



Sexual Isolation among Populations of *Drosophila mojavensis*

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- Diss. University of Pennsylvania, Philadelphia, Pennsylvania, USA.
- GALBRAITH, D. F., AND C. H. FERNANDO. 1977. The life history of *Gerris remigis* in a small stream in southern Ontario. *Can. Entomol.* 109:221–228.
- I STOCK, C. A. 1978. Fitness variation in a natural population, pp. 171–190. *In* H. Dingle (ed.), *Evolution of Insect Migration and Diapause*. Springer, Heidelberg, Germany.
- . 1981. Natural selection and life history variation: Theory plus lessons from a mosquito, pp. 113–127. *In* R. F. Denno and H. Dingle (eds.), *Insect Life History Patterns*. Springer, Heidelberg, Germany.
- KÖPFLI, R., R. HAUSER, AND M. ZIMMERMANN. 1987. Diapausendetermination bei Wasserläufern (Hemiptera, Gerridae). *Rev. Suisse Zool.* 94:533–543.
- LANDE, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* 63:607–615.
- MASAKI, S. 1967. Geographic variation and climatic adaptation in a field cricket. *Evolution* 21:725–741.
- . 1972. Climatic adaptation and photoperiodic response in the band-legged ground cricket. *Evolution* 26:587–600.
- MATTHEY, W. 1974. Contribution à l'écologie de *Gerris remigis* sur les deux étangs des Montagnes Rocheuses. *Bull. Soc. Entomol. Suisse* 47:85–95.
- MAYR, E. 1963. *Animal Species and Evolution*. Harvard Univ. Press, Cambridge, MA.
- MOUSSEAU, T. A. AND D. A. ROFF. 1989. Adaptation to seasonality in a cricket: Patterns of phenotypic and genotypic variation in body size and diapause expression along a cline in season length. *Evolution* 43:1483–1496.
- PARK, O. 1949. Application of the converse Bergmann principle to the carabid beetle, *Dicaeleus purpuratus*. *Physiol. Zool.* 22:359–372.
- ROFF, D. A. 1980. Optimizing development time in a seasonal environment: The “ups and downs” of clinal variation. *Oecologia (Berlin)* 45:202–208.
- . 1983. Phenological adaptation in a seasonal environment: A theoretical perspective, pp. 253–270. *In* V. K. Brown and I. Hodek (eds.), *Diapause and Life Cycle Strategies in Insects*. Dr. W. Junk, The Hague, Netherlands.
- RUBENSTEIN, D. 1989. Sperm competition in the water strider, *Gerris remigis*. *Anim. Behav.* 38:631–636.
- SPENCE, J. R. 1989. The habitat template and life-history strategies of pondskaters: Reproductive potential, phenology, and wing dimorphism. *Can. J. Zool.* 67:2432–2447.
- SPENCE, J. R., D. H. SPENCE, AND G. G. E. SCUDDER. 1980. The effects of temperature on growth and development of water strider species (Heteroptera: Gerridae) of central British Columbia and implications for species packing. *Can. J. Zool.* 58:1813–1820.
- STEARNS, S. C. 1976. Life-history tactics: A review of ideas. *Quart. Rev. Biol.* 51:3–47.
- . 1977. The evolution of life-history traits: A critique of the theory and a review of the data. *Annu. Rev. Ecol. Syst.* 8:145–171.
- TAUBER, M. J., C. A. TAUBER, AND S. MASAKI. 1986. *Seasonal Adaptations of Insects*. Oxford Univ. Press, Oxford, England.
- VEPSÄLÄINEN, K. 1973. Development rates of some Finnish *Gerris* species in laboratory cultures. *Entomol. Scand.* 4:206–216.
- . 1974. Determination of wing length and diapause in water striders. *Hereditas* 77:163–176.
- . 1978. Wing dimorphism and diapause in *Gerris*: Determination and adaptive significance, pp. 218–253. *In* H. Dingle (ed.), *Evolution of Insect Migration and Diapause*. Springer, Heidelberg, Germany.
- VIA, S., AND R. LANDE. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39:505–522.
- ZERA, A. 1981. Genetic structure of two species of water striders with differing degrees of winglessness. *Evolution* 35:218–225.

