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Sensitivity to larval density in populations of *Drosophila mojavensis*: influences of host plant variation on components of fitness

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Summary. Chromosomally polymorphic populations of *Drosophila mojavensis* from Baja California feed and breed on agria cactus, *Stenocereus gummosus*; whereas, monomorphic Arizona populations are associated exclusively with organ pipe cactus, *S. thurberi*. The effects of this host plant shift in expanding the kinds of feeding and breeding sites were assessed by manipulating larval density and recording differences in egg to adult development time and viability, and adult thorax size in both populations on artificially rotted substrates of both cactus species. Older agria rots increased development time but had no effect on viability. Organ pipe rots were qualitatively poorer substrates than agria rots for both monomorphic and polymorphic populations of *D. mojavensis*, especially at higher larval densities causing longer egg to adult development times, lower viabilities, and smaller thorax sizes than agria.

The Baja population expressed shorter development times, higher viabilities, and smaller thorax sizes than the Arizona population on both cactus substrates. No evidence for cactus host race formation was found. The Baja population was less sensitive to increasing larval densities for all fitness characters studied on both cactus substrates indicating greater developmental homeostasis than in the monomorphic Arizona population. These data support the hypothesized central-marginal population structure within this species coincident with the distribution of host plants and lend insight into the process of adaptive divergence at different life history stages caused by host plant shifts.

Key words: Drosophila – Polymorphism – Stenocereus – Host-plant-shift – Developmental homeostasis

Of the four *Drosophila* species endemic to the Sonoran desert in Arizona, Baja California, and Sonora, Mexico, two are considered polyphagic, using different host cacti for feeding and breeding within the geographical boundaries of their respective species ranges (Heed and Mangan 1986). Both of these species, *D. mojavensis* and *D. mettleri*, are widespread yet differ in a fundamental way: *D. mojavensis* breeds only in fermenting cactus tissues (Fellows and Heed 1972) where *D. mettleri* breeds only in soil soaked with cactus rot exudate (Heed 1977). Variation in host plant use by *D. mojavensis* suggests ongoing adaptation to different host cacti due to cactus specific differences in plant chemistry, growth form, and susceptibility to bacterial and yeast induced necrosis, "rot pockets", where this species carries out its entire life cycle (Heed 1978; Johnson 1980; Heed 1981).

In Arizona and Sonora, Mexico, *D. mojavensis* uses organ pipe cactus, *Stenocereus thurberi*, for breeding and feeding. Even though organ pipe is present in Baja California, *D. mojavensis* uses agria cactus, *S. gummosus*, there and in a small coastal area in Sonora (Fig. 1). Thus, agria is the preferred host plant even in areas where organ pipe is present (Fellows and Heed 1972). In the Mojave desert, California barrel cactus, *Ferocactus acanthodes*, is a major host plant, and *D. mojavensis* has also been found breeding in *Opuntia demissa* on Santa Catalina Island, California (Heed and Mangan 1986).

Such geographical variation in host plant use is coincident with a high degree of inversion polymorphism in the agria breeding Baja populations and nearly complete chromosomal monomorphism in the organ pipe and barrel cactus populations (Johnson 1980). Mettler (1963); Johnson (1980); and Heed (1981) have interpreted this pattern as a case of central-marginal population structure (Dobzhansky 1951; Lewontin 1957; Carson 1959; Brussard 1984) in which the older polymorphic populations have dispersed from Baja onto the mainland by shifting host plants.

The present study is concerned with variation in three fitness components, egg to adult viability and development time and adult thorax size, between Baja and mainland populations as potential adaptive responses to the host plant shift from agria to organ pipe cactus. Agria cacti are presumably more predictable feeding and oviposition sites than organpipe because agria rots are more abundant than organ pipe rots where they occur (Mangan 1982). However, stem diameters of agria are smaller than those of organ pipe and thus agria rots should be more prone to dessication. Organ pipe rots are considered more unpredictable for adult feeding and oviposition because they are less abundant, but last longer because stem diameters are twice that of agria (Heed 1981; Mangan 1982). Agria-inhabiting *D. mojavensis* may thus exhibit faster developmental rates than organ pipe populations. If adaptation to these host plants has occurred, each population may also be expected to exhibit higher relative fitness on its own host plant.

