

## LACK OF NONADDITIVE GENETIC EFFECTS ON EARLY FECUNDITY IN *DROSOPHILA MELANOGASTER*

J. FERNÁNDEZ,<sup>1,2,3</sup> S. T. RODRÍGUEZ-RAMILO,<sup>1</sup> A. PÉREZ-FIGUEROA,<sup>1</sup> C. LÓPEZ-FANJUL,<sup>2,4</sup> AND  
A. CABALLERO<sup>1,5</sup>

<sup>1</sup>Departamento de Bioquímica, Genética e Inmunología, Facultad de Ciencias, Universidad de Vigo, 36200 Vigo, Spain

<sup>2</sup>Departamento de Genética, Facultad de Ciencias Biológicas, Universidad Complutense, 28040 Madrid, Spain

<sup>4</sup>E-mail: clfanjul@bio.ucm.es

<sup>5</sup>E-mail: armando@uvigo.es

**Abstract.**—Fecundity is usually considered as a trait closely connected to fitness and is expected to exhibit substantial nonadditive genetic variation and inbreeding depression. However, two independent experiments, using populations of different geographical origin, indicate that early fecundity in *Drosophila melanogaster* behaves as a typical additive trait of low heritability. The first experiment involved artificial selection in inbred and non-inbred lines, all of them started from a common base population previously maintained in the laboratory for about 35 generations. The realized heritability estimate was  $0.151 \pm 0.075$  and the inbreeding depression was very small and nonsignificant ( $0.09 \pm 0.09\%$  of the non-inbred mean per 1% increase in inbreeding coefficient). With inbreeding, the observed decrease in the within-line additive genetic variance and the corresponding increase of the between-line variance were very close to their expected values for pure additive gene action. This result is at odds with previous studies showing inbreeding depression and, therefore, directional dominance for the same trait and species. All experiments, however, used laboratory populations, and it is possible that the original genetic architecture of the trait in nature was subsequently altered by the joint action of random drift and adaptation to captivity. Thus, we carried out a second experiment, involving inbreeding without artificial selection in a population recently collected from the wild. In this case we obtained, again, a maximum-likelihood heritability estimate of  $0.210 \pm 0.027$  and very little nonsignificant inbreeding depression ( $0.06 \pm 0.12\%$ ). The results suggest that, for fitness-component traits, low levels of additive genetic variance are not necessarily associated with large inbreeding depression or high levels of nonadditive genetic variance.

**Key words.**—Artificial selection, dominance, genetic variance, heritability, inbreeding depression.

Received July 12, 2002. Accepted October 24, 2002.

Establishing the genetic properties of life-history traits has been the objective of a large number of studies, bearing on many evolutionary and conservation genetics issues. Compilations of empirical data (Mousseau and Roff 1987; Roff and Mousseau 1987; Crnokrak and Roff 1995) indicate that traits closely connected to fitness usually exhibit lower levels of additive genetic variance and higher levels of nonadditive genetic variance (both relative to the total phenotypic variance) than other traits more distantly related to fitness (typically morphological traits). Furthermore, life-history traits usually show higher levels of inbreeding depression, implying directional dominance, than morphological traits (DeRose and Roff 1999). These generalizations have been interpreted in light of theoretical mechanisms that are not mutually exclusive: (1) natural selection erodes the additive variance of life-history traits more effectively and, therefore, most of their genetic variance must be nonadditive (Fisher 1930; Robertson 1955); (2) life-history traits are composites of multiple morphological traits and, consequently, the residual variances of the former should be larger, as they are subjected to more numerous sources of environmental variation (Price and Schluter 1991); and (3) the majority of deleterious mutations segregating in natural populations are partially recessive (e.g., Charlesworth and Charlesworth 1999). The genetic architecture of life-history traits should be established empirically, however, because the above conclusions do not necessarily apply to particular cases.

We present the results of two independent experiments started from populations of different geographical origin, aimed at investigating the relative importance of the additive and nonadditive components of the genetic variance for a life-history trait, early fecundity, in *Drosophila melanogaster*. In both instances, a comparison between inbred and non-inbred lines was involved, allowing the estimation of: the additive genetic variance of the trait, the inbreeding depression, and the changes in the between- and the additive within-line components of variance due to inbreeding. In the first experiment a laboratory population was analyzed, the results indicating that early fecundity behaved as a typical additive trait of low heritability, in contrast to previous work showing substantial dominance and inbreeding depression for this trait. Nevertheless, all these studies have been carried out on populations maintained in the laboratory for a variable, usually long, period of time. Because the genetic changes that occur in captivity may alter the original genetic architecture of metric traits, inferences from laboratory to wild populations should be taken with caution. This prompted us to carry out a second experiment, using a population recently collected from the wild, but the results obtained were similar to those in the first experiment.

### MATERIALS AND METHODS

#### *Experiment 1*

**Base population, culture conditions, and trait scored.**—The Proaza population was started from 35 inseminated females collected in Asturias (northern Spain) and it was maintained thereafter in a population cage for two years (about 35 gen-

<sup>3</sup> Present address: Departamento de Mejora Genética Animal, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain; E-mail: jmj@inia.es.

