The only other species about which some aspects of the genetics of oviposition behaviour are known are species of *Papilio* and *Drosophila*. In the *Papilio machaon* species group, preference is largely X-linked, with some autosomal effects, and specificity and preference are under partly separate genetic control[9,10]. X-linked inheritance of oviposition preference is also suggested in the tiger swallowtails *P. glaucus* and *P. canadensis*[30], and in the moth *Heliothis virescens*[31]. In both the latter studies, the genetic relationship between preference and specificity was not addressed. In *D. tripunctata*, preference is known to be largely additive and autosomal[18,19], and long-distance attraction to oviposition sites and laboratory preference seem to have a different genetic basis[32]. The distribution of preference within populations of *D. tripunctata* is unimodal[19], although this may be a consequence of assaying preference on groups of females together which could mask the effects of high individual specificity for different food media. Preference is also known to be largely additive in the specialist *D. seychellia*[33]; in this case too, the genetic relationship of preference and specificity is not known.

Overall, we feel that it is worthwhile to further examine this pattern in *individual* oviposition behaviour, wherein a population shows a combination of high specificity and variation for preference, because such variation in nature could be the starting point for the evolution of host-race formation or host-shifts via founder effects. A bimodal distribution of preference has recently been reported from a wild population, and in conjunction with a recent host-shift[27], supporting the view that further genetic studies on the evolutionary genetic relationships between preference and specificity may help to advance our understanding of the evolution of host specialization in insects.

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ACKNOWLEDGEMENTS. We thank V. Gohil for assistance in the laboratory. This work was supported by funds from the Department of Science and Technology, Government of India.

Received 26 April 1999; accepted 10 August 1999

Mating success in *Drosophila ananassae*: Evidence for greater variation in receptivity of females compared to male mating ability

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Mating success was studied by direct observation in Elens–Wattiaux mating chamber to test mating propensity in six mass culture wild-type strains of *Drosophila ananassae* originating from different geographic localities. The results indicate that the mean number of matings varies significantly among the stocks tested which is attributable to genetic heterogeneity among the stocks. Diallel analysis showed that the variation observed between the strains is due to differences in sexual activity of both sexes. However, females show more variation than males. In 15 pairwise comparisons between the strains, 10 comparisons showed greater variation in receptivitiy of females than in sexual activity of males. In 3 comparisons there is greater difference in male mating ability than in female

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Table 2. Mean number of matings ($\bar{X} \pm$ SE) in 60 min out of 15 pairs (5 replicates) tested in diallel crosses involving six wild-type strains of *D. ananassae*

Strains of female parent	Strains of male parent						
	PAT	TIR	Bhutan	CHIN	ELEN	DP	Total
PAT	0.0 ± 0.00	1.8 ± 0.37	3.4 ± 0.68	1.4 ± 0.25	1.2 ± 0.20	2.6 ± 0.39	10.4 (52)
TIR	5.8 ± 0.37	5.0 ± 0.00	9.0 ± 0.32	4.6 ± 0.25	4.0 ± 0.32	8.8 ± 0.37	37.2 (186)
Bhutan	7.0 ± 0.32	8.0 ± 0.32	9.0 ± 0.54	9.0 ± 0.54	8.8 ± 0.37	11.0 ± 0.32	52.8 (264)
CHIN	4.2 ± 0.37	3.8 ± 0.20	7.0 ± 0.45	3.0 ± 0.00	3.4 ± 0.25	7.0 ± 0.32	28.4 (142)
ELEN	6.8 ± 0.36	6.6 ± 0.25	8.4 ± 0.51	6.6 ± 0.25	6.2 ± 0.19	8.0 ± 0.45	42.6 (213)
DP	5.6 ± 0.25	5.8 ± 0.37	8.6 ± 0.25	7.8 ± 0.20	6.8 ± 0.37	8.0 ± 0.32	42.6 (213)
Total	29.4 (147)	31.0 (155)	45.4 (227)	32.4 (162)	30.4 (152)	45.4 (227)	214 (1070)

Total number of matings are given in parentheses.

female receptivity than in male sexual activity. Only in 3 comparisons there is greater variation in male mating ability than in female receptivity. However, differences in male mating activity and female receptivity are nearly identical in two comparisons.

Certain aspects of behaviour genetics of *D. ananassae* have been studied by different investigators[12]. Positive response to selection for phototaxis, pupation height, oviposition site choice, and mating propensity provides evidence for substantial amount of additive genetic variation for these behavioural traits in natural populations of *D. ananassae*[13,17,19,22]. Genetic control of sexual activity in this species has been demonstrated on the basis of significant variation in mating propensity of isofemale strains and inversion karyotypes, diminishing effects of certain mutations on sexual activity of males, and positive response to selection for high and low mating propensity[14–18,25]. Interestingly, females and males of *D. ananassae* with high number of sternopleural bristles are more successful in mating than those with low number of sternopleural bristles[21]. The results of earlier investigations on mating propensity in *D. ananassae* demonstrated that males contribute more to variation than females and males are principal determiners of efficient mating. Thus males are more subject to intrasexual selection than females[14–17].

