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PHOTOTACTIC BEHAVIOR OF *DROSOPHILA* SPECIES AT DIFFERENT TEMPERATURES

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A growing interest in the response of *Drosophila* to the environmental variable light is evidenced by the many laboratory procedures devised to measure phototactic behavior in this genus (see review by Rockwell and Sieger 1973). One apparatus, the Hadler phototaxis maze, has been popularized as a tool for evolutionary studies by the classical studies of Dobzhansky and his coworkers (Dobzhansky and Spassky 1969; Dobzhansky et al. 1969, 1972).

In the phototaxis maze, flies make a series of light-dark choices and are assigned a phototactic score which reflects their preference for light or darkness. While a given species may show characteristic photoscores, individual variation in maze phototaxis does exist among members of a population. A genetic component to this variation has been demonstrated by numerous selection experiments which have led to the creation of highly divergent photopositive and photonegative strains of *Drosophila pseudoobscura* (Dobzhansky and Spassky 1969), *D. melanogaster* (Hadler 1964a; Markow 1975), *D. persimilis* (Polivanov 1975) and *D. simulans* (Markow and Smith 1977). The heritability of maze phototactic behavior is only about 16% in *D. pseudoobscura* (Richmond 1969), suggesting that environmental factors modify phototactic behavior.

Hadler (1964b) mentioned that variables such as age, food, temperature, and humidity all affect behavior of *Drosophila* in the maze, but no data showing the nature of the effects of these factors were presented. Markow and Scavarda (1977) reported that older *D. melanogaster* are much more photoneutral than are younger flies. I wished to explore how phototaxis was affected by several other environmental variables. Below I report on the responses of five *Drosophila* species to light under conditions of high and low temperatures and humidities.

MATERIALS AND METHODS

Five species of *Drosophila* were compared. Populations of each species were founded by combining several laboratory strains in a population cage for four generations prior to the experiments. The species and their origins were *D.*

melanogaster (Tempe, Ariz., 1975; Amherst, Mass., 1974; Orlando, Fla., 1975), *D. simulans* (Tempe, Ariz., 1975; Cornville, Ariz., 1975), *D. pseudoobscura* (Mather, Calif., 1975; McDonald Ranch, Calif., 1974; Amecameca, Mexico, 1975), *D. ananassae* (U. Texas no. 3021.2; no. 3114.1), *D. willistoni* (U. Texas no. 1156.4, no. 1802.2). All stocks were raised in population cages containing 2.8 liters of standard cornmeal-molasses-agar medium with Tegosept-M. Flies were raised and stored at 24° C unless stated otherwise.

Phototaxis mazes (Hadler 1964a) were constructed so that flies entering the starting tube must make 15 light-dark choices before emerging in 16 numbered collecting tubes. Flies appearing in tube number 1 made all dark choices while flies in tube number 16 always chose the light. Three hundred flies were tested together in a maze, and the number appearing in each collecting tube was used to calculate a mean phototactic score which ranged from 1 (highly photonegative) to 16 (highly photopositive). Photoneutrality (equal numbers of turns to and from the light) is represented by a phototactic score of 8.5. Males and females were tested in separate mazes when 2-days old. Mazes were illuminated by G.E. cool white lamps giving an intensity of 45.6 m · cd at the surface. The temperature inside each maze was uniform.

A pair of mazes was placed in a Forma programmable environmental room which was set at particular combinations of temperature and humidity. Photomaze behavior was tested under conditions of low relative humidity (RH 10%) and temperatures of 20°, 22.5°, 25°, 31°, 34°, 36°, and 38° C. At temperatures below 20° C flies were inactive and remained in the starting tubes. Above 38° C flies only survived a few hours. Flies were later tested at the higher temperatures (36° and 38° C) at the higher relative humidity of 50%.

RESULTS

Photoscores of each species at different temperatures and 10% humidity are shown in figures 1–5. Although it was possible to include several tests of *Drosophila melanogaster* at 35° and 37° C, in addition to the other temperatures, it was not possible to test *D. annanassae* at 36° C due to demand for the environment room by other investigators. The photoscores from all the replications at a given temperature were plotted against the temperatures and subjected to regression analysis. Relationships were found to be either linear, where $y = a + bx$, or curvilinear, where $y = a + bx + cx^2$. *Drosophila melanogaster*, *D. simulans*, and *D. pseudoobscura* all become more photopositive at higher temperatures. The relationship is curvilinear in *D. melanogaster* and *D. pseudoobscura*, but linear in *D. simulans*. In *D. willistoni* and *D. ananassae*, photoscores were positive at lower temperatures but flies become increasingly photonegative at higher temperatures. The same photoscores were found for flies tested at 36° C and 38° C and either 50% or 10% humidity (table 1).