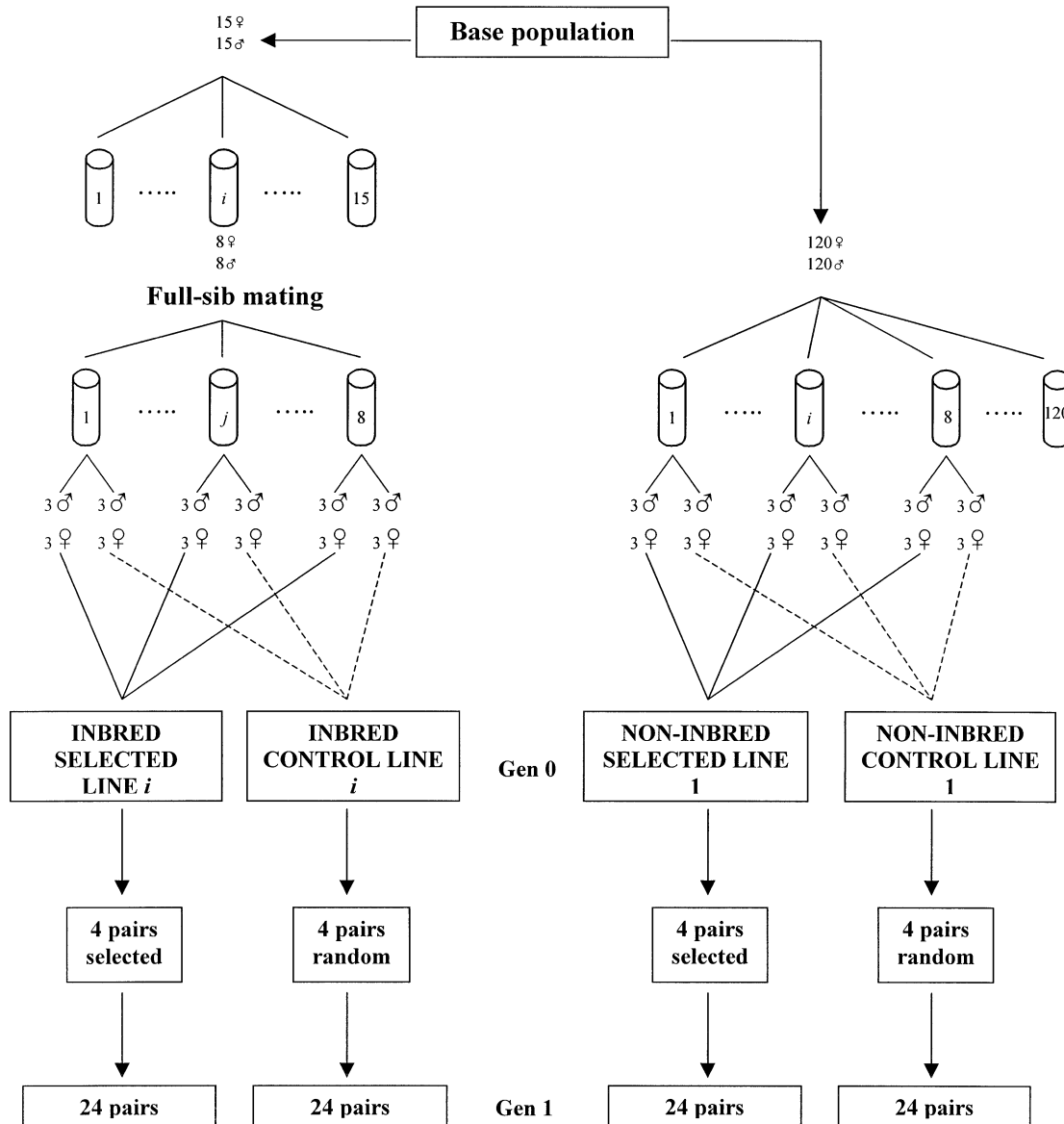


FIG. 1. Design of experiment 1 (see text for further explanation).

erations) before the start of this experiment. Flies were reared in a standard medium formula composed of 1 L water, 100 g brewer's yeast, 12 g agar, 100 g sucrose, 2.5 g NaCl, and 5 ml propionic acid. All cultures were incubated at  $25 \pm 1^\circ\text{C}$  and maintained under continuous lighting. Flies were handled at room temperature under ether anesthesia. The trait considered was early female fecundity. Because females take about six days to reach their maximum rate of egg production (McMillan et al. 1970), we evaluated that trait as follows: four-day-old virgin females were individually mated to males of the same age in glass vials (20-mm diameter, 100-mm height) with 10 ml medium added. After two days, both parents were transferred to a new vial with fresh medium to which food coloring was added to visualize the eggs. Oviposition was allowed for 24 h, after which the number of eggs laid was recorded. Untransformed data were used, and

matings with no eggs laid (3.2%) were excluded from the analysis.

*Inbred lines.*—The experimental design is shown schematically in Figure 1. A sample of 15 males and 15 virgin females was taken from the population cage (with assumed inbreeding coefficient  $F = 0$ ). These individuals were mated at random in pairs and each mating was kept in a separate vial. From the offspring of each mating, eight brother-sister matings were established and, from the corresponding inbred progeny ( $F = 0.25$ ), two lines were started, each formed by three males and three virgin female offspring per sib mating. These individuals were mated at random (24 pairs per line), and the fecundity of females was evaluated. In one of those lines one generation of upward selection was carried out, using as parents the four females laying more eggs (and their partners) of the 24 scored. The other line was used as a

control, and it was reproduced by four pairs of parents taken at random. In each line (control or selected), the fecundity of six female offspring per pair of parents was evaluated (24 females scored). In total, there were 15 inbred selected lines and 15 inbred control lines. In both sets of lines, full-sib mating (other than the initial) was always avoided, ensuring that the rate of inbreeding was negligible during the period considered (less than 0.01 per generation). Each selected line and its associated control line were scored within the same day to minimize environmental differences. In each generation, different selected and control lines were scored within the same week.

