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Female Remating in *Drosophila ananassae:* Bidirectional Selection for Remating Speed

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In *Drosophila ananassae*, artificial selection was carried out for fast and slow remating speed for 10 generations. Response to selection resulted in rapid divergence in remating time in each of two replicates of both fast and slow lines. There were significant differences in mean remating time in females among fast, slow, and control lines. Regression coefficients for both fast and slow lines are significantly different from zero. The realized heritability over 10 generations of selection is from 0.26 to 0.33 for two replicates of fast line and from 0.23 to 0.27 for two replicates of slow line. These findings suggest that female remating time in *D. ananassae* is under polygenic control. Remating frequency of females showed a correlated response in both fast and slow lines. At generation 10, correlated response to selection was also investigated. Mating propensity of *D. ananassae* of fast and slow lines was observed in an Elens-Wattiaux mating chamber. Fifteen pairs per test showed that on the average, the fast lines (11.20, 11.60) were more successful in mating than those of slow (6.40, 5.60) and control (8.00) lines. Productivity of once-mated females was measured in terms of number of progeny produced per female and the results of productivity analysis indicate that females of fast lines (157.83, 130.83) produced more progeny compared with slow (72.70, 85.83) and control (109.23) lines.

KEY WORDS: *Drosophila ananassae;* selection; fast and slow remating; mating propensity; productivity; polygenes.

INTRODUCTION

Reproductive capacity is particularly a good index of fitness in organisms that go through repeated cycles of rapid population growth. In such organisms any feature of the reproductive biology that increases reproductive rate will be favored by natural selection. Remating and sperm storage are specific features that can play important roles in determining female fecundity and male mating success and, hence, fitness (Levine *et al.,* 1980). Female remating is an important component of genus *Drosophila* mating systems because females store the sperm after mating in the paired spherical spermathecae and a single elongate tubular seminal receptacle (Pitnick, Markow, and Spicer, 1999) and utilize them to fertilize eggs as they are laid. Once a virgin female *D. melanogaster* has mated, she is usually unwilling to accept another male for some time because after mating behavioral and physiological changes occur, including decreased attractiveness to males (Tram and Wolfiner, 1998); decreased receptivity to further mating (Fuyama, 1995); elevation of egg laying (Hihara, 1981); storage and utilization of sperm (Pitnick, Markow, and Spicer, 1999); and decreased lifespan (Chapman *et al.,* 1995). In *D. melanogaster*, these behavioral changes are due in part to sperm and in part to seminal fluid (Hihara, 1981; Scott, 1987).

Remating in females is common for many species of *Drosophila* under both natural and laboratory conditions (Anderson, 1974; Richmond and Ehrman, 1974; Levine *et al.*, 1980; Loukas, Vergini, and Krimbas, 1981; Markow and Ankey, 1984; Barbadilla *et al.*, 1991; Joly, Carlou, and Lachaise, 1991; Etges and Heed, 1992; Aspi and Lankinen, 1992; Ochando *et al.*,

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1996; Service and Vossbrink, 1996; McRobert *et al.*, 1997; Price, 1997; Clark, Begun, and Prout, 1999; Bundgaard and Barker, 2000). The phenomenon of remating by females is a prerequisite for the occurrence of sperm competition between males (Parker, 1970; Birkhead and Moller, 1998; Price, Dyer, and Coyne, 1999; Civetta, 1999). The total impact of sperm competition on male fitness (Gromko and Pyle, 1978) and the significant effect of remating on the fitness of the female (Pyle and Gromko, 1978), make an excellent example of sexual selection. According to Rice (1996), sperm competition offers a unique opportunity to study adaptations shaped by the interacting forces of natural, sexual, and antagonistic selection. Remating by females is insurance against male sterility and subfertility (Gibson and Jewell, 1982). According to Pyle and Gromko (1978), remating results in increasing the genetic heterogeneity of offspring. It is known that female remating depends on the amount of sperm stored (Letsinger, and Gromko, 1985), the components of the male seminal fluid (van-Vianen and Bijlsma, 1993), level of nutrition and egg laying (Chapman and Partridge, 1996), and in the laboratory by different experimental designs (Newport and Gromko, 1984).

According to Parsons (1973), extreme phenotypes continuously favored during selection will be controlled by genotypes which are likely to be more homozygous than the unselected base populations. Manning (1961, 1968) selected for fast and slow mating speed in *D. melanogaster* and *D. simulans* and demonstrated the contributions of phototaxis and general activity to variation in mating speed. Manning found that general activity was different from the sexual activity and concluded that mating speed is the outcome of the complex interaction of several factors and that fast and slow mating speed may be achieved by different routes. Genetic control of female remating speed in *Drosophila* has been reported only in *D. melanogaster* (Pyle and Gromko, 1981; Gromko and Newport, 1988a, 1988b; Fukui and Gromko, 1991a, 1991b, 1991c; Sgro, Chapman, and Partridge, 1998).