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SEXUAL ISOLATION AMONG POPULATIONS OF *DROSOPHILA MOJAVENSIS*

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Drosophila mojavensis, a cactophilic fruit fly endemic to the Sonoran Desert of North America (Fig. 1), has become a popular model system for studies of speciation. Mettler (1963) originally divided the species into two geographic host races: race A breeds in necrotic barrel cactus (*Ferrocactus acanthodes*) in southern California; race B inhabits Baja California where it breeds in agria cactus (*Stenocereus gumosis*), Sonora

and southern Arizona where organ pipe cactus (*S. thurberi*) is the primary host plant. Flies of race A are larger and more yellow than those of race B (Mettler, 1963). These two races also show distinct differences in chromosomal inversions and allozyme frequencies (Zouros, 1974). Zouros (1974) further subdivided race B into subrace B₁, denoting populations from the mainland, and subrace B_{II} for the populations in the Baja Pen-

insula, on the basis of cytological (Johnson, 1973) and genetic (Zouros, 1974) differentiation.

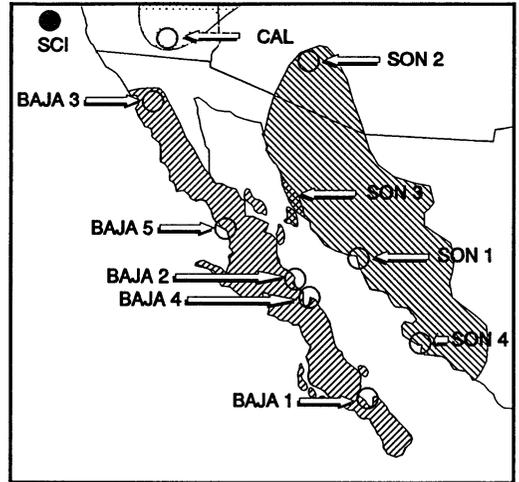
Flies from the two races and subraces may be crossed to produce fertile offspring (Mettler, 1963; Zouros, 1974) indicating the lack of postzygotic isolation. However, Zouros and d'Entremont (1980) discovered significant sexual isolation between subrace B_I and B_{II} such that females from Sonora show reduced matings with males of Baja California populations. The observed behavioral isolation has subsequently been shown to be under genetic control (Koeper, 1987a, 1987b; Krebs, 1990) and the responsible courtship behaviors identified (Krebs and Markow, 1989).

Drosophila mojavensis was later collected from prickly pear cactus (*Opuntia demissa*) on Santa Catalina Island, California (Heed, 1982) revealing the existence of still another geographically isolated (SCI, Fig. 1) host race. Though the two *D. mojavensis* populations from California are geographically separate and utilize very different host plants from the populations in Baja and Sonora, the possibility of sexual isolation between them and other geographic host races has not yet been examined. In the present study testing for behavioral isolation was extended to include strains of the other geographic host races of *D. mojavensis*; one from Santa Catalina Island and one from the Anza Borrego Desert of California. Based upon the degree of genetic differentiation reported earlier for flies from southern California significantly greater isolation was expected between race A flies (California) and race B (Baja or Sonora) than within race B.

MATERIALS AND METHODS

Strains and Rearing Conditions.—Strains of *Drosophila mojavensis* (Fig. 1) were obtained from the University of Arizona (with A stock numbers), or were collected by the author. For ease of reference, strains are denoted by abbreviations for geographic area: the Sonora desert mainland (SON1, SON2, etc.), the Baja Peninsula (BAJA1, BAJA2, etc.), Santa Catalina Island (SCI), and southern California (CAL). One set of sexual isolation experiments was conducted in 1981 and 1982, employing the same Baja and Sonora strains utilized in previous experiments (Markow, 1981; Markow et al., 1983): BAJA1 (La Paz, A791), BAJA2 (Santa Rosalia, A800), BAJA3 (Catevena, A761), SON1 (San Carlos, A798), SON2 (Santa Rosa Mountains, AZ), a strain from Santa Catalina Island, SCI (A826) and a strain from the Anza Borrego Desert, California, CAL (A753). Strains utilized in the second set of experiments, conducted between 1987 and 1989, include SON3 (Demboque, Sonora), SON4 (Las Bocas, Sinaloa A891), BAJA4 (San Lucas A920), and BAJA5 (Punta Prieta A859). The SON3 strain was collected in the small area where agria cactus occurs in Sonora and though agria appears to be preferred over organ pipe, those flies show no genetic differences from the flies using organ pipe nearby. Thus, they serve as a control for the influences of host plant in the following behavioral isolation tests.

