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EQUILIBRIUM ANALYSIS OF SEXUAL SELECTION IN *DROSOPHILA MELANOGASTER*

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Abstract.—Several models for sexual selection, both by male-male competition and female choice, predict that a character which covaries with mating success should be near an equilibrium where the intensity of sexual selection opposes viability selection. This prediction was used to design experiments for estimating the intensity of sexual and viability selection on wing length in a recently captured population of *Drosophila melanogaster*. Observations of matings by males color-marked for wing length indicated that the standardized sexual selection differential on wing length was 0.24 under a wide range of effective sex ratios. After estimating the heritability of wing length to be 0.62, the expected standardized response due to sexual selection was calculated as 0.15 (SE = 0.15). The response due to viability selection was then estimated by comparing wing lengths of progeny of flies that had been randomly mated, thereby preventing sexual selection, with progeny of flies that had been allowed to acquire mates in a mass-mating chamber. The results support an equilibrium model in that the standardized response due to viability selection (−0.31, SE = 0.08) was opposite in sign and similar in magnitude to the estimated response due to sexual selection.

Observations of females orienting in front of males which differed in wing length indicated that the mating advantage accruing to long-winged males was not due to female choice. Instead, male-male competition in which the larger of two randomly chosen males succeeded in mating, explains the observed sexual selection. An experimental analysis of genotype-environment interaction revealed that larval density had a nonlinear effect on mean wing length within sibships. If a population is displaced from equilibrium, therefore, the evolutionary trajectory of mean wing length will depend both on the intensity of selection and the environment in which that selection is operating.

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Sexual selection operates when mating success covaries with the phenotypic expression of a character. If there is heritable variation for that character, sexual selection will change the population mean unless opposed by selection for a different component of fitness, such as viability. Given a constant opposing force of selection, an equilibrium will be reached eventually when the intensity of sexual selection, due either to male-male competition or female choice, equals the intensity of viability selection. Charlesworth (1984) and Maynard Smith and Brown (1986) have demonstrated that a stable equilibrium can be attained for a trait which increases male competitive ability for mates if there is an escalating cost associated with exaggeration due to fighting or metabolic production of the trait. Most models of female choice (e.g., Lande, 1981; Kirkpatrick, 1982; Lande and Arnold, 1985; Seger, 1985), in contrast, predict lines of equilibria between the male trait and female preference which can be either stable or unstable depending on the magnitude of the genotypic regression of female preference on male trait and the slope of the line of equilibrium (Lande, 1981; Seger, 1985). These authors assume that an increase in the character reduces male viability without affecting females, but differ in their assumptions about genetic control and female choice. Their models show that when female choice evolves the intensity of sexual selection changes, and a stable equilibrium is attained only when viability selection opposes the sexual selection induced by female choice.

This brief discussion of equilibrium models suggests an experimental method for estimating the response to selection episodes acting on a specified trait, z, prior to sexual selection if z is at equilibrium. The response to selection acting on z in opposition to sexual selection can be estimated by imposing random mating on an experimental population. Random mating eliminates the potential for sexual selection and any change in $\bar{z}$ must be due to episodes of selection acting prior to sexual selection. To simplify discussion, I henceforth refer to these earlier selection episodes as viability

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selection. At equilibrium, then, the standardized response to viability selection can be measured as

$$R_v = \frac{\bar{z}_r - \bar{z}_c}{\sigma}, \quad (1)$$

where $\bar{z}_r$ is the mean z of offspring from a random mating sample of the population, $\bar{z}_c$ is the mean z of offspring from an undisturbed mating sample, and σ estimates the standard deviation of the trait in the population. The intensity, i, of sexual selection can be calculated directly as one-half the standardized selection differential, $S/2\sigma$, where S is the difference between $\bar{z}$ for mating males and $\bar{z}$ for all males. The factor 1/2 accounts for sex-limited selection assuming autosomal inheritance (Lande, 1981). Frankham (1968) demonstrates how to estimate this factor when there is sex linkage. After estimating the proportion of additive genetic variation or heritability, h^2, of z using parent-offspring regression or sib correlation (Falconer, 1981 p. 151), the expected standardized response to sexual selection is

$$R_s = h^2 i. \quad (2)$$

This reasoning generates the quantitative prediction that $|R_v| = |R_s|$ when $\bar{z}$ is at equilibrium. Furthermore, the equilibrium assumption makes the qualitative prediction that $\bar{z}$ for offspring of the randomly mated sample will be less than $\bar{z}$ for offspring from parents that experienced sexual selection. In other words, R_v should be negative and R_s should be positive.