*Non-inbred lines.*—The experimental design is also shown in Figure 1. A sample of 120 males and 120 virgin females was taken from the population cage and mated at random in pairs in separate vials. From these, 15 groups of eight matings per group were randomly established. From each group, two lines were started, each formed by three male and three virgin female offspring per mating. These individuals were mated at random (24 pairs per line) and, thereafter, they were maintained following the same procedure as in the inbred lines. Full-sib mating was avoided in all instances. Thus, 15 non-inbred selected lines and their companion non-inbred controls were obtained and these were kept contemporary to the inbred lines (selected and control). One of the non-inbred selected lines was accidentally lost.

### Experiment 2

*Base population, culture conditions, and trait scored.*—A total of 306 inseminated females were collected in a wine cellar close to Vigo (northwestern Spain). The trait scored and the experimental conditions in which the flies were maintained were as in experiment 1, except that the medium had twice as much yeast and half the sugar content and CO<sub>2</sub> was used instead of ether for anesthesia. Previous to the start of the inbreeding experiment, flies were maintained by single-pair matings in vials for three generations (denoted with a minus sign; see Fig. 2) as follows. From those wild females producing at least two offspring of each sex (232 of 306), 120 were randomly taken as ancestors of the experimental lines (generation -3). These females were randomly divided into three groups of 40 to form the three replicates of the experiment. In each group (replicate), two male and two virgin female offspring were taken from each vial and mated in pairs following a circular scheme (see Fig. 2), to produce two lines of 40 matings each (inbred and non-inbred lines were eventually derived from these lines, see below). Thus, the three replicates of the experiment were derived from three different groups of 40 wild females each, whereas the two treatments for each replicate (inbred and non-inbred) were derived from the same set of 40 wild females. Each replicate line was subsequently maintained with circular mating for two additional generations before the start of the inbreeding experiment (generation 0). The circular scheme used guaranteed no inbreeding at generation 0 (see Fig. 3).

*Inbred lines.*—At generation 0, the 40 pairs of virgin individuals from each of the replicates were mated and the fecundity was evaluated. From these, 10 pairs were randomly chosen and kept in separate vials, each mating contributing

four male and four virgin female offspring. From each vial, three male and three female offspring were mated in pairs and the remaining male and female were mated to individuals from other randomly chosen vials. Therefore, three-quarters of the crosses were made between full-sibs and one-quarter of them were made between unrelated individuals, and the fecundity of these 40 matings was evaluated (generation 1). Note, however, that all females evaluated at generations 0 and 1 were non-inbred. The procedure followed between generations 0 and 1 was repeated in consecutive generations.

*Non-inbred lines.*—The procedure was the same as that for the inbred lines, except that all 40 matings were made at random but avoiding mating between full-sibs. The experiment was carried out for five generations and fecundity was scored simultaneously in all inbred and non-inbred lines and replicates within the same day. Pooling replicates and generations, the proportion of sterile matings (zero eggs laid) was 4.7% in the inbred lines and 2.4% in the non-inbred lines.

Genealogies were kept from the start of the experiment (generation -3), allowing the calculation of the expected inbreeding coefficient of every individual. The average inbreeding coefficient for each of the inbred and non-inbred replicate lines is shown in Figure 3. At generation 5, the inbreeding coefficient reached a mean value of 0.37 in the inbred lines and of 0.07 in the non-inbred lines. As stated above, inbreeding of evaluated females started at generation 2, thus all estimates from generations 0 and 1 refer to non-inbred individuals (average  $F = 0.005$ ).

*Analysis.*—Inbreeding depression was estimated as the regression of fecundity on inbreeding coefficient, correcting for environmental trends as indicated by Lynch and Walsh (1998). Basically, the method is a partial regression of the inbred lines' mean at generation  $t$ ,  $\bar{Z}_I(t)$ , on the non-inbred lines' mean,  $\bar{Z}_C(t)$ , and the mean inbreeding coefficient,  $F(t)$ :

$$\bar{Z}_I(t) = a + b\bar{Z}_C(t) + IF(t) + e(t), \quad (1)$$

where  $I$  is the estimated inbreeding depression corrected for environmental trends and  $e(t)$  is the deviation of the mean at generation  $t$  from the regression line. The means of the inbred lines corrected for environmental trends are obtained as

$$\bar{Z}_I^*(t) = \bar{Z}_I(t) - b[\bar{Z}_C(t) - \bar{Z}_C], \quad (2)$$

where  $\bar{Z}_C$  is the non-inbred mean over generations. Note that  $I$  can also be estimated as the regression of  $\bar{Z}_I^*(t)$  on  $F(t)$ .

