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SEXUAL SELECTION OPERATING IN A WILD POPULATION OF *DROSOPHILA ROBUSTA*

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Almost 60 years have elapsed since the discovery of variation in the polytene chromosomes of *Drosophila* (Sturtevant and Dobzhansky 1936). Inversion polymorphism studies have revealed some of the intricacies of evolutionary change, but even now, when interest in them has waned, there is little understanding of the particular alleles contained within them that alone or in relation to other genes influence any component of fitness. Perhaps the most important rule about inversion polymorphisms learned from a long history of laboratory experiments (cf. Lewontin et al. 1981) is their sensitivity to environmental features such as temperature and nutrition. Therefore, laboratory studies alone may not predict the consequences due to genotype (karyotype) by environment interactions of selection in wild populations.

Only a few studies have documented selective mechanisms associated with preserving inversion polymorphisms in natural populations beyond establishing correlations with temperature, rainfall, humidity, elevation, and other environmental features. Despite the long history of interest in the ecology of *Drosophila* breeding and feeding sites (cf. Carson 1951, 1971; Heed 1957, 1968, 1971), experimental analyses of inversion polymorphisms involving natural breeding substrates are few because the mating sites and larval ecology of most species with well described inversion polymorphisms are poorly known, e.g., *D. pseudoobscura*. An early exception to this problem was the comprehensive study of inversion polymorphism in *D. flavopilosa*, a flower breeder from South America (Brncic 1962). Egg to adult viability differences among karyotypes were observed among preadult stages in flowers returned to the lab and exposed to contrasting temperatures (Brncic 1968). More recently, analysis of the "sex-ratio" meiotic drive system in natural populations of *D. pseudoobscura* suggested that most selection responsible for maintaining this polymorphism must be operating in preadult stages (Beckenbach 1996). A notable non-*Drosophila* example is the chromosome I polymorphism in seaweed flies, *Coelopa frigida*, that carry out their life cycle on decomposing seaweed on beaches around the north Atlantic and North Sea. Gene arrangement–based differences in egg to adult development time, adult body size, and mate preference have been demonstrated in seaweed-reared flies (Day et al. 1983; Engelhard et al. 1989; Gilburn et al. 1992).

For species that can be collected in nature throughout their life cycle, karyotype frequencies can be estimated from life stages reared in the wild and comparisons can be made between stages of the life cycle in selection component analyses (e.g., Prout 1971; Bundgaard and Christiansen 1972). Inversion polymorphisms in cactophilic *D. buzzatii* have been studied this way, a species that feeds and breeds in the fermenting tissues of several species of prickly pear cactus. In general, cactophilic *Drosophila* have taught us much about maintenance of genetic variability, host specificity, chemical ecology, trophic adaptation, and life history evolution (Barker and Starmer 1982; Barker et al. 1990). Despite the fact that 48% (44/91) of all described and undescribed *D. repleta* group species possess inversion polymorphism (Wasserman 1992), in only a few species has there been concerted effort to unravel the causes for maintenance of inversion polymorphism in nature, that is, *D. buzzatii* and *D. mojavensis*. Inversion polymorphism in the latter species, along with *D. pachea*, a cactophilic member of the *D. nannoptera* group, has been recently summarized (Etges et al., in press). Ruiz et al. (1986) demonstrated endocyclic selection, directional selection in opposing directions during the life cycle, on gene arrangements of *D. buzzatii*. However, this pattern is population and host specific (Hasson et al. 1991) and not surprisingly is limited to a few components of fitness including egg to third instar viability and adult body size, but not mating propensity (Santos et al. 1992; Barbadilla et al. 1994). Adult size in *Drosophila* can be correlated with increased fitness as larger flies typically have greater reproductive potential (Robertson 1957) and dispersal ability (Mangan 1982). These studies of *D. buzzatii* deserve special note because they illustrate the complexity of factors that must be addressed in understanding the maintenance of inversion polymorphisms in natural populations.