Among cactophilic *Drosophila*, differences in cactus tissue composition (Kircher 1982; Fogleman et al. 1982) and

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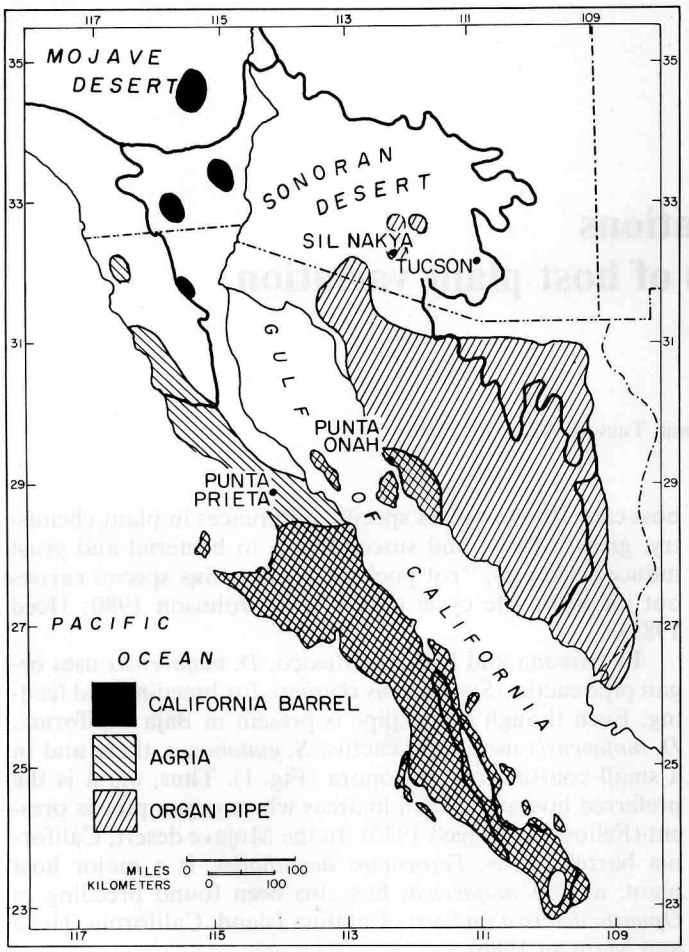

Fig. 1. Geographical boundaries of the species range and host cacti of *Drosophila mojavensis* in the Sonoran and Mojave deserts of the southwestern USA and Mexico. Collecting sites and cactus names are discussed in the text

variation in the microbial flora within rots may also influence development time. Larvae of *D. mojavensis* feed upon the yeasts, bacteria, and stem decomposition by-products in both agria and organ pipe rots (Fogleman et al. 1981; Fogleman et al. 1982). A major factor determining the yeast species present in both agria and organpipe rots is presumed to be the stage of decomposition of the rot (Starmer 1982a; Fogleman and Starmer 1985). The influence of rot age on components of fitness was assessed in this study.

Variation in larval development time in *Drosophila* is influenced mainly by temperature (Chiang and Hodson 1950; Tantaway and Malluh 1961) and food supply (Sokoloff 1966; McFarquhar and Robertson 1963). Considerable evidence for genetic variation in development time also exists (Sang and Clayton 1957; Hiraizumi 1961; Marien 1965; Spiess and Spiess 1966), but adaptive significance of such variation in developmental rates is obscured by lack of breeding site data. Adult thorax size in *D. mojavensis* is correlated with ovariole number in females (Mangan 1978; Heed, unpublished work) which is related to adult reproductive performance in several *Drosophila* species (Robertson 1957; Atkinson 1979). Because *D. mojavensis* rarely shares breeding sites with other species (Fellows and Heed 1972; Heed and Mangan 1986), interspecific competition is probably uncommon (Mangan 1978).

Use of different host cacti within the species range of *D. mojavensis* allows for direct experimental manipulation of both flies and cacti to determine possible genetic-environment interactions which may evidence adaptation to different host plants. Thus, the specific objectives of this study were; 1) to determine the effect of rot age on egg to adult development time and viability, 2) to determine the degree to which differences between agria and organ pipe rots influence expression of these fitness components and adult thorax size, 3) to determine the effects of larval density on these fitness components on both agria and organpipe rots, and 4) to assess differences in these components of fitness as related to adaptation to both agria and organ pipe cacti.

