D. malerkotliana* where large males prefer to mate with large females and small males with small females; we also proposed a "bigger is better" hypothesis on the basis of mating and courtship activities performed by males and females of different size during courtship. However, in view of contradictory information in *D. subobscura* (Steele & Partridge, 1988), more studies are needed in other species of *Drosophila* to test the role of body size in courtship and mating success. Therefore, the present study was undertaken using three sympatric species, belonging to the *melanogaster* species group viz., *D. rajasekari*, *D. bipectinata* and *D. nasuta*. The aims of this study are: 1) the role of body size in sexual selection; 2) whether size-assortative mating occurs in other species of *Drosophila*, and 3) whether the "bigger is better" hypothesis is applicable to other species or not.

MATERIALS AND METHODS

The stocks used in the present study originated from 150 naturally inseminated (wild caught) females of *D. bipectinata*, *D. ra-*

jasekari and *D. nasuta* from Mysore, Karnataka, India. There are natural differences of size in these species, *D. bipunctinata* being the smallest and *D. nasuta* the largest. Not only is the mean body size of these three species different, but variations in size exist within each species. All experiments were carried out separately but in the same environment for each species under study. Females were placed together in a culture bottle (250 ml). When progeny appeared, the flies were distributed over different culture bottles and maintained under constant temperature and humidity (for details of the procedure, see Hegde & Krishna, 1997). After ten generations, when adults emerged, virgin females and males were isolated within 3 h of their eclosion and maintained separately at 22 ± 1 °C and 70% relative humidity. Wing lengths of four to five-day-old male and female flies were measured separately and individually following the procedure of Hegde & Krishna (1997). After measuring the wing length, each fly was placed separately in a fresh food vial for 24 h and later was used to study courtship and mating success.

Pair-wise mating

The male with the longest wings was placed with the female with the longest wings in an Elens-Wattiaux mating chamber (a circular chamber with a diameter of 9 cm). The male with the second longest wings was allowed to mate with the female having second longest wings, and so on. This experimental design allowed us to study size-related mating latency and mating success under a pair-wise mating (uncompetitive) situation. Mating latency (time between introduction of male and female together into the mating chamber until initiation of copulation of each pair) and mating success (number of pairs mated in every 15-min period) was recorded. A total of 125 pairs was observed for 1 h; flies that did not mate after 1 h were considered unmated. Correlation matrices were calculated for wing length and mating latency data. Two-factors ANOVA followed by Duncan's Multiple Range Test (DMRT) was also carried out on mating success and mean wing length of flies mated in different time intervals (0-15 min, 16-30 min, 31-45 min, 46-60 min).

Male and female pairing (male and female choice matings)

Flies aged 5-6 days with long and short wings (see Table I for chosen wing lengths) were used to see whether there was any difference in mating success between long- and short-winged flies. In male mating experiments (male choice), a male with long wings was introduced to a female with long wings and another female with short wings in the mating chamber. A reciprocal mating was made with a male with short wings and two females, one with long wings and the other with short wings. Similarly, in the female mating experiments (female choice), a female with long wings was introduced into the mating chamber with a male with long wings and another male with short wings. Reciprocal matings were also made with a female with short wings and two males, one with long wings and another with short wings.

TABLE I - Chosen wing lengths of males and females.

Species	Male wing length (mm)		Female wing length (mm)	
	Long	Short	Long	Short
<i>D. bipunctinata</i>	1.72-1.74	1.58-1.60	1.93-1.95	1.78-1.80
<i>D. rajasekari</i>	1.80-1.82	1.68-1.70	1.97-1.99	1.82-1.84
<i>D. nasuta</i>	2.35-2.37	2.07-2.09	2.62-2.64	2.39-2.41

To identify the male or female with long or short wings, one of the two males or females in each of the above pairings was painted with Indian ink on the scutellum. The effect of painting was tested before the experiment by painting the short-winged flies with Indian ink and allowing them to mate. The results indicated that painting had no effect on the performance of these flies. For each set, 50 trials were made and a χ^2 test was applied to the data.

