

Positive Relation between Male Size and Remating Success in Some Populations of *Drosophila bipectinata*

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Positive relation between male size and remating success in some populations of *Drosophila bipectinata*. *Zoological Studies* 47(1): 75-83. In the present study, an apparent association between male size and male remating components was studied in 4 different geographical populations of *Drosophila bipectinata* using the no-choice method. Male size and remating components such as male mating latency (percentage of males remating), male remating latency, male mating ability, and copulation durations with the 1st and 2nd females varied significantly between different geographical populations, but all showed positive relations between male size and male remating components. Male size and remating components were significantly correlated in these populations suggesting that large males mated faster, copulated longer, remated faster and more frequently, and inseminated more females, while small males mated faster, copulated for a shorter duration, remated more slowly and less frequently, and inseminated fewer females. It was also noted that the duration of copulation was shorter in the 2nd mating (remating) by males than the 1st mating. Thus, in *D. bipectinata*, these studies suggest the occurrence of interpopulational variations in male size and male remating components, and support the hypothesis of bigger is better. <http://zoolstud.sinica.edu.tw/Journals/47.1/75.pdf>

Key words: *Drosophila bipectinata*, Male remating, Wing length, Body size.

The sexual behaviors of various species of *Drosophila*, with particular reference to their basic courtship patterns, genetic control, role of stimuli, and contributions of the 2 sexes to variations in mating activity and repeated mating, have been extensively studied (Parsons 1973, Banerjee and Singh 1977, Gromko and Pyle 1978, Casares et al. 1998). Size also has been an important theme in many investigations of *Drosophila* (Partridge and Farquhar 1983, Markow 1985, Hoffmann 1987, Santos et al. 1988, Hegde and Krishna 1997, Krishna and Hegde 2003, Sisodia and Singh 2004). Partridge et al. (1987) 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 (Ewing 1961, Monclús and Prevosti 1971, Partridge and Farquhar 1983, Partridge et al. 1987, Santos et al. 1988, Hegde and Krishna 1997,

Krishna and Hegde 1999 2003).

Very few studies of *Drosophila* male mating success have been conducted in the field (Markow 1985, Partridge et al. 1987, Santos et al. 1988 1992, James and Jaenike 1992). Partridge et al. (1987) demonstrated that in *D. melanogaster*, large males have a mating advantage over small males, while in females, size imparts no mating advantage. Contrary to this, Hegde and Krishna (1997) showed in the laboratory the occurrence of size assortative mating in *D. malerkotliana*, where large males prefer to pair with large females and small males with small females. Similar size assortative matings were also noted in other species of *Drosophila* such as *D. bipectinata*, *D. rajasekari*, *D. nasuta* (Krishna and Hegde 2003), and *D. ananassae* (Sisodia and Singh 2004). Those studies also indicated that the sizes of both males and females influenced mating success in

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Drosophila.

It has been widely demonstrated that males of different species of *Drosophila* can inseminate more than 1 female, and the mating ability of males is influenced by genetic and other factors (Prakash 1967, Singh and Chatterjee 1987, Sanchez Prado and Blanco Lizana 1989, Singh and Singh 1999). According to Gromko (1992), multiple mating is widely believed to be advantageous to males, and selection by males can produce a correlated response in females. In *Drosophila* and other organisms, the importance of male size in courtship and mating has also been studied (Hegde and Krishna 1997).

The importance of male size on sexual behavior is not straightforward, and in most cases, only 1 or a few aspects of male fitness like success in inter-male competition, fecundity, fertility, and longevity have been studied (Partridge and Farquhar 1983, Markow 1985, Partridge et al. 1987, Santos et al. 1988, Hegde and Krishna 1997, Krishna and Hegde 1999, Sisodia and Singh 1996 2004). In fact, remating is also a strategy for improving the fitness of individuals of polygamous populations. In *Drosophila*, the influence of female remating on fitness has been studied (Sisodia and Singh 2004). The further influence of male size on male remating components has been largely ignored. However, the influence of male size on male mating on fitness components has not been studied in *Drosophila*. Therefore the present investigation was undertaken in *D. bipectinata* to test the hypothesis that male size has a positive correlation with aspects of mating success in populations of the same species with individuals of different sizes.