D. ananassae, a cosmopolitan and domestic species, belongs to the *ananassae* species complex of the *ananassae* subgroup of the *melanogaster* species group. This species occupies a unique status in the whole of the genus *Drosophila* owing to certain peculiarities in its genetic behavior (Singh, 2000). These peculiarities are spontaneous male crossing-over, varied chromosomal polymorphism, heterosis without coadaptation, segregation distortion, high mutability, extrachromosomal inheritance, parthenogenesis, and Y-4 linkage of the nucleolus organizer. In *Drosophila*, usually an X-Y linked nucleolus organizer is found. The Y-4 association of the nucleolus organizer suggests that a translocation of the nucleolus organizer region from X to 4 has occurred during speciation of *D. ananassae*. *D. ananassae* has been used extensively for genetic studies, particularly population genetics, behavior genetics, and crossing over (see Singh, 1996). Recently, female remating and male remating in *D. ananassae* have been studied by present authors (Singh and Singh, 1999, 2000). The results have shown that: (1) male remating occurs more frequently than female remating, (2) strain variation for remating time exists for both males and females, and (3) shorter duration of copulation exists in second mating compared with first mating. Evidence for sperm displacement and greater productivity of remated females has also been reported in *D. ananassae* (Singh and Singh, 2001).

The genetic control of female remating speed in *D. melanogaster* has been studied extensively. However, the results of these studies differ. The genetic control of female remating speed in *D. ananassae*, another cosmopolitan species, has not been tested. In view of this, we conducted bidirectional artificial selection experiments for fast and slow remating time in *D. ananassae*. We also investigated other aspects of mating behavior related to selection for the timing of remating at generation 10, such as mating propensity and productivity of once-mated females of all the selection lines and the control line. The results of these experiments are reported herewith.

MATERIALS AND METHODS

Selection Experiment

Five mass culture wild type strains of *D. ananassae* derived from different geographic localities (Baripada, Orissa; Chinsura, West Bengal; Elenthikara, Kerala; Jammu, Jammu and Kasmir and Rameswaram, Tamil Nadu) in India were reciprocally crossed with each other. Hybrids were mixed to construct the base population. The base population was maintained for 6 generations before starting the selection experiment. From the base population, groups of virgin females and males were collected and aged for 4 to 5 days in food vials separately. To obtain once-mated females, 4- to 5-day-old virgin females were placed individually in food vials with a single 4- to 5-day-old male. The vials were carefully and continuously examined, and at 10-minute intervals those vials containing newly copulating pairs were gently set aside. Observation was

continued until 50 females had mated, usually within an hour. Following the completion of copulation, males were removed by aspiration. The next morning, 50 once-mated females were individually paired with virgin males and observed at 10-minute intervals for 2 hours daily at the time of transfer, until they remated or 14 days had elapsed. Females that remated on any one of the 14 testing days were no longer given the opportunity to remate. The first 10 females to remate were used to establish the high (fast) line and the last 10 females to remate (up to 14 days) were used to establish the low (slow) line. In each generation, the remating time (in days) for 50 once-mated females in each replicate of selection lines was noted and the first 10 females to remate in the fast line were used as parents for the subsequent generation. The last 10 females to remate (up to 14 days) in the slow line were taken as parents for the subsequent generation. From the same base population, 10 remated females were selected randomly to establish the control line. In each generation, remating time (in days) was noted for 50 once-mated females, and from these remated females, 10 females were selected randomly to serve as parents for the subsequent generation in the control line. Two replicates were maintained in each of the two lines (fast and slow) for selection. In each generation, remating frequency was also noted for all lines. Selection was continued for 10 generations.

Correlated Response to Selection

In order to test the correlated response to selection, both mating propensity and productivity of once-mated females were studied at generation 10 of selection in all selected lines and the control line.

Mating Propensity

For mating propensity experiments, virgin females and males were collected from each selected line and from the control line and aged for 4 to 5 days in food vials. Females and males were stored separately in food vials in groups of 15 individuals in each vial. This experiment was carried out by direct observation in an Elens-Wattiaux (1964) mating chamber. In each trial, 15 females and 15 males were used. Females were introduced first into the mating chamber and, in all five trials, were run for each selected line and for the control line. Mating was directly observed in the mating chamber at 5-minute intervals for 30 minutes. When a pair commenced mating, it was aspirated out and the time was noted. In this way, the total number of matings (15 females $\times$ 15 males–5 replicates) was recorded for each replicate of fast and slow lines and for the control line.