Below, I describe experiments on *Drosophila melanogaster* which test these qualitative and quantitative predictions of the equilibrium assumption and measure the intensity of sexual selection on wing length. Since wing length or any other sexually selected character could be involved both in male-male interactions and female choice, I conducted female preference tests to determine if females preferred males with wings longer or shorter than the mean. I assumed that male wing length covaried with mating success because male *D. melanogaster* court females by producing bursts of sound from wing vibrations (Ewing and Bennet-Clark, 1968), and Ewing (1964) has demonstrated that males with artificially shortened wings require more time before achieving a copulation than unaltered males. This result might be due to female choice because longer-winged males sing more loudly, but their songs do not differ in any spectral component (Partridge and Ewing, unpubl.). But, in addition, wing length is genetically correlated with body size (Robertson and Reeve, 1952). Long wings, therefore, indicate large males, which may displace small males when in direct competition for a female. Previous experiments have indicated that large males are more successful at mating than small males when paired with a female (Partridge and Farquar, 1983) or when housed in small groups (Ewing, 1961). Fighting for mates can occur between *D. melanogaster* males (Dow and von Schilcher, 1975). Consequently, current evidence does not preclude either male-male competition or female choice from favoring long wings.

Since density affects wing size and varies throughout the year (Tantawy, 1964; Atkinson, 1979), I also tested for any genotype-by-density interaction. If density interacts with the genotype to produce a nonlinear response in wing length, then any prediction of the response of individual genotypes to sexual selection in a nonequilibrium situation becomes dependent on larval rearing conditions. To determine the effect of this interaction on changes in mean phenotypes requires consideration of the evolution of phenotypes exposed to multiple environments (Via and Lande, 1985).

Materials and Methods

Stocks and Culture Conditions

The flies used in all of the experiments described here were descended from 30 female and 20 male *D. melanogaster* which I captured in baited traps at a fruit market warehouse in Brighton, U.K., from 10–15 June, 1984. These flies were maintained at 25 ± 1.5°C on a 12:12 hr light-dark cycle in a population cage containing 16 half-pint milk (stock) bottles. Each bottle held approximately 250 ml of medium made by adding 20 g agar, 22 g flaked yeast, 150 g maize meal, 130 g treacle, 5 g nipagin, and 5 ml propionic acid to 1.3 liters of water.

Each week, four fresh food bottles were added to the cage and four old (4 weeks) bottles were removed. The effective population size in this type of population cage has been estimated to be 5,000 (L. Partridge, pers. comm.). The flies used in these experiments were 2–12 generations removed from the founders. All measurements were performed under CO_2 anesthesia.

In the experiments discussed below untransformed data are used because, in all cases, the mean from untransformed data proved to be more independent of the variance than that from log-transformed data. All experiments were performed at 25 ± 1.5°C.

Sexual Selection Intensity and Heritability

Virgin adults were collected from stock bottles after eclosion, separated by sex into groups of 20, and kept with food for 2–3 days. Wing length from thoracic articulation to tip of radial vein was measured at 50 × with an ocular micrometer. The males were separated by wing length into six groups, each representing classes of 0.06 mm, and dusted with a unique fluorescent powder (4 micron particle diameter, Flare 610 pigment, Sterling Industrial Colours, Ltd., 133/135 High Street, Stratford, London E15 2RB). I ensured that the wing remained perpendicular to the line of sight by increasing the light level to reduce the depth of field. This technique yielded greater than 90% repeatability. After permitting marked flies to remove powder for 24 hr, mating tests were performed. Between 35 and 100 marked males were aspirated into a ventilated clear plastic box (11.3 × 17.2 × 5 cm), the bottom of which had been covered with 0.5 cm of food. Mates were allowed to habituate to the environment for 0.5 hr. Ten or 20 virgin females were aspirated into the chamber at 1- or 2-hr intervals, respectively, until 40 females each had at least 1 hr to mate. The color of all mating males was recorded with the aid of UV light. A pilot study with marked females showed that under these conditions 95% of females mate within 30 min after male introduction, only about 5% remate a second time during the 4-hr mating period, and there is no assortative mating for wing length. The sexual selection intensity was calculated by dividing the difference between the mean wing length of the marked mating males and the mean of all males introduced into the chamber by the standard deviation of the wing length of all males introduced. This experiment was replicated nine times. For each replicate the number of introduced females was held constant while the number of males introduced was varied to produce effective male : female sex ratios from 1.75:1 to 12:1.