Materials and methods

Rot age experiment. Natural rots of agria cactus, *S. gummosus*, containing immature *D. mojavensis* were collected in Punta Onah, Sonora in November, 1984 (Fig. 1, site and collection A879). Of three fermenting arms returned to the lab, one (8 × 30 cm) was immersed in an equal volume of distilled water, mashed, and thoroughly strained with cheese cloth to collect the juice containing yeasts and bacteria to create laboratory microbial cultures (Mangan 1982). Fresh agria pieces were immersed in a 10 percent solution of this rot juice in 5 gallon jars and incubated at 37° C. These cultures were changed onto fresh cactus at 10–14 day intervals for two months until the experiment began. Then, four fresh agria arms (10 × 30 cm) were injected with 10 ml of rot juice and placed in airtight containers. These inoculated arms were used throughout the experiment.

About 100 adult flies emerged from the two other agria rots and were introduced into a population cage. To provide fresh food and a place for oviposition, two of eight cups on this cage containing banana-malt-yeast-agar food were changed on alternate days, were retained and fitted with a plastic beaker in which a hole had been drilled large enough for a sponge cork. All eclosed adults were returned to the cage from these cups ensuring a large population size.

Eggs were collected on fresh food in cups on this cage over 6 h intervals. After removal from the food surface, the eggs were surface sterilized by repeated washing in sterile water and immersion in 70 percent ethanol for 10 min. Groups of 100 eggs were counted out onto 1 cm^2 squares of filter paper and placed onto 25 g of rotted agria, inoculated as described above, in sterile cups fitted with corked plastic tops. Eight replicate cultures were obtained from each of 15 samples of rotted agria aged from 5 to 34 days. All cultures were grown in an incubator with a 16:8 hr LD photoperiod with temperatures of 27° C during the day and 16° C at night (Mangan 1982).

Egg to adult viability and development time were calculated for each replicate by counting the number of eclosing adults daily. The number of dead and unfertilized eggs were counted and subtracted from the total to calculate combined larval-pupal viabilities.

Density sensitivity experiment. About 200–300 *D. mojavensis* emerging from an organ pipe rot, collected from the Santa Rosa Mountains near Sil Nakya, Arizona (A900)

Table 1. Inversion frequencies in natural populations of D. mojavensis from Punta Prieta, Baja California Norte, the Santa Rosa Mountains near Sil Nakya, Arizona, and Punta Onah, Sonora. Year and reference number of collection are given

Site	*N*[a]	*Chromosome 2*[b]				*Chromosome 3*	
		LP	ST	BA	SL	MU	ST
Punta Prieta, B.C.N. 1985 (A896)	230	0.43	0.31	0.25	0.01	0.94	0.06
Santa Rosa Mtns., Sil Nakya, Ariz. 1985 (A900)	214	1.00	0.00	0.00	0.00	0.01	0.99
Punta Onah, Sonora. 1984 (A856)[c]	40	0.98	0.02	0.00	0.00	0.05	0.95

[a] N refers to the number of chromosomes sampled
[b] Gene arrangements are labelled following Mettler (1963) and Johnson (1980); Second chromosome: *LP* La Paz, *ST* Standard, *BA* Baja, and *SL* San Lucas. Third chromosome: *MU* Mulege, *ST* Standard
[c] Data from Ruiz (unpublished work)

were used to start a population cage, as described above. About 2,000 *D. mojavensis* emerging from 17 agria rots from Punta Prieta, Baja California Norte (A896) were used to start another population cage. Both populations were scored for chromosomal polymorphism (Table 1).

In this experiment, rots were initiated with pure cultures of bacteria and yeast species for comparison with the rot juice method described above. Fresh 25 g pieces of cactus on 75 g of sand in 1/2 pint milk bottles sealed with a sponge cork were autoclaved. Each was inoculated with a pectolytic bacterium, *Erwinia carnegieana*, and seven species of yeast common to natural rots of both cactus species (Starmer 1982a; Fogleman and Starmer 1985). Yeasts used were: *Pichia cactophila*, *P. mexicana*, *P. amethionina* var. *amethionina*, *Cryptococcus cereanus*, *Candida valida*, *C. ingens*, and *C. sonorensis*.

Eggs were collected from each population cage, surface sterilized as described above, counted out onto filter paper in lots of 50, 100, 200, and 400, and placed on freshly inoculated agria or organ pipe cactus. Eggs from both populations were counted onto both species of cactus at each density each day. All cultures were grown at 25° C with a 14:10 LD photoperiod.

Egg to adult viability and development time and adult thorax size were recorded as described above. All data from this 2 populations × 2 cactus × 4 densities design were analyzed in an ANOVA (SAS, Helwig and Council 1979). Viability data were arc sin transformed and development time data were log transformed prior to analysis.