Productivity of Once-mated Females

For the productivity analysis, virgin females and males were collected from each replicate of the two selected lines and the control line and aged for 4 to 5 days in separate vials. In each of the selected lines and the control line, a single virgin female was placed in a food vial with a single virgin male. The pair was observed for 30 minutes and any pair not mating during this period was recorded as unmated. The male was aspirated out of the observation vial following copulation. Each mated female was kept in an individual food vial for a period of 3 days and then was transferred to a fresh food vial every third day. Three successive changes were made and then the females were discarded. Thus, there were four sets of vials (total time: $4 \times 3 = 12$ days) for counting the progeny. The total number of flies that emerged from each vial was counted. Data were pooled and the mean number of progeny per female was calculated in each selected line and the control line. A total of 30 females were tested for progeny analysis in each replicate of selected lines and the control line.

During the course of the study, a simple culture medium containing agar-agar, brown sugar (crude sugar), dried yeast, maize powder, nipagin, propionic acid, and water was used. All the experiments were carried out at a room temperature of approximately 24°C (75°F) with 60% to 80% relative humidity (RH) and 12-hour light/dark cycle.

RESULTS

The mean remating time (days) in females during the 14-day (2 hours daily observation design) observation period in each generation for all selection lines and the control line is presented in Table I. The results of selection are shown in Fig. 1. Over the 10 generations of selection, the mean remating time (days) was 4.39 and 4.50 days in the two replicates of high (fast) line, 10.30 and 9.59 days in the two replicates of low (slow) line, and 8.31 days in the control line (Table II). From Fig. 1 it is apparent that the response to selection was immediate from the fifth generation of selection, with rapid divergence in female remating time in both high (fast) and low (slow) lines. Although there were some

Table I. Mean Remating Time (days ± SE) During 14 days (2-hr Daily Observation Design) in Various Generations of the Selection Experiment in Both Replicates of Fast and Slow Lines in *D. ananassae* (Control is Also Given for Comparison)

Generation	F_1	F_2	S_1	S_2	Control
0	—	—	—	—	7.46 ± 0.27
1	6.42 ± 0.35	6.30 ± 0.17	6.86 ± 0.36	6.93 ± 0.62	8.80 ± 0.43
2	5.25 ± 0.41	5.52 ± 0.36	11.26 ± 0.48	6.50 ± 0.29	6.26 ± 0.41
3	5.60 ± 0.39	6.20 ± 0.42	10.90 ± 0.44	8.30 ± 0.34	5.50 ± 0.34
4	4.74 ± 0.52	6.00 ± 0.40	10.15 ± 0.34	7.05 ± 0.17	6.50 ± 0.28
5	5.69 ± 0.36	3.76 ± 0.86	8.50 ± 0.34	9.79 ± 0.27	10.80 ± 0.48
6	4.16 ± 0.58	4.87 ± 0.49	8.20 ± 0.33	11.09 ± 0.29	9.55 ± 0.49
7	3.33 ± 0.67	4.34 ± 0.55	9.09 ± 0.29	10.43 ± 0.54	8.25 ± 0.24
8	3.07 ± 0.78	2.60 ± 0.89	11.55 ± 0.53	11.45 ± 0.51	8.90 ± 0.52
9	2.91 ± 0.87	2.85 ± 0.97	11.60 ± 0.51	12.10 ± 0.55	9.20 ± 0.26
10	2.70 ± 0.84	2.55 ± 0.99	11.40 ± 0.54	12.25 ± 0.64	8.35 ± 0.32

fluctuations between the two replicates of fast and slow lines, there were no significant differences between the two fast lines and between the two slow lines (Table II). Table III presents the values of realized heritability and regression coefficient and results of the test of significance for fast and slow lines. Realized heritability was estimated in the lines undergoing selection for fast and slow remating time, according to Falconer and Mackay (1996). Realized heritability over 10 generations of selection are 0.33 (F_1), 0.26 (F_2), 0.27 (S_1)

