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Male Remating in *Drosophila ananassae*: Evidence for Interstrain Variation in Remating Time and Shorter Duration of Copulation during Second Mating

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ABSTRACT—In *Drosophila ananassae*, male remating was studied using ten mass culture stocks which were initiated from flies collected from different geographic localities. Male remating occurs at a high frequency and varies within narrow limits (84–96 percent) in different strains. Interestingly, male remating time (in min) varies from 7.41 (Bhutan) to 21.59 (PAT) in different strains and the variation is highly significant. Further, the results also show that males copulate for shorter duration during second mating. This is the first report in the genus *Drosophila* which provides evidence for interstrain variations for male remating time as well as for shorter duration of copulation during second mating as compared to first mating in *D. ananassae*.

INTRODUCTION

Since sexual behaviour of male and female affects and modifies the contribution of different genotypes to the gene pool of succeeding generations, it becomes an important component of fitness. In *Drosophila*, successful mating depends on male activity and female receptivity (Bastock, 1956). The fact that males can mate with more than one female forms one of the bases for sexual selection, especially because female generally accepts a limited number of mates (Petit *et al*., 1980). According to Gromko (1992), multiple mating is widely believed to be advantageous to males and selection on males could produce a correlated response in females. Studies on sexual behaviour in numerous species of *Drosophila* with particular reference to its genetic control, contribution of two sexes to the variation in mating activity and repeat mating are well documented (Spiess, 1970; Parsons,1973; Gromko and Pyle, 1978; Spieth and Ringo, 1983; Singh, 1996; Banerjee and Singh, 1997; Casares *et al*., 1998). It is widely demonstrated that males of different species of *Drosophila* can inseminate more than one female and mating ability of males is influenced by genetic and other factors (Prakash, 1967; Sharp, 1984; Singh and Chatterjee, 1986, 1988a; Sanches Prado and Blanco Lizana, 1989; Krishna and Hegde, 1997).

Drosophila ananassae is a cosmopolitan and domestic species. It possesses several genetic peculiarities and is of common occurrence in India (Singh, 1985). Population and behaviour genetics of Indian *D. ananassae* has been extensively studied by Singh and his coworkers (Singh, 1996, 1998). The results of mating propensity tests have clearly indicated that sexual behaviour in *D. ananassae* is under genetic control (Singh and Chatterjee, 1986, 1987, 1988a,b). Furthermore, males contribute more to variation in sexual activity than females and thus more subject to intrasexual selection than females. There is a positive correlation between duration of copulation and fertility in *D. ananassae* (Singh, S R and Singh, B N, 1999). Significant variation in mean number of matings among the wildtype stocks of *D. ananassae* has been found and receptivity of females shows more variation as compared to male mating ability (Singh, B N and Singh, S R, 1999a). Female remating has also been studied in *D. ananassae* and results indicate that there is significant variation in remating days among the stocks tested and the duration of copulation is shorter in second mating as compared to first mating (Singh, B N and Singh, S R, 1999b). Although it is well known that males can inseminate more than one female in different species of *Drosophila*, male remating has not been investigated with respect to remating time and duration of copulation in first and second matings. In view of this we studied male remating in *D. ananassae* by employing ten geographic strains and scored male remating frequency, remating time and duration of copulation in first and second matings. The results of these experiments are reported.

MATERIALS AND METHODS

To study the male remating in *D. ananassae*, ten mass culture wild type strains derived from different geographic localities were used. All the localities are shown on the map (Fig. 1). Details of these stocks and year of collection are given in Table 1. All these stocks are being maintained on simple culture medium by transferring 50 flies (females