MATERIALS AND METHODS

In the present study, mass culture stocks of *D. bipectinata* populations collected at 4 different geographic localities of Baroda (Ba), Kuppe Forest (KF), Shiradi Ghat (Sh G), and Mysore (Mys) were used. Each of these stocks was established from 50 wild-caught females collected from the above localities. Mass-cultured stocks carry a greater fraction of genetic variability than that originally present in the population. These stocks were maintained on wheat cream agar medium by transferring 50 flies (containing an equal number of males and females) to fresh culture bottles (containing 250 ml wheat cream agar medium) in each generation, and 10 generations were propagated

in the laboratory. In each stock, virgin females and bachelor males were collected and aged for 5-6 d.

A virgin female and a bachelor male from each population were aspirated into a fresh food vial and allowed to mate. They were observed for 1 h, and if no mating occurred, then the pair was discarded. When mating occurred, the male mating latency (time elapsed between the transfer of the male and female into the mating chamber until initiation of copulation by each pair) was recorded. Then the copulating pair was allowed to complete copulation, and the duration of copulation (time elapsed between copulation initiation to termination by each pair) was noted. The mated female was aspirated out, and she was replaced with another virgin female; this new pairing was observed for 2 h. When the male remated, the male remating latency (time elapsed between the introduction of the 2nd female into the mating chamber until initiation of copulation with her) and the duration (min) of copulation with the 2nd female were also recorded. If no male remating occurred within 2 h, that pair was discarded. This process was repeated, and the total number of females inseminated by each male within 2 h was recorded. This was considered the male remating ability (number of females inseminated by each male). After this, the male size was measured using wing length as an index (Hegde and Krishna 1997). In total, 50 males were observed for each strain, and the male remating frequency (% of males remating), male mating latency, remating latency, male remating ability, durations of copulation with the 1st and 2nd females, and male size (in terms of wing length) were recorded. All these experiments were carried out at $22 \pm 1^\circ\text{C}$ between 07:00 and 11:00. Analysis of variance followed by Duncan's multiple Range Test was carried out on male size, mating latency copulation duration, remating latency, copulation duration with 2nd female and mating ability. Correlation matrices also been calculated between male size and male remating components with in the population and general linear model (repeated measures) between male size and copulation duration with 1st and 2nd female was applied using spss 11.5

RESULTS

Male size showed variations in all 4 different geographic populations studied (Table 1a). It was noted that males of the Shiradi Ghat population had the longest wings (1.85 mm) while those of the

Baroda population had the shortest wings (1.33 mm). One-way analysis of variance (ANOVA) followed by Duncan's multiple-range test (DMRT) carried out on mean male size of 4 different geographic populations showed significant variations

(Table 1b). DMRT applied to the mean male size of different populations showed that male size of the Baroda population (1.37 mm) significantly varied from those of other populations. Similarly, Kuppe forest males (1.62 mm) had significantly

Table 1a. Male size and male remating components of *Drosophila bipectinata*

Parameter	Geographic population			
	Kuppe Baroda	Shiradi Forest	Ghat	Mysore
No. of pairs	50	50	50	50
Male size (mm)	1.37 ± 3.51 ^a	1.62 ± 8.69 ^b	1.83 ± 1.04 ^c	1.63 ± 6.53 ^b
Male mating latency I (min)	6.19 ± 0.11 ^d	4.77 ± 9.06 ^c	3.44 ± 8.82 ^a	3.98 ± 9.54 ^b
Copulation duration with 1st male (min)	7.26 ± 0.12 ^a	8.29 ± 6.77 ^b	9.95 ± 9.87 ^b	8.47 ± 0.11 ^b
Male remating latency II (min)	19.9 ± 19.1 ^c	13.0 ± 0.37 ^b	8.46 ± 0.24 ^a	12.2 ± 0.26 ^b
Copulation duration with 2nd male (min)	5.44 ± 9.28 ^b	5.57 ± 0.10 ^b	6.78 ± 7.61 ^c	5.13 ± 0.11 ^a
Male remating ability (no. of times)	1.80 ± 0.16 ^a	2.50 ± 0.18 ^a	3.32 ± 0.12 ^b	2.12 ± 0.14 ^a

Values are presented as the mean ± SE. Values in a row with the same letter do not significantly differ by Duncan's multiple-range test.