Narrow-sense heritability was calculated from mid-offspring/mid-parent regressions (Falconer, 1981 p. 152) using parents and four sibs of each sex reared in one of the "random" selection response treatments. This measurement represents, therefore, the heritability of wing length for the approximate larval density under which the selection response was measured.

Viability Selection Response

Forty inseminated adult females were removed from stock bottles, and each was isolated in a vial (75 × 25 mm) with food for 24 hr. The emerging progeny were separated by sex and used in mating tests after 3–4 days. Each fly was allocated to the "random" or "choice" treatment at random. The "random" treatment consisted of 40 males and 40 females paired at random into individual vials with food for 4 hr. The "choice" treatment was created by aspirating 20 females into a mating chamber containing 80 males, and after 2 hr aspirating a second group of 20 females into the chamber, as described above for measuring selection differentials. After mating, each female was allowed 24 hr to oviposit on 15 ml of food in a standard vial. Emerging progeny were separated by treatment, sex, eclosion date, and sibship. Selection response was calculated as the standardized difference in mean male wing length between the "choice" and "random" treatments. To obtain this number, a maximum of four male flies was measured per sibship each day and the mean of these sibship means was compared between treatments. Since including sibs would underestimate the population variance, I estimated the population standard deviation by sampling

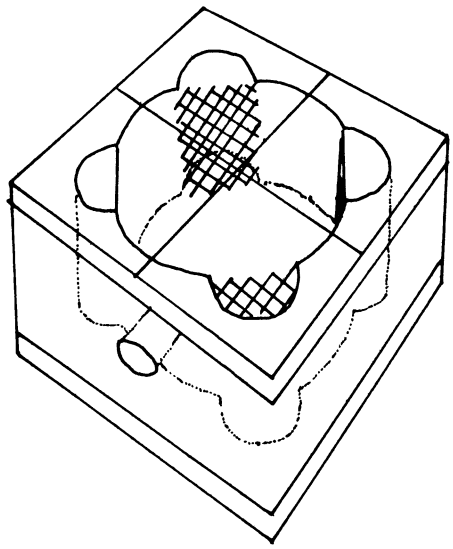

FIG. 1. Plexiglas chamber for measuring female preferences for male wing length. The inner chamber measures 1 cm in height × 3 cm in diameter. Side chambers are 1 cm in diameter and are separated from the inner chamber by nylon mesh. The Plexiglas top is inscribed to demarcate each male's "quadrant" and swivels to permit access to the side chambers. Entry to the inner chamber is via an aspiration hole on the side of the chamber.

one offspring at random from each sibship on each day from the "random" treatment. I did not estimate the population standard deviation from the "choice" treatment because these flies experienced both natural and sexual selection which reduced the population variance more than just the natural selection experienced by the "random" treatment flies. Ideally, one should measure the variance prior to any selection, but selection occurring during the larval stage precludes such measurement since it occurs prior to the expression of adult wing length. This experiment was replicated twice. I tested for a significant difference in male wing length between treatments with a repeated measures analysis of variance (Keppel, 1982), in which experiment and treatment were fixed factors and eclosion day was the repeated measure. This test is appropriate for these data because the flies which emerge on successive days from a given vial are primarily full-sibs and, therefore, cannot be considered as independent samples.

