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Heritability of phototactic behavior in Drosophila.

Heritability is an estimate of the genetic component of the observed phenotypic variance and may be computed in a number of different ways. We chose the estimates of the realized heritability (h_r^2, Table 1) of 6 selection lines of D. melanogaster and D. simulans, the heritability from regression of offspring on mid-parent values ($h^2_{\bar{P}O_2}$, Table 2), and the heritability in the narrow and broad sense (h_n^2, h_b^2, Table 3) from a 4x4 diallel analysis with two selected photonegative and two unselected photopositive strains (Falconer, 1970; Mather and Jinks, 1971).

The base populations of all selection lines were established by reciprocally crossing a wild-type laboratory strain and a marker strain carrying the X-chromosomal markers vermilion and garnet, or white. These markers were fixed in the photonegative lines during the first 3 or at most 7 generations (Köhler, 1977). Estimating the realized heritabilities after 7 and 10 generations of selection, respectively, these varied between 3.5% and 21.7% in D. melanogaster and between 6.1% and 11.5% in D. simulans. After 22 and 30 generations of selection respectively the estimated values generally show a slight decrease. Above all this may depend on ceasing of the selection response and the artificial selection limit in a Hirsch-Hadler maze.

The heritabilities of phototactic behavior which result from the regression of offspring on mid-parent values (Table 2) are lying in the same range but their standard errors (SE) are very high so that there is no significant difference from zero.

Table 1. Realized heritabilities (h_r^2) of negative phototactic behavior estimated from 6 different selection lines in D. melanogaster (1-4) and D. simulans (5-6).

Strain	Marker	Fixed in gener.	h_r^2(%) ♂	h_r^2(%) ♀	Number of gen.	h_r^2(%) ♂	h_r^2(%) ♀	Number of gen.
1 K1NEG	v g	6	11.4 ***	21.7 ***	7	1.9 *	0.9 n.s.	22
2 K2NEG	v g	7	6.4 **	11.9 ***	7	4.3 ***	5.9 ***	22
3 N2	w	3	5.9 **	3.5 *	10	7.4 ***	5.1 ***	30
4 N3	w	3	3.7 n.s.	5.5 *	10	2.6 ***	2.8 ***	30
5 N24	w	3	10.9 ***	11.3 ***	10	6.0 ***	7.8 ***	30
6 N34	w	3	6.1 *	11.5 **	10	5.2 ***	7.9 ***	30

Significant deviation from zero (t-test) is indicated by asterisks for an acceptance probability of 5% (*), 1% (**), or 0.1% (***).

Table 2. Heritability of phototactic behavior estimated by the mid-parent - offspring regression method for 2 unselected wild-type strains of D. m.

	$h^2_{\bar{P}O}$(%)	SE
KOK	6.2	3.0
K2KON	3.2	4.5

All these values are in accordance with those summarized by Grossfield (in: Ashburner and Wright, 1978). He noted that the overall picture is "that heritabilities are low, decrease with the number of generations of selection and seem to be somewhat higher for maze studies than for open field designs". We would like to remark that it could in addition depend on the method of estimation because in our third design we got heritabilities much higher than those of Hadler, for example.

We used in our diallel analysis the selected lines 1 and 2 of Table 1 after about 90 generations of selection and 2 unselected photopositive laboratory strains. The various tests described in Mather and Jinks (1971) provided no reason to doubt the adequacy of the simple model and therefore the components of variation could be estimated.

Table 3. Components of variation and heritability of phototaxis in D. melanogaster estimated from a 4x4 diallel with 3 replicates in 6 different Hirsch-Hadler mazes with 4 light-dark choices. In the last row the pooled data were used (4x4 diallel with 18 replicates). Nomenclature according to Mather and Jinks (1971).

Maze	D	F	H1	H2	E	$\overline{uv}$	h^2_n	h^2_b	h^2_{CA}
KK1	2.50	-0.18	0.55	0.39	0.09	0.17	0.88	0.94	0.69
KK2	1.88	-0.11	0.46	0.32	0.08	0.17	0.87	0.94	0.68
KK3	1.46	-0.15	0.32	0.21	0.09	0.17	0.86	0.91	0.64
KK4	1.31	-0.46	0.18	0.13	0.13	0.17	0.85	0.88	0.53
KK5	1.50	-0.09	0.16	0.10	0.13	0.15	0.84	0.86	0.66
KK6	1.62	-0.23	0.76	0.52	0.09	0.17	0.83	0.94	0.55
Total	1.71	-0.21	0.39	0.27	0.10	0.17	0.86	0.91	0.63

h^2_n, h^2_b heritability in the narrow and broad sense, h^2_{CA} heritability of Crumpacker and Allard (computer program of Lee and Kalisikes, Univ. of Manitoba, Winnipeg)

It is clear cut that the additive component D compared with E (error) and H_1 and H_2 (dominance components) is extremely high. This leads to heritability estimates between 83% and 88% in the narrow sense and between 86% and 94% in the broad sense. There exist only slight differences between the estimates from the data in the 6 mazes so that these could be handled as one diallel with 18 replicates. The negative F values indicate that there are more recessive alleles present in the 4 lines than dominant alleles, irrespective of whether these have photopositive or photonegative effects. The average frequencies of the alleles for increasing or decreasing phototactic behavior are about 40% if we assume that they are equally distributed ($\overline{uv} > 0.16$).

These extremely high heritabilities of a behavioral trait are probably a result of using selected and control lines in a diallel cross and therefore these estimates are not valid to describe the heritability of phototactic behavior in a normal population. Similarly the estimates of Hadler (1964) were computed from differences in the variances of selected ("isogenic") lines and their control. Furthermore, there exists a scale effect in the Hirsch-Hadler mazes (variance depends on the mean in a binomial distribution). In summary, heritabilities of phototactic behavior in Drosophila are low in general and the higher estimates may depend on the computational method in connection with the strains used.

References: Ashburner, M. and T.R.F. Wright 1978, The Genetics and Biology of Drosophila, Academic Press, New York; Falconer, D.S. 1970, Quantitative Genetics, Ronald Press, New York; Hadler, N.M. 1964, Genetics 50:1269-1277; Köhler, W. 1977, Genetica 47:93-104; Mather, K. and J.L. Jinks 1971, Biometrical Genetics, Chapman and Hall, London.

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Oviposition preferences in D. melanogaster.

Mainardi (1968) has shown that the females of D. melanogaster (Oregon) are able to (1) distinguish between food sites "scented" by previous exposure to adult males of their strain and intact ones, and (2) prefer to lay eggs in the former ones.

Ayala and Ayala (1968) have repeated Mainardi's experiment. They found that the females are able to recognize the previous presence of males, but their females showed an egg-laying