CHANGES IN GENETIC PARAMETERS FOR FITNESS-RELATED TRAITS IN A CAPTIVE POPULATION OF *DROSOPHILA MELANOGASTER*

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INTRODUCTION

The genetic architecture of fitness-related traits in *Drosophila* is usually studied using populations that have been maintained in the laboratory for some period of time, sometimes years (*e.g.*, Ehiobu *et al.* 1989; Santiago *et al.* 1989; García *et al*. 1994). A population in captivity may suffer from the joint action of random drift and adaptation to captivity, with variable outcomes, depending on particular circumstances. For example, frequent bottlenecks occurring in the laboratory may induce a purge of deleterious recessive genes (see, *e.g.*, Wang *et al.* 1999). In contrast, deleterious recessive alleles may become more common under benign laboratory conditions, as a consequence of adaptation to captivity (Hoffmann *et al*. 2001; Woodworth *et al*. 2002). It is therefore possible that the genetic constitution of a captive population substantially differs from the wild population of origin. We compared estimates of genetic parameters for fitness-related traits (additive genetic variance and inbreeding depression) obtained from a recently captured population (Rodríguez-Ramilo *et al*. 2004) with those obtained from the same population after two years of captivity in laboratory conditions.

MATERIAL AND METHODS

Base population, culture conditions and traits scored. Three hundred pregnant females were captured in a wine cellar in Vigo (Spain) at the end of 2000. These females were put individually into glass vials with 10 ml medium added, and one male and one female progeny were collected from each vial. For the next two generations matings were made following a circular mating scheme that avoided matings between relatives, with one male and one female offspring contributed by each couple. After these two generations an experiment of inbreeding and artificial selection for five generations was carried out (described below; see Figure 1). Flies were reared in the standard medium formula of our laboratory (brewer's yeast-agar-sucrose) and handled at room temperature under CO_2 anaesthesia. All cultures were incubated at 25 ± 1^{o}C and maintained under continuous lighting. The trait under artificial selection was egg-to-adult viability, which was evaluated as follows. Four-day-old virgin females were individually mated to males of the same age in vials. After two days, both parents were transferred to a new vial with fresh medium to which food colouring was added. Oviposition was allowed for 24 hours. Thirty eggs were transferred to a fresh vial and allowed to develop into adults. The egg-to-adult viability was the proportion of adults emerged from the 30 eggs laid. Fecundity was also measured as the total number of eggs laid by each female.

Progeny from the wild females not used at the start the experiment were employed to set up a single large population that was maintained in captivity for about two years (30 generations; Figure 1). This population was maintained with a dozen of numbered bottles with about 50 males and 50 females each. Bottles´ contributions to each generation followed a circular scheme in order to keep the population with a large effective size. Every generation, each bottle was constituted by about 50 individuals from the bottle of the previous generation with the same code and 50 from the bottle with the following code. After this period of captivity, an experiment identical to the previous one was performed, except that artificial selection for viability was only carried out for two generations. The results of the initial experiment were

presented previously (Fernández *et al.* 2003; Rodríguez-Ramilo *et al.* 2004). Here we present the results of the latter experiment comparing them with the previous one.

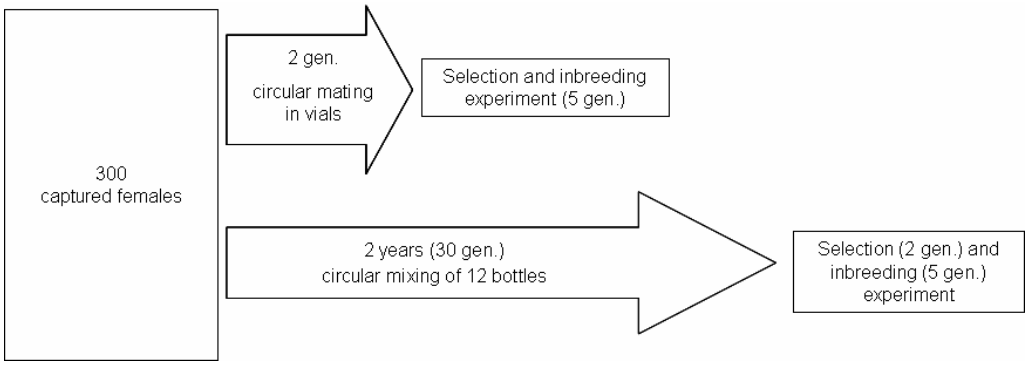

Figure 1. Experimental scheme

Selection and inbreeding procedure. A series of treatments were carried out in both experiments: SN (Selected non-inbred) - 40 males and 40 females were mated at random in vials avoiding full-sib matings, the viability of their offspring was evaluated and the 25% families with the largest viability (4 males and 4 females of each of the top 10 vials) were selected as parents for the next generation; CN (Control non-inbred) - As SN, except that selection of parents was at random; SI (Selected inbred) - As SN except that 75% of matings (30 out of 40) were between full sibs; and CI (Control inbred) - As SI except that selection of parents was at random. Each treatment was carried out for five generations (only two generations for selected lines in the experiment carried out after captivity) and replicated three times. The response to upward artificial selection was calculated for each replicated selected line (SN and SI) as the regression of the mean values of the selected lines, deviated from the corresponding control mean values (CN and CI), over generations. Under the assumption that the trait is fully dependent on the mother genotype, realised heritabilities were estimated from the regression of the selection response on the cumulative selection differential. Additive variances were estimated by multiplying the phenotypic variance by the realised heritability. Inbreeding coefficients were obtained from the pedigree, which was recorded for the two selection and inbreeding experiments. Inbreeding depression was estimated by a partial regression of the mean of CI lines on the mean of CN lines and the mean inbreeding coefficient (Lynch and Walsh 1998).