Thus, studies of selection on inversion polymorphisms in species with hard-to-find breeding sites have been restricted to adult flies because they can be captured in the wild. If we include the recent *D. buzzatii* studies mentioned above, several studies of genetic variation in male mating success (Anderson et al. 1979; Levine et al. 1980; Salceda and Anderson 1988), the recent analysis of the "sex-ratio" polymorphism in *D. pseudoobscura* (Beckenbach 1996), and mate choice in seaweed flies (Gilburn et al. 1992), most of what we know of selection operating on inversion polymorphisms under natural conditions has only recently been documented. It is interesting to note that not one example documenting an identifiable selective agent operating on inversion polymorphisms was cited by Endler (1986) in his review, "Natural Selection in the Wild," despite the long history of population genetics

research in *Drosophila* and other organisms with chromosome polymorphisms.

Studies of inversion polymorphisms in *D. robusta* over the last 40 years have revealed a wealth of information on clinal variation (Stalker and Carson 1948; Levitan 1978; Etges 1984), temporal frequency changes (Carson 1958; Levitan 1973; Etges 1984, 1991), linkage disequilibrium (Carson 1953; Levitan 1958, 1992), and population structure (Carson 1959; Prakash 1973). Variation of karyotype-related fitness components including viability, fertility, mating speed, egg-to-adult development time, age at first reproduction, and adult longevity under laboratory conditions has also been assessed (Prakash 1967a,b, 1968; Etges 1989). This species is one of the more common members of the noncosmopolitan *Drosophila* fauna in the east-central United States and Canada with a species range roughly coincident with the eastern deciduous forest (Carson 1958).

Drosophila robusta breeds in sap fluxes of several deciduous tree species, particularly American elm, *Ulmus americana* (Carson and Stalker 1951). Fourteen gene arrangements distributed over the three metacentric chromosomes (X, 2, 3) have been found segregating in natural populations. Those on the X and second chromosomes are often encountered in nonrandom associations (reviewed in Levitan 1992) suggesting fitness interactions between arrangements on opposing chromosome arms. Even now, it remains impractical to perform experiments with sap flux–reared larvae.

The focus of the present study was to estimate karyotypic variation in a natural population of *D. robusta* and compare frequencies of wild caught adults and their offspring to detect the effects of natural selection and possible karyotype related differences in male mating success. This study represents the first attempt to identify selection on particular components of fitness in *D. robusta* under natural conditions.

Materials and Methods

Adult *D. robusta* were collected over buckets of fermenting bananas in an old growth, shortleaf pine–mixed deciduous forest in the Mill Creek Recreation Area (Ouachita National Forest) in Scott County, Arkansas. The buckets were left exposed continuously from 16–25 July 1990. Because of the long generation time of *D. robusta* (ca. 16 d for egg to adult development time plus 5 d posteclosion to reach sexual maturity at 25°C for females and longer for males under optimal conditions; Etges 1989), this 10-d collecting period was short enough to minimize sampling different cohorts from nature. Seasonal variation in chromosome frequencies has not been measured at Mill Creek, but has been observed elsewhere in Arkansas (Etges 1991). adults attracted to bait are thought to be a random sample of the local population as Carson (1958) found no differences in karyotypes of baited flies and those collected on sap fluxes. The first 41 females collected were separated into food vials immediately after capture to insure that all inseminated females had mated with males in the wild rather than in the capture vials. To increase sample sizes, I returned to this site two more times. All flies collected on these two trips were returned to the laboratory within 4 h in 12–15°C chilled coolers to minimize activity in the vials.

All remaining adult *D. robusta* were individually separated into different food vials in the laboratory. Each wild male was mated to a stock homokaryotypic female and wild females were allowed to oviposit until they were depleted of stored sperm. Remating is frequent in both sexes with copulations lasting less than a minute (Prakash 1967a) and no insemination reaction is formed (Grant 1983). However, there is little evidence of multiple insemination, that is, mixtures of sperm from more than one male stored by wild females, in the egg samples of *D. robusta* females from Fayetteville, Arkansas (Etges 1991, unpubl. data). Therefore, five offspring from each wild female were karyotyped, and in a subset of 20 females, up to 10 larvae were scored to ascertain whether five larvae were a representative egg sample in this population. In no cases were additional gene arrangements observed in the expanded progeny sets, suggesting that sampling five larvae per female provided an adequate sample of the offspring each female would have contributed to nature. Wild females were transferred to fresh food vials every few days until no larvae were seen. They were then mated to stock homokaryotypic males. The karyotypes of at least seven F_1 larvae from each of the wild adults crossed to stock homokaryotypes were determined to infer the karyotypes of the wild adults.