Table 1b. Analysis of variance of male size, copulation duration, male remating latency, and male remating ability

Source of variation	Degrees of freedom	SS	MSS	F value
I. Male size				
Between populations	3	5.165	21.498	17.656**
Within populations	196	3.579	1.218	
Total	199			
II. Male mating latency I				
Between populations	3	213.927	71.309	151.222***
Within populations	196	92.424	0.472	
Total	199			
III. Copulation duration with the 1st female				
Between populations	3	78.753	61.769	119.699*
Within populations	196	89.971	0.516	
Total	199			
IV. Male remating latency				
Between populations	3	3422.7	1140.925	212.209***
Within populations	196	1053.7	5.376	
Total	199			
V. Copulation duration with the 2nd female				
Between populations	3	78.753	26.271	57.187*
Within populations	196	89.971	0.459	
Total	199			
VI. Male remating ability				
Between populations	3	64.495	21.498	94.282**
Within populations	196	238.660	1.218	
Total	199			

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

longer wings than others, while the difference in lengths was insignificant between it and the Mysore population.

Male mating latency (with the 1st female) was higher (6.19 min) in the Borada population while it was lowest (3.44 min) in the Shiradi Ghat population. Data on the mean mating latency of all 4 populations were subjected to ANOVA followed by DMRT, which revealed significant variations among populations (Table 1b).

Data on the mean copulation duration along with the standard error of all 4 geographic populations are given table 1a. The Shiradi Ghat population had a longer copulation duration (9.95 min), while the Baroda population had a shorter copulation duration (7.26 min). Analysis of variance applied to the mean copulation duration of the 4 different geographic populations showed significant variations. ANOVA followed by DMRT carried out on the mean copulation durations of different populations showed that the copulation duration of the Baroda population (7.26 min) was significantly longer than those of the other populations. However, variations in copulation duration of these

populations were not significant.

Male mating latency with the 2nd female (male remating latency) of the 4 different geographic populations of *D. bipunctata* are provided in table 1a. It was noted that the male remating latency was shortest in the Shiradi Ghat population (8.46 min), and it was longest in the Baroda population (19.90 min). ANOVA followed by DMRT applied to the mean values of male remating latency between populations showed significant variations. The mean male remating latency of the Shiradi Ghat population (8.46 min) was significantly shorter than those of the other populations, while the mean male remating latency of the Baroda population (19.9 min) was significantly longer than those of the other populations. However, the male remating latency of Kuppe forest (13.0 min) males did not significantly vary from that of the Mysore population (12.2 min) but showed significant variations with the Baroda (19.9 min) and Shiradi Ghat populations (8.46 min).

Data on the copulation duration of males with the 2nd female are given in table 1a. It was noted that the copulation duration of males with the 2nd

Table 2. General linear model (repeated measures) between male size and mating latency with the 1st and 2nd females by the same male

Source Mat lat	Type III sum of squares	d.f.	Mean square	F value	Significance
Mat lat Linear	4930.101	1	4930.101	1558.31	0.000
Mat lat x male size Linear	1127.920	59	19.117	6.043	0.000
Error (Mat lat) Linear	442.923	140	3.164	-	-

Mat lat, Mating latency.

Table 3. General linear model (repeated measures) between male size and copulation duration with the 1st and 2nd females

Source CD	Type III sum of squares	d.f.	Mean square	F value	Significance
CD Linear	356.150	1	356.150	782.149	0.000
CD x male size Linear	57.334	59	0.972	2.134	0.000
Error (CD) Linear	63.749	140	0.455	-	-

CD, copulation duration.

Table 4. Logistic regression of mating ability with male size and population

Effect	-2 log likelihood of reduced model	Chi-squared	d.f.	Significance
Male size	87.545	50.475	59	0.778
Population	38.516	1.446	3	0.695

female was highest in the Shiradi Ghat population (6.78 min) while it was lowest in the Mysore (5.13 min) population. ANOVA followed by DMRT carried out on the copulation duration of males with the 2nd female showed significant variations among different populations (Table 1b).

Results of the GLMs (repeated measures) between male size and mating latency of males with the 1st and 2nd females are provided in table 2 and figure 1. A positive relation between male size and male mating latency was noted with the 1st and 2nd females suggesting that larger males mated faster than smaller males. Furthermore, the mating latency of males with the 1st female significantly differed from that of males with the 2nd female.

Table 3 and figure 2 show results of the GLM (repeated measures) between male size and the copulation duration of males with the 1st and 2nd females in the 4 different geographic populations of *D. bipectinata*. Significant positive relations were found for copulation durations with the 1st and 2nd females with male size and male copulation durations with the 1st and 2nd females. Furthermore, table 1 also shows significant variations between copulation durations of the male with the 1st and 2nd females.

