Female remating in *Drosophila ananassae*: shorter duration of copulation during second mating as compared to first mating

B N SINGH* and S R SINGH

Genetics Laboratory, Department of Zoology, Banaras Hindu University, Varanasi 221 005, India

**Corresponding author (Fax, 91-542-317074; Email, bnsingh@banaras.ernet.in).*

Drosophila ananassae, a cosmopolitan and domestic species, belongs to the *ananassae* subgroup of the *melanogaster* species group. Female remating was observed in ten mass culture stocks of this species, which were initiated from flies collected from different geographic localities. The frequency of female remating ranges from 24% to 56% in different strains. Strains show significant variation in remating latency (days). Significant variation has also been found in all the stocks for duration of copulation between first and second matings. The duration of copulation is shorter in second mating as compared to first mating in *D. ananassae*.

1. Introduction

Since sexual behaviour of males and females 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 because usually the female is the discriminating partner in the mating act, i.e., she actively accepts or rejects a courting male (Bateman 1948; Bastock 1956). A large number of investigations on sexual behaviour in various *Drosophila* species have been carried out by numerous investigators (for references see Spiess 1970; Parsons 1973; Spieth and Ringo 1983; Sisodia and Singh 1996; Yamamoto *et al* 1997; Casares *et al* 1998).

Female remating is an important aspect of sexual behaviour in *Drosophila* because females store the sperm after mating in the spermathecae and ventral receptacles and utilize them to fertilize eggs as they are laid. Once a virgin female *Drosophila* has mated, she is usually unwilling to accept another male for some time. The length of this refractory period varies between species and in different strains of the same species (Manning 1962). Remating is common in females of many species of *Drosophila* under both natural and laboratory conditions (Dobzhansky and Pavlovsky 1967; Anderson 1974; Richmond and Ehrman 1974; Milkman and Zeitler 1974; Cobbs 1977; Gromko and Pyle 1978; Craddock and Johnson 1978; Loukas *et al* 1981; Markow and Ankey 1984; Markow 1985; Barbadilla *et al* 1991; Etges and Heed 1992; Aspi 1992; Aspi and Lankinen 1992; Schwartz and Boake 1992; Joly and Lachaise 1993; Chapman *et al* 1994; Service and Vossbrink 1996; McRobert *et al* 1997; Singh and Singh 1997). The phenomenon of remating by females is a prerequisite for the occurrence of sperm competition between males (Parker 1970). 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) combine to make an excellent example of sexual selection. In *Drosophila melanogaster*, a longer delay of female remating is due to the transfer of a large amount of sperm (Letsinger and Gromko 1985). However, Service and Vossbrink (1996) found that a longer delay in remating was associated with a slower use of stored sperm.

Drosophila ananassae, a cosmopolitan and domestic species, belongs to the *ananassae* subgroup of the *melanogaster* species group. It occupies a unique status among *Drosophila* species due to certain peculiarities in its genetic behaviour such as spontaneous meiotic male recombination, varied chromosomal polymorphism, high mutability, Y-4 linkage of the nucleolus organizer, segregation distortion, parthenogenesis, extra chromosomal inheritance and lack of coadaptation (Singh 1985, 1996). *D. ananassae* has been extensively used for genetical

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studies particularly population genetics, behavioural genetics and crossing over (Singh 1985, 1996; Tobari 1993). The results of mating propensity tests in wildtype strains, mutant strains and inversion karyotypes and the results of selection experiment provide evidence for genetic control of sexual behaviour in *D. ananassae* (Singh and Chatterjee 1986, 1987, 1988a, b; Chatterjee and Singh 1987, 1988). Further, males contribute more to the variation in sexual activity than females and thus are more subject to intrasexual selection than females (Singh and Chatterjee 1987). A positive correlation between mating activity and fertility has been found in isofemale strains of *D. ananassae* (Singh and Chatterjee 1987). The existence of rare male mating advantage has also been reported in *D. ananassae* (Singh and Chatterjee 1989). Evidence for polygenic control of pupation site preference and oviposition site preference has been presented in *D. ananassae* (Singh and Pandey 1993; Srivastava and Singh 1996). Mating propensity, courtship time, duration of copulation and fertility have been tested in mass culture wildtype strains of *D. ananassae* derived from different geographic localities and the results indicate that receptivity of females shows more variation than male mating ability and there is a positive correlation between duration of copulation and fertility in *D. ananassae* (Singh B N and Singh S R 1999; Singh S R and Singh B N 1999).

In this paper, we report the results of our studies on female remating in *D. ananassae* with particular reference to the frequency of female remating, remating days and duration of copulation in first and second matings in several mass culture wildtype strains.