All flies were reared in half-pint milk bottles containing standard cornmeal-molasses-yeast medium with buffered propionic acid and seeded with live yeast. Virgin males and females were separated under light ether anesthesia 1 to 6 hours after eclosion and stored in 8-dram vials with live yeast, with five flies per vial.



-  agria *Stenocereus gummosis*
-  organ pipe *Stenocereus thurberi*
-  barrel cactus *Ferrocactus acanthodes*
-  prickly pear *Opuntia demissa*

FIG. 1. Collection localities for strains of the geographic host races used in this report. Host plant use distributions are presented according to the key.

The flies were kept in a 13:11 hour light:dark cycle with temperatures at 26 to 27°C day and 20 to 21°C night.

Measuring Sexual Isolation between *D. mojavensis* Strains from Different Localities.—Sexual isolation was tested as in Markow (1981) by placing 10 pairs of sexually mature virgin flies from each of two geographic strains in a Plexiglas observation chamber for one hour and scoring the strain identities of the males and females mating. Flies had been colored with fluorescent dust to distinguish strains, and the colors were alternated between each of the four replications to eliminate possible marking effects. The joint isolation index (*I*) and female isolation indices (*I*₁, *I*₂) from each strain were calculated according to the following formulae:

$$I = [(n_{11} + n_{22}) - (n_{12} + n_{21})]/n$$

$$I_1 = (n_{11} - n_{12})/(n_{11} + n_{12})$$

$$I_2 = (n_{22} - n_{21})/(n_{22} + n_{21})$$

where *n*₁₁ is the number of matings between females from Strain 1 and males from Strain 1, *n*₁₂ is the number of matings between females of Strain 1 and males of Strain 2, etc., and *n* is the total number of matings (Stalker, 1942). The standard error of these indices is

given by $SE = \sqrt{\frac{1 - I^2}{n}}$ (Malagolowkin-Cohen et al., 1965).

RESULTS

Sexual Isolation between Geographic Host Races.—Sexual isolation indices derived from the first set pooled

TABLE 1. Isolation indices for *Drosophila mojavensis* from a and d) southern California with flies from Baja and Sonora, b and e) Santa Catalina with flies from Baja, Sonora, and southern California, c and f) Baja with flies from Sonora. Observations a, b, and c were made in 1981 and 1982 while observations d, e, and f were made in 1989.

	P1	P2	I (SE)	I_1 (SE)	I_2 (SE)
1A.					
a.	CAL	BAJA1	0.04 (0.20)	0.09 (0.28)	0.00 (0.28)
	CAL	BAJA2	0.18 (0.17)	-0.23 (0.24)	0.57 (0.19)*
	CAL	BAJA3	0.33 (0.13)*	0.19 (0.19)	0.53 (0.16)*
	CAL	SON1	0.05 (0.11)	-0.14 (0.16)	0.27 (0.16)
	CAL	SON2	0.01 (0.16)	-0.02 (0.13)	0.03 (0.13)
b.	SCI	BAJA1	0.00 (0.14)	-0.41 (0.15)*	0.44 (0.16)*
	SCI	BAJA2	-0.14 (0.14)	-0.15 (0.21)	-0.27 (0.18)
	SCI	BAJA3	0.16 (0.14)	0.44 (0.18)*	-0.12 (0.19)
	SCI	SON1	0.10 (0.14)	0.11 (0.19)	0.36 (0.19)
	SCI	SON2	0.02 (0.13)	0.08 (0.19)	-0.10 (0.18)
	SCI	CAL	0.15 (0.14)	0.68 (0.14)*	-0.36 (0.18)*
c.	BAJA1	SON1	0.23 (0.08)**	0.13 (0.09)	0.30 (0.10)**
	BAJA1	SON2	0.15 (0.07)*	0.08 (0.08)	0.81 (0.11)**
	BAJA2	SON1	0.19 (0.09)*	0.16 (0.12)	0.69 (0.08)**
	BAJA2	SON2	0.21 (0.11)	-0.09 (0.06)	0.77 (0.10)**
	BAJA3	SON1	0.31 (0.07)**	0.21 (0.07)**	0.33 (0.10)**
	BAJA3	SON2	0.25 (0.09)*	0.19 (0.08)*	0.59 (0.23)**
1B.					
d.	CAL	BAJA4	0.09 (0.18)	-0.12 (0.17)	0.16 (0.20)
	CAL	BAJA5	0.18 (0.14)	-0.03 (0.09)	0.14 (0.08)
	CAL	SON3	0.07 (0.10)	-0.11 (0.11)	0.26 (0.15)
	CAL	SON4	0.24 (0.16)	0.19 (0.09)*	0.40 (0.12)**
e.	SCI	BAJA4	0.01 (0.14)	-0.12 (0.11)	0.19 (0.15)
	SCI	BAJA5	0.20 (0.19)	-0.11 (0.09)	0.26 (0.18)
	SCI	SON3	0.18 (0.18)	0.04 (0.15)	0.37 (0.15)*
	SCI	SON4	0.10 (0.10)	0.11 (0.15)	0.22 (0.11)*
f.	BAJA4	SON3	0.16 (0.08)*	0.12 (0.16)	0.54 (0.13)**
	BAJA4	SON4	0.20 (0.10)*	0.09 (0.14)	0.60 (0.19)**
	BAJA5	SON3	0.22 (0.07)**	0.12 (0.08)	0.71 (0.20)**
	BAJA5	SON4	0.16 (0.07)*	-0.10 (0.06)	0.69 (0.22)**
	BAJA4	BAJA5	0.09 (0.10)	-0.02 (0.04)	0.07 (0.13)
	SON3	SON4	0.20 (0.19)	0.12 (0.16)	0.14 (0.19)