All inversion frequency data were tested for heterogeneity between sexes and life stages using likelihood ratio or *G*-tests (Sokal and Rohlf 1981) with Williams's correction (Williams 1976). Data for each chromosome arm were also tested for Hardy-Weinberg equilibrium. Analyses of linkage disequilibrium of gene arrangements on the X and second chromosomes at Mill Creek and four other Arkansas populations are presented in Levitan and Etges (1995) and so are not presented here in detail. They found strong nonrandom association among gene arrangements on the left and right arms of the X chromosome, but not the second chromosome in the Mill Creek population.

Results and Discussion

Karyotypes were inferred for most of the 115 adult females and 108 males collected at Mill Creek in this study. There were 17 (15 %) adult females that produced no offspring. Five of these 17 females proved to be fertile after crossing to stock males, but the remaining 12 produced no offspring in the presence of several stock males each. These 12 wild females were sterile or preferred not to mate with the stock males. All but four of the 108 wild caught males mated with stock females and produced offspring. There was no evidence of sperm from more than one male in the egg samples of each wild-caught female. However, since most females were not placed into separate vials prior to transport of the flies to the laboratory, there may be a bias in the offspring frequencies.

Frequencies of observed second chromosome, left arm karyotypes (TWL) differed marginally between wild adult males and females ($G = 12.96$, 7 df, $P = 0.07$). When analyzed separately, male and female TWL karyotypes were in Hardy-Weinberg equilibrium. Pooling adult karyotypes for this chromosome arm yielded a small departure from Hardy-Weinberg equilibrium, expected if male and female karyotypes differ in frequency ($G = 15.22$, 8 df, $P = 0.06$). All observed

karyotypes for the X and third chromosomes conformed to Hardy-Weinberg expectations. Gene arrangement frequencies did not differ among adult females and males for the X , right arm of the second (TWR), or the third chromosome (THR: all $P > 0.30$). TWL gene arrangement frequencies differed significantly between wild males and females ($G = 9.27$, 3 df, $P = 0.03$).

Frequencies of TWL gene arrangements of wild adult females differed significantly from those of their offspring ($G = 11.96$, 3 df, $P = 0.01$). Such heterogeneity for the other chromosome arms was not found. Offspring frequencies were homogeneous with those of the wild males for all chromosome arms. There were no frequency differences between male and female offspring ($P > 0.5$).

The differences between adult male and female TWL gene arrangement frequencies suggests that sex-specific viability selection is operating in Mill Creek. Viability selection could be operating at any stage of the life cycle from zygote through adult life stages. Similar observations were made in New Jersey (Levitan 1951a) and Virginia populations (Levitan 1951b). In the latter study, frequencies of gene arrangement 2L-2 shifted seasonally in wild-caught adults of both sexes, but shifts in 2L-3 were confined to males. Further, seasonal frequency shifts in XL and XL-1 were documented in males only. These observations strongly suggest sex-specific natural selection in response to seasonal variability. Levitan (1992) also described field experiments where he perturbed inversion frequencies in two New Jersey populations by releasing adults descended from Alabama, Mississippi, and South Carolina with known karyotypes. After verifying that the introduced adults had mated with resident flies, he documented that inversion frequencies for all five polymorphic chromosome arms returned to preperturbation levels in one year for both populations, strongly suggesting that these gene arrangements influence some components of fitness in nature.