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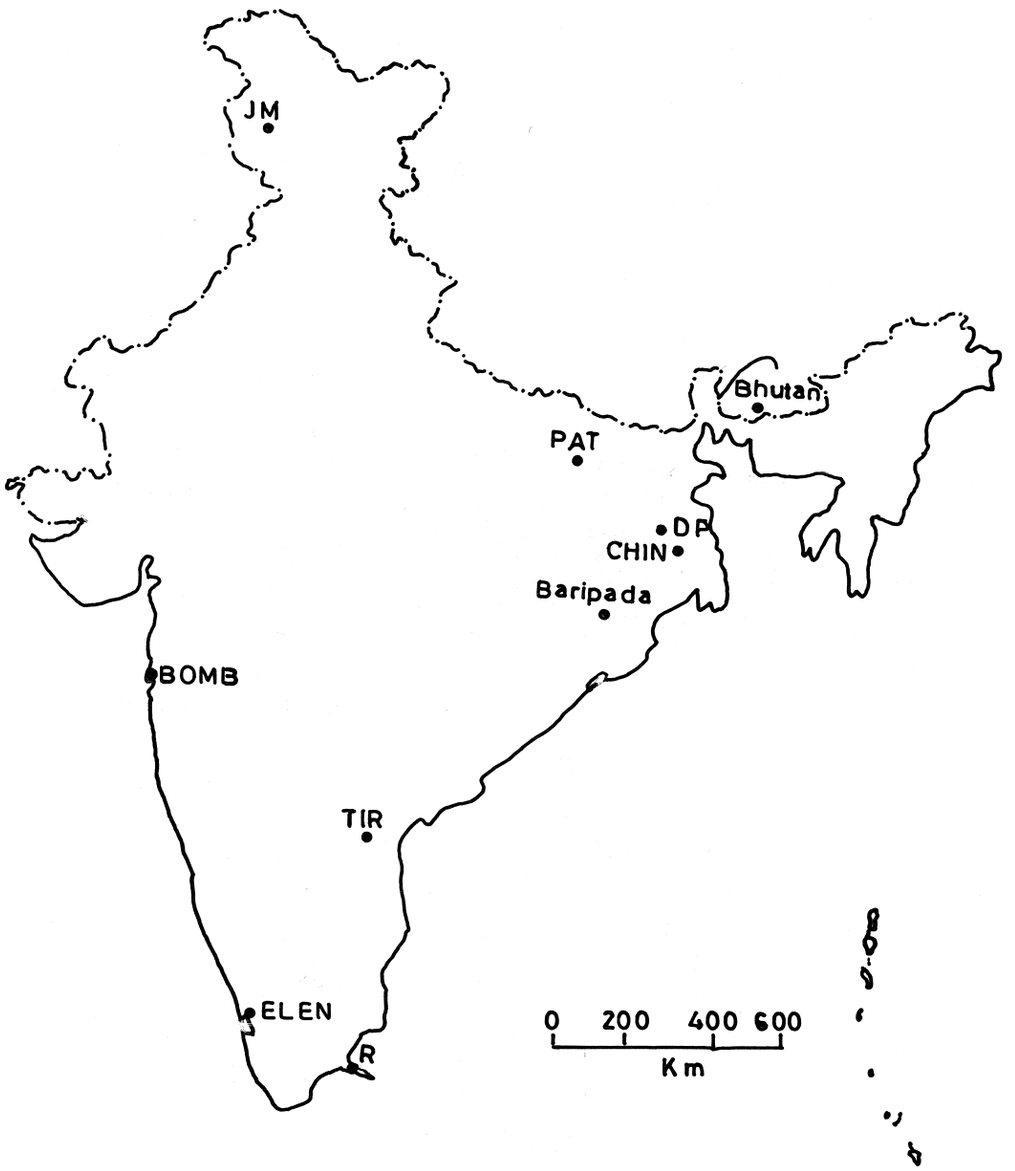

Fig. 1. Map of India showing the geographic localities from which *D. ananassae* flies were collected.

Table1. Strains of *Drosophila ananassae* used for male remating experiment

Strain	Place of origin	Year of collection
R	Rameswaram, Tamil Nadu	1984
Bomb	Bombay, Maharashtra	1985
Baripada	Baripada, Orissa	1987
JM	Jammu, Jammu & Kashmir	1987
PAT	Patna, Bihar	1990
TIR	Tirupati, Andhra Pradesh	1990
Bhutan	Phuntsholing, Bhutan	1993
Chin	Chinsurah, West Bengal	1993
Elen	Elenthikara, Kerala	1993
DP	Dubrajpur, West Bengal	1994

and males in equal number) to fresh culture bottles in each generation and have spent varying numbers of generations in the laboratory. In each stock, virgin females and males were collected and aged for seven days in food vials. A single virgin female was placed in a fresh food vial with a single virgin male and the pair was observed for 60 min. When mating occurred, the pair was allowed to complete copulation. Courtship time and duration of copulation were recorded for each mated pair. After copulation, the mated female was aspirated out and replaced with another virgin female and observed for 2 hr. When remating occurred, mating time and duration of copulation were recorded for each pair. If there was no remating within 2 hr, then the pair was discarded. In this way 50 males were observed in each of the ten strains for remating frequency, remating time and duration of copulation in first and second matings (remating). All the tests were performed in a room maintained at approximately 24°C temperature under normal laboratory light condition during morning hours (7–11 AM).

RESULTS AND DISCUSSION

The number of remated males and percentage of remating in ten mass culture wild type strains of *D. ananassae* are presented in Table 2. The male remating percentage varies from 84 to 96. All the strains show very high male remating frequency. Table 3 shows the mean remating time (minutes) in different strains of *D. ananassae*. The mean remating time(min) varies from 7.41 (Bhutan) to 21.59 (PAT). The analysis of variance (ANOVA) of mean remating time (Table 4) shows highly significant variation ($F = 6.81$, $P < 0.001$) among different strains. Thus the wild laboratory stocks of *D. ananassae* show significant variation in male remating time. Table 5 presents the comparison of duration of copulation (minutes) between first and second matings (remating) in different strains of *D. ananassae*. The duration of copulation is shorter in the second mating than the first mating in all the strains tested. The difference in the mean duration of copulation between first and second matings (remating) has been tested by calculating t-values which show that differences are significant in all strains. Thus *D. ananassae* males show shorter duration of copulation in second mating (remating) as compared to the first mating .

