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SHORT COMMUNICATION

Genetics of Phototactic Behavior in *Drosophila ananassae*, a Member of the *melanogaster* Species Group

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Using Hirsch-Hadler phototaxis mazes, selection for photopositive and photonegative behavior was carried out for 21 generations in Drosophila ananassae. *The chromosomes that are important in influencing photomaze behavior in* D. ananassae *are different from what has been observed for other members of the* melanogaster *species group, and the differences cannot be entirely attributed to the chromosome rearrangements which have occurred during the evolution of these related species.*

KEY WORDS: phototaxis maze; sex-linked behavior; *Drosophila;* chromosomal homologies; species differences.

INTRODUCTION

Hirsch-Hadler photomazes (Hadler, 1964) have been used in genetic investigations of phototactic behavior in several species of *Drosophila*. Results of selection experiments and reciprocal hybridizations largely support a polygenic, additive mode of inheritance for photomaze behavior in all species examined so far (Hadler, 1964; Walton, 1970; Markow, 1975*a*; Dobzhansky and Spassky, 1969; Woolf, 1972; Polivanov, 1975; Markow and Smith, 1977). Within a given species, particular chromosomes have been consistently shown to have a greater influence than others on phototactic responses (Dobzhansky *et al.*, 1975; Markow, 1975*b*; Markow and Smith, 1977), suggesting that genes influencing photomaze behavior are not

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randomly scattered among the chromosomes. The importance of particular chromosomes in maze phototaxis has been investigated previously in two members of the *melanogaster* species group, *D. melanogaster* (Markow, 1975*b*) and *D. simulans*. Genetic analysis of phototactic behavior in another species of the *melanogaster* group, *D. ananassae*, is reported below. The findings are discussed with respect to what is known about the genetic architecture underlying phototaxis in related species.

MATERIALS AND METHODS

Phototaxis Mazes

The Hirsch-Hadler phototaxis maze has been described extensively elsewhere (Hadler, 1964; Markow, 1975*a*; Markow and Smith, 1977). Flies enter the maze and make a series of 15 light/dark choices, emerging in 16 numbered collecting tubes. Flies emerging in tube 1 have made 15 dark choices and receive a photoscore of 1 (highly photonegative). Highly photopositive flies appear in tube 16, having made all light choices. Three-hundred flies are tested at one time, and, based on the number of flies in each collecting tube, a mean phototactic score is computed. In the current study males and females were tested separately at 4 days of age. General Electric cool white lights provided 2150 lux at the surfaces of the mazes.

Stocks

Cultures of *D. ananassae*, originally collected at three different localities (Papua New Guinea; Honolulu, Hawaii; Mysore, India) were obtained from the University of Texas Stock Center. The three strains were pooled in a population cage for five generations (1000 flies each generation) to establish a heterogeneous base population.

Selection

Three-hundred virgin females and 300 virgin males were tested in the mazes. The most photonegative 50 males and 50 females were chosen as the parents of the first generation of the photonegative line. A photopositive line was begun with the 50 most photopositive pairs. Each generation, the most extreme (i.e., photopositive or photonegative) 50 pairs were selected.

Reciprocal Hybridizations

After 21 generations of selection, reciprocal hybridizations were conducted between the photopositive and photonegative lines. Twenty virgin

males from the photopositive strain were placed with 20 virgin females of the photonegative strain in each of five half-pint culture bottles. The reciprocal cross was set up in the same way. The flies were transferred to fresh culture bottles every 3 days to give several successive F_1 broods for testing in the mazes. An F_2 generation was produced by setting up replicates of crosses between F_1 flies.

All flies were reared at 24 ± 1°C on standard cornmeal-molasses-agar medium with propionic acid.

RESULTS AND DISCUSSION

The response of *D. ananassae* to 21 generations of photopositive and photonegative selection is shown in Fig. 1. The original base population was slightly photopositive. In most generations, male photoscores were more positive than female photoscores. Realized heritabilities were calculated (Falconer, 1960) over the first ten generations and are shown in Table I.