* $P < 0.05$.

** $P < 0.01$.

of behavioral isolation tests (1981–1982) are reported in Table 1a. Only once was the joint isolation index significantly different from zero, between the CAL strain and the northern-most Baja strain, BAJA3. The degree of assortative mating or isolation attributable to females of each strain is reflected by I_1 and I_2 values. Males from the CAL strain had reduced mating success with females from other localities, and positive assortative mating occurred in tests with the Baja strains, BAJA2 and BAJA3. While no significant joint isolation indices were found in tests involving SCI flies, strong positive assortative mating was found for SCI females paired with BAJA3 and CAL males. Females from BAJA1 and SCI showed a significant excess of matings with BAJA1 males although no negative assortative mating was found between these strains. As expected, all comparisons with Baja and Sonora flies showed reduced mating success between Baja males and Sonora females. The significant positive assortative mating was primarily a function of the disproportionate

number of matings by Sonora females with males of their own strain.

Sexual isolation indices from the second group of experiments are shown in Table 1B. Similar patterns of isolation were observed in the more recent tests. Almost all significant isolation indices were found in tests between Sonora and Baja strains. Tests for isolation among Baja or among Sonora strains indicated no isolation within these regions (Table 1B, at bottom).

DISCUSSION

To understand the evolution of behavioral isolation among *D. mojavensis* flies, the extent to which all four populations of *D. mojavensis* are isolated from each other was examined. A number of generalizations can be made. First, the most consistent and significant behavioral isolation is found between Sonora females and Baja males. This is true of females from the SON3 strain, which came from the same host plants as the Baja strains, suggesting host adaptation is not in itself

a major determinant of isolation. Second, the discrimination by some females against Baja males does not necessarily extend to all males from the other geographic host races. For example, males from southern California show reduced mating success with females of most other races, and in some tests, reduced success with their own females. Third, the lack of isolation between flies of the northern-most Sonora strain (SON2) and that of southern California (CAL) may reflect a history of gene flow between these populations. Fourth, males from Sonora and from the Santa Catalina Island strain tend to show the greatest relative mating success with females of other races. Finally, the fact that flies from the La Paz region (BAJA1), at the southern tip of the Baja Peninsula, appear to behave differently from other Baja strains is suggestive of some sort of differentiation, perhaps clinal in nature, within Baja itself.