During the course of the present investigation, six mass culture stocks of *D. ananassae* established from flies collected in different geographical localities were tested for mating success by direct observation in Elens–Wattiaux mating chamber. There is a significant variation in mean number of matings among the strains tested which is attributable to genetic heterogeneity among the strains resulting from original geographical location and genetic drift during laboratory rearing. To assess the relative sexual activity of two sexes, diallel crosses were also made. It is evident from the results of diallel analysis that both sexes contribute to the variation in mating propensity of these strains. However, variation is more for females than for males. Although ANOVA applied to the data of diallel crosses has demonstrated that there is greater variation in receptivity of females than in male mating ability, the pairwise comparisons (Table 3) have been made to measure the differences between sexual activity of the two sexes. Out of 15 comparisons, 10 show greater variation in female receptivity than in male sexual activity and only 3 comparisons show more variation in male sexual activity than in female receptivity. However, only two comparisons show nearly identical differences

Table 3. Pairwise comparisons to test the differences between male activity and female receptivity based on the marginal totals of mean number of matings in diallel crosses

Pairs of strains	Range of variation		Difference
PAT vs TIR	Male activity	29.4–31.0	1.6
	Female receptivity	10.4–37.2	26.8
PAT vs Bhutan	Male activity	29.4–45.4	16.0
	Female receptivity	10.4–52.8	42.4
PAT vs CHIN	Male activity	29.4–32.4	3.0
	Female receptivity	10.4–28.4	18.0
PAT vs ELEN	Male activity	29.4–30.4	1.0
	Female receptivity	10.4–42.6	32.2
PAT vs DP	Male activity	29.4–45.4	16.0
	Female receptivity	10.4–42.6	32.2
TIR vs Bhutan	Male activity	31.0–45.4	14.4
	Female receptivity	37.2–52.8	15.6
TIR vs CHIN	Male activity	31.0–32.4	1.4
	Female receptivity	37.2–28.4	8.8
TIR vs ELEN	Male activity	31.0–30.4	0.6
	Female receptivity	37.2–42.6	5.4
TIR vs DP	Male activity	31.0–45.4	14.4
	Female receptivity	37.2–42.6	5.4
Bhutan vs CHIN	Male activity	45.4–32.4	13.0
	Female receptivity	52.8–28.4	24.4
Bhutan vs ELEN	Male activity	45.4–30.4	15.0
	Female receptivity	52.8–42.6	10.2
Bhutan vs DP	Male activity	45.4–45.4	0.0
	Female receptivity	52.8–42.6	10.2
CHIN vs ELEN	Male activity	32.4–30.4	2.0
	Female receptivity	28.4–42.6	14.2
CHIN vs DP	Male activity	32.4–45.6	13.0
	Female receptivity	28.4–42.6	14.2
ELEN vs DP	Male activity	30.4–45.4	15.0
	Female receptivity	42.6–42.6	0.0

between two sexes. Even if the comparisons involving PAT strain (very low receptivity or high mating threshold of females) are excluded, 5 comparisons (out of 10) indicate that there is greater variation in female receptivity than in male mating ability but only 3 show more variation in male activity than in female receptivity. Based on the analysis of data of diallel crosses by ANOVA and pairwise comparisons to measure the difference in sexual activity of the two sexes, it is suggested that receptivity of females shows more variation than sexual activity of males in these strains of *D. ananassae* although the earlier work on this species demonstrated that there was greater variation in male mating ability than in female receptivity.

It is known that male activity and female receptivity are the main factors responsible for successful mating in *Drosophila*[6]. Intra-specific variation in mating activity has been reported in *D. melanogaster*, *D. subobscura*, *D. robusta* and *D. bipectinata*[26–31]. The dependence of successful mating on a particular sex varies between species and within species between genotypes such that males may often be more important if mating is rapid, while if mating is slow, females play a progressively more important role[2,27]. In *D. pseudoobscura*, mating is so rapid that variation in female receptivity may be relatively unimportant[2]. In *D. persimilis*, it has been found that females are critical over a 1 h period because of an interaction between copulation and avoidance tendencies[32]. Thus the results concerning the contribution of a particular sex to variation in sexual activity as well as the dependence of mating success on a particular sex may vary within the species depending upon the genetic constitution of strains. In different species of *Drosophila*, it has been demonstrated that sexual activity of males and receptivity of females have a genetic basis[1,2,4,5,9,33].

The present observation clearly shows that receptivity of females shows more variation than male mating ability in the mass culture strains of *D. ananassae* employed during the present study. However, the earlier work on *D. ananassae* in which isofemale lines were used demonstrated that there was greater variation in male mating ability than in female receptivity[15]. The mass culture stocks utilized during the present study and the isofemale strains tested earlier were derived from different geographic localities and had spent varying number of generations in the laboratory. Thus these strains vary in the genetic constitution which may explain the variation in the results concerning the contribution of a particular sex to variation in sexual activity as well as dependence of mating success on a particular sex within the species. Such intra-specific variation regarding the contribution of a particular sex to variation in sexual activity as well as dependence of mating success on a particular sex depending on the genetic constitution of the strains have been demonstrated earlier in certain species of *Drosophila*[2,27,32]. The differences in the degree of behavioural reproductive isolation between mass culture stocks and isofemale lines of *D. ananassae* originating from different geographic localities have been reported by Singh and Chatterjee[34,35], who found that isolation was stronger among isofemale lines compared to mass culture stocks which demonstrated genetically based divergence in mating behaviour of *D. ananassae*.

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ACKNOWLEDGEMENTS. The present work has been supported by UGC, New Delhi in the form of a research project to B.N.S. and a project fellowship to S.R.S.

Received 20 March 1999; revised accepted 20 August 1999