Reciprocal hybridizations were carried out between the photopositive and photonegative strains after 21 generations of selection. Photoscores of F_1 and F_2 females and males are presented in Table II. In the cross between photopositive females and photonegative males, the F_1 males are significantly more photopositive than their sisters. Since males inherit their X chromosomes from their mothers, this finding shows a strong influence

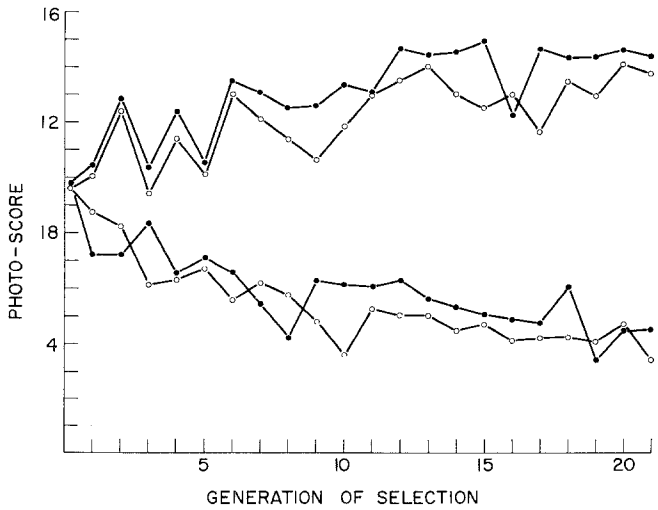

Fig. 1. Response to selection for photopositive and photonegative behavior in *D. ananassae*. ●, Male scores; O, female scores.

Table I. Realized Heritabilities of Positive and Negative Phototactic Behavior in *D. ananassae*

Behavior	Sex	Realized $h^2 \pm$ SE
Photonegative	Females	0.081 ± 0.001
Photonegative	Males	0.062 ± 0.003
Photopositive	Females	0.046 ± 0.004
Photopositive	Males	0.066 ± 0.003

of the X chromosome on positive phototactic behavior. However, an autosomal contribution to photopositive behavior is suggested by the fact that F_1 males are not so photopositive as the females or as males from the photopositive parental strain. In the reciprocal cross, F_1 males received their X chromosome from their photonegative mothers, but these F_1 males are no more photonegative than their sisters. In fact, when F_1 scores are pooled, the slightly more photopositive behavior of these males becomes statistically significant. Apparently, photonegative behavior is predominantly under the influence of autosomal loci.

The difference in the photoscores of the F_2 females and males from the cross of photonegative females and photopositive males is probably a function of recombination and of the photopositive influence of the X chromosome in the hemizygous males. While alleles causing recombination in males are present in some *D. ananassae* populations, the strains used in the present study do not show male recombination (Moriwaki and Tobari, 1975; Kikkawa, 1938). An increase in all F_2 variances over the F_1 variances supports a polygenic mode of inheritance for phototaxis, as suggested by the gradual response to selection and low heritabilities.

In all species of *Drosophila* examined so far, photomaze behavior has been found to be a polygenic, additive trait. One goal of genetic analysis of polygenic traits is to reveal any underlying organization of genes involved. In other words, are the loci controlling a particular polygenic trait randomly scattered throughout all chromosomes or are they found primarily within particular chromosomes or chromosomal regions? To our knowledge, studies of various polygenic traits in *Drosophila* have always shown some degree of organization of loci influencing the trait in question.

