

INDEX SELECTION FOR A NON-ADDITIVE TRAIT: PRODUCTIVITY IN *DROSOPHILA MELANOGASTER*

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SUMMARY

A comparison of three family indices to increase productivity in *Drosophila* is reported. Seven generations of selection were carried out in each of two replicated lines. It was found that the simplest index, that based only on the dam performance, was the more efficient in both replicates. Possible explanations of this result are discussed: reduction of selection differentials, inbreeding depression, and the use of a wrong genetic model and/or wrong parameters.

INTRODUCTION

The recent popularity of selection nucleus, i.e. MOET schemes, has aroused great interest in the study of the response to selection in small populations. In parallel, there has been an emphasis in the use of family information, via indices or BLUP, to improve evaluation accuracy. However, the use of family indices in finite populations presents some undesirable features that are sometimes disregarded: 1) a greater increase in inbreeding is induced compared to mass selection; 2) standard deviations of indices in finite populations lower than expected. In addition, experimental evidence on the possible advantage of family indices over the individual phenotype is inconsistent and refers mainly to additive traits (Mc Bride & Robertson, 1963; Wilson, 1974; Campo & Tagarro, 1977; Avalos & Hill, 1981, among others). Another fact that has not been experimentally analysed is the effect of using a wrong model on the response attained.

Thus, it seems necessary, given the lack of a theory and the limitations of computer simulation, to check experimentally the effectiveness of index selection for non-additive traits. Here, we report a selection experiment comparing the relative efficiency of three family indices to increase productivity in *Drosophila melanogaster*.

MATERIAL AND METHODS

Three lines of *Drosophila melanogaster* were selected for productivity, measured as the number of pupae offspring developing from the first 3-day lay of single females. Each line was selected according to one of the following indices: 1) D, based simply on the productivity of the dam; 2) HD, which also included the dam's full sib and half sib records; and 3) HS, that added information on the sire's full sib and half sibs.

In this scheme each of the 10 males was mated to 6 females. Each full sib family consisted of 1 male and 3 females. The best 10 males and the best 60 females were selected.

Since some matings failed to reproduce and no attempt was made to replace them, a separate index was calculated for each family. The indices were computed using a heritability estimate of 0.30, which was obtained from ANOVA and regression analysis in the base population. Seven generations of selection were carried out, the experiment being replicated twice. In the 2-nd replicate,

a control line was also included. The mean pupae number in the base population was 70, with a standard deviation of 20.

At the end of the experiment, double hierarchical ANOVA and within sire regression were used to estimate h^2 in each generation. By combining the different variance components, three estimates can be obtained, as listed in Table 1. In the 2-nd replicate, realized h^2 's were computed from the regression of phenotypic means deviated from control on the selection differentials. Additionally, genetic parameters were also obtained in the control line by REML. The linear model fitted was:

$$y_{ijk} = \mu + g_i + l_{ij} + a_{ijk} + b F_{ijk} + \epsilon_{ijk} \quad (1)$$

where y_{ijk} is the productivity record; μ the overall mean; g_i is a fixed effect of the i -th generation; l_{ij} , a random effect of the j -th family; a_{ijk} , the breeding value of an individual; b , a linear regression coefficient on the inbreeding of the ijk -th animal, in order to account for inbreeding depression (Kennedy, 1989); and ϵ_{ijk} , the residual term. The family effect includes common environment effects, and possibly part of dominance and maternal effects.

This model was fitted to obtain BLUP of breeding values using the REML estimates. All lines in each replicate (including control) were derived from the same individuals and, thus, they were evaluated together to obtain more precise estimates. All genealogies were known and inbreeding was taken into account to construct the inverse of the additive relationship matrix.

RESULTS AND DISCUSSION

The evolution of the means for the two replicates is plotted in Figure 1. In the 2-nd replicate, realized heritabilities could only be calculated until generation 5, since the response was negative from that generation. They were 0.19 ± 0.03 , 0.01 ± 0.04 and 0.08 ± 0.02 for the D, HD and HS lines, respectively. In Figure 2, the results obtained from the BLUP of the breeding values are plotted. The following REML estimates were used: $h^2 = 0.04$ and "I2" (due to family effects) = 0.22. The genetic trend, estimated as the regression of mean breeding value on generation number, were: 0.93 ± 0.07 and 0.96 ± 0.13 (lines D), 0.35 ± 0.03 and -0.08 ± 0.05 (lines HD), and -0.06 ± 0.15 and -0.02 ± 0.15 (lines HS). The most interesting point, noticed in Figures 1 and 2, is that the base index (D) is significantly better than both HD and HS indices in the last generations. There are several reasons that may explain this result.

1) Selection differentials being smaller than expected, due to the increased correlation among family members. In Table 2 the observed and expected standard deviations of the indices are shown. In agreement with the results of Toro *et al.* (1988), the loss in variance increases as amount of information included in the index increases. Nevertheless, the selection differential increased in absolute terms.