Female Choice Experiment

I constructed small Plexiglas mate choice chambers (Fig. 1) to determine if virgin females displayed a preference for long-winged males by orienting towards them. Each side chamber contained a 3–4-day-old virgin male and female obtained from stock bottles. The females in the side chambers were incapacitated by partially severing their thoracic-head junction. This treatment prevented females from mating, but enabled them to move enough to elicit long bouts of courtship from the confined males. The four males differed in wing length. The wing length of one male was within 1 SD of the mean, the wing length of another male was longer than 1 SD from the mean, and the wing length of the third male was shorter than 1 SD from the mean. The fourth male's wings were clipped off. Males were introduced at random into the side chambers under CO_2 anesthesia and allowed to recuperate for at least 20 min. A single 3–4-day-old virgin female was then aspirated into the center of the chamber. After allowing her to habituate for at least 5 min, observations were conducted for 5 min. The time the female spent in each of the four males' quadrants was recorded on a microcomputer. At the end of a 5-min session, the female was removed from the chamber by aspiration, a new female was introduced into the chamber, and the computer ranked each male by the amount of time that female spent in his quadrant. A rank of 1 indicated the largest proportion of time. Fourteen sets of four males were each exposed to between five and 10 virgin females.

Genotype-by-Density Interaction

Fifty-six pairs of virgin males and females were collected from stock bottles, kept isolated with food for 3–4 days, and then transferred to mating/laying pots. The mating pots were inverted 50 ml plastic pill vials with 15% agar in the lid and yeast paste on the side. After 48 hr, the lids were removed to permit collection with a trimmed paintbrush of first-instar larvae. Three densities were created with equal-sized full-sib larvae from each pot: density A—15 larvae on 15 ml food using standard vials; density B—15 larvae on 1.5 ml food using small (50 ×

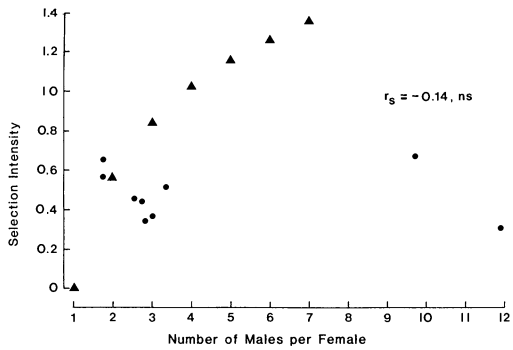

FIG. 2. Solid circles represent standardized selection differentials, *i*, plotted against effective sex ratio for nine mating cage experiments using color-marked males. Solid triangles represent the expected *i* for a best-of-*N* mating rule where *N* is the number of males per female.

12 mm) vials; and density C—30 larvae on 1.5 ml food in small vials. At the high density, development takes longer and smaller flies eclose, but mortality does not increase significantly.

Wing lengths of four progeny of each sex from each of the 44 parental families at the three densities were measured on mounted wings along the radial vein from the radiomedial cross-vein to the wing tip at 40 × with an ocular micrometer. Since flies reared at different larval densities were full sibs within a family, wing lengths of flies from one density could not be considered independent of wing lengths of their sibs raised under different larval conditions. Therefore, I used a repeated measures analysis of variance (Keppel, 1982 p. 423), with density as the repeated measure and both family and sex as between-subject treatments to determine the significance of any interaction between family and density. Since no progeny eclosed from 11 vials in the highest density treatment due to mold, I have analyzed these data twice; once with all families in two densities (mean family size for density A = 7.2, for density B = 7.4) and a second time with only the 33 producing families at all three densities (mean family size = 7.9 for all densities). I also calculated product-moment correlations across environments to provide approximations to the genetic correlations. These are only approximate genetic correlations because the variances contain a portion of the within-family error variance (Via, 1984). Since I did not have half-sib groups, I was unable to separate the additive genetic variation from dominance and maternal components of variation (Falconer, 1981 p. 290).

TABLE 2. Selection response from "choice"—"random" mating experiments. R = random, C = choice.

Replicate	Treatment	Male wing length		Number of families	Day of eclosion	Standardized response
		Mean	SD			
I	R	2.315	0.046	35	10	0.500
	C	2.346	0.037	28		
	R	2.311	0.039	28	11	0.098
	C	2.315	0.032	20		
II	R	2.218	0.058	25	10	0.328
	C	2.240	0.056	25		
	R	2.204	0.065	30	11	0.306
	C	2.228	0.052	36		

RESULTS

Sexual Selection Intensity and Heritability

The selection intensities for each of the nine mass mating experiments using marked males are presented in Figure 2. In each experiment, the mean wing length of the mating males was significantly greater than the mean of all males in the cage. There was no significant Spearman rank correlation between either male density or effective sex ratio and the standardized selection differential ($r_S = -0.25$ and $r_S = -0.14$, respectively). Table 1 provides the data on mating frequency within each of five size-classes

TABLE 1. Pooled distribution of fly wing lengths from seven experiments which estimate the sexual selection differential.