Similarity in frequencies between adult males and the pooled offspring in Mill Creek suggests that gene arrangement frequencies in the zygote pool were influenced differentially by males because the egg sample frequencies are expected to be the arithmetic mean of their parents' frequencies. Several mechanisms may be operating: sperm displacement, meiotic drive, or differential male mating success (Salceda and Anderson 1988). Studies of sperm displacement and meiotic drive have not been undertaken with *D. robusta* and could be responsible. One way to assess meiotic drive using the present data is to test for differences in frequency between X chromosome arrangements in adult females and the pooled male offspring. These frequencies are expected to be the same unless certain chromosomes from the adult females enjoy biased rates of transmission to their sons. There were no significant differences in X chromosome frequencies between adult females and their male offspring (all $P > 0.25$). Of course, male-based meiotic drive could be responsible, but it cannot be estimated with the present data.

Changes in gene arrangement frequencies among the wild adults and the offspring of the females inseminated in nature can be used to estimate differential male mating success using the procedures developed by Salceda and Anderson (1988) for the third chromosome system of inversions in *D. pseudoobscura*. This technique allows for the estimation of the

TABLE 1. Adult second and third chromosome gene arrangement[1] frequencies contributed to their offspring in a natural population of *D. robusta*. Estimation of males' sperm contribution to wild caught females and the change in frequency in one generation, Δp, due to differential male mating success is shown.

	2L	2L-1	2L-2	2L-3	n_{TWL}	2R	2R-1	n_{TWR}	3R	3R-1	n_{THR}
1. Combined adult frequencies	25.81	49.87	23.56	0.75	399	81.95	18.05	399	1.75	98.25	399
2. Offspring frequencies	29.51	48.06	20.94	1.49	1003	81.92	18.08	1001	1.59	98.41	1004
3. Adult female frequencies	20.94	54.97	24.08	0.0	191	80.10	19.90	191	1.57	98.43	191
4. Adult male frequencies	30.29	45.19	23.08	1.44	208	83.65	16.35	208	1.92	98.08	208
5. Female parents' contribution to offspring[2]	10.47	27.49	12.04	0.0		40.05	9.95		0.79	49.22	
6. Males contribution to offspring (row 2 − row 5)	19.04	20.57	8.90	1.49		41.87	8.13		0.80	49.19	
7. Frequencies in sperm stored by wild females (row 6 × row 2)	38.08	41.14	17.80	2.98		83.74	16.26		1.60	98.38	
8. Δp: difference in frequency due to male mating success (row 7 − row 4)	7.79	−4.05	−5.28	1.54		0.09	−0.09		−0.32	0.30	
9. % change in frequency = 100(row 8/row 7)	20.46	−9.84	−29.66	51.68		0.11	−0.11		−20.00	0.30	
10. *P*-value associated with Δp	0.028	0.285	0.095	0.119		0.975	0.975		0.756	0.771	

[1] Gene arrangements are labelled by chromosome number and arm, e.g., 2L-3 refers to gene arrangement 3 on the left arm of the second chromosome. The number of chromosome arms sampled, n_{TWL}, is the number of left arm, second chromosomes examined. See Etges (1989) for details.
[2] Females' contribution to their offspring is assumed to be 50% because 5–6 offspring per wild-caught female were karyotyped.

TABLE 2. Adult gene arrangement frequencies contributed to their offspring for the X chromosome in a natural population of *D. robusta*. Estimation of males' sperm contribution to wild caught females and the change in frequency in one generation, Δp, due to differential male mating success is shown. *P*-values are associated with the hypothesis that Δp = 0.

