

morphology and the morphological gap between *Zachaeus* and *Cycloramphus* is sufficiently large that they should be maintained in separate genera. This decision rests on the recognition of genera as adaptive units<sup>15</sup>, not strictly time

differentiated units. This conclusion implies the time history of evolution is an additional and independently resolvable aspect which helps elucidate the classification but does not determine it.

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- 3 J. D. Lynch, Univ. Kans. Publs Mus. nat. Hist. 53, 1 (1971); W. R. Heyer, Smithsonian Contrib. Zool. 199, 1 (1975). Morphological descriptions of the 3 generic units can be extracted from these papers.
- 4 W. R. Heyer, Variation and systematics of frogs of the genus *Cycloramphus* (Amphibia, Leptodactylidae), unpublished.
- 5 W. R. Heyer and L. R. Maxson, Relationships and zoogeography of frogs of the genus *Cycloramphus* (Amphibia, Leptodactylidae), unpublished.
- 6 L. R. Maxson, R. Highton and D. B. Wake, *Copeia* 1979, 502.
- 7 L. Karig and A. C. Wilson, *Biochem. Genet.* 5, 211 (1971).
- 8 A. B. Champion, E. M. Prager, D. Wachter and A. C. Wilson, in: *Biochemical and Immunological Taxonomy of Animals*. Ed. C. A. Wright. Academic Press, London 1974.
- 9 L. R. Maxson and A. C. Wilson, *Science* 185, 66 (1974).
- 10 L. Maxson, *Experientia* 32, 1149 (1976); B. E. Scanlan, L. R. Maxson and W. E. Duellman, *Evolution* 34, 222 (1980); L. R. Maxson, *Copeia* 1981, in press.
- 11 L. R. Maxson and A. C. Wilson, *Syst. Zool.* 24, 1 (1975).
- 12 A. C. Wilson in F. J. Ayala, ed., *Molecular Evolution*. Sinauer Assoc. Inc., Mass. 1976.
- 13 A. C. Wilson, S. S. Carlson and T. J. White, *A. Rev. Biochem.* 46, 573 (1977).
- 14 R. K. Selander, S. Y. Yang, R. C. Lewontin and W. E. Johnson, *Evolution* 24, 402 (1970).
- 15 R. F. Inger, *Evolution* 12, 370 (1958).

### Behavioral differentiation between two species of cactiphilic *Drosophila*. 1. Adult geotaxis and phototaxis<sup>1</sup>

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**Summary.** Using Hirsch-Hadler geotaxis and phototaxis mazes, we measured the responses of 2 cactiphilic species of *Drosophila*, *D. mettleri* and *D. nigrospiracula*, to gravity and to light. Both species were found to be photonegative but they differed significantly from each other in their geotactic behavior. *D. mettleri* was geonegative while *D. nigrospiracula* was geopositive. This result was surprising in that natural populations show a contrasting vertical distribution with *D. nigrospiracula* located higher than *D. mettleri* on rotting saguaro substrates.

An interesting case of niche separation occurs between 2 cactiphilic species of *Drosophila* of the Sonoran Desert. The larvae of 1 species, *D. nigrospiracula*, utilize the necrotic tissue of cardon (*Pachycereus pringlei*) on the Baja peninsula and saguaro (*Carnegiea gigantea*) on mainland Mexico. *Drosophila mettleri* larvae live in the soil permeated with the fermenting juices from these rotting cacti<sup>2,3</sup>. While the larval niche separation appears quite complete, considerable overlap exists in the distribution of adult flies. Table 1 shows a typical distribution of adult males and females of both species were aspirated off a rotting saguaro near Tucson, Arizona in October of 1979. The saguaro trunk was necrotic from the ground to a height of about 3 m, and feeding sites were available over the entire area. While *D. nigrospiracula* adults prefer feeding sites located higher up on the cactus trunk, *D. mettleri* are found both on the cactus and on the soil below. *D. mettleri* females are found more often on the ground, frequently under loose rocks. The  $\chi^2$  statistic is extremely high indicating that the 2 species are quite different in their distributions. Considering males only from both species, an inhomogeneity  $\chi^2$  of 50.87 is obtained, compared to 84.77 for females. Females of *D. mettleri* and *D. nigrospiracula* are even more different than are the males. These data are similar to those reported by Heed<sup>2</sup>.

The strong difference in vertical distribution between the 2 species suggested to us that gravity might be a factor in their niche separation. Geotaxis, the behavioral response to

gravity, is easily measured in *Drosophila* using Hirsch-Hadler geotaxis mazes. The response of flies to another ecological variable, light, is measurable in a 2nd type of device, the phototaxis maze. This report concerns the geotactic and phototactic behavior of *D. mettleri* and *D. nigrospiracula*.

Hirsch-Hadler phototaxis and geotaxis mazes are described in detail in many studies<sup>4-6</sup>. Flies make a series of choices with respect to light or gravity and are assigned a score of 1 (highly photo- or geonegative) to 16 (highly photo- or geopositive). Photo- or geoneutrality is indicated by a mean score of 8.5. The flies used in these studies were descendants of a multi-female collection of *D. nigrospiracula* reared from a saguaro rot in May 1979. The *D. mettleri* came from a multi-female collection of individuals reared from soil beneath the same rotting saguaro. All stocks were maintained in the laboratory on banana media (University of Texas recipe) until tested in mazes in September, 1979. Males and females were separated under light ether anesthesia 2 days prior to testing. 3 replications were carried out for each sex of each species with each replication consisting of several hundred individuals.