2. Materials and methods

To study female remating frequency in *D. ananassae*, ten mass culture wildtype strains established from large numbers of flies collected from different geographic localities were used. Details of these stocks and the year of collection are given in table 1. All these stocks are being maintained on a simple culture medium by transferring 50 flies (females and males in equal numbers) to fresh culture bottles in each generation and have spent varying number of generations in the laboratory. In each stock, males and females were collected as virgins under ether anaesthesia and aged for seven days in food vials. First time female matings were obtained by placing seven days old virgin females individually in a food vial with a single male seven days of age. The pair was observed for 60 min. When mating occurred, courtship time and duration of copulation were recorded for each mated pair. Females failing to mate during a 60 min observation period were discarded. Males were aspirated out from the observation vial within 30 min of the completion of copulation. The next morning, fertilized females were paired with new mate partners in fresh food vials and were observed continuously for 2 h. After these 2 h, the males were discarded from the vials and the same procedure was repeated on twelve consecutive mornings with fresh males (Gromko and Pyle 1978). When remating occurred, the duration of copulation was noted for each pair. Remating days (the number of days spent after the first mating until the female accepts to copulate again within 12 days) were also noted for each mated pair. The females remating during this time were no longer given the opportunity to remate. In this way 50 females were observed in each of the ten strains for remating frequency, remating days and the 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 (about 1000 lux; 12 : 12 light : dark regime) during morning hours (7–11 AM). All the strains were tested concurrently.

The χ^2 test was used to test the hypothesis that the frequency of remating is equal in all strains. An analysis of variance (one-way ANOVA) was applied to test the variation in mean remating days among different strains. To test the differences in the mean duration of copulation between first and second matings, the Student's t-test (paired, for dependent samples) was used.

Table 1. Strains of *D. ananassae* used in the female remating test, frequency of remating and mean remating latency (days) in different strains.

Abbreviation	Place of origin	Year of collection	Frequency of remating (%)	Remating latency (mean ± SE)
R	Rameshwaram, Tamil Nadu	1984	44	7·82 ± 0·56
BOMB	Bombay, Maharashtra	1985	44	6·95 ± 0·58
Baripada	Baripada, Orissa	1987	50	7·08 ± 0·77
JM	Jammu, Jammu and Kashmir	1987	56	6·75 ± 0·53
PAT	Patna, Bihar	1990	24	8·58 ± 0·95
TIR	Tirupati, Andhra Pradesh	1990	34	6·47 ± 0·39
Bhutan	Phuntsholing, Bhutan	1993	40	6·15 ± 0·46
CHIN	Chinsura, West Bengal	1993	32	8·75 ± 0·51
ELEN	Elenthikara, Kerala	1993	36	6·11 ± 0·57
DP	Dubrajpur, West Bengal	1994	34	7·06 ± 0·57

3. Results

Table 1 shows the remating frequency and remating latency in ten mass-cultured wild-type strains of *D. ananassae*. The remating percentage varies from 24% (PAT) to 56% (JM). However, the variation is not statistically significant as indicated by the χ^2 test ($\chi^2 = 10{\cdot}10$; df = 9, $P > 0{\cdot}05$). JM (56%) and Baripada (50%) strains show the highest remating frequency, while PAT (24%) shows the lowest. The JM and Baripada strains were established in 1987 and the PAT strain was established in 1990. Thus there is no direct relation between the number of generations the strains have been maintained in the laboratory and the remating frequency. The mean number of remating days varies from 6·11 (ELEN) to 8·75 (CHIN). The analysis of variance (ANOVA) for mean number of remating days (table 1) shows a significant variation ($F = 2{\cdot}05$, $P < 0{\cdot}05$) among different strains. The longest remating latency was observed in the CHIN strain and the shortest in ELEN strain, although both strains were established in 1993. Thus, there is no relation between the number of generations the strains have been kept in the laboratory and the remating latency. Table 2 presents a comparison of the duration of copulation (in min) between first and second matings (remating) in different strains of *D. ananassae*. In all the strains, duration of copulation is significantly shorter in second matings as compared to first matings. However, the level of significance varies between the different strains.

4. Discussion

During the course of the present study, ten mass culture wildtype strains of *D. ananassae* derived from flies collected from different geographic localities were tested for female remating frequency, remating days and the duration of copulation in first and second matings (remating). In the present experiments, female remating frequency varied from 24% to 56% among the strains of *D. ananassae* tested. However, this variation is not statistically significant. Significant variation has been observed for remating days in different strains (table 1). Female remating in *D. ananassae* occurs after at least 6 days using the periodic confinement technique. In female remating studies primarily two techniques, i.e., continuous confinement and periodic confinement, have been used by various investigators and female remating frequency varies considerably in different species (Smith 1956; Richmond and Ehrman 1974; Prout and Bundgaard 1977; Gromko and Pyle 1978; Pyle and Gromko 1978; Beckenbach 1981; Loukas *et al* 1981; Wu 1983; Turner and Anderson 1984; Markow and Ankey 1984; Markow 1985; Barbadilla *et al* 1991; Aspi 1992; McRobert *et al* 1997). There are only few studies, in which female remating has been observed in natural populations in certain species of *Drosophila* (Richmond and Powell 1970; Anderson 1974; Milkman and Zeitler 1974; Cobbs 1977; Craddock and Johnson 1978; Levine *et al* 1980; Griffiths *et al* 1982; Aspi and Lankinen 1992; Harshman and Clark 1998).