Group	Median wing length (mm)					*N*	Mean	SD
	1.7	1.79	1.87	1.95	2.05			
All males	47	61	85	97	98	388	1.902	0.115
Mating males	10	25	32	62	114	243	1.960	0.103

TABLE 3. ANOVA on male wing length in the "choice-random" mating experiments.

Source	Sum of squares	*d.f.*	Mean square	*F*
Main effects	60.190	3	20.063	82.52***
Treatment	2.143	1	2.143	8.815**
Replicate	55.274	1	55.274	227.348***
Day	1.104	1	1.104	4.540*
Interactions	0.371	4	0.093	0.382
Treatment × Replicate	0.040	1	0.040	0.164
Treatment × Day	0.163	1	0.163	0.672
Replicate × Day	0.001	1	0.001	0.000
Treatment × Replicate × Day	0.185	1	0.185	0.762
Error	53.973	222	0.243	

* $0.01 < P < 0.05$; ** $P < 0.001$.

pooled across seven experiments in which the mean wing lengths were not significantly different. In the other two experiments mean wing lengths were shorter because the flies emerged from older stock bottles and therefore experienced higher larval densities and greater larval competition. More mating males than total males in the largest size-class indicated that these individuals mated more than once. The mean i for the nine experiments in Figure 2 was 0.478 (SD = 0.133).

Male and female flies eclosing 10 days after laying in selection response replicate IIR (Table 2) were used to estimate heritability under the larval density conditions for that experiment. Since single-sex regressions showed no evidence of a maternal effect, midparent-midoffspring regression was performed (Falconer, 1981 p. 152). This regression estimated $h^2 = 0.62$ (SE = 0.12).

Viability Selection Response

Progeny of female flies which were allowed to mate in chambers containing 80 males had significantly longer wings than progeny of randomly paired females (Table 3). Replicate number and eclosion day also significantly affected male wing length but none of the interactions were signficant (Table 3). The difference between replicates was due to higher fecundity by the females in replicate II. The higher larval density in that replicate resulted in smaller eclosing flies (Table 2). Examination of the mean wing lengths for each treatment in the two replicates (Table 2) reveals a mean standardized selection response, over replicates and eclosion days, of 0.308 (SD = 0.165). This estimate could be biased if there was differential fecundity between treatments. Female fecundity did not directly bias the estimate of R_v because four males were measured from each vial on each day. Fecundity could have affected this measurement indirectly, however, if the females in the two treatments differed in body size, since fecundity correlates with female thorax length (Robertson, 1957) and thorax length decreases with density (Atkinson, 1979). However, there was no significant difference in wing length ($P = 0.35$, t test) between females in the two treatments for the replicate in which parental wing lengths were measured. Furthermore, there was no significant difference between treatments in the number of eclosing progeny emerging from vials in either replicate I or II ($P = 0.53$ and $P = 0.29$, respectively, Mann-Whitney test).

TABLE 4. Sums of ranked time each of 85 females spent orienting towards males of a given wing length in 5 min. A assumes females orient randomly to all four males, B assumes females orient randomly to those males with wings.

Male wing length	Sum of ranks	Expected sum of ranks	
		A	B
>1 SD	197	212.5	198.5
±1 SD	202.5	212.5	198.5
<1 SD	196	212.5	198.5
0	254.5	212.5	
		$G = 10.76$*	0.12

* $P < 0.01$.

Female Choice Experiment

A goodness-of-fit G test (Sokal and Rohlf, 1981 p. 705) shows (Table 4) that the 85

females do not move randomly in front of the four males in the display chamber (Fig. 1) during the 5-min observation periods. If females showed no preference between any of the four males, then the expected sum of ranks for each male class would be equal. Examination of Table 4 shows that females are clearly spending more time in front of displaying males with wings. If females moved independently of male wing length, then the expected sum of ranks should be the same for each of the three males with wings. A goodness-of-fit G test does not reject this null hypothesis (Table 4). The conclusion from these orientation experiments is that although females approach displaying males with wings, they display no preference for males with longer than average wings.