In another series of experiments *D. melanogaster* and *D. willistoni* were acclimated to 32° C for 24 h prior to testing at 36° C and 10% humidity. This exposure had little effect on the photoscores of either species (table 2).

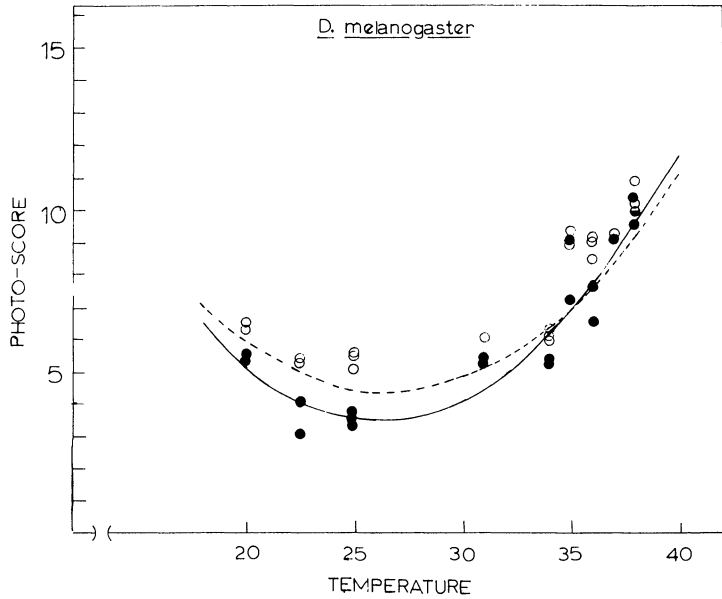


FIG. 1.—Photoscores of *D. melanogaster* at various temperatures. Open circles = female photoscores, dark circles = male photoscores; broken line = female regression, $Y = 2.25 + .24X + .99X^2$, $r = .88$; solid line = male regression line, $Y = .94 + .32X + 1.60X^2$, $r = .94$.

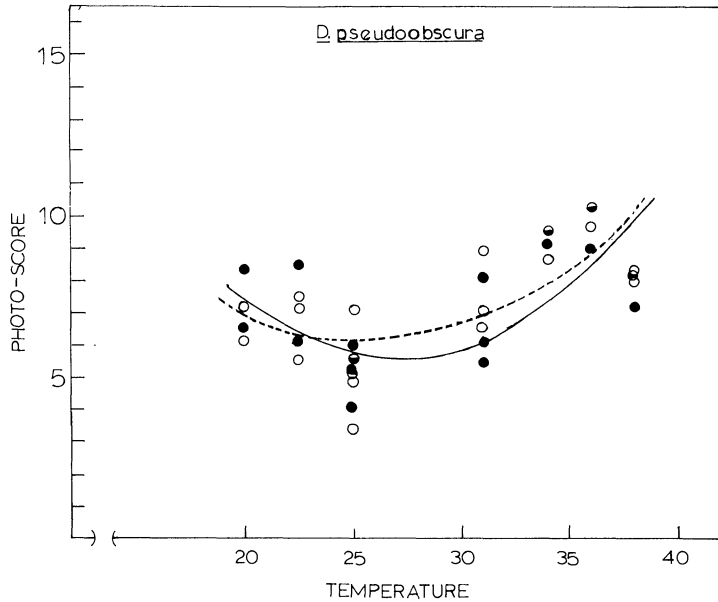


FIG. 2.—Photoscores of *D. pseudoobscura* at various temperatures. Open circles = female photoscores, dark circles = male photoscores; broken line = female regression, $Y = 3.48 + .70X + .72X^2$, $r = .82$; solid line = male regression, $Y = 3.71 + .98X + .60X^2$, $r = .66$.