Body size, mating activity and courtship pattern

Large and small virgin females and males (see Table I) aged 5-6 days were used to study mating activities and courtship patterns. Different matings were made (large male with large female; large male with small female; small male with large female; small male with small female). A total of 50 pair-wise matings were made for each of the crosses. Courtship latency was the time between introduction of a male and a female together into a mating chamber until the male had oriented itself towards the female. Mating latency was the time between introduction of male and female together into a mating chamber until initiation of copulation of each pair. Copulation duration was the time between initiation and termination of copulation for each pair. In addition, courtship acts such as tapping, scissoring, vibration, licking, circling, ignoring, extruding and decamping were quantified following the procedure of Hegde & Krishna (1997). Two-way ANOVA was applied to the data.

RESULTS

Correlation matrices of mating latency and wing length of three sympatric species are presented in Table II. It is clear from these data, that the time taken for initiation of copulation increased with increasing wing length. With pairs of flies (Fig. 1), the highest percentage of mating occurred in 0-15 min. Further, mating success varied significantly between different time intervals (two-way ANOVA: $F = 121.51$, $df = 3, 6$, $P < 0.0001$) between species ($F = 56.21$, $df = 2, 6$, $P < 0.001$) and also between species and time intervals ($F = 61.51$, $df = 5, 6$, $P < 0.001$). Duncan's Multiple Range Test (DMRT) showed that, irrespective of the species, a greater percentage of flies paired during the 0-15 min intervals than in subsequent periods. In *D. bipunctinata* and *D. rajasekari*, the percentage of flies mating during the 16-30 min period did not vary significantly from those

TABLE II - Correlation matrices between wing length and mating latency.

Parameters	<i>D. bipunctinata</i> $n = 116$ $df = 114$	<i>D. rajasekari</i> $n = 120$ $df = 118$	<i>D. nasuta</i> $n = 122$ $df = 110$
Mating latency	-	-	-
Female wing length (mm)	0.589*	0.492*	0.505*
Male wing length (mm)	0.625*	0.598*	0.512*

*, $P < 0.001$

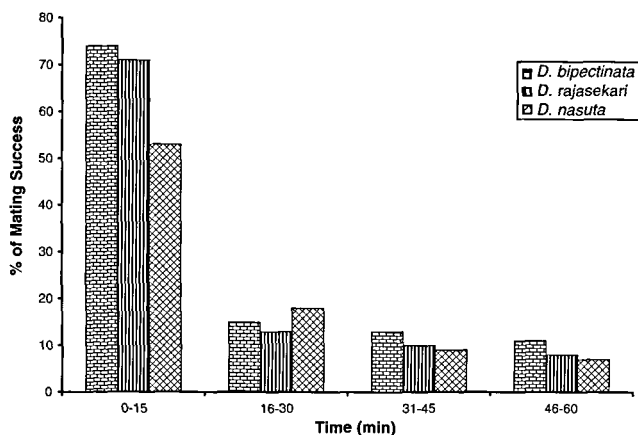


Fig 1 - Percentage of mating success in different time intervals.

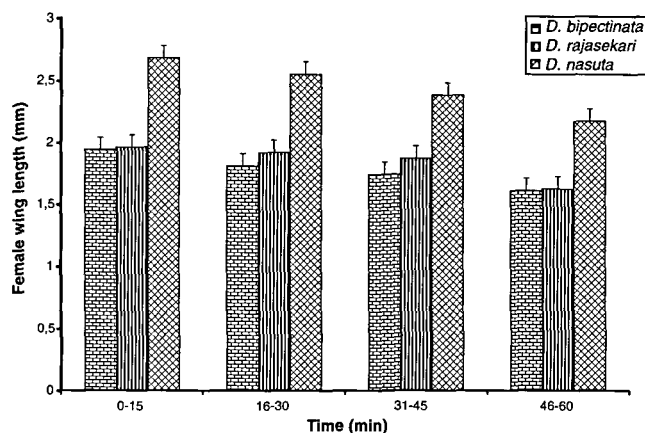


Fig. 3 - Average female wing length according to mating success in different time intervals.

during the 31-45 min period, but was significantly greater than the percentage of flies mating during the 46-60 min period. In *D. nasuta*, the percentage of flies mating in 16-30 min was significantly different from that during subsequent intervals.