	XL	XL-1	XL-2	n_{XL}	XR	XR-1	XR-2	n_{XR}
1. Combined adult frequencies	26.62	5.46	67.92	293	11.95	3.07	84.98	293
2. Combined offspring frequencies	30.77	6.03	63.20	780	14.63	2.57	82.80	779
3. Offspring female frequencies	29.68	5.93	64.39	556	14.21	2.16	83.63	556
4. Offspring male frequencies	33.48	6.25	60.27	224	15.70	3.59	80.72	223
5. Adult female frequencies	29.84	4.71	65.45	191	13.61	2.62	83.77	191
6. Adult male frequencies	21.57	6.86	71.57	102	8.82	3.92	87.26	102
7. Female parents' contribution to female offspring[1]	14.92	2.36	32.73		6.81	1.31	41.89	
8. Males contribution to female offspring (row 3 − row 7)	14.76	3.57	31.66		7.40	0.85	41.74	
9. Frequencies in sperm stored by wild females (row 8 × row 2)	29.52	7.14	63.32		14.80	1.70	83.48	
10. Δp: difference in frequency due to male mating success (row 9 − row 6)	7.95	0.28	−8.25		5.98	−2.22	−3.78	
11. % change in frequency = 100 (row 10/row 9)	26.93	3.92	−13.03		40.41	−130.58	−4.53	
12. *P*-value associated with Δp	0.078	0.918	0.093		0.061	0.267	0.301	

[1] We assume the females' contribution to their female offspring is 50% and to their male offspring is 100% because we karyotyped 5–6 offspring per wild-caught female.

genetic composition of the sperm carried by the adult females by subtracting the frequencies of the females' contribution to their offspring from the offspring frequencies. I applied this technique to all of the polymorphic chromosomes in the Mill Creek population of *D. robusta*, including the X chromosome where there is no paternal contribution to sons (Tables 1 and 2).

Since the autosomal gene arrangement frequencies in the offspring (Table 1, row 2) are composed of 50% maternal and 50 percent paternal contributions, the females' contributions are assumed to be 50% of the adult frequencies (row 5). Gene arrangement frequencies in the stored sperm are therefore the differences between the offspring frequencies and the adult males (row 6) multiplied by two (row 7). The difference between the observed adult male frequencies (row 4) and those in the females' stored sperm therefore represent changes in gene arrangement frequencies most likely due to differences in male mating success (Salceda and Anderson 1988).

Of the four TWL gene arrangements, three were in moderate frequencies in Mill Creek and one, 2L-3, was quite rare. Arrangement 2L increased by 20.5% while 2L-1 and 2L-2 decreased markedly due to differences in male mating success. Statistical significance of the changes in frequencies due to males, Δp, can be evaluated by calculating $\Delta p / \sqrt{\{[p_a(1 - p_a)/n_a] + [p_s(1 - p_s)/n_s]\}}$, which is distributed as a standard normal deviate. The subscript *a* refers to the adult male frequencies and *s* refer to the estimated frequencies in the sperm stored by the wild females. The null hypothesis is Δp = 0. The increase in frequency of gene arrangement 2L was larger than that expected due to chance ($Z = 2.20$, $P = 0.03$) and the decrease in 2L-2 due to male mating success was not significant ($Z = -1.07$, $P = 0.1$). Thus, the rarest gene arrangement, 2L-3, increased in frequency by over 50%, consistent with the "rare male" advantage in mating success, but this was not statistically significant (Table 1).

Three X chromosome gene arrangements, XL, XL-2, and XR also varied in frequency due to differences in male mating success, but these changes were marginally significant (Table 2). It is much more difficult to interpret the dynamics of single gene arrangements on the X chromosome here because of strong linkage disequilibria between left and right arm arrangements (Levitan and Etges 1995). Sample sizes were probably inadequate to achieve statistical significance, particularly with low frequency gene arrangements (Anderson et al. 1979). Despite this, both XL and XR seem to have increased in frequency due to male mating success ($P = 0.08$ and 0.06, respectively) and coincidentally were in strong linkage disequilibrium in this population (Levitan and Etges 1995).

XL-2 is an enigmatic gene arrangement because it is almost permanently linked to the right arm of the X chromosome containing XR-2, that is, wherever XL-2 is present, it almost always linked to XR-2. A handful of recombinants (XL-2 linked to XR and one to XR-1) have been found in nature out of the thousands of wild adults karyotyped, so "wrong" combinations cannot be lethal (Levitan 1992; M. Levitan, unpubl. data). This strong association between XL-2 and XR-2 has been known since Carson and Stalker (1949) first observed the association in the egg samples of flies collected from 1946 to 1948 near St. Louis, Missouri, yet there is no experimental evidence that the XL-2.XR-2 association has any effect on fitness. The frequency of the XL-2.XR-2 association at Mill Creek is the highest yet observed in the entire species range of *D. robusta*. Both XL-2 and XR-2 decreased marginally in frequency due to male mating success (Table 2), so perhaps further analysis of this and other Ouachita populations of *D. robusta* will resolve the mechanisms responsible for preserving this extreme case of linkage disequilibrium.

