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Source: *Evolution*, Vol. 37, No. 3 (May, 1983), pp. 649-652
Published by: Society for the Study of Evolution
Stable URL: http://www.jstor.org/stable/2408281
Accessed: 10/08/2009 17:02

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Corresponding Editor: R. MacIntyre

Evolution, 37(3), 1983, pp. 649–652

REPRODUCTIVE ISOLATION IN SONORAN DESERT *DROSOPHILA*

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Received May 10, 1982. Revised September 16, 1982

The *Drosophila* literature contains numerous examples of sexual isolation between different populations of the same species (Patterson and Stone, 1952; Dobzhansky, 1972). Certain species, such as *D. immigrans* (Ehrman and Parsons, 1980) and *D. virilis,* show isolation between strains from different geographic areas while others, such as *D. melanogaster,* do not (Petit et al., 1976). Since detailed ecological data on populations showing isolation are often lacking, it is difficult to assess the role of geographic isolation or host plant shifts in producing behavioral divergence. An exception to this case is the group of *Drosophila* species endemic to the Sonoran Desert of North America. Four species are known to breed in the necrotic tissues of various species of cacti in this desert which includes a large portion of northern Mexico (including Baja California) and parts of southwestern United States. The Gulf of California and the sand dunes near the mouth of the Colorado River act as major geographic barriers between pop-

TABLE 1. *Indices of reproductive isolation between populations of* D. nigrospiracula, D. mettleri, D. pachea, *and* D. mojavensis.

Species	Localities†		Number of each type of mating (females × males)				I ± SE
	A	B	A × B	A × B	B × A	B × B	
D. nigrospiracula	Santa Rosa (M) ×	Pto. Balandra (P)	25	25	20	19	−.01 ± .106
	San Esteban (I) ×	Pto. Balandra (P)	17	19	24	17	−.12 ± .113
	Santa Rosa (M) ×	San Esteban (I)	16	22	22	17	−.14 ± .112
D. mettleri	Tucson (M) ×	Pto. Balandra (P)	11	15	21	11	−.24 ± .127
D. pachea	Hermosillo (M) ×	La Paz (P)	13	17	24	13	−.22 ± .073
	Zaragosa (M) ×	Cuñaño (P)	24	24	24	24	.00 ± .000
	Zaragosa (M) ×	Miraflores (P)	10	32	22	16	−.35 ± .073*
	Desemboque$^+$ (M) ×	Todas Santos (P)	26	18	30	25	.03 ± .100
	Desemboque$^+$ (M) ×	La Paz (P)	16	17	22	20	−.04 ± .013
	San Bartolo (P) ×	Cuñaño (P)	16	6	10	7	.18 ± .158
	La Paz (P) ×	Cuñaño (P)	6	10	9	5	−.10 ± .182
D. mojavensis	Punta Onah (M) ×	San Telmo (P)	28	6	17	21	.36 ± .106*
	Santa Rosa (M) ×	San Telmo (P)	31	9	21	29	.33 ± .099*

† M = Mainland, P = Peninsula (Baja), I = Island in Gulf of California.
$+$ = del Rio San Ignacio.
* $P < .05$.

ulations of the four desert species. Moreover, three of the species are known to change host plants on opposite sides of the Gulf (Heed, 1978).

Drosophila mojavensis utilizes rotting stems of agria cactus (*Stenocereus gummosus*) in Baja California while populations in Sonora grow on organ pipe cactus (*Stenocereus thurberi*), where agria does not exist (except in the region of Desemboque del Rio San Ignacio including the collection site, Punta Onah). *Drosophila nigrospiracula* reproduces in cardón (*Pachycereus pringlei*) in Baja California, but shifts to saguaro (*Carnegiea gigantea*) on the mainland except along the coastal areas where both cacti exist. Another species, *D. mettleri,* shares the same host plants with *D. nigrospiracula* also shifting to saguaro on the mainland from cardón in Baja California. *Drosophila mettleri,* however, utilizes the soil which has been soaked with juice from a rotting cactus (Heed, 1977). These three species are all members of the large repleta species group. The fourth species found in the desert is *D. pachea,* a member of the nannoptera species group (Ward and Heed, 1970). This species has a unique nutritional dependency on senita cactus (*Lophocereus schottii*) which necessitates its association with this host plant on both sides of the Gulf of California (Heed and Kircher, 1965).