Wing length of males (Fig. 2) varied significantly between time intervals (two-way ANOVA and subsequent DMRT: $F = 45.25$, $df = 3, 6$, $P < 0.01$), between species ($F = 51.62$, $df = 2, 6$, $P < 0.01$) and also between species and time intervals ($F = 42.41$, $df = 5, 6$, $P < 0.01$). Males that mated during the 0-15 min period had longer wings than flies that mated during subsequent time intervals. Female wing length (Fig. 3) also varied significantly between intervals (two-way ANOVA and subsequent DMRT; $F = 58.73$, $df = 3, 6$, $P < 0.01$), between species ($F = 61.75$, $df = 2, 6$, $P < 0.01$) and also between species and time intervals ($F = 35.64$, $df = 5, 6$, $P < 0.05$). Females that mated within 0-15 min had significantly longer wings than females that mated in subsequent intervals by DMRT.

Table III reports data on wing length and mating success in three sympatric species of *Drosophila* using female choice matings. In *D. rajasekari*, in 42 out of 50 trials, the female with short wings was mated by a male

with long wings, while in the remaining eight trials she mated with short-winged males. In reciprocal matings, in 40 out of 50 trials, long-winged females mated with long-winged males, while in 10 trials they mated with short-winged males. In *D. nasuta*, in 44 out of 50 trials, the female with short wings was mated by a male with long wings, and in the remaining six trials short-winged females mated with short-winged males. Instead, in reciprocal matings, in 41 out of 50 trials, long-winged females mated with long-winged males and in the remaining nine trials she mated with short-winged males. Similarly in *D. bipectinata*, in 39 out of 50 trials, the female with short wings was mated by a male with long wings and in the remaining 11 trials short-winged females mated with short-winged males. While in reciprocal crosses, in 40 out of 50, trials long-winged females mated with long-winged males and in the remaining 10 trials long-winged females paired with short-winged males. Chi-square values of all three sympatric species of *Drosophila* showed significant difference in all the crosses studied.

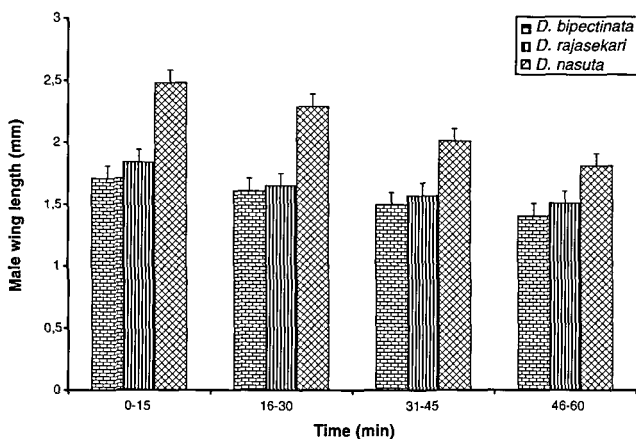


Fig. 2 - Average male wing length according to mating success in different time intervals.

TABLE III - Wing length and mating success using male choice experiments.

Males	Females		χ^2	P
	Large	Small		
<i>D. rajasekari</i>				
Large	41	9	31.15	<0.01
Small	16	34	21.16	<0.01
<i>D. nasuta</i>				
Large	39	11	28.19	<0.01
Small	13	37	21.15	<0.01
<i>D. bipectinata</i>				
Large	33	17	22.15	<0.01
Small	16	34	26.17	<0.01

TABLE IV - Wing length and mating success using female choice experiments.

Females	Males		χ^2	P
	Large	Small		
<i>D. rajasekari</i>				
Large	40	10	33.00	<0.01
Small	42	08	30.12	<0.01
<i>D. nasuta</i>				
Large	41	09	25.19	<0.01
Small	44	06	29.11	<0.01
<i>D. bipectinata</i>				
Large	40	10	30.15	<0.01
Small	39	11	26.31	<0.01

Data on wing length and mating success in the sympatric species of *Drosophila* using male choice matings are provided in Table IV. In *D. rajasekari*, in 45 out of 50 trials, short-winged males mated with short-winged females and in the remaining 16 short-winged males mated with long-winged females. In reciprocal crosses, in 41 out of 50 trials, long-winged males mated with long-winged females and in the remaining nine trials long-winged males mated with short-winged females. In