The male remating abilities (number of females inseminated by each male) of the 4 different geographic populations of *D. bipectinata* are also given in table 1a. It was noted that males of the Shiradi Ghat population had a greater remating ability (3.32) and they inseminated more females, while males of the Baroda population had a lower remating ability (1.80) and inseminated fewer females in a given unit of time. One-way ANOVA followed by DMRT of the mean male remating ability showed significant variations among populations (Table 1b). DMRT showed that male mating ability of the Shiradi Ghat population significantly differed from those of the other populations. The other populations showed no significant differ-

ences.

Male remating frequency varied in the 4 geographic populations of *D. bipectinata* (Fig. 3). For example in the Baroda population, it was 82%, while in Shiradi, it was 96%. However, the logistic regression applied to the remating frequency data showed non-significant variations in male size and population (Table 4).

Correlation matrices between male size and male remating components are given in table 5. Male size was negatively correlated with remating latency, while positively correlated with the percentage of males remating and remating ability, suggesting that larger males had greater remating fitness than small males.

DISCUSSION

Body size in male insects may affect the reproductive activities including success in intra-sexual counters, sperm precedence, and female fecundity. For many of these activities, a larger size confers a reproductive advantage. In the present study, the influence of male size on male remating components was evaluated in 4 different geographic populations of *D. bipectinata*. It was noted that male size significantly varied among the different geographic populations (Table 1a). Males

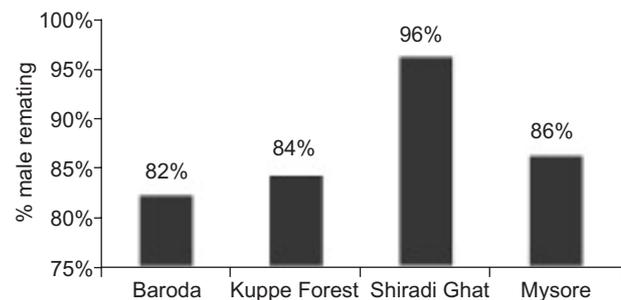


Fig.1. Chart showing percentage of male remating in different geographical populations.

Table 5. Correlation matrices between male size and male re-mating components within a population

Population	Parameter	Percent of males mating with the 2nd females	Male mating latency with the 2nd female (male re-mating latency)	Male mating ability
Baroda	Male size ($n = 41$, $d.f. = 39$)	0.79*	- 0.69*	0.82*
Kuppae Forest	Male size ($n = 42$, $d.f. = 40$)	0.81*	- 0.72*	0.69*
Shiradi Ghat	Male size ($n = 48$, $d.f. = 46$)	0.71*	- 0.67*	0.80*
Mysore	Male size ($n = 43$, $d.f. = 41$)	0.64*	- 0.79*	0.72*

* $p < 0.01$.

of the Shiradi Ghat population had the longest wings, while males of the Baroda population had the shortest wings suggesting the existence of interpopulational size differences in *D. bipectinata*. This agrees with earlier studies of body size variations in geographic strains of other species of *Drosophila* (Sokoloff 1966, Anderson 1973, Coyne and Beecham 1987). They also found inter-strain variations in morphometric traits. According to Coyne and Beecham 1987, phenotypic variations in wing length and abdominal bristle number among individuals and populations in nature have a substantial genetic component, and environmental variations within and among population do not completely obfuscate a fly's genetic endowment. There is evidence for the presence of a significant amount of additive genetic variations for body size in both laboratory and natural populations (Robertson 1987, Ruiz et al. 1991). Simple conclusions can be drawn from these types of studies that the population is not at an equilibrium and that the mean body size increases with time, or if the population is indeed at equilibrium, then positive selection for large size during the adult stage must be counterbalanced by selection in some other parts of the life cycle. In other words, a trade off exists between opposing selective forces.

It was noted that male mating latency (with

the 1st female) and remating frequency (with the 2nd female) (Table 1a, b) showed significant variations among the different populations. The Baroda population had a significantly higher male mating latency with both the 1st and 2nd female, while the least male mating latency was recorded in the Shiradi Ghat population. As speed is the reverse of time, individuals which had a higher mating latency are considered to be slow maters, while those populations with shorter mating latencies were fast maters. Therefore among the 4 population of *D. bipectinata* studied, the Shiradi Ghat population consisted of fast maters while the Baroda population consisted of slow maters. This confirms earlier studies on the influence of male size on mating components (Santos et al. 1988 1992, Hegde and Krishna 1997). Those studies also found positive correlations between male size and male mating components. A similar trend was also seen in male remating latency (mating latency of a male with the 2nd female). In the present study, the GLM carried out on data of male mating latency with the 1st and 2nd females (Table 2, Fig. 1) showed a positive relation between male size and male mating latency with the 1st and 2nd females in all populations. Similarly, it was also noted that the male remating ability (Table 1a, b) significantly varied among the different popula-

