Zoological Studies **35**(1): 25-29 (1996)

Zoological Studies

Evidence for Positive Correlation between Duration of Copulation and Fertility in *Drosophila bipectinata*

Seema Sisodia and Bashisth Narayan Singh*
Genetics Laboratory, Department of Zoology, Banaras Hindu University, Varanasi-221 005, India

(Accepted October 2, 1995)

Seema Sisodia and Bashisth Narayan Singh (1996) Evidence for positive correlation between duration of copulation and fertility in *Drosphila bipectinata*. *Zoological Studies* **35**(1): 25-29. *Drosophila bipectinata* is a member of the *bipectinata* species complex of the *ananassae* subgroup of the *melanogaster* species group. This species commonly occurs in India. During the course of present study, courtship time, duration of copulation, and fertility were tested in seven wild laboratory stocks of *D. bipectinata* originating from different localities in India. The results show that there is significant variation among the strains tested with respect to courtship time, duration of copulation, and fertility. The strains showing a longer duration of copulation produce more progeny. These findings provide evidence that there is a positive correlaton between duration of copulation and fertility in *D. bipectinata*.

Key words: Wild strains, Sexual behavior, Postmating fitness.

Behavioral studies on different species of *Drosophila* are well documented (Spieth 1952, Parsons 1973, Grossfield 1978, Spieth and Ringo 1983, Chatterjee and Singh 1989). Sexual and non-sexual behavior of adult *Drosophila* and behavior of larva *Drosophila* have been investigated in various species. Courtship in mature flies consists of an interchange of visual, acoustic, and chemical stimuli that culminate in copulation. Mating speed, the time from the beginning of courtship to copulation (Spieth and Ringo 1983) is a good estimate of sexual receptivity of females and mating propensity in males. It has been widely demonstrated that sexual behavior in *Drosphila* is under genetic control (Spiess 1970, Parsons 1973, Spieth and Ringo 1983). It is known that male activity and female receptivity are the main factors responsible for successful mating in *Drosophila* (Bastock 1956). Different aspects of the sexual behavior of *Drosophila*, such as mating speed, duration of copulation and a correlation between fertility and sexual activity, have also been tested in certain species of *Drosophila* (Maynard Smith 1956, Kaul and Parsons 1965, Fulker 1966, Prakash 1967, Gilbert and Richmond 1982, Ringo et al. 1986, Singh and Chatterjee 1987). There is a positive correlation between mating activity and fertility in certain species (Maynard Smith 1956, Fulker 1966, Prakash 1967, Singh and Chatterjee 1987). Parsons (1973) has suggested that mating speed and duration of copulation may possibly be regarded as an integrated system controlled mainly by the males and that there is some selective advantage in completing mating and copulation rapidly. *D. melanogaster* males that mate faster also copulate more successfully and leave more progeny (Fulker 1966). In *D. robusta* males, Prakash (1967) observed an association between fast mating, repeat mating, and the number of offspring produced. At 16 °C, *D. melanogaster* males with active esterase-6 mate sooner, copulate for a shorter duration and produce more progeny per mating than males without esterase-6 (Gilbert and Richmond 1982). However, a negative correlation between male mating success and productivity has been reported in certain strains of *D. simulans* (Ringo et al. 1986) with the lower productivity of males which are more successful in mating

*To whom all correspondence and reprint requests should be addressed.

perhaps being caused in part by an exhaustion of rapidly synthesized components of the ejaculate (Fowler 1973).

Drosophila bipectinata is a member of the *bipectinata* species complex of the *ananassae* subgroup of the *melanogaster* species group. It has wide geographic distribution and commonly occurs in India. It is characterized by genetic polymorphism in its natural populations (Singh and Das 1991, Banerjee and Singh 1995) and shows incomplete sexual isolation with the closely related members of the *bipectinata* complex (Singh et al. 1981). Incipient sexual isolation among certain geographic strains of *D. bipectinata* has also been reported (Singh and Chatterjee 1991). Evidence for genetic control of sexual activity, and existence of sexual selection in *D. bipectinata*, has been presented on the basis of mating propensity tests carried out on geographic strains, their hybrids and diallel crosses (Singh and Sisodia 1995, and unpublished data). The sepia eye color mutation detected for the first time in this species has been found to diminish the sexual activity of males (Singh et al. unpublished data). During the present study, courtship time, duration of copulation, and fertility were tested in seven wild stocks of *D. bipectinata* and the results are reported in this communication.