A restricted maximum likelihood (REML) estimate of heritability for fecundity was obtained from the whole set of replicates, lines (or treatments), and generations, using the VCE program (Groeneveld and García-Cortés 1998). The model fitted was

$$y_{ijkl} = \mu + R_i + T_j + G_k + a_{ijkl} + e_{ijkl} \quad (3)$$

where  $y_{ijkl}$  is the fecundity measure of the  $l$ th female within a particular combination of fixed factors;  $\mu$  is the mean fecundity;  $R_i$ ,  $T_j$ , and  $G_k$  are the effects of replicate  $i$ , treatment (line)  $j$ , and generation  $k$ , respectively;  $a_{ijkl}$  is the genetic value of the female; and  $e_{ijkl}$  the residual (or environmental) effect. Estimates were also obtained for reduced models where some or all fixed effects (except the mean) were removed.

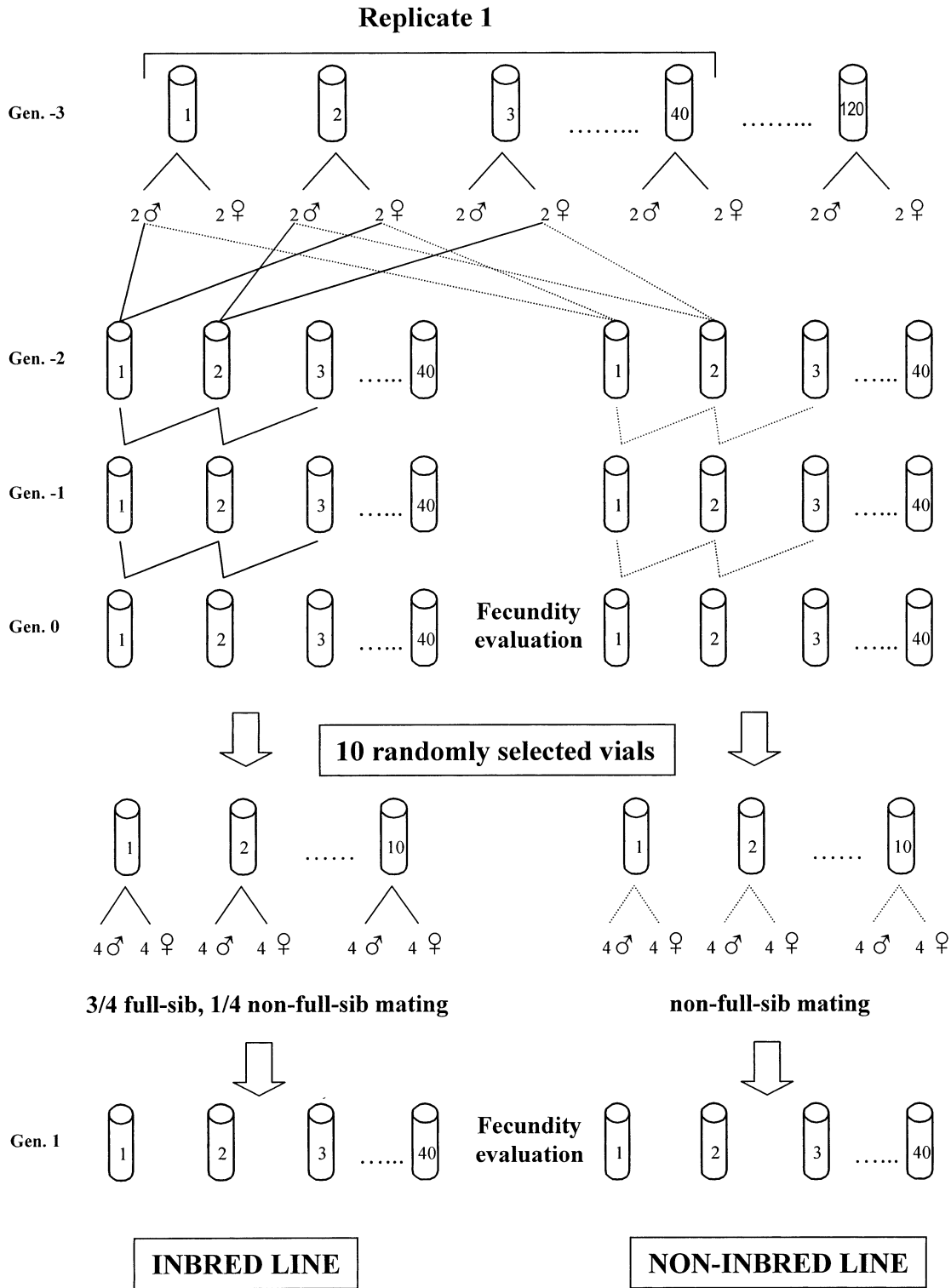


FIG. 2. Design of experiment 2 (see text for further explanation).

RESULTS

*Experiment 1*

The average fecundity and the within- and between-line phenotypic variance components are shown in Table 1 for

the non-inbred and inbred control lines. Both the mean and the within-line variance were higher at generation 1, which could be ascribed to an unidentified environmental trend. Over generations, however, no significant differences were detected between the values of these two parameters for the

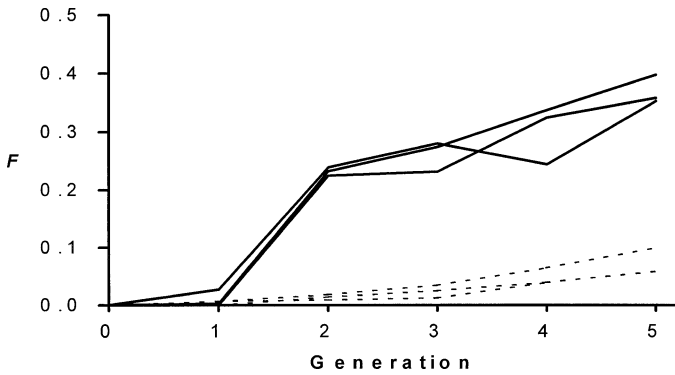


FIG. 3. Average inbreeding coefficient ( $F$ ) per generation for the non-inbred (broken) and inbred (continuous) lines in experiment 2.