RESULTS AND DISCUSSION

Table 1 shows the average estimates of selection response, realised heritability and additive genetic variance obtained from the experiment carried out with the wild population, and that after a period of two years in captivity in the laboratory. The responses to selection were very small in both experiments and non-significantly different from each other, though there was a slight tendency for a larger response after captivity. Such small responses to selection are compatible with the expectations assuming mutation-selection balance frequencies for deleterious viability alleles in the natural population (Rodríguez-Ramilo *et al.* 2004).

Table 1. Estimates of genetic parameters in both experiments[A]

Parameter	Treatment	Recently captured[B]	After captivity
R viability	SI	0.027 ± 0.006	0.035 ± 0.010
	SN	0.011 ± 0.006	0.025 ± 0.022
h_r^2 *viability*	SI	0.128 ± 0.028	0.172 ± 0.038
	SN	0.064 ± 0.071	0.130 ± 0.102
V_A *viability*	SI	0.004 ± 0.001	0.006 ± 0.001
	SN	0.003 ± 0.002	0.004 ± 0.003
ID viability	CI	0.702 ± 0.110	–0.006 ± 0.102
ID fecundity	CI	0.060 ± 0.123	1.033 ± 0.425

[A]Mean (± s.e.) estimates of selection response (R), realised heritability (h_r^2), and additive genetic variance (V_A) for egg-to-adult viability across three replicates in the selected inbred (SI) and selected non-inbred (SN) treatments. Estimates of inbreeding depression (ID) per 1% increase in inbreeding in the control inbred (CI) lines, expressed as a deviation from the corresponding initial means. [B]Data from Rodríguez-Ramilo *et al*. (2004) and Fernández *et al.* (2003).

Table 1 also shows the estimated inbreeding depression rates for egg-to-adult viability and fecundity per 1% increase in inbreeding, expressed as a percentage of the corresponding initial means, and figure 2 shows the average means over replicates plotted against the average inbreeding coefficient. Average inbreeding coefficients at the fifth generation were 0.41 and 0.34 for the CI lines for the first and second experiment, respectively, assuming no inbreeding at the beginning of each of them. Whereas in the first experiment, the rate of inbreeding depression for viability (0.7%) was significant and of the same order of magnitude as in previous experiments (0.82%, López-Fanjul and Villaverde 1989; 0.54% García *et al.* 1994; 0.42-0.96%, Ehiobu *et al.* 1989), the rate obtained after captivity (–0.006%) was non-significant. In contrast, the rate of inbreeding depression for fecundity, that was non-significant in the first experiment (0.06%), became significant (1.03%) after captivity, in agreement with other estimates obtained from captive populations (*e.g.*, 1%, Ehiobu *et al.* 1989).

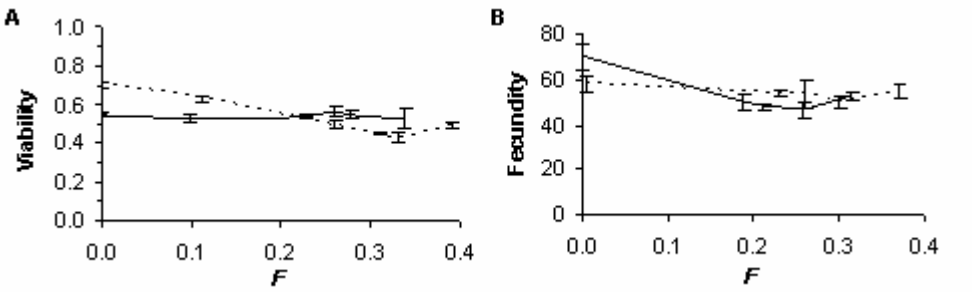

Figure 2. Average egg-to-adult viability (A) and average fecundity (B) of control inbred (CI) lines corrected for environmental effects, plotted against the average inbreeding coefficient. Continuous line: captive population; dotted line: recently captured population. Bars represent standard errors

CONCLUSION

The genetic architecture of fitness-related traits may change substantially in populations maintained for long periods of time in captivity. Although the estimates of additive genetic variance for viability obtained from response to artificial selection did not change substantially after the period of captivity, inbreeding depression for viability decreased significantly, and

that for fecundity increased significantly. The results suggest that inferences on genetic parameters from populations previously maintained in the laboratory should be taken with caution.

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