In female remating studies the 2 h periodic confinement technique has been used by Gromko and Pyle (1978) in *D. melanogaster* and by McRobert *et al* (1997) in *D. biarmipes* and *D. melanogaster*. In *D. melanogaster*, it was found that about 80% of the females remate when remating was observed for 12 days (Gromko and Pyle 1978). McRobert *et al* (1997) studied remating in *D. melanogaster* and *D. biarmipes* during 2 h periodic confinement for 14 days and compared the post-copulatory behaviour of *D. biarmipes* and *D. melanogaster* females. Females from both species were shown to undergo a series of behavioural changes following mating, including significant reduction in both sexual attractiveness and receptivity. However, while both attractiveness and receptivity return to "virgin like" levels within a few days in *D. melanogaster*, *D. biarmipes* females which regained their sexual attractiveness within a few days, remained unreceptive to copulation for at least two weeks. They also tested remating frequency in both species and found that about 26% of *D. biarmipes* females mated at least twice and that the mean remating latency was 10·8 days. In contrast, in *D. melanogaster*, 87% of the females remated and remating latency was 6·4 days. We have also followed the 2 h periodic confinement technique in *D. ananassae* and observed remating for 12 days. In *D. ananassae* the average female remating frequency is 39·4% and the mean remating latency is 7·17 days. *D. melanogaster* and *D. ananassae* are cosmopolitan and domestic species and belong to the *melanogaster* species group. The differences observed between these two species in female remating frequency may be due to

Table 2. Comparison of the duration of copulation (min) between first and second matings (remating) in different strains of *D. ananassae*.

Strain	Duration of copulation for first mating (min)	Duration of copulation for second mating (min)	t	df	P (<)
R	4·54 ± 0·39	3·33 ± 0·09	2·41	21	0·05
BOMB	4·58 ± 0·15	3·68 ± 0·12	5·00	21	0·001
Baripada	4·61 ± 0·21	3·04 ± 0·12	2·56	24	0·05
JM	4·19 ± 0·12	3·97 ± 0·19	5·73	27	0·001
PAT	4·08 ± 0·26	3·77 ± 0·17	4·52	11	0·01
TIR	4·40 ± 0·15	3·35 ± 0·19	4·20	16	0·001
Bhutan	4·22 ± 0·15	3·38 ± 0·15	7·43	19	0·001
CHIN	4·11 ± 0·17	3·50 ± 0·39	4·70	15	0·001
ELEN	4·06 ± 0·22	3·45 ± 0·19	3·40	17	0·01
DP	4·21 ± 0·21	3·18 ± 0·11	3·94	16	0·01

Data are presented as means ± standard error of mean.

differences in the reproductive biology of females between these two species.

Joly *et al* (1991) and Joly and Lachaise (1993) studied female remating and compared the duration of copulation in first and second matings in two geographic strains of *D. teissieri*, which originated from two geographic localities in Africa [(i) Mount Silinda, Zimbabwe, established in 1970; (ii) Tai forest, Ivory Coast, established in 1981]. Joly and collaborators used periodic confinement techniques (8 h) and scored remating after 24, 48 and 72 h delay. Joly and Lachaise (1993) found a significant strain variation in female remating frequency. In one stock (Mount Silinda) all females remated, while only about 16% females of the other strain (Tai) remated. In both these strains the duration of copulation was longer during second mating (Joly *et al* 1991). Interestingly, the two strains of *D. teissieri* differ in sperm morphology. The Silinda males have very large sperm and females of this strain remate with a high frequency. Based on the findings in *D. teissieri*, Joly *et al* (1991) proposed that the stable coexistence of two fertile sperm morphs (short and long) in one ejaculate is a mixed strategy, which has evolved via sperm competition possibly in response to female facultative polyandry. Bressac *et al* (1991) found high recurrence polyandry in *D. littoralis* and *D. latifasciaeformis* (up to 3 mates within up to 8 h) and low recurrence polyandry in *D. affinis* (female have only two rematings every 7 days). Furthermore, they also measured the duration of copulation in first as well as in subsequent matings. Interestingly, their results clearly indicate that there is no significant difference in the duration of copulation when compared between different matings in *D. littoralis* and *D. latifasciaeformis*. However, there is a significant decrease in the duration of copulation from first to second mating in *D. affinis*, which is characterized by low recurrence polyandry. The duration of copulation was measured in first as well as second matings in all ten strains of *D. ananassae*. It is interesting to note that invariably all the strains show a significantly shorter duration of copulation during second mating (remating). In our preliminary study (Singh and Singh 1997) we also observed a shorter duration of copulation during second matings in *D. ananassae*. If the results of *D. teissieri*, *D. littoralis*, *D. latifasciaeformis*, *D. affinis* and *D. ananassae* are compared with respect to the incidence of rematings and duration of copulation, it may be concluded that significant variation exists between the species and the species with low incidence of rematings takes less time for copulation in second matings.

It is known, that the higher the level of stored sperm supply, the longer the latency for remating (Scott 1987). It is also known that remating shortens the life span of females because components of ejaculates have toxic effects (Chapman *et al* 1995). Thus, it may be suggested that different species may vary in the incidence of remating and duration of copulation due to differences in their reproductive biology and adaptation.

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