Results

Chromosomal polymorphism

The population from Punta Prieta was polymorphic for the LP, ST, BA, and SL second chromosome gene arrangements and for both third chromosome gene arrangements (Table 1). The SL gene arrangement has not been previously recorded from this locality (Johnson 1980). The Arizona population was fixed for the LP gene arrangement, and only 2/214 individuals were heterozygous for the third chromosome. This is the first record of the MU gene arrangement in this region. Overall, these inversion frequency differences conform with earlier cytological surveys (Johnson 1980; Ruiz (unpublished work).

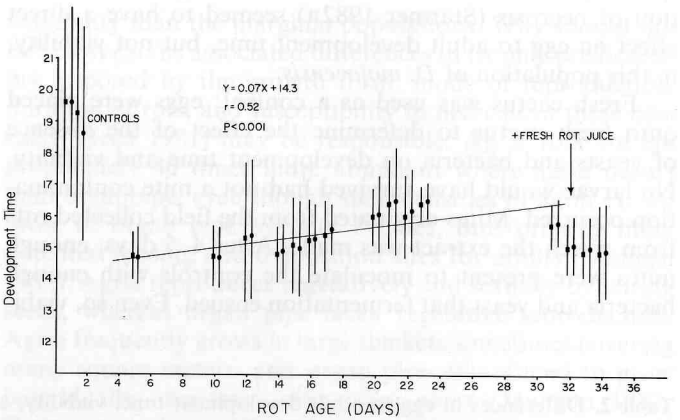

Fig. 2. Correlation between egg to adult development time (days) and age of rotted agria. Female (squares) and male (circles) means (±2 SE) are the averages of 8 replicates each. Linear regression of development time on rot age is plotted. Control groups were grown on fresh, unrotted cactus (see the text for details)

Rot age experiment

Egg to adult development time increased with age of the fermented tissue (Fig. 2). Male and female development times were not significantly different ($P > 0.05$). However, egg to adult viability increased as the rots aged suggesting that as cactus tissue softens with increasing decomposition, larval survivorship increases. Egg to adult development time and viability were positively correlated over age of rots ($r = 0.247$, $P < 0.05$).

That the cause for increased development times was related to changes in the abundance and/or composition of the yeasts and bacteria present was demonstrated by adding fresh rot juice to the oldest three rot samples when the eggs were placed onto the tissue (Fig. 2). This extract was obtained from freshly collected agria rots in Punta Onah after the experiment began, and presumably contained a richer yeast flora than the rots experimentally aged for over a month. Development times in this set of treatments were shortened by 1.14 days from the previous three aged rot sets (1 tailed t-test, $P < 0.001$, Fig. 2). Thus, changes in yeast

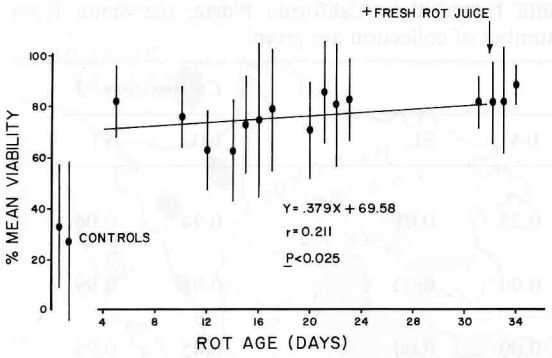

Fig. 3. Association between egg to adult viability and age of agria rots. Means (±2 SE) are the averages of 8 replicates each. The linear regression between viability and rot age is plotted. Control groups were grown on fresh, unrotted cactus (see the text for details)

species present and their abundance throughout the duration of necrosis (Starmer 1982a) seemed to have a direct effect on egg to adult development time, but not viability, in this population of *D. mojavensis*.

Fresh cactus was used as a control: eggs were placed onto fresh cactus to determine the effect of the absence of yeasts and bacteria on development time and viability. No larvae would have survived had not a mite contamination occurred. Mites originated from the field collected rots from which the extract was made. After 4–5 days, enough mites were present to inoculate the controls with enough bacteria and yeast that fermentation ensued. Even so, viability was very low and development times were elongated in the controls (Figs. 2 and 3). Using axenic flies and sterile cactus, Starmer (1982b) demonstrated that microbe-free cactus tissue cannot support larval growth.

Density sensitivity experiment

Development time. The *D. mojavensis* population from Arizona expressed longer egg to adult development times than the Baja population indicating geographical variation in development time between these two populations (Tables 2 and 3). On organ pipe cactus still longer development times resulted in both populations, and most notably when initial egg densities were greater than 100 ($P<0.05$). Average development time lengthened with increasing density, i.e. 12.71 days (50 eggs) ≅13.33 days (100 eggs) <14.33 days (200 eggs) <17.36 days (400 eggs), accounting for a significant interaction between cactus and density (Table 3).