The results of the maze experiments are presented in table 2. There were several striking features of the performance of these 2 species in the geotaxis mazes. First, in natural conditions, *D. nigrospiracula* are found in higher positions on the cactus than *D. mettleri*, which are primarily on or near the ground. If these 2 species were selecting their

Table 1. Vertical distribution of *D. nigrospiracula* and *D. mettleri* on a saguaro trunk

Height above ground (cm)	<i>D. nigrospiracula</i>		<i>D. mettleri</i>		Total
	Males	Females	Males	Females	
0-15	2	1	12	54	69
15-60	16	15	61	29	121
above 125	93	62	44	14	213
Total	111	78	117	97	403

$\chi^2 = 207.94$ ;  $p \ll 0.001$ .

Table 2. Geotactic and phototactic scores of *D. nigrospiracula* and *D. mettleri*

	Repetition	Females		n	Males		n
		$\bar{X}$	$\pm$ SE		$\bar{X}$	$\pm$ SE	
<b>Geotaxis</b>							
<i>D. nigrospiracula</i>	1	9.17	$\pm 0.28$	352	9.89	$\pm 0.23$	381
	2	9.52	$\pm 0.20$	340	9.61	$\pm 0.24$	271
	3	11.15	$\pm 0.21$	295	10.94	$\pm 0.17$	411
pooled		9.88	$\pm 0.13$	987	10.21	$\pm 0.12$	1063
<i>D. mettleri</i>	1	5.34	$\pm 0.26$	254	4.73	$\pm 0.22$	290
	2	5.87	$\pm 0.26$	268	5.21	$\pm 0.28$	219
	3	7.27	$\pm 0.23$	245	7.00	$\pm 0.25$	209
pooled		6.14	$\pm 0.15$	767	5.65	$\pm 0.146$	718
<b>Phototaxis</b>							
<i>D. nigrospiracula</i>	1	4.15	$\pm 0.20$	259	4.90	$\pm 0.20$	362
	2	5.50	$\pm 0.22$	238	5.21	$\pm 0.15$	225
	3	4.43	$\pm 0.15$	288	4.52	$\pm 0.17$	324
pooled		4.60	$\pm 0.12$	785	4.82	$\pm 0.11$	911
<i>D. mettleri</i>	1	5.79	$\pm 0.24$	237	5.81	$\pm 0.23$	226
	2	5.44	$\pm 0.24$	269	6.07	$\pm 0.19$	314
	3	5.19	$\pm 0.24$	242	6.64	$\pm 0.20$	420
pooled		5.46	$\pm 0.14$	749	6.27	$\pm 0.12$	950

niches on the basis of gravity, their geotactic score would reflect their distributions as shown in table 1. Instead, the opposite was found: *D. mettleri* were quite geonegative while *D. nigrospiracula* were slightly geopositive. Statistically, this difference is highly significant ( $t = 12.988$ ,  $p < 0.001$ ). The differences between male and female *D. mettleri* are not significant, unlike the situation on the rot. Furthermore, *D. mettleri* differed from *D. nigrospiracula* in the rapidity with which maze runs were completed. The average period of time required for 200 to 300 *D. nigrospiracula* to pass through the maze was about 2 days. On the other hand, all samples of *D. mettleri* had finished going through in just a few hours. There may be some relationship between the maze geonegativity of *D. mettleri* and the speed with which they went through the device. Among certain *Drosophila* species, an 'escape response' is well known<sup>4,7</sup>. When flies are in any way agitated, they tend to become very active, highly geonegative, and photopositive. Species differ in whether or not they exhibit the escape response. Possibly the response would be more likely to occur in species of flies that live on or near the ground. In any event, geotaxis mazes do differentiate between the behavior of these 2 species. While the difference is not of the nature anticipated, it is, nevertheless, a function of some previously unknown behavioral difference, the ecological significance of which remains unclear.

Both species were characterized by photonegative behavior. This might have been expected considering that they are inhabitants of a desert environment. Any tendency to avoid a sunny location would also be a potential tendency to avoid desiccation and heat stress in a hot, dry environment. *D. mettleri* also traversed the photomazes much more rapidly than did *D. nigrospiracula*. Although *D. mettleri* are signi-

ficantly less photonegative than *D. nigrospiracula* ( $t = 2.31$ ,  $p < 0.05$ ), we feel that a difference of this magnitude has little biological significance. The same is true for the difference within a species between males and females (table 2).

We interpret the above findings to indicate that behavioral differentiation with respect to gravity (as measured in geotaxis mazes) is not of primary importance in either the observed differences in adult distributions or the larval niche separation between *D. nigrospiracula* and *D. mettleri*. The fact that both species are very photonegative correlates well with the observation that, in nature, adults are found in the shade rather than in the sun during the hotter parts of the day. Additional experiments on the oviposition site preference of these species with respect to gravity, light, and substrate type (cactus or soaked-soil) have shown them to be behaviorally differentiated in directions expected on the basis of the known larval habitats (unpublished). Thus, behavioral differentiation may be intrinsically involved with oviposition. These investigations are being pursued.

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- 2 W. B. Heed, Proc. Ent. Soc. Wash. 79, 649 (1977).
- 3 W. B. Heed, Ecology and Genetics of Sonoran Desert *Drosophila* in Brussard, Ed. Proceedings in Life Sciences: Ecology and Genetics. Springer, New York 1978.
- 4 T. Dobzhansky and B. Spassky, Proc. natl Acad. Sci. USA 63, 75 (1969).
- 5 C. M. Woolf, H. Sasmor and T. A. Markow, Behav. Genet. 8, 65 (1978).
- 6 T. A. Markow, Am. Nat. 114, 884 (1979).
- 7 T. A. Markow, Genetics 79, 527 (1975).