inbred and non-inbred lines. A very slight, nonsignificant inbreeding depression of  $0.033 \pm 0.033$  eggs per 1% increase in inbreeding coefficient ( $0.09 \pm 0.09\%$  of the non-inbred mean) was observed. This result strongly suggests the absence of directional dominance for fecundity in the population considered. In parallel, the similarity of the average within-line phenotypic variance in inbred and non-inbred lines could be tentatively ascribed to a greater susceptibility of inbred flies to environmental heterogeneity being compensated for a reduction of the additive variance due to inbreeding (see below). The variance between inbred lines was higher than that for non-inbred lines in both generations. However, this comparison may be biased, as the value obtained for the inbred lines at generation 0 was, unexpectedly, much larger than the remaining estimates. Thus, we have also considered the between-line variances of the selected lines (Table 1). These values should be comparable to those corresponding to the control lines if the heritability of the selected trait is small (see below). In this case, estimates obtained in different generations were similar, and the average value of the variance between non-inbred selected lines was about three-quarters of that corresponding to the inbred selected lines, as expected from additive gene action.

Table 2 shows the averages over lines (inbred or non-inbred) for: (1) the response to one generation of upward selection ( $R$ ), expressed as deviation from the associated control; (2) the selection differential applied ( $S$ ), calculated as the difference between the average number of eggs laid by the selected females and that for all females scored; (3) the phenotypic variance at generation 0 ( $V_P$ ); (4) the realized heritability ( $R/S$ ); and (5) the additive variance ( $V_A$ ) obtained by multiplying the phenotypic variance by the realized her-

TABLE 2. Average parameters ( $\pm$  standard errors) for selected lines in experiment 1.  $R$ , response to selection;  $S$ , selection differential;  $V_P$ , phenotypic variance;  $V_A$ , additive genetic variance;  $h_r^2$ , realized heritability.

	Non-inbred lines	Inbred lines
$R$	$2.496 \pm 1.404$	$2.406 \pm 2.077$
$S$	$17.269 \pm 1.065$	$16.257 \pm 1.365$
$V_P$	$162.894 \pm 18.636$	$143.050 \pm 19.030$
$V_A$	$24.594 \pm 13.367$	$17.175 \pm 17.996$
$h_r^2$	$0.151 \pm 0.075^*$	$0.120 \pm 0.140$

\*  $P < 0.05$ .

itability. Figure 4 shows the additive variance estimates for each inbred or non-inbred selected line.

A negative response to upward selection was observed in some lines (five non-inbred and eight inbred selected lines), resulting in negative estimates of the corresponding realized heritabilities and additive variances. This should be mainly ascribed to random drift as, in lines of effective size eight selected with intensity 0.72 for a trait with heritability 0.12–0.15, the expected chance of success after one generation of artificial selection is about 70% (fig. 2 of Nicholas 1980). This implies that, on the average, four or five of the selected lines in each group (non-inbred or inbred) are expected to go backward. However, negative realized heritability estimates were not set equal to zero, as this procedure results in biased estimates of the average realized heritability of each group of lines (Toro and Pruñonosa 1984). The average realized heritability only departed significantly from zero ( $P < 0.05$ ) for the non-inbred lines and it was about 20% larger than that for the inbred lines. The average additive variance within inbred lines was 30% lower than that for non-inbred lines, in agreement with the expectation for additive gene action (25% lower). In parallel, an estimate of the variance among inbred lines, corrected for environmental causes of resemblance, can be obtained by subtracting the between-line variance for non-inbred selected lines from that for the inbred selected lines. This value ( $47.8 - 35.3 = 12.5$ ) was nearly equal to the corresponding additive expectation  $2FV_A = 2 \times 0.25 \times 24.594 = 12.3$ .

### Experiment 2

Figure 5 shows the mean fecundity for each of the replicates, plotted against generation number. The average fecundity of the inbred lines at generations 0 and 1 ( $57.76 \pm 3.11$ ) was slightly lower than that of the non-inbred lines ( $64.01 \pm 5.38$ ), although the difference was not significant.

TABLE 1. Phenotypic parameters for fecundity  $\pm$  standard errors for Experiment 1.

	Generation	Mean	Control lines		Selected lines
			Average within-line variance	Between-line variance	Between-line variance
Non-inbred	0	$33.51 \pm 1.32$	$155.40 \pm 16.20$	17.95	39.49
	1	$38.60 \pm 1.16$	$160.92 \pm 21.45$	12.08	31.11
	Average	$36.06 \pm 0.97$	$158.16 \pm 12.96$	15.02	35.30
Inbred	0	$33.46 \pm 2.17$	$145.70 \pm 17.61$	64.78	48.82
	1	$37.01 \pm 1.50$	$169.09 \pm 30.64$	26.78	46.78
	Average	$35.23 \pm 1.32$	$157.39 \pm 17.20$	45.78	47.80

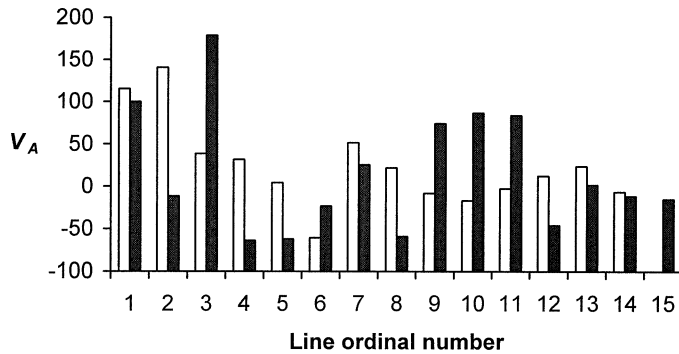


FIG. 4. Estimated additive genetic variance ( $V_A$ ) for each of the non-inbred (white) and inbred (black) selected lines in experiment 1.