All the strains of *D. ananassae* used in the present investigation were initiated from flies collected at different geographic localities and have spent varying number of generations in the laboratory. It is known that Indian natural populations of *D. ananassae* are genetically heterogeneous (Singh, 1996) and there is substantial genetic variations in natural populations for different behavioural traits such as mating behaviour , larval pupation behaviour and oviposition behaviour (Singh and Chatterjee, 1988b, Singh and Pandey, 1993; Srivastava and Singh, 1996).

It is evident from the present results that there is a high incidence of male remating in *D. ananassae* and it occurs very quickly. Further, the remating time shows highly significant variation among the strains. This may be attributable to genetic heterogeneity among the founders of strains used. Although the strains vary in remating time, there is no correla-

Table 2. Number of remated males and percentage of male remating in different strains of *D. ananassae* (50 males were tested in each strain.)

Strain	Remated males	Percentage of remating
R	46	92
Bomb	44	88
Baripada	47	94
Jm	45	90
PAT	42	84
TIR	46	92
Bhutan	48	96
Chin	43	86
Elen	42	84
DP	48	96

Table 3. Remating time (in minute) in different strains of *D. ananassae*

Strain	Remating time Mean ± SE
R	8.60 ± 1.38
Bomb	9.36 ± 1.68
Baripada	8.04 ± 0.78
Jm	10.03 ± 1.68
PAT	21.59 ± 1.95
TIR	12.11 ± 1.48
Bhutan	7.41 ± 0.98
Chin	12.31 ± 0.83
Elen	12.62 ± 1.81
DP	12.30 ± 2.09

Table 4. ANOVA for remating time

Source	SS	df	MS	F	P
Total	52746.73	450			
Between strains	6437.31	9	715.26	6.81	< 0.001*
Within strains	46309.42	441	105.01		

*Significant

Table 5. Comparison of duration of copulation (min) between first and second matings (remating) in different strains of *D. ananassae*

Strain	Duration of copulation in first mating (min)	Duration of copulation in second mating (min)	t	df	P
R	5.00 ± 0.11	3.36 ± 0.09	13.67	44	< 0.001*
Bomb	5.04 ± 0.12	3.17 ± 0.11	10.39	42	< 0.001*
Baripada	4.95 ± 0.10	3.65 ± 0.09	10.83	45	< 0.001*
Jm	4.86 ± 0.12	3.29 ± 0.11	11.21	43	< 0.001*
PAT	4.22 ± 0.12	2.81 ± 0.11	10.07	40	< 0.001*
TIR	5.81 ± 0.20	3.76 ± 0.12	9.76	44	< 0.001*
Bhutan	4.54 ± 0.12	3.25 ± 0.10	10.75	46	< 0.001*
Chin	4.45 ± 0.18	3.10 ± 0.14	10.38	41	< 0.001*
Elen	4.83 ± 0.33	3.05 ± 0.15	9.37	40	< 0.001*
DP	4.89 ± 0.11	2.99 ± 0.06	9.5	46	< 0.001*

Data are presented as mean ± SE.
* Significant

tion with geographic distances. The PAT stain shows highest remating time (21.59 min) as compared to other strains and duration of copulation is also shorter in both matings in this strain. PAT strain is also characterized by low mating success, shorter duration of copulation, low number of progeny and higher courtship time (Singh, S R and Singh, B N, 1999; Singh, B N and Singh, S R, 1999a). In female remating experiment, PAT strain showed lowest remating frequency and highest remating days when compared with other stains (Singh, B N and Singh, S R, 1999b). Thus the PAT strain is characterized by low female receptivity (or high mating threshold of females) as indicated by our earlier studies (Singh, B N and Singh, S R, 1999a) which is the characteristic of this strain.

We have also compared the duration of copulation during the first and second matings. It is interesting to note that males copulate for shorter duration during the second mating as compared to the first mating in all the strains and differences are highly significant in all 10 comparisons. It is known that the duration of copulation is male determined and is an expression of the rate of sperm transfer (Spiess, 1970). It has also been demonstrated that *D. bipectinata* males copulating for longer durations produce more progeny which is likely due to a higher number of sperm transferred (Sisodia and Singh, 1996). The shorter duration of copulation during the second mating of *D. ananassae* males is likely to be due to depletion in the amount of sperm and accessory gland secretion. As far as we know this is the first report in the genus *Drosophila* that demonstrates intraspecific variations in male remating time as well as shorter durations of copulation during the second mating in *D. ananassae*. Thus *D. ananassae* is characterized by high incidence of male remating and interstrain variation with respect to male ramating time which is likely to be due to genetic heterogeneity among the strains as they were derived from different geographic localities. This provides evidence for sexual selection on males in *D. ananassae*. Recently cryptic female choice has been demonstrated in several species but it is not clear whether it is as widespread as it has been suggested (Eberhard, 1994). Selection in the form of cryptic female choice may be acting on the males (Eberhard, 1991, 1996). Although we have not tested the effect of cryptic female choice on male mating ability in *D. ananassae*, the possibility for selection via cryptic female choice may not be eliminated.

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