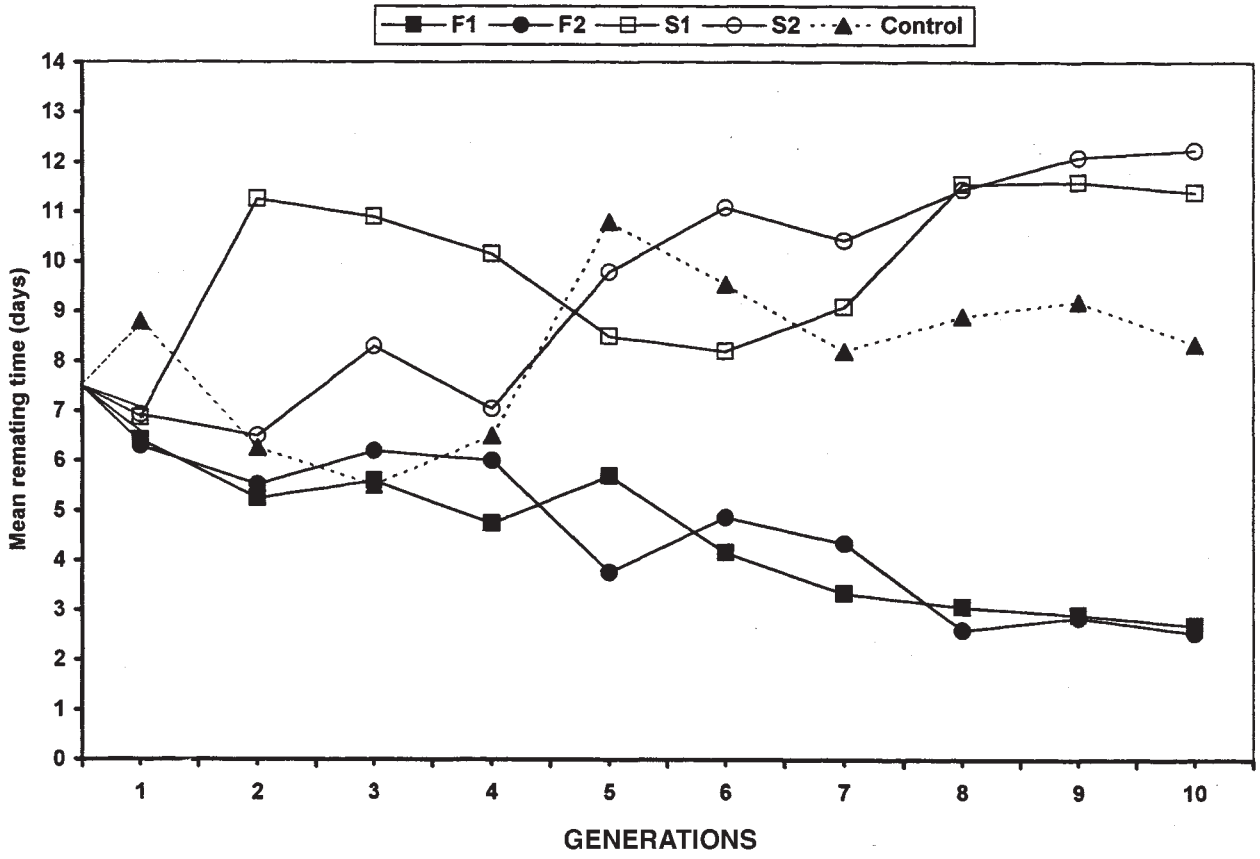

Fig. 1. Response to selection for fast and slow female remating (time in days) in *D. ananassae.* F1 and F2, fast lines; S1 and S2, slow lines.

Table II. Comparison of Mean Remating Time (Days) Over 10 Generations of Selection Between Control and Selected Lines and Between Fast and Slow Lines by *t*-tests in *D. ananassae*

Line	Mean ± SE	Comparison	*t*	df	*P*
F_1	4.39 ± 0.42	Control vs. F_1	5.37	18	<0.001
		Control vs. F_2	4.33	18	<0.001
F_2	4.50 ± 0.47	Control vs. S_1	2.29	18	<0.05
		Control vs. S_2	2.21	18	<0.05
S_1	10.30 ± 1.80				
		F_1 vs. S_1	6.96	18	<0.001
S_2	9.59 ± 0.70	F_1 vs. S_2	4.82	18	<0.001
		F_2 vs. S_1	6.74	18	<0.001
Control	8.31 ± 0.29	F_2 vs. S_2	4.45	18	<0.001
		F_1 vs. F_2	0.39	18	ns
		S_1 vs. S_2	0.95	18	ns

and 0.23 (S_2). Regression coefficients over 10 generations of selection are −0.51 and −0.63 for F_1 and F_2 lines, respectively, and +0.73 and +0.89 for S_1 and S_2 lines, respectively. These values and the results of the test of significance indicate that significant progress was achieved in both fast and slow directions.

The mean remating time (days) in females over 10 generations of selection was calculated for each replicate of fast and slow lines as well as for the control line. These values are shown in Table III. The differences between control and each replicate of selected lines and between fast and slow lines were tested by *t*-test. The differences were significant in all the comparisons, which also shows that significant progress has been made during selection for fast and slow remating speed. Remating frequency (%) for females in each generation of the selection in both replicates of fast and slow lines and in the control line is given in Table IV. The mean percentage of remating over 10 generations of selection was calculated in each replicate of the high, low, and control lines (Table V). The differences between the control and selected lines and between the fast and slow lines were tested by *t*-test after transforming the percentage to angle by Arcsine square root transformation. The differences were significant in all comparisons. These results indicate that fast line females remate more frequently than those of slow and control lines and control line females also remate more frequently than those of slow line. The two replicates of each selection line did not differ significantly from each other.