2) Inbreeding depression. The final inbreeding coefficient was 0.12, 0.17 and 0.20 for the D, HD and HS lines, respectively. The negative values obtained for the regression coefficients of performance on inbreeding coefficient (-3.3 and -4.3 per 10% increase in F , in replicates 1 and 2) evidence inbreeding depression. However, the regression coefficients obtained and the different final inbreeding in the three lines only account for approximately 15% of the phenotypic differences between the base index (D) and other indices.

3) Wrong genetic parameters. The heritabilities, averaged over generations and lines by the inverse of their variances, are shown in Table 1. It can be seen that the half sib estimate, which is the only one unbiased,

is much lower than the others, especially than the full sib estimate, which is greatly inflated. The REML estimate for the control was 0.04 for h^2 and 0.22 for "I2". Thus, our results show that the heritability of productivity was lower than the value used to construct the indices. They also indicate a large common environment and/or dominance. It should be kept in mind that, although the D index is independent of the heritability estimate, HD and HS indices are not. Nevertheless, Sales & Hill (1976) showed that indices are very robust to wide departures of estimate from real values and it is unlikely that this effect per se can explain the observed differences.

4) Wrong genetic model. In constructing the indices, it was implicitly assumed that the full sib intraclass correlation was $h^2/2$ and that there were neither common environment nor inbreeding effects. As can be seen from Table 1, this is unlikely to be true. Thus, HD and HS indices would not have been optimal strategies. It is also remarkable that correlations between BLUP and selection criteria, averaged over generations and replicates, were 0.41, 0.35 and 0.25 for D, HD and HS, respectively. This means that, if we admit that the model in (1) is more realistic than the simplest one: $y = \mu + g + a + \epsilon$ selecting via HS or HD will lead to choose worse animals than if we rely exclusively upon the individual phenotype.

In conclusion, our results emphasize that if sophisticated evaluations, either BLUP or indices, are to be used, a model that correctly describes the biological background needs to be chosen carefully, especially with complex (reproductive) traits. In practical programs, some restrictions should also be imposed in order to avoid inbreeding depression as much as possible.

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Table 1. Heritabilities (s.e.) averaged over lines and generations.

	Replicate:	1	2	Mean
Half sib correlation		0.04(0.04)	0.14(0.04)	0.09(0.03)
Wihing sire regression		0.42(0.02)	0.21(0.05)	0.30(0.03)
Full sib correlation		1.15(0.08)	1.07(0.08)	1.11(0.06)

Table 2. Expected and observed standard deviations of the index.

Index	Replicate: 1		Replicate: 2	
	Exp.	Obs.	Exp.	Obs.
D	3.41	3.40	4.23	4.08
HD	3.98	3.37	5.21	4.60
HS	5.18	4.00	7.06	5.11

Figure 1a. Phenotypic averages. Replicate 1

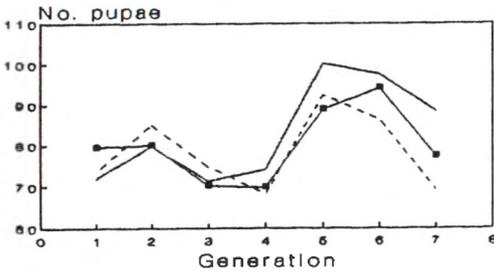


Figure 1b. Phenotypic averages deviated from control. Replicate 2

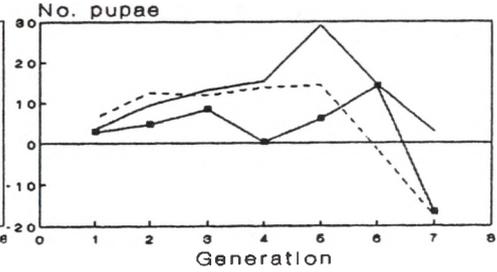


Figure 2a. BLUP averages. Replicate 1

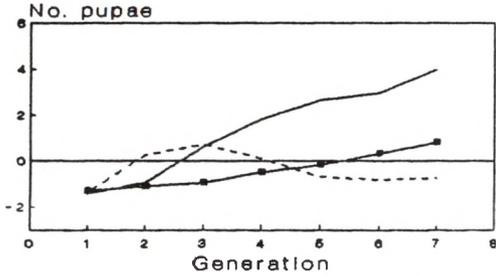
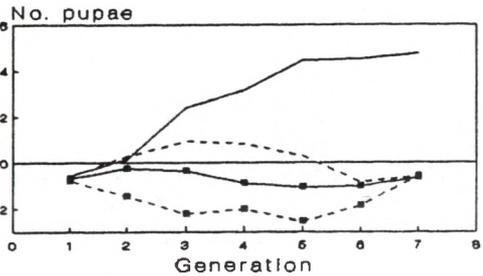


Figure 2b. BLUP averages. Replicate 2



— D —■— HD - - - HS - - - ■ - - - Control