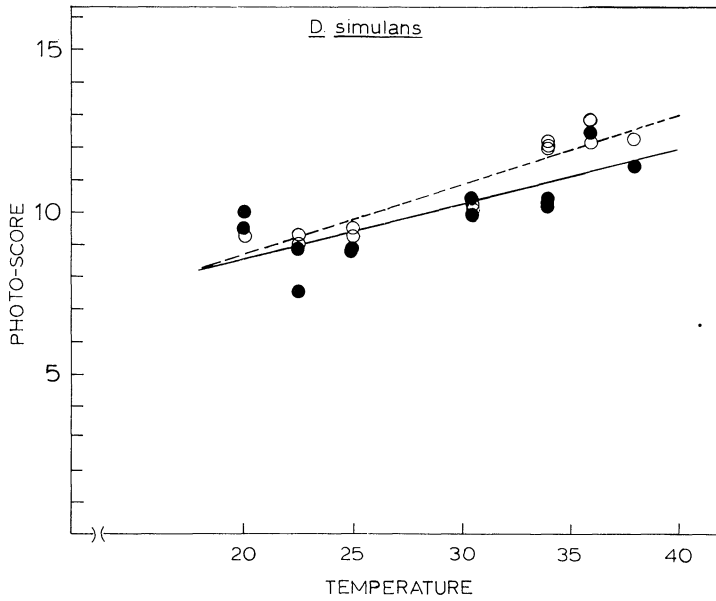


FIG. 3.—Photoscores of *D. simulans* at various temperatures. Open circles = female photoscores, dark circles = male photoscores; broken line = female regression line, $Y = 4.56 + .22X$, $r = .95$; solid line = male regression line, $Y = 6.00 + 0.16X$, $r = .88$.

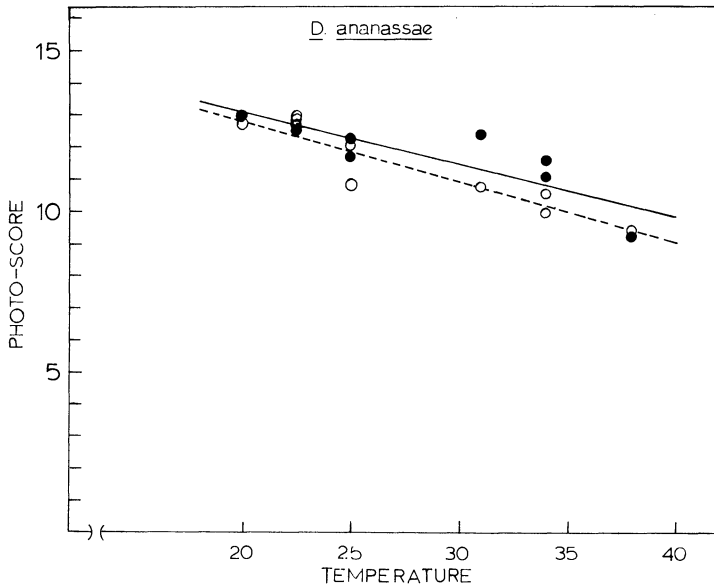


FIG. 4.—Photoscores of *D. ananassae* at various temperatures. Open circles = females photoscores, dark circles = male photoscores; broken line = female regression line, $Y = 15.91 - .19X$, $r = -.98$; solid line = male regression line, $Y = 16.33 - .16X$, $r = -.88$.

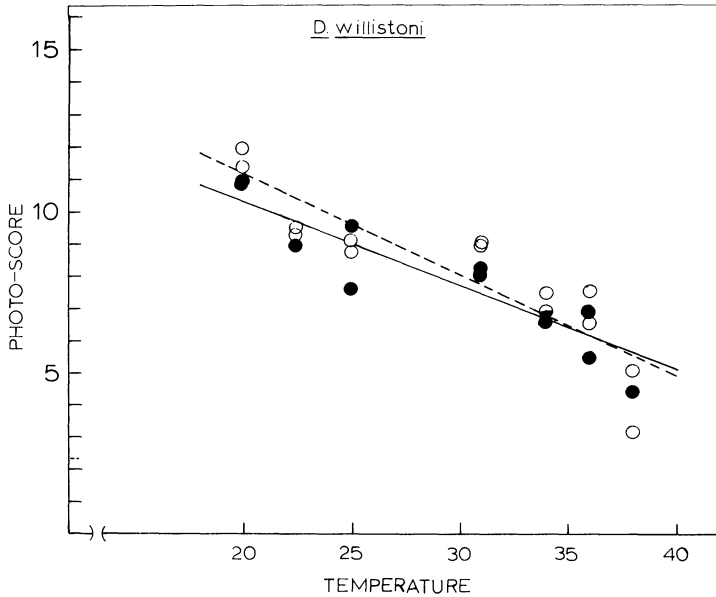


FIG. 5.—Photoscores of *D. willistoni* at various temperatures. Open circles = female photoscores, dark circles = male photoscores; broken line = female regression line, $Y = 16.69 - .31X$, $r = -.91$; solid line = male regression line, $Y = 15.94 - .28X$, $r = -.95$.