The reason for this discrepancy should be chance, as the two types of lines were extracted from the same group of wild females in each replicate. Nevertheless, mean fecundity was very similar for inbred and non-inbred lines throughout the experiment. Note that the mean fecundity in experiment 2 was about twice that of experiment 1, probably because the culture media used in each experiment were different, that of experiment 2 being much richer in yeast.

The estimated inbreeding depression, averaged over the three replicates and corrected for environmental changes, was very small,  $0.036 \pm 0.075$  eggs per 1% increase in inbreeding, or  $0.060\% \pm 0.123$  of the average fecundity of non-inbred females at generations 0 and 1. These figures are in good agreement with those obtained in experiment 1 (0.033 and 0.090%, respectively).

The REML estimate of heritability for fecundity, using the complete model, was  $0.210 \pm 0.027$ , in good agreement with the estimates of experiment 1 (Table 2). Estimates for reduced models were very similar, giving estimates of heritability higher but not significantly different from the above one. The largest estimate ( $0.248 \pm 0.029$ ) was obtained when the only fixed factor included in the model was the mean.

#### DISCUSSION

Early fecundity is usually considered to be a major determinant of female fitness, which can be negatively correlated with a number of other life-history traits. Of these, the negative correlation between early fecundity and survival is particularly well documented (Sgrò and Partridge 2000). Culture conditions (age, crowding, temperature) have been shown to affect both fecundity (Huey et al. 1995) and the trade-offs between this and other traits (Gasser et al. 2000). Thus, the following discussion will be restricted to early female fecundity, defined as the daily number of eggs laid by a single 5- to 10-day-old inseminated female at 25°C.

The heritability of early fecundity has commonly been found to be low. Estimates ranging from 0.02 to 0.18 (generally not significantly different from zero) have been obtained for populations of widely different geographical origins: Australia (Sgrò and Hoffmann 1998), Egypt (Tantawy and El-Helw 1970), Scotland (Robertson 1957), Serbia (Tucic et al. 1988) and the United States (Reeve and Fairbairn 1999). Thus, the estimates obtained in our study (0.15–0.21) are in agreement with previous values. Exceptionally, a somewhat

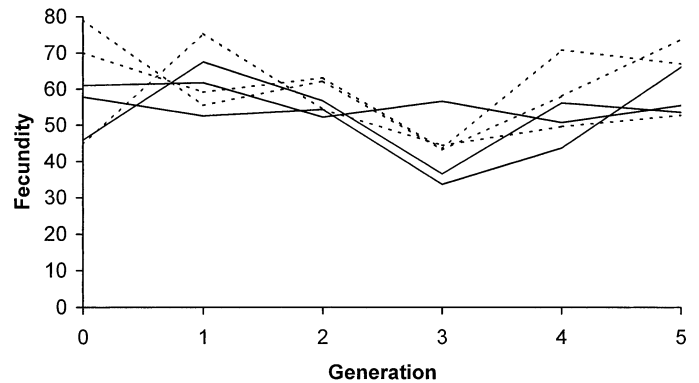


FIG. 5. Average fecundity per generation for the non-inbred (broken) and inbred (continuous) lines in experiment 2.

larger heritability (about 0.30), together with a nonsignificant dominance variance component, have been estimated for a U.S. population (Rose and Charlesworth 1981; Rose 1984).

A previous experiment following a similar design as that of experiment 1 but using a different base population showed substantial inbreeding depression (0.82%) for egg-to-pupa viability and a fivefold significant increase of the additive variance with inbreeding (López-Fanjul and Villaverde 1989). These results were later confirmed in a second experiment with other base population (García et al. 1994) and are in agreement with the hypothesis that egg-to-pupa viability is a trait closely related to fitness, with genetic variance essentially caused by segregation of rare deleterious recessives. Experiment 1 was carried out expecting that the behavior of early fecundity would be similar to that observed for egg-to-adult viability. However, we found a small, non-significant inbreeding depression (0.09%), suggesting little or no directional dominance of the genes involved. Furthermore, at  $F = 0.25$ , the observed between-line and additive within-line variances agreed closely with their pertinent additive expectations. Because experiment 1 was based on a captive population, we carried out experiment 2 using recently caught flies. In this case, the observed inbreeding depression for early fecundity was 0.06%, in agreement with the results obtained in experiment 1. The inbreeding depression for egg-to-adult viability obtained in experiment 2 was about 1% (unpubl. data), also in agreement with previous estimates.