MATERIALS AND METHODS

Seven mass-culture wild stocks of *Drosophila bipectinata* were used in tests for mating propensity and fertility. Details of these stocks are given in Table 1 and strains are arranged according to the year of collection. In each stock, virgin females and males were collected and aged for seven days. A single male was placed in a food vial with a single female and allowed to acclimatize to the vial for 30 seconds. The pair was observed and courtship time and duration of copulation were recorded for each pair. The time elapsed until mating of pair from 30 seconds after mixing male and female is taken as courtship time. Duration of copulation was measured from the time copulation began until the time when copulation terminated. Pairs were watched for 30 minutes and any pair not mating during this period was recorded as unmated. Experiments were carried out in a room maintained at approximately 24°C temperature under normal laboratory light conditions between 7-11 a.m. The fertility of all strains was tested by counting the number of offspring produced by each pair. For testing fertility, each mated pair was kept in an individual food vial for a period of three days and was then transferred to fresh food vials every third day. Three successive changes were made and the total number of flies which emerged from each vial was counted. Data were pooled and the mean number of flies per female was calculated. The number of pairs tested varied for different strains.

Table 1. Strains of *Drosophila bipectinata* used in the mating propensity and fertility tests

Abbreviation	Place of origin	Year of collection
BHU	Banaras Hindu University Varanasi, Uttar Pradesh	1987
UL	Unchawa Lodge, near Udai Pratap College, Varanasi, Uttar Pradesh	1987
MY	Mysore, Karnataka	1988
KER	Ernakulam, Kerala	1990
KOT	Kottayam, Kerala	1993
NL	Nilgiris, Tamil Nadu	1993
AD	Alipur Dwar, West Bengal	1993

RESULTS

Mean courtship time, mean duration of copulation and mean number of progeny/female are given in Table 2. Mean courtship time varied from 4.79 min (UL) to 10.93 min (MY) for different stocks. Analysis of variance for mating time (Table 3) shows that there is significant variation among the stocks tested. Mean duration of copulation varied from 9.62 min (UL) to 13.14 min (NL) in different stocks and ANOVA (Table 3) shows that there is significant variation among the stocks tested. Mean number of progeny produced per female varied from 99.57 (BHU) to 217.03 (NL) for different stocks and ANOVA (Table 3) indicates significant variation among the stocks.

Correlation coefficients were calculated in order to test the relationship between courtship time and fertility and between duration of copulation and fertility. There is no relation between courtship time and fertility (r = 0.31; df = 5, $p >$ 0.05). However, there is a positive correlation between duration of copulation and fertility (r = 0.88; df = 5, $p <$ 0.01). The strain showing a longer duration of copulation produced more progeny.

Table 2. Courtship time, duration of copulation, and number of progeny/female for different wild strains of *Drosophila bipectinata*

Strain	Number of pairs tested	Courtship time (min)	Duration of copulation (min)	Number of progeny produced/female
BHU	24	7.69 ± 1.05	9.85 ± 0.29	99.50 ± 5.89
UL	23	4.79 ± 1.12	9.62 ± 0.40	164.04 ± 10.23
MY	23	10.93 ± 1.19	12.16 ± 0.45	137.60 ± 15.46
KER	17	7.99 ± 1.45	10.56 ± 0.39	147.23 ± 10.30
KOT	30	6.90 ± 1.02	10.69 ± 0.41	166.73 ± 11.77
NL	28	7.53 ± 1.14	13.14 ± 0.67	217.03 ± 6.13
AD	26	8.76 ± 1.36	11.18 ± 0.39	166.53 ± 7.39

Data are presented as mean ± standard error of mean.

Table 3. Summary of analysis of variance

	F	*p*
Courtship time	2.33	< 0.05*
Duration of copulation	7.52	< 0.001**
Fertility	16.40	< 0.001**

*Significant at the level of 0.05.
**Significant at the level of 0.001.

The productivity of a strain in which flies copulate earlier is lower. A correlation coefficient was also calculated to test the relationship between courtship time combined with duration of copulation and the number of progeny produced per female and there is a significant positive relationship (r = 0.77; df = 5, $p < 0.05$).