D. nasuta, in 37 out of 50 trials, short-winged males mated with short-winged females and in the remaining 13 trials short-winged males mated with long-winged females. In reciprocal crosses, in 39 out of 50 trials, long-winged males mated with long-winged females and in remaining 11 long-winged males with short winged females. Similarly, also in *D. bipectinata*, in 34 out of 50 trials, short-winged males mated with short-winged females while in the remaining 16 short-winged males mated with long-winged females. In reciprocal crosses, in 33 out of 50 trials, long-winged males mated with long-winged females and in the remaining 17 trials long-winged males mated with short-winged females. These indicates that size-assortative mating existed in all the species of *Drosophila* studied, and that the χ^2 -value showed significant difference in all the crosses.

Tables V and VI show courtship and mating activity in all three sympatric species; the number of pairs copulating was highest in pairs involving short-winged males and long-winged females. Courtship and mating latency were the highest in pairs of short-winged males and long-winged females and the lowest in pair of short-winged males and long-winged females, indicating that short-winged males oriented towards long-winged females slowly and initiated copulation more slowly than did long-winged males. Courtship patterns such as tapping, scissoring, vibration, licking, and circling were more frequent in long-winged pairs, while rejection responses such ignoring, extruding, and decamping were greater in pairs of long-winged females and short-

TABLE V - Mating activities of different sized flies in *Drosophila*.

Species	Large male × large female	Large male × small female	Small male × large female	Small male × small female	F	P
Percent of mating						
<i>D. rajasekari</i>	94	80	68	86	$F_1 = 312.75$	<0.0001
<i>D. nasuta</i>	84	61	62	78	$F_2 = 220.58$	<0.0001
<i>D. bipectinata</i>	96	84	74	88	$F_3 = 11.91$	<0.05
Courtship latency						
<i>D. rajasekari</i>	3.10 ± 0.19	3.46 ± 0.32	6.47 ± 0.40	4.05 ± 0.51	$F_1 = 5.35$	<0.05
<i>D. nasuta</i>	5.10 ± 0.18	1.10 ± 0.19	8.10 ± 0.19	10.36 ± 0.52	$F_2 = 17.36$	<0.05
<i>D. bipectinata</i>	3.30 ± 0.19	3.40 ± 0.16	5.10 ± 0.19	4.10 ± 0.15	$F_3 = 1.22$	>0.05
Mating latency						
<i>D. rajasekari</i>	3.38 ± 0.42	3.71 ± 0.21	6.49 ± 0.14	4.25 ± 0.31	$F_1 = 5.29$	<0.05
<i>D. nasuta</i>	5.29 ± 0.31	8.05 ± 0.41	8.56 ± 0.16	11.15 ± 0.15	$F_2 = 19.69$	<0.05
<i>D. bipectinata</i>	3.66 ± 0.29	3.74 ± 0.16	5.44 ± 0.20	4.89 ± 0.15	$F_3 = 1.49$	>0.05
Copulation duration						
<i>D. rajasekari</i>	9.54 ± 0.32	11.35 ± 0.01	10.01 ± 0.12	8.05 ± 0.06	$F_1 = 6.27$	<0.05
<i>D. nasuta</i>	19.25 ± 0.47	17.05 ± 0.37	16.71 ± 0.47	14.27 ± 0.17	$F_2 = 88.27$	<0.01
<i>D. bipectinata</i>	9.64 ± 0.09	9.45 ± 0.13	9.39 ± 0.09	7.29 ± 0.07	$F_3 = 1.27$	>0.05

F_1 , between crosses; F_2 , between species; F_3 , between species and crosses

-winged males. Further, mating activities and courtship patterns were significantly different between species. The data on these activities and patterns were found statistically significant by two-way ANOVA (Tables V, VI).