Zouros and d'Entremont (1980) have shown that there is partial reproductive isolation between Baja California and mainland populations of *D. mojavensis.* They argue that, with respect to behavioral isolation, host plant differences and geographic location are secondary in importance compared to the fact that *D. arizonensis,* the sibling species of *D. mojavensis,* is present on the mainland, sympatric with mainland *D. mojavensis.* The presence of a related species is thought to have put pressure on the mate recognition system of mainland *D. mojavensis,* thereby bringing about isolation through behavioral character displacement (Wasserman and Koepfer, 1977, 1980; Markow, 1981). The other three desert species have no close relatives sharing their ranges to any extent and should therefore be comparative material in this respect. The present report documents experiments designed to look for behavioral isolation between peninsular and mainland populations of *D. pachea, D. mettleri,* and *D. nigrospiracula.*

MATERIALS AND METHODS

The collection localities of the various *Drosophila* strains used are shown in Table 1. With the exception of *D. pachea,* and one strain of *D. mettleri* (from Tucson), all experiments were conducted within two or three generations after collection from nature. All flies were reared on rotting cactus (*D. nigrospiracula* and *D. mettleri*) or on banana medium supplemented with rotting cactus (*D. pachea* and *D. mojavensis*). Eclosing flies were aspirated out and virgin males and females were separated under light ether anesthesia. Flies were aged 10 days before being used in experiments.

All observations were conducted in plexiglass chambers constructed from a model kindly provided by Dr. Lee Ehrman. In each experiment, 20 pairs of flies (10 pair from each locality) were observed for one hour and the type and number of each mating combination were recorded. Each experiment was replicated at least three, and in some cases five, times. Flies were lightly dusted with pink or blue microdust (R-103-G119 from the U.S. Radium Corporation) 24 hs prior to the experiments so that flies from different localities could be distinguished. The color of each strain was alternated between replications. Mating experiments always commenced at 8:30 AM. Upon completion of a mating trial, females were dissected and checked for the presence of sperm in order to

TABLE 2. *Records of* D. mojavensis *and* D. arizonensis *reared from the same cactus rot.*

Collection number	Date	Locality	Cactus	Number of flies *D. arizonensis*	Number of flies *D. mojavensis*
A 131	Sept. 15, 1965	Caborca, Sonora	Saguaro fruit	24	16
A 155	Dec. 27, 1967	San Carlos, Sonora	Cina	3	20
A 233	Jan. 26, 1969	Navojoa, Sonora	Cina	80	3
A 240	Jan. 29, 1969	Hermosillo, Sonora	Cina	127	37
A 301	Jan. 30, 1971	Navojoa, Sonora	Cina	71	2
A 749	Oct. 8, 1979	Desemboque, Sonora	Agria	35	198
A 786	Nov. 10, 1980	Desemboque, Sonora	Agria	87	1,182

see if the number of females inseminated was the same as the number of matings observed. This procedure was followed because females of *D. nigrospiracula* and *D. mettleri* can multiply mate in one hour. In only one trial was multiple mating found and that particular mating trial (for *D. mettleri*) was not included in the data.

Joint isolation indices were calculated according to the following formula:

$$I = \frac{(n_{11} + n_{22}) - (n_{12} + n_{21})}{n}$$

where n_{11} is the number of matings between females of strain 1 and males of strain 1, n_{12} is the number of matings between females of strain 1 and males of strain 2, etc. (Stalker, 1942). The standard error of I is obtained from the formula devised by Malagolowkin-Cohen et al., (1965):

$$SE = \frac{(1 - I^2)}{n}.$$

RESULTS AND DISCUSSION

The observed matings and joint isolation indices are shown in Table 1. Most indices are in the negative direction suggesting a slight tendency toward outbreeding. The only significant positive isolation indices are those calculated for *D. mojavensis* which are similar to what has been previously reported by Zouros and d'Entremont (1980). Tests between *D. mojavensis* from the two regions show significant sexual isolation while combinations of the other three species do not.