Table III. Realized Heritability (h^2), Regression Coefficient (*b*), Standard Deviation of Regression Coefficient (*Sb*), and Results of the Test of Significance for F_1, F_2, S_1 and S_2 Lines in *D. ananassae*

Line	h^2	*b*	*Sb*	df	*t*	*P*
F_1	0.33	−0.51	0.22	8	2.32	<0.05
F_2	0.26	−0.63	0.23	8	2.74	<0.05
S_1	0.27	+0.73	0.31	8	2.35	<0.05
S_2	0.23	+0.89	0.36	8	2.47	<0.05

Table IV. Remating Frequency (%) in Various Generations of the Selection Experiment for Female Remating Time in Both Replicates of Fast and Slow Lines and the Control Line in *D. ananassae*

Generation	F_1	F_2	S_1	S_2	Control
0	—	—	—	—	48
1	52	66	58	60	52
2	64	54	46	48	54
3	60	60	40	54	44
4	68	60	38	38	48
5	58	74	52	38	50
6	62	62	50	46	62
7	60	64	64	56	64
8	58	60	44	44	60
9	66	64	40	42	50
10	60	68	46	40	62

At generation 10, correlated response of selection was tested by scoring mating propensity of all the selection lines and the control line and by measuring productivity of once-mated females. Mean number of matings in 30 minutes in the Elens-Wattiaux mating chamber out of 15 pairs (15 females × 15 males–5

Table V. Comparison of Mean (Arcsin Tranformed) Remating Frequencies Over 10 Generations of Selection Between Control and Selected Lines and Between Fast and Slow Lines by *t*-tests in *D. ananassae**

Line	Mean ± SE	Comparison	*t*	df	*P*
F_1	51.26 ± 0.84	Control vs F_1	2.19	18	<0.05
		Control vs F_2	3.15	18	<0.01
F_2	52.70 ± 1.03	Control vs S_1	3.01	18	<0.01
		Control vs S_2	2.63	18	<0.02
S_1	43.74 ± 1.52				
		F_1 vs S_1	3.49	18	<0.01
S_2	43.04 ± 1.41	F_1 vs S_2	2.12	18	<0.05
		F_2 vs S_1	6.01	18	<0.001
Control	47.09 ± 0.96	F_2 vs S_2	4.98	18	<0.001
		F_1 vs F_2	0.90	18	ns
		S_1 vs S_2	0.51	18	ns

**t*-test was performed after transforming percentage to angles by arcsin transformation.

Table VI. Number of Matings (mean ± SE) in 30 Minutes, out of 15 Pairs (15 Female × 15 Male—Replicates) Tested in Selected Lines and in the Control Line at Generation 10 in *D. ananassae**

Line	Mean ± SE	Comparison	*t*	df	*P*
F_1	11.20 ± 0.38	Control vs. F_1	8.53	8	<0.001
		Control vs. F_2	7.06	8	<0.001
F_2	11.60 ± 0.51	Control vs. S_1	6.40	8	<0.001
		Control vs. S_2	4.71	8	<0.01
S_1	6.40 ± 0.24				
		F_1 vs. S_1	9.79	8	<0.001
S_2	5.60 ± 0.40	F_1 vs. S_2	8.24	8	<0.001
		F_2 vs. S_1	7.88	8	<0.001
Control	8.00 ± 0.32	F_2 vs. S_2	7.23	8	<0.001
		F_1 vs. F_2	0.66	8	ns
		S_1 vs. S_2	2.10	8	ns

* *t*-test was performed for comparison of mean number of matings between control and selected lines and between fast and slow lines.

replicates) in both replicates of selected lines and in the control line at generation 10 are shown in Table VI and mating propensity (%) at 5-minute intervals in 30 minutes is shown in Fig. 2. *T*-test was used to compare the mean number of matings observed in control line with mean number of matings observed in each replicate of high and low lines. The differences between the control and selected lines and between the high and low lines were statistically significant (Table VI). These results of mating propensity tests indicate that the flies of high (fast) line are more successful in mating compared with those of the low and control lines.