Our results contrast with others obtained in previous fecundity studies reporting inbreeding depression or heterosis in crosses among inbred lines. Ehiobu et al. (1989) found a substantial inbreeding depression for early fecundity (about 1%) using full-sib and other types of inbred lines (all with an expected  $F = 0.25$ ), and Santiago et al. (1989) detected heterosis for early fecundity of the order of 34%, after crossing inbred lines derived from a wild population. Other estimates of heterosis (Robertson and Reeve 1955; Ehiobu et al. 1990) or of the nonadditive component of the genetic variance (Robertson 1957) can hardly be general, as they were based on a small number of inbred lines derived from populations descended from one or two impregnated wild females. Heterosis for female fecundity has also been reported in other experiments (e.g., Fry et al. 1998, and references

therein). However, either the trait studied was a composite trait including other fitness components (e.g., hatch rate of eggs) in addition to early egg-laying or crosses were made between inbred lines from different wild populations. Therefore, these results do not have a bearing on the present ones and will not be discussed.

For fecundity mutations accumulated on the second chromosome, a nonsignificant estimate of inbreeding depression was obtained by Houle et al. (1997), although the estimated coefficient of dominance for fecundity mutations appeared to be more recessive than those for other fitness components. On the other hand, genomewide mutational heterozygous effects on fecundity detected by Fernández and López-Fanjul (1996) were of variable sign, but the degree of directional dominance could not be established.

The fact that some populations exhibit substantial inbreeding depression for early fecundity, while others do not show it at all, is an intriguing issue; it is generally expected that traits tightly connected to fitness should present directional dominance (for a review see DeRose and Roff 1999). In the interpretation of the between-population differences in inbreeding depression or heterosis, a factor that must be taken into account is the previous history of the populations studied. Many of those populations have not been recently caught from the wild, but have been maintained in the laboratory for some period of time (sometimes years). This is, for example, the case of the population in our experiment 1, and that of Ehiobu et al. (1989), which was maintained for a year in the laboratory before the start of the assays. The same consideration applies to the inbred lines crossed by Santiago et al. (1989), which were started from individually captured females, maintained by full-sib mating for 60 generations, and subsequently kept in bottles for an unrecorded time before the crosses were made (A. Domínguez, pers. comm.). It is possible that there are real differences in the inbreeding depression of early fecundity between wild populations but, unfortunately, the scarcity of pertinent data does not allow to substantiate this hypothesis. In parallel, it is highly likely that the genetic architecture of life-history traits in wild populations will considerably change after a period in the laboratory. However, the joint action of random drift and adaptation to captivity may produce variable outcomes, depending on particular circumstances. On the one hand, the likely bottlenecks suffered by laboratory populations may purge deleterious recessive genes (e.g., Wang et al. 1999). If this is the case, the inbreeding depression observed in populations kept in the laboratory would be an overestimation of that in the wild. On the other hand, deleterious recessive alleles segregating at low frequencies in nature may become more common under benign laboratory conditions, as a consequence of adaptation to captivity. This would result in underestimates of the inbreeding depression. In addition, there may be a large variation in inbreeding depression among small populations subjected to bottlenecks (Fowler and Whitlock 1999). These issues notwithstanding, the population used in our experiment 2 was a recently caught population and, therefore, the original genetic architecture of fecundity in nature is unlikely to have been distorted by subsequent random fluctuations in allele frequency or adaptation to laboratory conditions.

Summarizing, for early fecundity, a low heritability and no inbreeding depression were detected in the only recently collected population so far studied in this context (experiment 2). This suggests that the genetic architecture of this trait may differ from that of other fitness-component traits (e.g., viability); that is, low levels of additive variance do not necessarily need to be associated to large inbreeding depression or high levels of nonadditive genetic variance. However, contrasting results were obtained in laboratory populations, ranging from pure additivity (experiment 1) to considerable dominance, expressed as inbreeding depression or heterosis (experiments by Ehiobu et al. 1989; Santiago et al. 1989). Thus, the genetic properties of early fecundity varied considerably among those populations, depending on their previous laboratory history. This implies that the study of the genetic architecture of life-history traits in nature should be made from recently collected populations, rather than from those populations that have been maintained for a long time in laboratory conditions, as these may have induced critical genetic changes.

#### ACKNOWLEDGMENTS

We thank M. A. Toro for useful comments on the manuscript. This work was supported by grants PB98-0814-C03-01 (Ministerio de Educación y Cultura), 64102C124 (Universidade de Vigo), PGIDT01PX130104PN (Secretaría Xeral de Investigación e Desenvolvemento, Xunta de Galicia), and BOS2000-0896 (Plan Nacional de I + D + I, Ministerio de Ciencia y Tecnología). JF was supported by a Programa Ramón y Cajal contract.