DISCUSSION

Drosphila bipectinata is a member of the *bipectinata* species complex of the *ananassae* subgroup of the *melanogaster* species group. It has a wide geographical distribution and commonly occurs in India. Genetic and behavioral studies have been carried out on *D. bipectinata.* There is evidence for genetic variability at the level of chromosomal and allozyme polymorphisms in *D. bipectinata* (Yang et al. 1972, Singh and Das 1991, Banerjee and Singh 1995). Evidence for genetic heterogeneity among different strains with respect to mating propensity, polygenic control of sexual activity, effect of mutation on mating propensity, and ethological isolation between certain geographic strains has also been presented for *D. bipectinata* (Singh and Chatterjee 1991, Singh and Sisodia 1995 and unpublished data). Significant variations were found within *D. bipectinata* when comparing time until mating, duration of copulation, and mating frequency (Naseerulla and Hegde 1993). During the course of the present study, experiments were conducted to investigate courtship time, duration of copulation, and fertility by employing several strains of *D. bipectinata* orginating from different geographical localities. It is evident from the present results that all seven strains tested during the present study show significant variations with respect to courtship time, duration of copulation, and fertility. There is no correlation between courtship time and fertility although strains vary with respect to both characteristics. Interestingly, there is a significant positive correlation between duration of copulation and the number of progeny produced in different strains of *D. bipectinata.* The strain copulating for a longer time produces more progeny. While strains copulating for less time produce fewer offspring. For example, the NL strain copulated the maximum time and correspondingly produced the highest number of progeny per female. Similarly the UL and BHU strains copulated for shorter times and also produced fewer flies. Although there is no correlation between courtship time and fertility, courtship time combined with duration of copulation shows a significant positive correlation with productivity. Thus it is suggested that strains taking more time both in mating and during copulation may show higher productivity, other factors being equal.

Kaul and Parsons (1965) found a negative correlation between time to mating and duration of copulation for different inversion karyotypes in males of *D. pseudoobscura*, a species which may possibly be regarded as having an integrated system controlled mainly by the male. Parsons (1973) has suggested that the individual completing mating and copulation rapidly would most readily leave genes in subsequent generations and thus there is some selective advantage in completing mating and copulation rapidly. A positive correlation between male mating activity and fertility has been found in *D. subobscura* and *D. ananassae* (Maynard Smith 1956, Singh and Chatterjee 1987). Fulker (1966) investigated the relations between time to begin mating, duration of copulation, the number of copulations resulting in fertilization, and the number of progeny produced in *D. melanogaster.* All four measures appear to be general characteristics of male mating behavior and the males that mate more quickly also copulate successfully and leave more progeny. Prakash (1967) observed a relationship between fast mating, repeat mating, and the number of offspring produced in *D. robusta.* Gilbert and Richmond (1982) reported that at 16°C, *D. melanogaster* males with active esterase-6 mate sooner, copulate for a shorter duration and produce more progeny per mating than males without esterase-6. Ringo et al. (1986) found that there is a negative correlation between male mating success and postmating fitness in *D. simulans* as the males of certain strains had higher mating propensity, greater virility and lower productivity. The lower productivity of the males might be caused in part by an exhaustion of rapidly synthesized components of the ejaculate (Fowler 1973). Hay (1976) found a negative correlation between male mating speed and female fertility in certain laboratory strains of *D. melanogaster.* The line with faster males had females with lower fertility which resulted in a smaller number of progeny for that line. Thus it is not necessarily true that the fastest male genotypes also have greater reproductive fitness. The comparison of results with respect to the relationship among mating activity, duration of copulation, and fertility reported for *D. melanogaster, D. pseudoobscura, D. subobscura, D. robusta, D. ananassae*, and *D. simulans* clearly indicates that there are intra- and interspecific variations. We investigated certain aspects of sexual behavior and postmating fitness in *D. bipectinata* in tests employing several mass-culture laboratory stocks. There was a singificant variation among the strains tested with respect to courtship time, duration of copulation, and number of progeny produced. Furthermore, there is a positive correlation between duration of copulation, and number of progeny produced. Furthermore, there is a positive correlation between duration of copulation and fertility in *D. bipectinata.* The results obtained for *D. bipectinata* clearly show that it differs from other species in which fast mating and shorter durations of copulation have been considered advantageous, and also from those in which males copulate for a shorter duration of time and produce more progeny. Therefore various species of *Drosophila* may differ with respect to certain aspects of sexual behavior and postmating fitness. Duration of copulation is an expression of the rate of sperm transfer and is male determined (MacBean and Parsons 1967, Spiess 1970). *D. bipectinata* males copulating for longer durations produce more progeny which is likely due to higher sperm transfer and may be a species-specific characteristic.

Acknowledgements: The present work has been carried out during the tenure of a Banaras Hindu University research scholarship to Seema Sisodia. We thank the anonymous reviewers for their comments on the manuscript.

REFERENCES

Banerjee R, BN Singh. 1995. Evidence for selection and genetic drift in laboratory populations of *Drosophila bipectinata.* Proc. Zool. Soc. (Calcutta) **47:** 125-133.

Bastock M. 1956. A gene mutation that changes a behavior pattern. Evolution **34:** 421-439.