Second chromosome gene arrangement 2L at Mill Creek therefore influenced both viability and male mating success in a pleiotropic fashion (Table 1). These results also help to resolve the mechanisms responsible for maintaining inversion polymorphism in natural populations of *D. robusta*. While the differences in adult frequencies of 2L and 2L-1

suggest sex-specific viability selection in nature, the mechanism involved is unknown. Males with karyotypes 2L/2L-1 3R-1/3R-1 exhibited faster mating speeds than alternate karyotypes in a Missouri Ozarks population, but this was dependent on the second chromosome karyotypes of the females used in the courtship trials (Prakash 1968). Since 2L/2L-1 3R-1/3R-1 karyotypes are also very common in Mill Creek, it is likely that these males achieve more matings consistent with the large changes in frequency of 2L due to male mating success (Table 1). However, heterokaryotypes involving arrangement 2L-1, that is, 2L-1/2L-2 and 2L-1/2L-3, were associated with decreased egg-to-adult development times when compared with 2L/2L homokaryotypes and heterokaryotypes involving 2L, including 2L/2L-1, in populations from the Smoky Mountains. Furthermore, averaged across karyotypes, arrangements 2L-1 and 2L-2 were associated with shorter egg to adult development times than 2L and 2L-3 (Etges 1989). Care must be taken in generalizing these results to Mill Creek because the genic content of these inversions may vary geographically and so may not influence components of fitness the same way and these studies were performed with lab-reared flies. If the disadvantage to carriers of 2L imposed by longer development times in both sexes is expressed in nature then the mating advantage confirmed upon 2L males suggests natural selection and sexual selection are in opposition during the life cycle. More information on the effects of karyotypes including 2L at particular stages of the life cycle in the Mill Creek population will allow us to determine whether this is another example of endocyclic selection (Ruiz et al. 1986). Further studies of sperm displacement, meiotic drive, and mating behavior should also clarify the postulated role of the variation in male mating success in this population of *D. robusta*.

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FACULTATIVE ADJUSTMENT OF THE SEX RATIO IN AN INSECT (*PLANOCOCCUS CITRI*, PSEUDOCOCCIDAE) WITH PATERNAL GENOME LOSS

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The extent to which members of a species can modulate their sex ratio in response to local conditions is strongly influenced by the type of sex-determination mechanism the species possesses. The system that allows perhaps the greatest flexibility is haplodiploidy, where males develop from unfertilized eggs and females from fertilized eggs. By controlling the access of sperm to the egg, females of haplodiploid groups such as the insect order Hymenoptera can determine the sex of their offspring. There is now abundant evidence that many haplodiploid species have adaptive sex ratio strategies that are influenced by local conditions (Charnov 1982; King 1987; Werren 1987; Antolin 1993; Wrensch and Ebbert 1993; Godfray 1994). Paternal genome loss (PGL) is a sex-determination system that in many ways has similar population-genetic consequences to haplodiploidy. Females develop as normal diploid organisms, while in males the paternal chromosome set fails to enter the gametes. The stage and tissues in which the paternal genome is inactivated varies among taxa, although in many groups the father's chromosome set condenses early in development so that males are functionally haploid. It is less clear how mothers might control the sex ratio of their offspring in species with PGL and Bull (1983) has suggested that haplodiploidy might have evolved more often than PGL precisely because it allows sex ratio control. However, Sabelis and Nagelkerke (1987) and Nagelkerke and Sabelis (1991) demonstrated that phytoseiid mites with PGL were able to respond to changes in population density by biasing their sex ratio toward females as predicted

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