The observed isolation patterns suggest that the factors underlying sexual isolation in *D. mojavensis* populations are more complex than just host plant adaptation or degree of genetic differentiation. The geographic host races showing the greatest and most consistent isolation, Sonora and Baja, both utilize columnar cacti of the same genus (*Stenocereus*) while the southern California and Santa Catalina Island populations breed in barrel and prickly pear respectively. Analysis of their chemical constituents confirms that organ pipe and agria are more similar to each other than to prickly pear (Kircher, 1982). Other features of the breeding sites provided by these cacti, such as rot density and duration, may also place significant pressure on the resident *Drosophila* influencing their life histories (Etges, 1990), size (Krebs, 1990), and physiology (Toolson et al., 1990). These characters could indirectly underlie sexual isolation through their effects on general activity or vigor. But geographic host plant shifts in cactophilic *Drosophila* are not necessarily associated with sexual isolation. Host plant shifts between Baja and Sonora populations of both *D. mettleri* and *D. nigrospiracula* (from *Carnegiea gigantea* to *Pachycereus pringlei* respectively) were not found to be associated with any sexual isolation between geographic populations of either of these *Drosophila* species (Markow et al., 1983).

Other biotic and abiotic variables besides host plant ecology may contribute heavily to differentiation of *mojavensis* populations in ways influencing sexual isolation. For example, a class of lipid, the epicuticular hydrocarbons, underlies the ability to regulate water loss in desert-adapted arthropods (Toolson, 1988). In populations of many insect species, including *Drosophila*, hydrocarbon composition varies with regional climatic factors such as temperature and humidity (Toolson and Kuper-Simbron, 1989). Epicuticular hydrocarbons also act as mating pheromones in several insect species, and even slight changes in their composition have been shown to selectively and significantly influence mating success in *D. mojavensis* from Sonora (Markow and Toolson, 1990). While epicuticular hydrocarbon composition in *D. mojavensis* from Sonora and Baja differs in a way that could explain the sexual isolation observed between these two geographic populations (Markow and Toolson, 1989), nothing is known of the profiles of these lipids in the other *D. mojavensis* strains.

Because epicuticular hydrocarbons act as phero-

mones as well as regulators of cuticular permeability, their composition may also be sensitive to the presence of closely related species. In Sonora, there are considerable areas of sympatry between *D. mojavensis* and its sibling species *D. arizonae*. This sympatry is associated with increased sexual isolation between the two sibling species (Wasserman and Koepfer, 1977) and has been invoked to explain changes in the mate recognition of *D. mojavensis* in Sonora so as to increase their sexual isolation from Baja flies (Zouros and d'Entremont, 1980). *Drosophila mojavensis* from southern California and Santa Catalina Island experience no sympatry with closely related species; thus the flies from these populations would not be expected to be as discriminating as Sonora flies against flies from other geographic host races. However, if the presence of *D. arizonae* in Sonora has caused Sonora *D. mojavensis* females to be more generally discriminating against other *mojavensis* strains, we would have expected this to show up in tests with CAL and SCI males. The fact that it did not means that if the presence of *D. arizonae* has caused character displacement in the sexual recognition system of sympatric *D. mojavensis*, the effect for some reason is strongest in the latter's interaction with *D. mojavensis* from Baja. While reproductive character displacement may have occurred in Sonora *D. mojavensis*, the possibility that variation in mate recognition systems (Butlin, 1989) of the different geographic host races evolved independently is not eliminated. In my laboratory we are currently analyzing the epicuticular hydrocarbons of *D. mojavensis* from CAL and SCI populations in order to evaluate the relative importance of these compounds in the observed patterns of sexual isolation. However, we fully expect rigorous study will reveal that the factors controlling the evolution of sexual isolation in this species to be diverse and complex.

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LITERATURE CITED

- BUTLIN, R. 1989. Reinforcement of premating isolation. In D. Otte and J. A. Endler (eds.), *Speciation and Its Consequences*. Sinauer, MA.
- ETGES, W. 1990. Direction of life-history evolution in *Drosophila mojavensis*, pp. 37–56. In J. S. F. Barker, W. T. Starmer, and R. J. MacIntyre (eds.), *Ecological and Evolutionary Genetics of Drosophila*. Plenum Press, N.Y.
- HEED, W. B. 1982. Origin of *Drosophila* in the Sonoran Desert, pp. 65–76. In J. S. F. Barker and W. T. Starmer (eds.), *Ecological Genetics and Evolution. The Cactus-Yeast-Drosophila-Model System*. Academic Press, Sydney, Australia.
- JOHNSON, W. H. 1980. Chromosomal polymorphism in natural populations of the desert adapted species *Drosophila mojavensis*. Ph.D. Diss. University of Arizona, Tucson, AZ.
- KIRCHER, H. W. 1982. Chemical composition of cacti and its relationship to Sonoran Desert *Drosophila*,