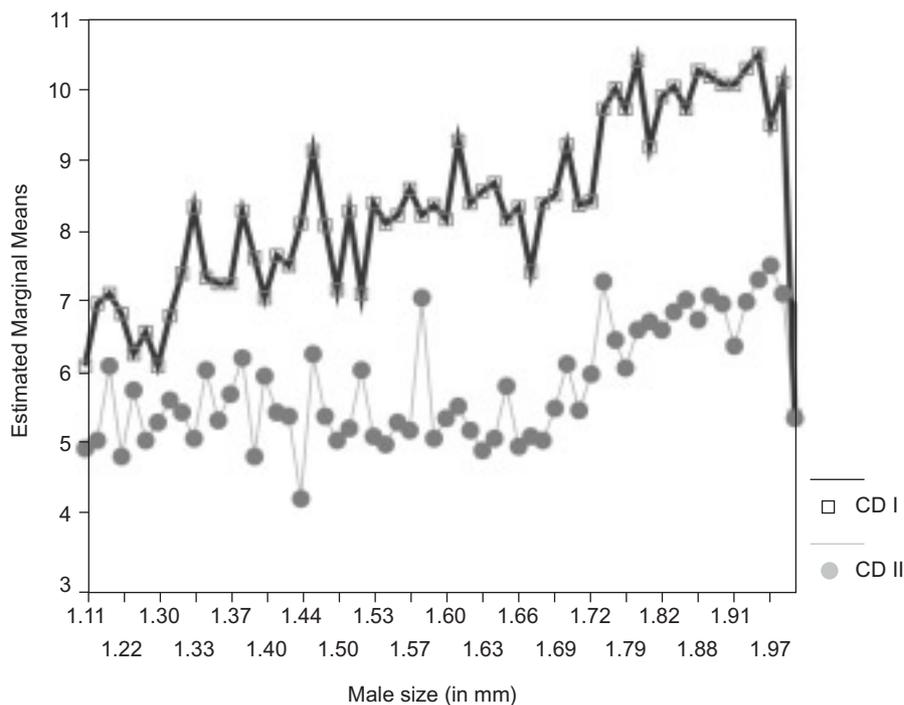


Fig. 2. Copulation duration in a repeated-measures general linear model. CD I, copulation duration with the 1st female; CD II, copulation duration with the 2nd female.

tions. The Shiradi Ghat population had the highest male remating ability, while the Baroda population had the lowest. This is because flies of Shiradi Ghat were larger when mated, remated faster, and inseminated more females in a given unit of time, while flies of the Baroda population mated and remated more slowly and inseminated fewer females. Thus in *D. bipectinata* irrespective of the geographic strains studied, larger males have greater vigor than smaller males.

In *Drosophila*, like other insects, studies have shown that although olfaction, visual, and auditory stimuli are some of the obvious influences on courtship behavior, physical characters such as body size and shape seem to be the determining factors of successful courtship and mating (Ewing 1961, Fulker 1966, Monclús and Prevosti 1971, Partridge et al. 1987, Santos et al. 1988, Krebs and Barker 1991, Ruiz et al. 1991, Naseerulla and Hegde 1992, Aspi and Hoikkala 1995, Hegde and Krishna 1997, Krishna and Hegde 2003). Those studies demonstrated the greater mating success of larger flies. This is because mating activities involve complicated sexual behaviors, because different actions by 1 sex may affect subsequent responses from the opposite sex.

In the present study, it was also noted that the copulation durations of males with the 1st and 2nd females significantly varied among populations

(Table 1a, b), which suggests the existence of intrapopulation variations in copulation duration. Further, it was also noted that the duration of copulation was shorter in the 2nd mating than in the 1st. This agrees with the work of Singh and Singh (2000) who while working with *D. ananassae* also found a variation in the durations of copulation between the 1st and 2nd matings. Joly et al. (1991) and Joly and Lachaise (1993) in their female remating studies of *D. teissieri* found that the duration of copulation in both strains was longer during the 2nd mating. Interestingly, Bressac et al. (1991) observed no significant difference in the copulation duration of the 1st and 2nd matings of different strains of *D. littoralis* or *D. latifasciaeformis*. If the results of *D. teissieri*, *D. littoralis*, *D. latifasciaeformis*, *D. affinis*, *D. ananassae*, and *D. bipectinata* are compared with respect to the incidence of remating and duration of copulation, it may be concluded that significant variations exist among species, and species with a low incidence of remating take less time to copulate in 2nd matings. This is because in *Drosophila* like other insects, the duration of copulation is male-determined (Parsons 1973). Further, a shorter duration of copulation of the 2nd mating is likely due to depletion of sperm and accessory gland secretions (Singh and Singh 2000).