Number of progeny produced per female (Mean ± SE) for each replicate of the fast and slow lines and the control line is given in Table VII. Fig. 3 shows the number of progeny produced per female (range, mean, and SE) in each replicate of the selected lines and the control line at generation 10. A comparison of mean number of progeny produced per female between the different lines was done using the *t*-test (Table VII). The results show that the differences are significant in all

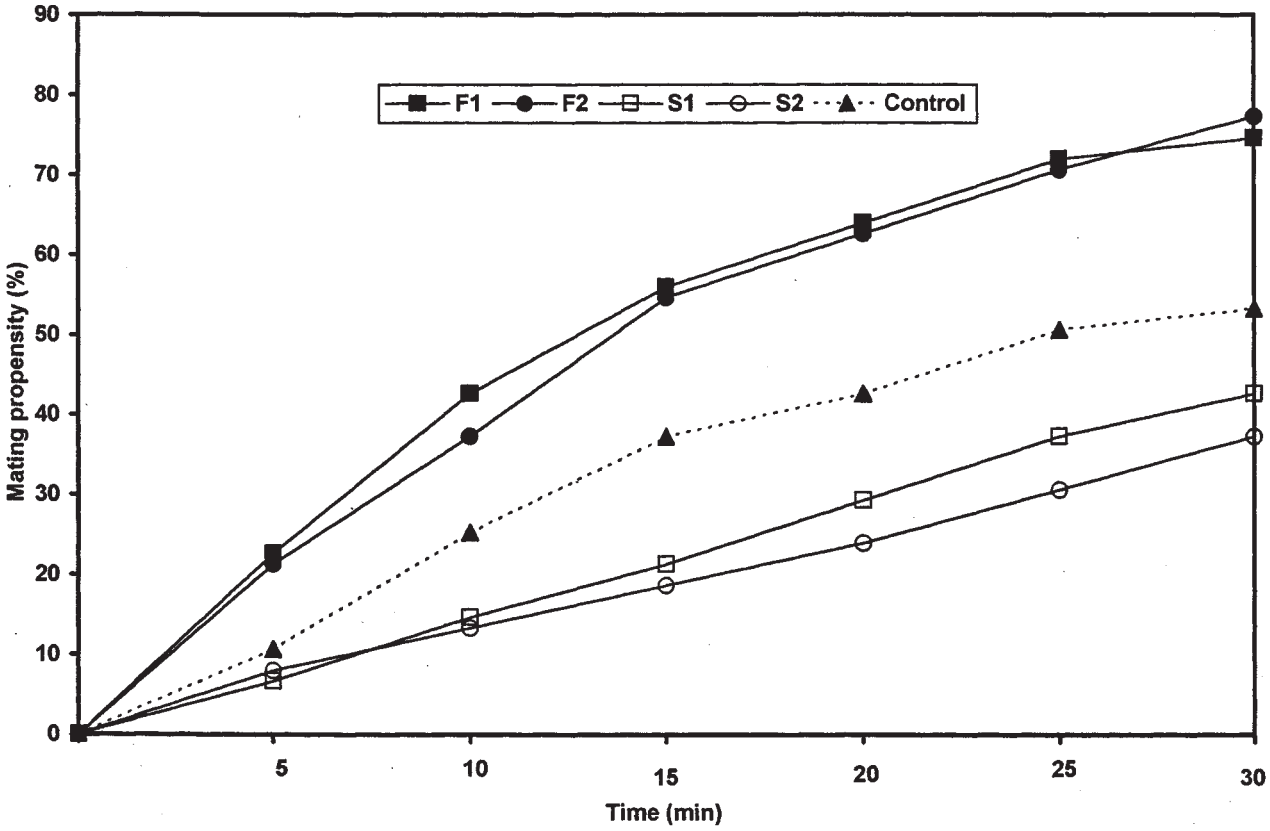

Fig. 2. Mating propensity (%) at 5-minute intervals for 30 minutes out of 15 pairs (15 female × 15 male—replicates) tested in each replicate of selected lines and the control line at generation 10 in *D. ananassae*.

Table VII. Number of Progeny Produced Per Female in Selected Lines and in the Control Line at Generation 10 in *D. ananassae**

Line	*N*	Number of progeny/female (Mean ± SE)	Comparison	*t*	*P*
F_1	30	157.83 ± 6.06	Control vs. F_1	5.06	<0.001
			Control vs. F_2	3.00	<0.01
F_2	30	130.83 ± 2.92	Control vs. S_1	4.51	<0.001
			Control vs. S_2	2.97	<0.01
S_1	30	72.70 ± 4.54			
			F_1 vs. S_1	5.06	<0.001
S_2	30	85.83 ± 5.32	F_1 vs. S_2	8.39	<0.001
			F_2 vs. S_1	8.65	<0.001
Control	30	109.23 ± 6.49	F_2 vs. S_2	9.41	<0.001

* *t*-test was performed for comparison of number of progeny produced per female between control and selected lines and between fast and slow lines, df = 58.