TABLE 1
PHOTOTACTIC SCORES AT HIGH TEMPERATURES AND
HIGH OR LOW RELATIVE HUMIDITY
(Females Only)

Species	Temperature	10% RH	50% RH	H^*
<i>Drosophila melanogaster</i>	36° C	8.87 ± .20	8.48 ± .19	1.021 (NS)
	38° C	10.29 ± .14	9.99 ± .12	.946 (NS)
<i>D. willistoni</i>	36° C	5.69 ± .24	6.06 ± .33	1.311 (NS)
	38° C	5.12 ± .28	4.86 ± .25	.922 (NS)

* The Kruskal-Wallis H nonparametric test does not assume normal distributions or homogeneous variances (Woolf 1968). A χ^2 table is used to determine P .

DISCUSSION

Temperature-dependent shifts in phototactic behavior are not unknown among insects. For example, in laboratory studies, *Malacosoma* larvae (tent caterpillar) are photopositive at low temperatures but become increasingly photonegative when the temperature is increased (Sullivan and Wellington 1953). Field observations on this genus show that when the temperatures outdoors are relatively cool larvae move toward the sun. The beetle, *Blastophagus*, on the other hand, becomes quite photonegative when temperatures go down (Perttunen 1958).

TABLE 2
EFFECT OF ACCLIMATION AT 32° C FOR TWENTY-FOUR
HOURS PRIOR TO TESTING AT 36 ± 1° C

Species	Acclimated ($\bar{X} \pm SE$)	Nonacclimated ($\bar{X} \pm SE$)	H*
<i>Drosophila melanogaster</i>			
Females (rep. no. 1)	8.67 ± .19	8.87 ± .10	.987 (NS)
Females (rep. no. 2)	8.49 ± .21	8.59 ± .14	.861 (NS)
Males (rep. no. 1)	9.36 ± .16	9.12 ± .14	.942 (NS)
Males (rep. no. 2)	8.99 ± .20	9.31 ± .17	1.002 (NS)
<i>D. willistoni</i>			
Females (rep. no. 1)	4.04 ± .25	4.12 ± .28	.775 (NS)
Females (rep. no. 2)	4.20 ± .19	4.35 ± .24	.629 (NS)
Males (rep. no. 1)	3.95 ± .24	4.36 ± .35	1.402 (NS)
Males (rep. no. 2)	3.61 ± .26	4.00 ± .29	1.223 (NS)

NOTE.—Rep. = replication.

* The Kruskal-Wallis H nonparametric test does not assume normal distributions or homogeneous variances (Woolf 1968). A χ^2 table is used to determine P.

Reports of photobehavioral differences between *Drosophila* species are numerous (e.g., see Spassky and Dobzhansky 1967; Rockwell et al. 1975; Parsons 1975; Polivanov 1973). While some of these studies vary with respect to the devices used to measure the response to light, in most studies temperature was either kept at a constant level or allowed to vary only within the daily range for a particular laboratory or testing room. Dobzhansky et al. (1974) found no phototaxis score difference among *Drosophila pseudoobscura* tested at 15°, 20°, or 27° C. The results of this study, based on more extreme temperature conditions, show that species differences in maze phototaxis are strongly dependent upon the temperatures at which flies are tested. At low temperatures *D. melanogaster* is quite photonegative and *D. willistoni* is photopositive. At high temperatures the opposite is found. It would be interesting to see if *Drosophila* phototactic behavior when measured by other techniques such as light gradient distribution (Parsons 1975) changes with differences in temperature.