DISCUSSION

The size of the three sympatric species used in the present study was different (see Table I) *D. nasuta* being the largest and *D. bipectinata* the smallest, and they showed significant variation in mating success (Fig. 1). This shows that in *Drosophila* species-specific difference occurs in mating success, which is in agreement with the work of Spieth (1968) who also found differences in the mating activity of 101 Hawaiian *Drosophila* species. However, in the present study, in each of the three sympatric species (Table II), mating latency was negatively correlated with both male and female wing

length, indicating that fast-mating flies had longer wings than slow-mating flies. This agrees with the work of Monclus & Prevosti (1971) on *D. subobscura* and Naseerulla & Hegde (1992) on *D. malerkotliana*. They also demonstrated a positive relationship between wing length and mating speed in a multiple choice situation where fast mating flies had longer wings than slow-mating flies. Even in nature, Partridge *et al.* (1987) and Santos *et al.* (1988) found that mating males had longer wings than non mating males in *D. melanogaster* and *D. buzzatii*. In the present study, Figures 1-3 also show that mating success and wing length varied significantly between time intervals. Flies mating within 0-15 min had greater mating success and longer wings than flies that mated in subsequent intervals. Therefore, in each of the species, irrespective of size, fast-mating flies had longer wings than slow-mating flies.

Males or females select their partner in order to increase their fitness. Large female mates are more fecund

TABLE VI - Courtship pattern of different sized flies in *Drosophila*.

Species	Large male × large female	Large male × small female	Small male × large female	Small male × small female	F	P
Tapping						
<i>D. rajasekari</i>	13.42 ± 0.52	10.16 ± 0.32	8.31 ± 0.31	8.05 ± 0.23	F ₁ = 5.87	<0.05
<i>D. nasuta</i>	4.15 ± 0.25	3.56 ± 0.35	3.00 ± 0.16	2.10 ± 0.51	F ₂ = 50.04	<0.01
<i>D. bipectinata</i>	8.90 ± 0.19	6.02 ± 0.20	11.81 ± 0.27	6.61 ± 0.19	F ₃ = 3.96	<0.05
Scissoring						
<i>D. rajasekari</i>	16.36 ± 0.15	14.36 ± 0.38	9.32 ± 0.42	12.92 ± 0.17	F ₁ = 6.51	<0.05
<i>D. nasuta</i>	3.52 ± 0.41	2.56 ± 0.51	2.31 ± 0.44	1.56 ± 0.41	F ₂ = 215.88	<0.0001
<i>D. bipectinata</i>	17.76 ± 0.22	12.61 ± 0.28	19.46 ± 0.34	15.92 ± 0.27	F ₃ = 2.51	>0.05
Vibration						
<i>D. rajasekari</i>	13.10 ± 0.11	9.12 ± 0.21	7.28 ± 0.16	8.32 ± 0.16	F ₁ = 4.09	<0.05
<i>D. nasuta</i>	15.21 ± 0.31	15.01 ± 0.41	13.32 ± 0.41	13.05 ± 0.51	F ₂ = 46.15	<0.01
<i>D. bipectinata</i>	7.14 ± 0.17	5.27 ± 0.14	11.19 ± 0.16	6.58 ± 0.21	F ₃ = 5.47	<0.05
Circling (twist dance in <i>D. rajasekari</i>)						
<i>D. rajasekari</i>	3.51 ± 0.31	3.35 ± 0.16	2.32 ± 0.08	2.05 ± 0.21	F ₁ = 2.27	<0.05
<i>D. nasuta</i>	8.41 ± 0.21	7.28 ± 0.25	6.27 ± 0.57	4.37 ± 0.37	F ₂ = 23.86	<0.01
<i>D. bipectinata</i>	2.46 ± 0.19	1.35 ± 0.07	2.73 ± 0.18	1.48 ± 0.10	F ₃ = 0.78	>0.05
Ignoring						
<i>D. rajasekari</i>	12.10 ± 0.16	10.64 ± 0.31	15.81 ± 0.32	12.05 ± 0.48	F ₁ = 2.93	>0.05
<i>D. nasuta</i>	11.21 ± 0.41	12.21 ± 0.61	15.05 ± 0.51	11.54 ± 0.54	F ₂ = 6.43	<0.05
<i>D. bipectinata</i>	14.67 ± 0.26	13.68 ± 0.26	17.78 ± 0.21	14.21 ± 0.21	F ₃ = 3.37	>0.05
Extending						
<i>D. rajasekari</i>	16.15 ± 0.31	11.31 ± 0.42	18.81 ± 10.42	13.21 ± 0.51	F ₁ = 6.25	<0.05
<i>D. nasuta</i>	2.15 ± 0.11	2.31 ± 0.61	3.25 ± 0.61	2.00 ± 0.31	F ₂ = 7.21	<0.01
<i>D. bipectinata</i>	18.29 ± 0.25	14.77 ± 0.24	20.00 ± 0.30	15.07 ± 0.39	F ₃ = 4.10	<0.05
Decamping						
<i>D. rajasekari</i>	16.32 ± 0.21	11.21 ± 0.51	18.52 ± 0.31	14.05 ± 0.61	F ₁ = 6.38	<0.05
<i>D. nasuta</i>	10.15 ± 0.61	11.51 ± 0.32	13.15 ± 0.16	9.25 ± 0.15	F ₂ = 77.28	<0.01
<i>D. bipectinata</i>	20.26 ± 0.35	16.73 ± 0.41	22.29 ± 0.55	17.31 ± 0.17	F ₃ = 4.59	<0.05