Egg to adult viability. Egg to adult viability was higher over all treatments in the Baja population than in the Sonoran population, 92.95 vs. 66.15 percent, respectively (Tables 2 and 3). Differences induced by the cactus substrates were not as great for this character, where viability in the organ pipe treatments averaged 73.85 percent vs. 84.55 percent in agria. In part, this resulted from density-induced differences in viability that were only apparent at the highest density level of 400 eggs and because organ pipe caused lower viabilities at this density than did agria (Table 2). Rankings of density specific percent viabilities, averaged over substrates, were: 97.81 (50 eggs) ≅89.15 (100 eggs)

Table 2. Differences in egg to adult development time, viability, and thorax size caused by density in two populations of *D. mojavensis* cultured on two host cacti, agria (AG), *Stenocereus gummosus* and organ pipe (OP), *S. thurberi*. Row 1 in each cactus treatment shows mean development time in days (SE), Row 2 shows percent mean viabilities (SE), and Row 3 shows mean female thorax sizes in mm (SE) over mean male thorax sizes in mm (SE). All data shown are means of 3 replicates, except where noted

		Population							
		Santa Rosa Mountains, AZ (A900)				Punta Prieta, B.C.N (A896)			
		Density (# eggs/25 g. cactus)							
		50	*100*	*200*	*400*	*50*	*100*	*200*	*400*
OP	1.	13.19 (0.40)	14.13 (0.25)	16.27 (0.32)	20.15 (0.40)	12.46 (0.14)	13.03 (0.35)	14.98 (0.60)	21.27 (0.45)
	2.	70.74 (6.99)	75.39 (2.73)	49.75 (5.28)	17.27 (6.49)	91.80 (4.70)	85.28 (6.90)	73.61 (6.63)	41.30 (5.35)
	3.	1.079 (0.011)	0.9566 (0.019)	0.8893 (0.023)	0.8080 (0.006)	1.017 (0.021)	0.9652 (0.037)	0.8842 (0.027)	0.7927 (0.017)
		0.9895 (0.009)	0.8888 (0.019)	0.8319 (0.037)	0.7769 (0.015)	0.9535 (0.028)	0.9041 (0.034)	0.8225 (0.031)	0.7542 (0.014)
AG	1.	12.86 (0.42)	13.26 (0.38)	13.22 (0.30)	14.35 (0.47)	12.37 (0.17)	12.99 (0.86)	12.56[a] (0.43)	13.66[a] (0.47)
	2.	73.55 (0.73)	59.36 (7.05)	78.43 (6.31)	52.75 (5.21)	85.55 (5.11)	84.28 (5.07)	84.23[a] (14.7)	63.54[a] (8.34)
	3.	1.086 (0.006)	1.065 (0.004)	1.015 (0.014)	0.9248 (0.015)	1.060 (0.003)	1.045 (0.003)	0.9363[a] (0.014)	0.9106[a] (0.025)
		0.9917 (0.010)	0.9775 (0.020)	0.9494 (0.003)	0.8686 (0.008)	0.9811 (0.014)	0.9638 (0.011)	0.9363[a] (0.014)	0.8448[a] (0.012)

[a] Data averaged over 2 replicates only

Table 3. Analysis of variance results for egg to adult viability and development time, female thorax size, and male thorax size in two populations of *D. mojavensis* reared at different larval densities on two species of columnar cactus, *Stenocereus gummosus* and *S. thurberi*. Viability data were arc sin transformed and development time data were $\log_{(10)}$ transformed prior to analysis

Source of variation	df	Viability		Development time		Female thorax size		Male thorax size	
		Sums of squares	F	Sums of squares	F	Sums of squares	F	Sums of squares	F
Model	15	3.424	6.90*****	0.224	29.50*****	0.388	28.16*****	0.268	14.67*****
Population	1	0.794	24.02*****	0.004	7.17***	0.004	4.08*	0.002	1.89
Cactus	1	0.139	4.22**	0.054	106.36*****	0.092	99.85*****	0.062	50.75*****
Pop* Cactus	1	0.016	0.47	0.000	0.00	0.000	0.00	0.000	0.01
Density	3	1.710	17.24*****	0.103	67.64*****	0.251	91.16*****	0.174	47.50*****
Pop* Density	3	0.029	0.30	0.001	0.93	0.003	0.98	0.001	0.32
Cactus* Density	3	0.524	5.28***	0.048	31.50*****	0.018	6.40**	0.016	4.34**
Pop* Cactus* Density	3	0.067	0.068	0.002	1.30	0.002	0.62	0.001	0.31
Error	30	0.992		0.015		0.028		0.037	