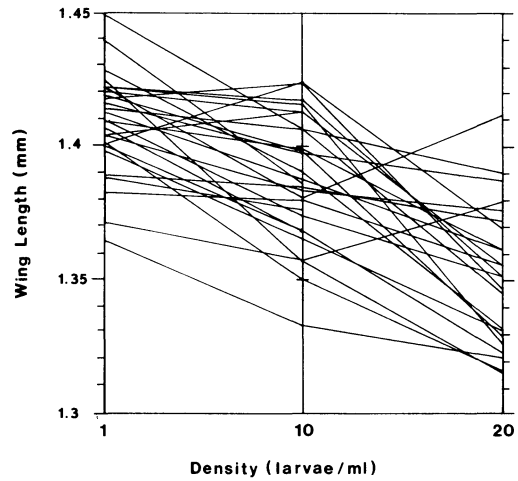

FIG. 3. Mean wing length for full sibs in each of 44 families plotted against larval density. Sibship means are connected by lines. Nonparallel lines indicate genotype-by-density interaction.

Genotype-by-Density Interaction

Nonparallel changes in family mean wing lengths at each of the three densities (Fig. 3) suggest that some genotype-by-environment interaction may have occurred in this experiment. Table 5 presents the results for the repeated measures analysis of variance using data from densities A and B, and Table 6 presents the analysis of variance results using all three densities. Both analyses show that sex explained more variation in wing length than any other factor, but the other factor, family, and the repeated measure, density, were still highly significant. The family-by-sex interaction term was not significant in either model, and the family-by-density interaction was highly significant in both analyses as Figure 3 suggests. Including the high-density treatment reveals, in addition, significant interactions between sex and density, and between family, sex, and density which were not significant when only the two lower densities were analyzed.

The variation in wing length among family means of males changed little across densities. At density A, SD = 0.0283 ($\bar{x}$ = 1.308, N = 43), at density B, SD = 0.0225 ($\bar{x}$ = 1.296, N = 43), and at density C, SD = 0.0233 ($\bar{x}$ = 1.262, N = 33). These three

TABLE 5. Repeated measures ANOVA for genotype-by-density interaction experiment using data from densities A and B.

Source	Sum of squares	*d.f.*	Mean square	*F*
Model	5.9499	171	0.0348	41.42*
Factors				
Family	0.5205	43	0.0121	14.17*
Sex	5.2124	1	5.2124	6,102.66*
Family × Sex	0.0503	41	0.0012	1.33
Within factor error	0.1794	210	0.0009	
Repeated measures				
Density	0.0381	1	0.0381	46.34*
Family × Density	0.0833	43	0.0019	2.35*
Sex × Density	0.0022	1	0.0022	2.66
Family × Sex × Density	0.0431	41	0.0011	1.28
Within measure error	0.1729	210	0.0008	

* $P < 0.001$.

TABLE 6. Repeated measures ANOVA for genotype-by-density interaction experiment using data from all three densities.

Source	Sum of squares	*d.f.*	Mean square	*F*
Model	6.9205	194	0.0357	45.77**
Factors				
Family	0.4965	32	0.0155	17.00**
Sex	5.7542	1	5.7542	6,304.91**
Family × Sex	0.0387	31	0.0013	1.37
Within factor error	0.1442	158	0.0009	
Repeated measures				
Density	0.3740	2	0.1870	263.94**
Family × Density	0.1694	64	0.0027	3.73**
Sex × Density	0.0050	2	0.0025	3.55*
Family × Sex × Density	0.0827	62	0.0013	1.88**
Within measure error	0.2239	316	0.0007	

* $0.01 < P < 0.05$; ** $P < 0.001$.

variances do not differ significantly across densities ($P = 0.37$, Friedman's test).