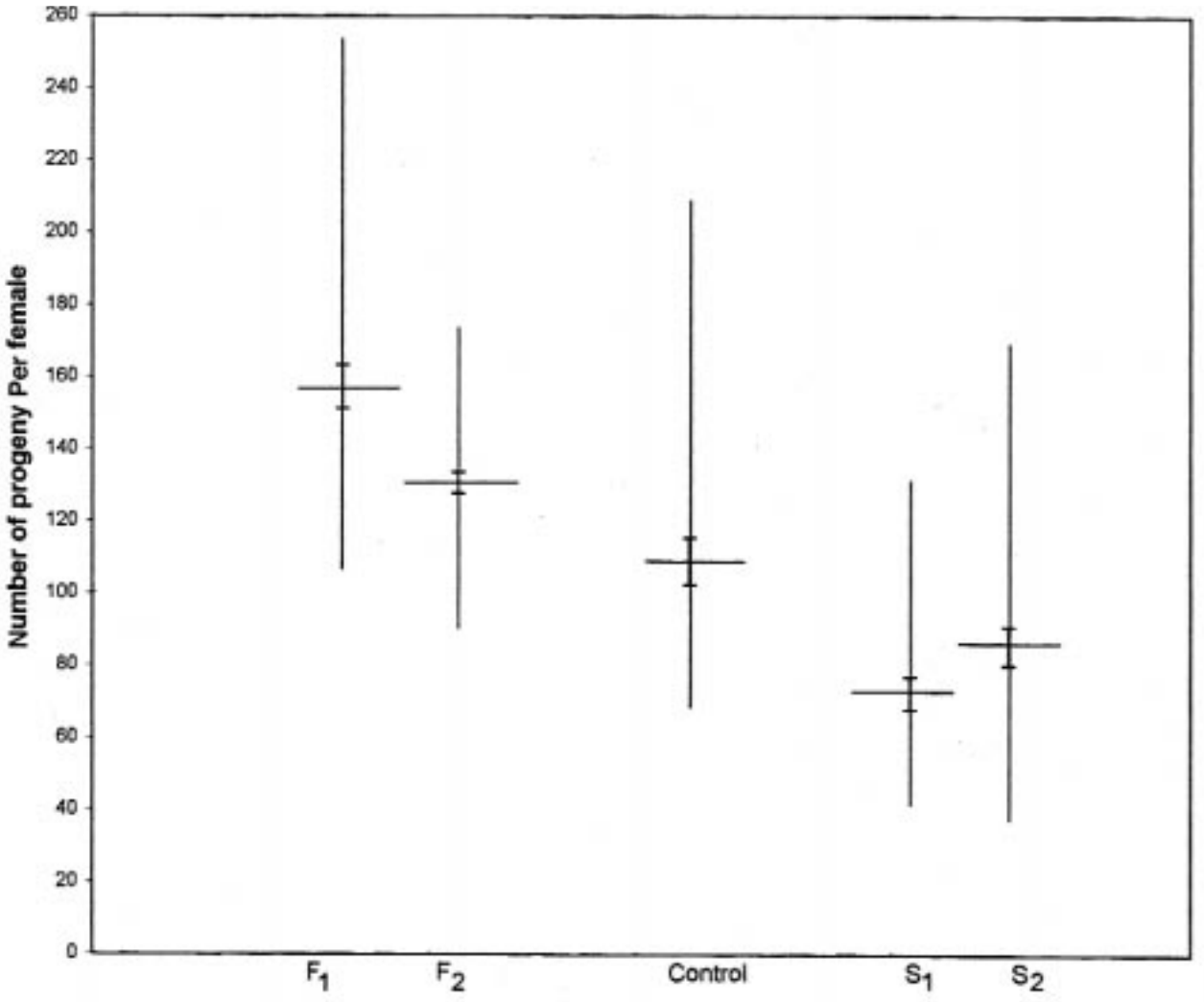

Fig. 3. Number of progeny per female with range, mean, and standard error in each replicate of selected lines and the control line at generation 10 in *D. ananassae*.

the comparisons and indicate that the once-mated females of the fast line are more productive compared with those of the slow and control lines.

DISCUSSION

It is evident from these results that selection for high (fast) and low (slow) remating time (in days) in female *D. ananassae* was effective and two lines, each with fast and slow remating time, were established. Fig. 1 shows clear divergence in both directions with respect to remating time in females *D. ananassae*. The response to selection for remating time in both directions provides evidence that there is substantial additive genetic variation for this trait in *D. ananassae*. Thus, remating time is under polygenic control in *D. ananassae*. Female remating frequency (%) was also recorded in each generation of selection in both replicates of fast and slow lines and in the control line. The comparison of remating frequency showed a correlated response to selection in both fast and slow lines and suggests that remating time is heritable and rapid remating is pleiotropically associated with frequent remating in *D. ananassae*. In *D. melanogaster*, Sgro, Chapman, and Partridge, (1998) found such association only in high lines.