Chatterjee S, BN Singh. 1989. Sexual isolation in *Drosophila.* Ind. Rev. Life Sci. **9:** 101-135.

Fowler GL. 1973. Some aspects of the reproductive biology of *Drosophila*: Sperm storage and sperm utilization. Adv. Genet. **17:** 293-360.

Fulker DW. 1966. Mating speed in male *Drosophila melanogaster*: A psychogenetic analysis. Science **153:** 203-205.

Gilbert DG, RC Richmond. 1982. Esterase 6 in *Drosophila melanogaster*: Reproductive function of active and null males at low temperature. Proc. Natl. Acad. Sci. USA **79:** 2962-2966.

Grossfield J. 1978. Non-sexual behavior in *Drosophila. In* M Ashburner, TRF Wright, eds. The genetics and biology of *Drosophila.* Vol. 3a. New York: Academic Press, pp. 2-126.

Hay DA. 1976. The behavioral phenotypes and mating behavior of two inbred strains of *Drosophila melanogaster.* Behav. Genet. **6:** 161-170.

Kaul D, PA Parsons. 1965. The genotypic control of mating speed and duration of copulation in *Drosophila pseudoobscura.* Heredity **20:** 161-170.

MacBean IT, PA Parsons. 1967. Directional selection for duration of copulation in *Drosophila melanogaster.* Genetics **56:** 233-239.

Maynard Smith J. 1956. Fertility, mating behavior and sexual selection in *Drosophila subobscura.* J. Genet. **54:** 261-279.

Naseerulla MK, SN Hegde. 1993. Lack of correlation between mating activity and EST-1 polymorphism in three natural and laboratory populations of *Drosophila bipectinata*. Ind. J. Exp. Biol. **31:** 215-218.

Parsons PA. 1973. Behavioral and ecological genetics: A study in *Drosophila*. Oxford: Clarendon Press.

Prakash S. 1967. Association between mating speed and fertility in *Drosophila robusta*. Genetics **57:** 655-663.

Ringo J, K Barton, H Dowse. 1986. The effect of genetic drift on mating propensity, courtship behavior and postmating fitness in *Drosophila simulans*. Behavior **97:** 226-233.

Singh BN, S Chatterjee. 1987. Variation in mating propensity and fertility in isofemale strains of *Drosophila ananassae*. Genetica **73:** 237-242.

Singh BN, S Chatterjee. 1991. Evidence for incipient sexual isolation within *Drosophila bipectinata*. Evol. Biol. **5:** 105-113.

Singh BN, A Das. 1991. Linkage disequilibrium between inversions in *Drosophila bipectinata*. Biol. Zent. bl. **110:** 157-162.

Singh BN, YN Dwivedi, JP Gupta. 1981. Sexual isolation among three species of the *Drosophila bipectinata* species complex. Ind. J. Exp. Biol. **19:** 898-900.

Singh BN, S Sisodia. 1995. Variation in mating propensity in laboratory strains of *Drosophila bipectinata*. Biol. Zent. bl. **114:** 95-101.

Spiess EB. 1970. Mating propensity and its genetic basis in *Drosophila*. *In* MK Hecht, WC Steere, eds. Essay in evolution and genetics in honor of Theodosius Dobzhansky. New York: Appleton Century Crofts, pp. 315-379.

Spieth HT. 1952. Mating behavior within the genus *Drosophila* (Diptera). Bull. Amer. Natural Hist. **99:** 395-474.

Spieth HT, JN Ringo. 1983. Mating behavior and sexual isolation in *Drosophila*. *In* M Ashburner, HL Carson, JN Thompson, eds. The genetics and biology of *Drosophila*. London: Academic Press, pp. 223-284.

Yang SY, L Wheeler, IR Bock. 1972. Isozyme variation and phylogenetic relationships in the *Drosophila bipectinata* species complex. Univ. Texas Publ. **7213:** 213-227.

Drosophila bipectinata 果蠅交尾時間與生育力之相關性

Seema Sisodia[1] and Bashisth Narayan Singh[1]

Drosophila bipectinata 屬於 *melanogaster* 種群，*ananassae* 亞群，*bipectinata* species complex 中的一種，在印度相當普遍。本研究比較了採自不同地區七個品系之果蠅在求偶、交尾時間及生育力上之差異，結果發現上述測量值在不同品系間具顯著差異，而交尾所需時間較長的品系可產生較多的子代，顯示此種果蠅之交尾時間與生育力間呈正相關。

關鍵詞：野生品系, 性行爲, 交配後的適應度。

[1] Genetics Laboratory, Department of Zoology, Banaras Hindu University, Varanasi-221 005, India