Rank correlations between sexes within each environment are consistently greater than zero (density A: $r_S = 0.383$, $N = 42$, $P = 0.006$; density B: $r_S = 0.610$, $N = 44$, $P < 0.001$; density C: $r_S = 0.398$, $N = 33$, $P = 0.011$) but do not differ significantly from those across densities ($X^2 = 2.31$, 2 *d.f.*, $P > 0.1$, Snedecor and Cochran, 1980 p. 187). Surprisingly, the mid-sib rank correlation between density A and B was significantly greater than zero ($r_S = 0.314$, $N = 42$, $P = 0.021$). The generally low value of all three correlations across densities (between densities A and C, $r_S = 0.213$, $N = 32$, $P = 0.12$, and between densities B and C, $r_S = 0.223$, $N = 33$, $P = 0.11$) reflects, however, the tendency for the mean value of a family in one density to be a poor predictor of the relative ranking of that family in another density.

DISCUSSION

These results provide support for an equilibrium model of sexual selection in which the intensity of sexual selection is opposed by viability selection. Assuming that all mating males have, on average, equal fecundity, the expected response due to sexual selection can be calculated from Equation (2). Substituting $h^2 = 0.62$ (SE = 0.12) and $i = 0.48/2 = 0.24$ (SD = 0.07) into Equation (2) yields the estimate, $R_s = 0.15$ (SE = 0.15). The standard error of this estimate was calculated using the expectation for the standard error of the product of two random variables with zero covariance (Kendall and Stuart, 1977 p. 247). This expected response is similar in magnitude and opposite in sign from the mean standardized selection response due to all episodes of selection acting prior to mating, $R_v = -0.31$ (SE = 0.08), calculated from Equation (1). The negative force of viability selection on wing size is due to the smaller wing size in the "random" treatment, which qualitatively supports the equilibrium assumption and indicates that flies which will have large wings as adults are more likely to experience mortality as eggs, larvae, or pupae.

Although the standard errors associated with these statistics indicate that they do not differ significantly, a more congruent result might appear if one other component of selection, adult longevity, is measured. Partridge and Farquar (1983) have demonstrated that large males survive longer and mate more times than small males. This selection episode, which could not operate under these experimental conditions, would further favor large males and therefore increase R_s. Further research is warranted to determine if that increase is sufficient to quantitatively validate the equilibrium model.

Evidence for Viability Selection on Body Size

Much evidence indicates that large adult flies are favored by natural selection. Partridge and Farquar (1983) have shown that

large males from a wild-type population of *D. melanogaster* have higher mating speeds, inseminate more females in the absence of competitors, and outcompete small males for copulations. Furthermore, large females are more fecund than small females (Robertson, 1957). These results suggest that natural selection does not act directly against large wing size in adult flies, but rather on some larval character which is correlated with wing or overall size (Roff, 1981). The imaginal discs which develop into the wings grow from the first through the third larval instar (Bryant and Simpson, 1984). Although the cue for pupation is not well understood, some evidence indicates that a predetermined number of cell divisions triggers pupation (Bryant and Simpson, 1984). Since no mutants have yet been discovered which increase the number of imaginal disc cell divisions (Bryant and Simpson, 1984) genetically large flies have to take longer to develop (Robertson, 1960). Consequently, they are exposed to contaminants in the media for longer periods of time. Botella et al. (1985) have shown recently that the larval metabolites, uric acid and urea, can decrease or even arrest larval growth. Genetically large flies may, therefore, suffer higher mortality in crowded larval environments. In support of this argument, flies which have been selected for large size for 20 generations produce fewer adults when in competition at high standardized densities with an outbred stock carrying the mutant *sparkling* than flies in unselected control lines (Partridge and Fowler, unpubl.).

The proposition that larval mortality increases with body size in conjunction with the results reported in this paper appears to contradict the well-known experiment by Partridge (1980) in which she showed that flies mated in a population cage produced larvae with higher competitive ability than flies mated at random. No obvious explanation exists for this difference; however, it should be noted that a recent attempt (Schaeffer et al., 1984) to replicate Partridge's experiment failed to reproduce her result. One explanation may be that the two experiments were carried out under different larval densities.

Female Choice or Male-Male Competition?