- pp. 143–158. In J. S. F. Barker and W. T. Starmer (eds.), *Ecological Genetics and Evolution: The Cactus-Yeast-Drosophila Model System*. Academic Press, Sydney, Australia.
- KOEPFER, H. R. 1987a. Selection for sexual isolation between geographic forms of *Drosophila mojavensis* I. Interactions between the selected forms. *Evolution* 41:37–48.
- . 1987b. Selection for sexual isolation between geographic forms of *Drosophila mojavensis* II. Effects of selection on mating preference and propensity. *Evolution* 41:1409–1412.
- KREBS, R. A. 1990. Genetics of sexual isolation in *Drosophila mojavensis*. *Behav. Genet.* 20:535–543.
- . 1991. Body size of laboratory and field populations of *Drosophila mojavensis*. *Dros. Inf. Ser. In press*.
- KREBS, R. A., AND T. A. MARKOW. 1989. Courtship behavior and control of reproductive isolation in *Drosophila mojavensis*. *Evolution* 43:908–912.
- MALOGOLOWKIN-COHEN, CH., A. S. SIMMONS, AND H. LEVENE. 1965. A study of sexual isolation between certain strains of *Drosophila paulistorum*. *Evolution* 19:95–103.
- MARKOW, T. A. 1981. Courtship behavior and control of reproductive isolation between *Drosophila mojavensis* and *Drosophila arizonensis*. *Evolution* 35:1022–1026.
- . 1982. Mating systems of cactophilic *Drosophila*, pp. 273–287. In J. S. F. Barker and W. T. Starmer (eds.), *Ecological Genetics and Evolution. The Cactus-Yeast-Drosophila-Model System*. Academic Press, Sydney, Australia.
- . 1988. Reproductive behavior of *Drosophila melanogaster* and *Drosophila nigrospiracula* in the field and in the laboratory. *J. Comp. Psychol.* 2: 167–173.
- MARKOW, T. A., J. C. FOGLEMAN, AND W. B. HEED. 1983. Reproductive isolation in Sonoran desert *Drosophila*. *Evolution* 37:649–652.
- MARKOW, T. A., AND E. TOOLSON. 1990. Temperature effects on epicuticular hydrocarbons and sexual isolation in *Drosophila mojavensis*, pp. 315–331. In J. S. F. Barker, W. T. Starmer, and R. J. MacIntyre (eds.), *Ecological and Evolutionary Genetics of Drosophila*. Plenum Press, N.Y.
- METTLER, L. E. 1963. *Drosophila mojavensis baja*, a new form of the *mulleri* complex. *Diss. Info. Services* 38:57.
- STALKER, H. D. 1942. Sexual isolation studies in the species complex *Drosophila virilis*. *Genetics* 27:238–257.
- TOOLSON, E. C. 1988. Cuticle permeability and epicuticular hydrocarbon composition of Sonoran Desert *Drosophila pseudoobscura*, pp. 505–510. In F. Schnal, A. Zaba, and D. L. Denzlinger (eds.), *Endocrinol Frontiers in Insect Physiological Ecology*. Wroclaw, Poland.
- TOOLSON, E. C., AND R. KUPER-SIMBRON. 1989. Laboratory evolution of epicuticular hydrocarbon composition and cuticular permeability in *Drosophila pseudoobscura*. *Evolution* 43:468–472.
- TOOLSON, E. C., T. MARKOW, L. JACKSON, AND R. HOWARD. 1990. Epicuticular hydrocarbon composition of wild and laboratory reared *Drosophila mojavensis*. *Ann. Entomol. Soc. Am. In press*.
- WASSERMAN, M., AND H. R. KOEPFER. 1977. Character displacement for sexual isolation between *Drosophila mojavensis* and *Drosophila arizonensis*. *Evolution* 31:812–823.
- ZOUROS, E., AND C. J. D'ENTREMONT. 1980. Sexual isolation among populations of *Drosophila mojavensis*: Response to pressure from a related species. *Evolution* 34:421–430.

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