There is considerable genetic variability in Indian populations of *D. ananassae* (Singh, 1996), and the base population was constructed by crossing five mass culture wild-type strains derived from eco-geographically different localities in India. Further, significant strain variation in female remating time was found, which indicates that there is substantial genetic variation for female remating time in populations of *D. ananassae* (Singh and Singh, 1999). During the present study, fluctuations in remating time occurred in early generations. Such fluctuations in early generations of selection experiments for mating propensity, spontaneous male recombination, pupation height, and choice of oviposition site preference have also been observed in *D. ananassae* (for references, see Singh, 2000). Falconer and Mackay (1996) claim that both directional dominance and directional gene frequencies would not be expected to exert such an effect in the early generations of selection.

Experiments on genetic basis of female remating in *Drosophila* are primarily restricted to *D. melanogaster*. Most of the experiments on this aspect have been carried out by Gromko and coworkers in *D. melanogaster* using various experimental designs. Their results vary with respect to remating speed (the time interval between the first and second mating). Pyle and Gromko (1981) found evidence for a relatively small number of genes, deviation from additive gene action, and involvement of X chromosomes in artificially selected single line for fast remating in both sexes of *D. melanogaster*. In selecting both fast and slow lines, which was based on behavior of one sex, they suggested that genes affecting remating speed in females are largely sex limited in their action (Gromko and Newport, 1988a). Moreover, Gromko and Newport (1988b) were able to demonstrate correlated responses to selection in virgin mating behavior, early fecundity, courtship elicited by mated females, and the relation between sperm use and remating interval. However, chromosome substitution analysis, biometrical and planned comparision analysis, and recombination analysis of their experiment for remating speed demonstrates the involvement of chromosome II, which contributed significantly to the differences in remating speed in selected lines (Fukui and Gromko, 1991a, 1991b, 1991c). Recently, Sgro, Chapman, and Partridge (1998) found significant direct response to selection for time to remating in *D. melanogaster* females for both selection lines (fast and slow) and suggested that remating time is heritable and rapid remating is pleiotropically associated with frequent remating. These results also suggest that remating time in females is under polygenic control.

At generation 10 of selection for remating time in females, correlated response to selection was also tested. The results of mating propensity experiments for virgin flies, a correlated response to selection, at generation 10 indicate that the flies of the high (fast) line are more successful in mating compared with those of the low (slow) line and the control line. Significant strain variation in mating propensity was found, which indicates that substantial genetic variation exists for mating propensity in populations of *D. ananassae* (Singh and Singh, 1999). Mating propensity is a complex trait based on interaction of both sexes. Successful mating depends on male activity and female receptivity. According to Ehrman and Parsons (1981), rapid mating is associated with male genotype, whereas in slow mating female genotype plays a progressively more important role.

Similarly, the results of productivity analysis of once-mated females at generation 10 indicate that high (fast) line females are producing significantly more progeny compared with low (slow) line females. However, Pyle and Gromko (1981) found that productivity of once-mated females decreased in the selected line

compared with the control line. This has been explained by suggesting that females that received a smaller supply of stored sperm would need to remate sooner to replenish stored sperm, hence low egg production rates. But their comparison was only between one line for decreased remating time and control line, whereas in the present study two different lines for high (fast) and low (slow) remating time (speed) in females were used, and it is likely that females of different lines received different amounts of sperm. In *D. ananassae*, significant strain variation for mating activity and productivity was reported (for references, see Singh and Singh, 1999). It has been reported that mating activity and productivity are correlated characters in *D. ananassae* (for references, see Singh, 1996). Fulker (1966) also found positive correlation between mating activity and productivity in *D. melanogaster*.

Thus, it is evident from the present results that there is a positive response to selection for remating speed in *D. ananassae*. Further, fast lines had a positive effect on productivity and initial mating speed, and slow lines had a significantly negative effect on productivity and mating speed. This shows that selection for remating speed resulted in correlated response for mating activity and fertility in *D. ananassae*. It is known that there is a positive correlation between mating activity and fertility in *D. ananassae* (for references, see Singh, 1996, 2000). The results of the present study and earlier studies demonstrate that all three traits—remating speed, mating propensity, and fertility—are under polygenic control. Further, it is also known that there is a positive correlation between duration of copulation and fertility in *D. ananassae*, which has been explained by suggesting that duration of copulation is an expression of the rate of sperm transfer (for references, see Singh and Singh, 1999).

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