F₁, between crosses; F₂, between species; F₃, between species and crosses.

and large male mates sire higher quality offspring (Robertson, 1957; Partridge *et al.*, 1987; Santos *et al.*, 1988, 1992). In the present study, in female choice matings large males were more successful irrespective of the size of the female, showing that large males had an advantage in intrasexual competition. This is because in female choice situations females appeared to use relative criteria thereby preferring longer-winged males. This agrees with the work of Krebs & Barker (1991) on *D. buzzatii* and Hegde & Krishna (1997) on *D. malerkotliana*. While studying *D. buzzatii*, Aspi & Hoikkala (1995) found that during courtship large males produced more courtship song than did small males. On the other hand, in male choice matings, large males preferred to mate with large females and small males with small females, showing size-assortative mating. This confirms our earlier work on *D. malerkotliana* (Hegde & Krishna, 1997). Therefore, these studies suggest that size-assortative mating occurs in several other species of *Drosophila*, too.

Greater mating success is also related to the activities of the pairs in courtship (Partridge *et al.*, 1987). This is because *Drosophila* males do not contribute resource to their mates or protect their mates or offspring. Therefore, the displays given by the males before mating are the only grounds on which the females can differentiate between potential mates (Hoikkala & Liimatainen, 1992). Since we could not check locomotor activity of courting pairs, only courtship acts such as tapping, scissoring, vibration, etc., which involve interaction of courting pairs, were recorded. These acts are important for pheromone exchange because, when touching and licking, each partner receives chemical stimuli from the other (Jallon, 1984; Scott *et al.*, 1988). If the interaction between the partners is a symmetrical (i.e., if one of the partners is not able to give the right stimuli) the courtship may become fixed at a certain phase for a longer period (Hoikkala & Liimatainen, 1992). The males and females which performed greater and faster courtship acts had greater mating advantage than the ones which showed less and slower courtship (Hegde & Krishna, 1997). Therefore, in the present study (Table V, VI), contrary to the observations of Partridge *et al.* (1987) and Steele & Partridge (1988), in all three sympatric species large males and females performed greater and faster courtship acts than did small males and small females, and had greater mating success. This confirms our hypothesis of "bigger is better" in *D. malerkotliana* (Hegde & Krishna, 1997). Further, courtship and mating activity varied significantly between species (Table V, VI). *D. nasuta* courted and mated more slowly than *D. rajasekari* and *D. bipectinata*. This shows that species-specific differences occur in courtship and mating activities. According to Spieth (1968), through these courtship acts the males not only convey sexual signals but also stimulate females. Therefore, *D. rajasekari* males with their greater courtship acts may be faster at stimulating the female than are *D. nasuta* and *D. bipectinata*. On the other hand, *D. ra-*

jasekari females may be more receptive than *D. nasuta* and *D. bipectinata*. Furthermore, in all three sympatric species, copulation duration was also the highest in pairs involving long-winged flies with respect to pairs involving short-winged flies (Table VI). Thus, these studies suggest that in all the three sympatric species large flies have courtship and mating advantage and size-assortative mating does occur in all the species.

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