#### LITERATURE CITED

- Charlesworth, B., and D. Charlesworth. 1999. The genetic basis of inbreeding depression. *Genet. Res.* 74:329–340.
- Crnokrak, P., and D. A. Roff. 1995. Dominance variance: associations with selection and fitness. *Heredity* 75:530–540.
- DeRose, M. A., and D. A. Roff. 1999. A comparison of inbreeding depression in life-history and morphological traits in animals. *Evolution* 53:1288–1292.
- Ehiobu, N. G., M. E. Goddard, and J. F. Taylor. 1989. Effect of rate of inbreeding on inbreeding depression in *Drosophila melanogaster*. *Theor. Appl. Genet.* 77:123–127.
- . 1990. Prediction of heterosis in crosses between inbred lines of *Drosophila melanogaster*. *Theor. Appl. Genet.* 80:321–325.
- Fernández, J., and C. López-Fanjul. 1996. Spontaneous mutational variances and covariances for fitness-related traits in *Drosophila melanogaster*. *Genetics* 143:829–837.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford, U.K.
- Fowler, K., and M. C. Whitlock. 1999. The variance in inbreeding depression and the recovery of fitness in bottlenecked populations. *Proc. R. Soc. Lond. B* 266:2061–2066.
- Fry, J. D., S. L. Heinsohn, and T. F. C. Mackay. 1998. Heterosis for viability, fecundity, and male fertility in *Drosophila melanogaster*: a comparison of mutational and standing variation. *Genetics* 148:1171–1188.
- García, N., C. López-Fanjul, and A. García-Dorado. 1994. The genetics of viability in *Drosophila melanogaster*: effects of inbreeding and artificial selection. *Evolution* 48:1277–1285.
- Gasser, M., M. Kaiser, D. Berrigan, and S. C. Stearns. 2000. Life-history correlates of evolution under high and low adult mortality. *Evolution* 54:1260–1272.
- Groeneveld, E., and A. García-Cortés. 1998. VCE4.0: a (co)-variance component package for frequentists and Bayesians.

- Proceedings of the 6th World Congress on Genetics Applied to Livestock Production 27:455–456.
- Houle, D., K. A. Hughes, S. Assimakopoulos, and B. Charlesworth. 1997. The effects of spontaneous mutation on quantitative traits. II. Dominance of mutations with effects on life-history traits. *Genet. Res.* 70:27–34.
- Huey, R. B., T. Wakefield, W. D. Crill, and G. W. Gilchrist. 1995. Within- and between-generation effects of temperature on early fecundity of *Drosophila melanogaster*. *Heredity* 74:216–223.
- López-Fanjul, C., and A. Villaverde. 1989. Inbreeding increases genetic variance for viability in *Drosophila melanogaster*. *Evolution* 43:1800–1804.
- Lynch, M., and B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sinauer, Sunderland, MA.
- McMillan, I., M. Fitz-Earle, and D. S. Robson. 1970. Quantitative genetics of fertility. II. Lifetime egg production of *Drosophila melanogaster*: experimental. *Genetics* 65:355–369.
- Mousseau, T. A., and D. A. Roff. 1987. Natural selection and the heritability of fitness components. *Heredity* 59:181–197.
- Nicholas, F. W. 1980. Size of populations required for artificial selection. *Genet. Res.* 35:85–105.
- Price, T., and D. Schluter. 1991. On the low heritability of life-history traits. *Evolution* 45:853–861.
- Reeve, J. P., and D. J. Fairbairn. 1999. Change in sexual size dimorphism as a correlated response to selection on fecundity. *Heredity* 83:697–706.
- Robertson, A. 1955. Selection in animals: synthesis. *Cold Spring Harbor Symp. Quant. Biol.* 20:225–229.
- Robertson, F. W. 1957. Studies in quantitative inheritance. XI. Genetic and environmental correlation between body size and egg production in *Drosophila melanogaster*. *J. Genet.* 55:428–443.
- Robertson, F. W., and E. C. R. Reeve. 1955. Studies in quantitative inheritance. VIII. Further analysis of heterosis in crosses between inbred lines of *Drosophila melanogaster*. *J. Anim. Breed. Genet.* 86:439–458.
- Roff, D. A., and T. A. Mousseau. 1987. Quantitative genetics and fitness: lessons from *Drosophila*. *Heredity* 58:103–118.
- Rose, M. R. 1984. Artificial selection on a fitness-component in *Drosophila melanogaster*. *Evolution* 38:516–526.
- Rose, M. R., and B. Charlesworth. 1981. Genetics of life-history in *Drosophila melanogaster*. I. Sib analysis of adult females. *Genetics* 97:173–186.
- Santiago, E., A. Domínguez, J. Albornoz, R. Piñeiro, and J. L. Izquierdo. 1989. Environmental sensitivity and heterosis for egg laying in *Drosophila melanogaster*. *Theor. Appl. Genet.* 78:243–248.
- Sgrò, C. M., and A. A. Hoffmann. 1998. Heritable variation for fecundity in field-collected *Drosophila melanogaster* and their offspring reared under different environmental temperatures. *Evolution* 52:134–143.
- Sgrò, C. M., and L. Partridge. 2000. Evolutionary responses of the life history of wild-caught *Drosophila melanogaster* to two standard methods of laboratory culture. *Am. Nat.* 156:341–353.
- Tantawy, A. O., and M. R. El-Helw. 1970. Studies on natural populations of *Drosophila*. IX. Some fitness components and their heritabilities in natural and mutant populations of *Drosophila melanogaster*. *Genetics* 64:79–91.
- Toro, M. A., and J. V. Pruñonosa. 1984. The use of prior information in the estimation of heritability by parent-offspring regression. *Genet. Sel. Evol.* 16:177–184.
- Tucic, N., D. Cvetkovic, and D. Milanovic. 1988. The genetic variation and covariation among fitness components in *Drosophila melanogaster* females and males. *Heredity* 60:55–60.
- Wang, J., W. G. Hill, D. Charlesworth, and B. Charlesworth. 1999. Dynamics of inbreeding depression due to deleterious mutations in small populations: mutation parameters and inbreeding rate. *Genet. Res.* 74:165–178.

Corresponding Editor: M. Whitlock