How can it be explained that in three species, geographic isolation, even in conjunction with host plant shifts, has not produced significant behavioral isolation? As previously mentioned, one major ecological difference which sets *D. mojavensis* apart from the other three species is the sympatry of its sibling species, *D. arizonensis,* in parts of mainland Sonora. This sympatry is illustrated by the fact that *D. mojavensis* and *D. arizonensis* have been reared together at times from the same cactus rot (Table 2). The co-occurrence of larvae of these two species in the same substrate has been observed for both agria (two out of 22 collections in the Desemboque region) and cina (*Stenocereus alamosensis*; four out of 12 collections), the latter being the normal host plant for *D. arizonensis* in Sonora, Mexico. *Drosophila nigrospiracula* and *D. pachea* do not have close relatives living sympatrically on either side of the Gulf of California. *Drosophila mettleri* is overlapped by its closest relative, *D. eremophila,* in southern Sonora and the Cape region of Baja California (Heed, 1982). In this case, however, the two species do not share a common host plant. Our data for *D. mojavensis* as well as that of Zouros and d'Entremont (1980) show that the reproductive isolation is asymmetrical, that is, due to the behavior of mainland *D. mojavensis.* The absence of premating reproductive isolation in *D. pachea, D. nigrospiracula,* and *D. mettleri,* and the host plant overlap between *D. mojavensis* and *D. arizonensis* lend strong support to Wasserman and Koepfer's (1980) contention that character displacement for mating behavior has occurred in mainland populations of *D. mojavensis.*

There are other factors which might explain why *D. mojavensis* is the only one of the four species to show isolation. If *D. mojavensis* had inhabited the desert for a longer period of time, it might be expected to be the first species to feel the effect of isolation by the Gulf of California. However, available evidence implicates this species to be among the most recently evolved, not the oldest (Heed, 1982).

Another possible factor might be the population structure change associated with the host plant shift in *D. mojavensis.* Even though three of the cactophilic species shift host plants between the peninsula (and its extension of plants to the islands in the Gulf and coastal Sonora) and the remainder of the mainland, the shift for D. *mojavensis* includes a unique characteristic. The shift from agria cactus on the peninsula to organ pipe cactus on the mainland imposes an apparent change in population structure for *D. mojavensis* due to differences in the distributions and life forms of the two host plants. These differences are reflected in the observed retention of considerable inversion polymorphism in the ancestral, Baja California populations utilizing agria cactus (Heed, 1981). There is no analogous change in the population structure of *D. nigrospiracula* and *D. mettleri* since cardón and saguaro have approximately the same spatial distributions and life forms on opposite sides of the Gulf. It is presently impossible to determine how this host plant-dependent difference in population structure could have directly

TABLE 3. *A comparison of ecological parameters for mainland and peninsular populations for Sonoran Desert* Drosophila *species.*

Species	Host shift	Population structure shift	Presence of sibling
D. pachea	−	−	−
D. mettleri	+	−	−
D. nigrospiracula	+	−	−
D. mojavensis	+	+	+

brought about behavioral isolation in *D. mojavensis* (pleiotropy could be indirectly responsible). In any event, if the population structure difference were a major factor, we would expect less isolation in tests with *D. mojavensis* from Punta Onah since agria is available to those populations.

A comparison of the four desert *Drosophila* species is summarized in Table 3. Observations on the first three species show that geographic isolation even accompanied by a host plant shift was not enough to bring about behavioral isolation. *Drosophila mojavensis* differs from the first three in that it shows both a population structure shift and ecological overlap with a sibling species. The presence of *D. arizonensis* on the mainland provides a more defined pressure on the mate recognition system of *D. mojavensis* than does the apparent change in population structure associated with the shift to organ pipe. In our opinion, the data presented here support the hypotheses that character displacement for reproductive isolation has occurred in mainland populations of *D. mojavensis* but do not preclude the possibility that other factors may have played a role.

SUMMARY

Four species of cactophilic *Drosophila* are endemic to the Sonoran Desert of North America. Populations of each species have been collected from Baja California and from across the Gulf of Sonora on the mainland and tested for reproductive isolation. Sexual isolation has only been detected between mainland and peninsular populations of *D. mojavensis*. No assortative mating was observed among geographically isolated populations of the other three species. Two of the species not showing isolation, *D. nigrospiracula* and *D. mettleri,* exhibit a host plant shift from Baja to Sonora while the other species, *D. pachea* does not. We have explored several possible factors which might explain why *D. mojavensis* from Baja and the mainland show a strong isolation not observed in the other species. *Drosophila mojavensis* is the only species of the four which shows appreciable sympatry with its sibling species on the mainland and we favor the idea that the observed behavioral isolation has been most strongly influenced by this fact.

ACKNOWLEDGMENT

The capable technical assistance of Ms. Rosa Tang is greatly acknowledged. This research has been supported by grant #NS 15263 to T. A. Markow from the National Institutes of Health and by grant #DEB 7912924 to W. B. Heed from the National Science Foundation.

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Corresponding Editor: R. J. MacIntyre