The relative roles of the X chromosome and autosomes in controlling positive and negative phototactic behavior in three related species of the melanogaster group are summarized in Table III. Several possible explanations for these differences exist: e.g., (1) loci could have been translocated between the X chromosome and autosomes during the evolutionary

Table II. Parental, F_1, and F_2 Photoscores from Reciprocal Hybridization of Photopositive and Photonegative Populations of *Drosophila ananassae*

		X	n			X	n	t
	P_1:	Photopositive ($\bar{X}$ = 13.721 ± 0.179, n = 300) $X^PX^PA^PA^P$			×	Photonegative ($\bar{X}$ = 4.524 ± 0.195, n = 300) $X^NYA^NA^N$		
F_1 ♀♀		8.312 ± 0.251	157	F_1 ♂♂		11.094 ± 0.213	170	8.487[b]
$X^PX^NA^PA^N$		8.011 ± 0.141	465	$X^PYA^PA^N$		10.612 ± 0.109	577	14.776[b]
		7.016 ± 0.172	313			10.454 ± 0.144	377	22.952[b]
Pooled		7.728 ± 0.102	935			10.638 ± 0.081	1084	22.656[b]
F_2 ♀♀		8.988 ± 0.255	247	F_2 ♂♂		9.507 ± 0.232	255	1.494
$X^PX^RA^RA^R$		8.832 ± 0.196	262	$X^RYA^RA^R$		8.687 ± 0.198	224	0.518
Pooled		8.908 ± 0.159	509			9.098 ± 0.154	449	0.852
	P_1:	Photonegative ($\bar{X}$ = 3.739 ± 0.144, n = 300) $X^NX^NA^NA^N$			×	Photopositive ($\bar{X}$ = 14.170 ± 0.132, n = 300) $X^PYA^PA^P$		
F_1 ♀♀		7.572 ± 0.134	369	F_1 ♂♂		8.045 ± 0.173	289	2.193
$X^NX^PA^NA^P$		8.248 ± 0.156	347	$X^NYA^NA^P$		8.379 ± 0.136	393	0.636
		7.995 ± 0.194	221			8.419 ± 0.180	227	1.599
Pooled		7.922 ± 0.091	937			8.283 ± 0.092	909	2.781[b]
F ♀♀		6.000 ± 0.205	250	F_2 ♂♂		8.395 ± 0.247	167	7.433[b]
$X^RX^RA^RA^R$		7.145 ± 0.192	220	$X^RYA^RA^R$		9.047 ± 0.220	148	6.436[b]
Pooled		6.536 ± 0.144	470			8.702 ± 0.220	315	9.723[b]

[a] X^P = X chromosome from photopositive strain; X^N = X chromosome from photonegative strain; A^P = autosomes from photopositive strain; A^N = autosomes from photonegative strain; X^R, A^R = recombinant X chromosome or autosomes.
[b] $P < 0.05$.

Table III. Roles of X Chromosomes and Autosomes in Positive and Negative Phototactic Behavior

Species	Photopositive	Photonegative	Source
D. melanogaster	Autosomal	X	Markow (1975*b*)
D. simulans	Autosomal	Autosomal	Makow and Smith (1977)
D. ananassae	X, autosomal	Autosomal	Present study

divergence of these species, or (2) positive phototactic behavior could be influenced by different loci in different species, and photonegative behavior could be influenced by different loci in different species.

D. melanogaster and *D. simulans* are sibling species which differ chromosomally in minor ways. These differences include some small inversions in several chromosomes and one translocation in which a small region in the distal portion of the *D. melanogaster* X chromosome appears to have moved to the second chromosome of *D. simulans* (Horton, 1939). The possibility that the translocated material contains genetic information involved in negative phototactic behavior has not been ruled out (Markow and Smith, 1977). The cytological relationships between *D. ananassae* and *D. melanogaster* also reflect the presence of inversions and translocations (Wharton, 1943). A proximal protion of the *D. melanogaster* X chromosome that includes the bobbed locus as well as some heterochromatin is found in the *D. ananassae* fourth chromosome. While the *D. melanogaster* X chromosome has a terminal centromere, an inversion has resulted in a metacentric X chromosome in *D. ananassae*. The *D. ananassae* X chromosome has not acquired by translocation any material from the *D. melanogaster* autosomes, which could account for the observed sex linkage for photopositive behavior. It is more likely that existing loci in the *D. ananassae* X chromosome, by accumulation of alleles from mutation or because of position effects following inversions, have acquired ability to influence photopositive behavior.

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