The range of temperatures used here are not beyond the normal diurnal and seasonal ranges where many of these species occur. The way *Drosophila* respond behaviorally to light and temperature may reflect their physiological ability to adapt to temperature extremes. Levins (1969) grouped species of *Drosophila* according to breadth of geographic distribution and ability to resist thermal stress. On the average, species which showed the most physiological plasticity were the most widely distributed, while the poor thermal acclimators were narrowly distributed. According to Levins (1969) and to Hunter (1964, 1965, 1966), *D. melanogaster* and *D. simulans* are able to acclimate to heat and are widely distributed. *Drosophila pseudoobscura* is not a good acclimator and has a much more limited range. The only exception found appears to be *D. willistoni*, which is fairly broadly distributed. Levins suggested that *D. willistoni* may be able to occupy various habitats because of possible behavioral avoidance of desiccating

situations. If light is an indicator of a hot sunny place, species having poor thermal acclimation capabilities may tend to avoid light at high temperatures. The pattern of changes in phototactic behavior observed at different temperatures by the species in the present study is consistent with such a hypothesis. While *D. ananassae* show a decrease in photopositivity with heat, no literature is available on the physiological plasticity of this species; therefore it is impossible to know just how similar to *D. willistoni* they actually are.

While the potential adaptive advantage of seeking darkness when temperatures are high can easily be seen, how can the increased photopositivity of *D. melanogaster*, *D. simulans*, and *D. pseudoobscura* be explained? It is possible that the changes observed in these species are related to the change in activity levels and in phototactic behavior that occur when flies become excited. The increased photopositivity of excited flies has been noted for *D. pseudoobscura* (Lewontin 1959), *D. persimilis* (Rockwell et al. 1975), *D. melanogaster* (Markow and Merriam 1977) and *D. simulans* (Markow, unpublished) and is probably widespread among *Drosophila*. This phenomena has been referred to as an "escape reaction" (Dobzhansky and Spassky 1969) in which excited flies become very active, highly geonegative, and photopositive, moving quickly upward and toward the light. The influence of temperature may be easily inferred from the observation that at room temperature (24° C) the time required for a sample of 300 flies to complete the maze is about 24 h. We noticed that at 36° C and 38° C all flies had gone through the maze in less than 2 h. The increased photopositivity of *D. melanogaster*, *D. pseudoobscura*, and *D. simulans* at higher temperatures may reflect their efforts to "escape" the maze. A factor which could potentially influence the behavioral responses of the populations of flies tested is the length of time the cultures have been maintained under laboratory conditions. While the strains of *D. pseudoobscura*, *D. melanogaster*, and *D. simulans* were freshly trapped, the strains of *D. willistoni* and *D. ananassae* have been cultured in the laboratory for a decade or more. It has been suggested that culturing in the laboratory selects for geopositive and photonegative behavior, as part of a "reverse escape response" (Wallace and Srb 1964). However, at normal laboratory temperatures *D. willistoni* and *D. ananassae* are quite photopositive. The strain differences in phototaxis appear at extreme temperatures. The exact nature of any effect of laboratory maintenance on the results reported above would be difficult to pinpoint. Testing freshly caught *D. willistoni* and *D. ananassae* would be of interest. While my findings and interpretations do not conflict with what is already known about certain physiological and behavioral responses of *Drosophila* to heat and light, the reasons for the observed shifts in phototactic behavior are still open to speculation.

In the laboratory intra- and interspecific variation in response to individual environmental factors such as light has been extensively documented. In nature, environmental variables do not occur independently of each other. Rarely do any of them remain static. When flies are collected in nature, the distribution of species recovered within a particular location depends upon geographic location, season, time of day, weather, and microhabitat (Dobzhansky and Pavan 1950; Dobzhansky et al. 1950; Charles Taylor, personal communication). Recently,

differences in phototactic behavior of certain Hawaiian *Drosophila*, *D. mimica*, *D. imparisetae*, and *D. kambysellisi* has been found to be related to their individual diurnal habitat preferences and leking activities (Richardson and Johnston 1975). No doubt light and temperature rank high in importance among the factors influencing habitat choices of most *Drosophila* species. In view of the wide variety of factors which influence habitat choice of *Drosophila* and the wide variety of responses shown between these species, it should not be surprising that these factors interact in the way they influence behavior. In the laboratory a multivariate approach, taking into account several environmental variables simultaneously, should provide a better understanding of the variation in behavioral and physiological adaptations found within this genus.

SUMMARY

Using Hirsch-Hadler phototaxis mazes, the light responses of five different *Drosophila* species were compared at a wide range of temperatures. At higher temperatures *D. pseudoobscura*, *D. simulans*, and *D. melanogaster* become more photopositive, while *D. ananassae* and *D. willistoni* become less photopositive. Humidity and prior acclimation to higher temperatures had no effect on the temperature-dependent shifts in phototaxis. The possible adaptive significance of these changes in relation to desiccation, predator defense, and social factors is discussed.

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