Figure 3 shows the percentages of males

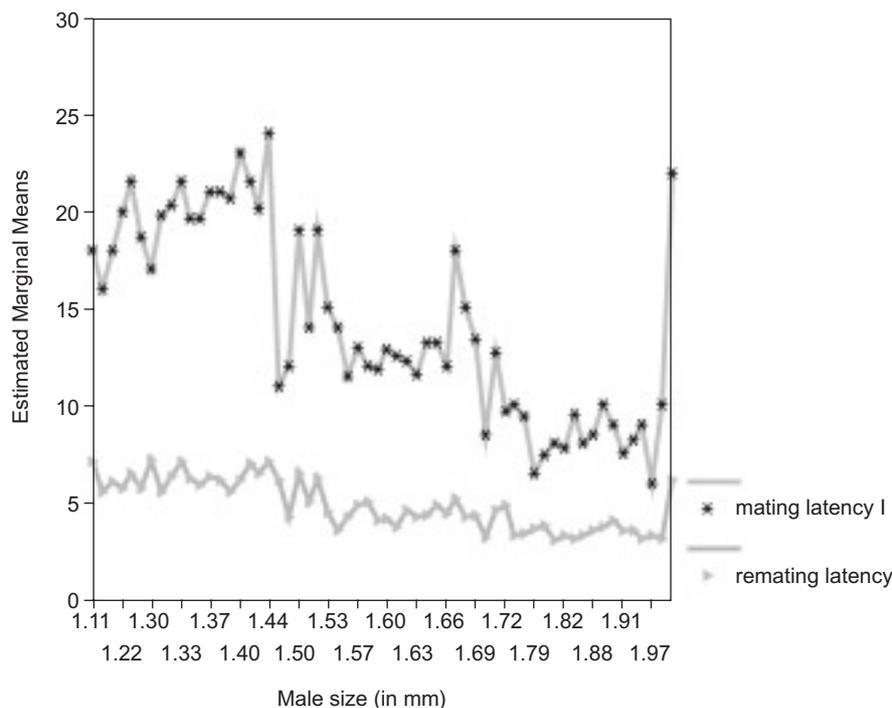


Fig 3. Mating latency in a repeated-measures general linear model.

remating in different geographic populations of *D. bipectinata*. It was noted that the percentage of males remating significantly varied among different geographic populations. The Shiradi Ghat population had the highest percentage of males remating while the Baroda population had the lowest. We already pointed out that the Shiradi Ghat population had longer flies (Table 2a). This means that individuals of a population which are larger in size remate more frequently, while others which are smaller in size remate less frequently. Thus, it is clear that there were significant variations in the male's remating ability among the 4 laboratory stocks of *D. bipectinata* originating from different geographic localities. Some populations had fast male rematers, while others had slow male rematers. Since these populations originated from different localities, the observed variations in male remating activities are attributed to genetic heterogeneity among the populations tested. Further, in the present study, mass-cultured populations were used, and they originally carry a greater fraction of the genetic variability. This agrees with earlier studies on *Drosophila* (Maynard Smith 1956, Parsons 1973, Singh and Chatterjee 1987 1992, Casares et al. 1998). Further, it was also noted that irrespective of the genetic variation among different geographic populations, male size and various components of male remating are positively related.

Correlation matrices calculated among male size, male remating latency, male remating ability, and the percentage of remating frequency are provided in table 5. It was noted that in all geographic populations, male size was negatively correlated with male remating latency, while positively correlated with male remating ability and male remating frequency, indicating that even within a population, larger males remated more rapidly and more frequently inseminated a greater number of females. This indicates that large males have a fitness advantage over small males. In the present study, the GLM applied to male size and copulation durations of males with the 1st and 2nd females (Table 3, Fig. 2) showed positive relations suggesting the influence of male size on copulation duration. This confirms earlier studies on body size and copulation duration in other species of *Drosophila*. (Hegde and Krishna 1997). Thus, the present study on *D. bipectinata* suggests the occurrence of interpopulational variations in male size and male remating and confirms the hypothesis that bigger is better (Hedge and Krishna 1997).

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