The results of the female orientation tests do not provide any evidence that females can discriminate between males with different sized wings. Although some workers claim to have documented female choice in *D. melanogaster* (see review by Spiess, 1982), most of these studies can be criticized either on experimental or statistical grounds. Usually, strains are used with genetic markers that may have pleiotropic effects on mating success, and females often are not permitted the opportunity to escape from courting males (Ewing, 1983). Furthermore, the most frequently cited experimental evidence: rare males experience increased mating success, can be generated by a number of non-frequency-dependent mechanisms including several forms of male-male competition (Partridge and Hill, 1984). The best evidence for female preference comes from a study by Heisler (1984) who recently demonstrated differential mating success by mutant *yellow* male *D. melanogaster* when mated in mass-mating chambers to two wild-type strains of females. Although her results implicate some role of female choice (such as a lack of preference for wild-type males in one strain), in no case did *yellow* males succeed in obtaining more mates than wild-type males. Thus, no evidence yet demonstrates female choice for natural variation in wing length or any other quantitatively varying character in *D. melanogaster.*

The estimated standardized selection differentials obtained from the experiments on males size-coded with colored powders provide indirect evidence that a very simple form of male-male competition could explain the intensity of sexual selection in this species. If mating success was determined by male tournaments in which the male with the longest wing in a group of N males obtained a copulation, then one would expect N to increase with the effective sex ratio. The expected i, given that N equals the sex ratio (commonly referred to as the first-order statistic, Janetos, 1980), is plotted in Figure 2. In these experiments a best-of-N mating rule is not found. Rather, at all effective sex ratios a best-of-2 ($i = 0.564$) rule is most consistent with the data.

A best-of-2 mate selection model is also compatible with direct observations of matings. Courtship in the cage was initiated when a male encountered a virgin female and began displaying. Usually, a nearby male would approach and also display. Invariably, the female would then run away with the courting males in pursuit. Although more than two males occasionally displayed to a female at rest, very rarely did more than two males pursue a departing female. Larger male *D. melanogaster* can pursue females more rapidly than smaller males (A. Ewing, pers. comm.). If the larger of two pursuing males succeeds in copulating with the departing female, then the standardized selection differential should equal the first-order statistic with $N = 2$ and be independent of the relative ratio of males to females as observed here. In support of this male competition interpretation, Dow and von Schilcher (1975) demonstrated that paired male *D. melanogaster* fight over females, and the winner almost always gains the copulation.

Effects of Larval Density on Response to Selection

The viability selection response experiments indicte that under the larval densities imposed during those experiments, sexual selection opposes viability selection. Further experiments are needed to determine if sexual selection would oppose viability selection under other larval densities. If viability selection did not exactly counterbalance sexual selection at some other larval density, then the proportion of additive genetic variation, in addition to the net selection differential, would determine how the mean wing length in the population would respond. Some indirect evidence suggests that the heritability may not change substantially at different larval densities. Since the phenotypic variance (V_p) at each density represented full sibships, V_p contains one-half additive genetic variation (V_a), one-quarter dominance variation (V_d), and environmental variation (V_e). Since V_p did not change with larval density, either V_a is also invariant or V_e is changing appropriately to compensate for changes in V_a to maintain a constant V_p. Accepting the first possibility as the more plausible one produces constant heritabilities. Consequently, the mean wing length of a nonequilibrium population should move directly toward the optimum at a rate determined by the net selection differential as long as the larval density remains constant. If the density changes between generations, then any prediction for the change in the mean at one density will depend on the genetic correlation between the expressions of the character at the two densities (Via and Lande, 1985).

Continued exposure to different larval densities, as occurs in most temperate regions (Tantawy, 1964; Atkinson, 1979), should lead to eventual attainment of the optimal mean wing length given stabilizing selection in each environment (Via and Lande, 1985). However, the rate and initial direction of the evolutionary trajectory depends on the genetic correlation between wing lengths expressed by flies reared at two larval densities. If the genetic correlation between characters expressed in two environments remains constant, then populations with high positive or negative genetic correlations can evolve away from their joint optima (Via and Lande, 1985). Very low genetic correlations allow the mean value of a character expressed in multiple environments to evolve independently in each environment (Via and Lande, 1985). Since most of the genetic correlations between densities measured in this study were not significantly greater than zero, this population should be evolving directly toward its optimal wing size for each of the densities used here if it is not already at equilibrium.

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