* $P=0.0525$; ** $P<0.05$; *** $P<0.01$; **** $P<0.005$; ***** $P<0.0001$

$\cong$82.03 (200 eggs) $\gg$44.25 (400 eggs). Organ pipe caused lower viabilities at the highest density level than agria, again accounting for an interaction between cactus and density (Table 3).

Thorax size. Male and female flies reared on agria were larger than those reared on organ pipe. Sonoran females were larger than Baja flies, but only marginally ($P=0.0525$, Table 3). Thorax sizes were significantly different from each other at each density for males and females (Tables 2 and 3). Organ pipe cactus produced significantly smaller flies at higher densities than agria, accounting for the significant cactus by density interaction terms (Table 3).

Discussion

Agria cactus is a qualitatively better breeding substrate than organ pipe as evidenced by shorter development times, higher viabilities, and larger thorax sizes expressed by both Baja and Arizona populations of *D. mojavensis*, especially at higher densities. Because thorax size is correlated with ovariole number (Mangan 1978), larger body sizes characteristic of the organ pipe populations may also imply greater potential fecundity. Organ pipe rots cannot support as many flies on a per gram basis as agria, thus supporting the hypothesis that organ pipe dwelling *D. mojavensis* are marginal populations (Mettler 1963; Johnson 1980; Heed 1981) not only geographically and chromosomally but also ecologically because they have made a trophic shift onto an poorer resource for larval growth and development. Baja California is assumed to be where agria breeding *D. mojavensis* originated because all inversions are present there, including a rare ancestral gene arrangement (Johnson 1980), all major host plants grow there yet agria is the preferred host plant and is most abundant there (Fellows and Heed 1972; Heed 1981; Heed 1982; Mangan 1982).

The greater relative fitness, i.e. shorter development times and higher viabilities, expressed by the Baja population across cactus substrates and larval densities suggests that the central, chromosomally polymorphic populations are more developmentally homeostatic than are the marginal populations. Developmental homeostasis in fitness characters (Lerner 1954) implies that the Baja populations of *D. mojavensis* are better buffered against environmental variability than the marginal populations. Why should this be? Host cactus associated differences in trophic predictability imposed by the growth form, mode of reproduction, duration of rots, and susceptibility to necrosis of these host cacti (Heed 1981) may be responsible. Agria rots are approximately 40 times more abundant where agria occurs than organpipe, even though stem densities of agria exceed those of organ pipe by only 7 times, thus offering more potential feeding and oviposition sites for adults (Mangan 1982). Agria reproduces vegetatively and sexually by setting seeds, whereas organ pipe lacks vegetative reproduction. Agria frequently grows in large thickets sometimes covering many square meters, and organ pipe plants tend to grow individually, dispersed over large areas (Mangan 1982; Etges, pers. observation). Agria stems are on average half the diameter of organ pipe stems, so individual agria rots tend to be smaller than those of organ pipe (Mangan 1982). Agria rots should be more prone to dessication than organ pipe rots. Shorter development times in the Baja populations may have resulted from selection for faster developmental rates due to rot dessication. Duration of natural rots is not known, but is assumed to be positively correlated with stem diameter. Stage of rot decomposition can influence egg to adult development time and viability because of changes in microbial food abundance (Figs. 2 and 3) or accumulation of secondary plant compounds (Fogleman et al. 1986). Thus, greater homeostasis in larval fitness components in the agria inhabiting populations may have resulted from occupying a more stressful larval environment due to rot dessication.

The results of this study suggest that natural populations of organ pipe breeding *D. mojavensis* encounter nutritionally poorer substrates than agria populations. Abundance of yeast cells in organ pipe rots can be 3–4 fold lower than in agria (Fogleman and Starmer 1985). However, thorax sizes of wild-caught females of *D. mojavensis* from organ pipe in Sonora are larger than those from agria in Baja, $\cong$1.0 vs. 0.8–0.9 mm, respectively (Mangan 1982). Thorax sizes of Sonoran organ pipe breeders are similar to those of flies reared on organpipe at densities of between 50–100 eggs per 25 g of organ pipe (Table 2). Similarly, thorax sizes in natural populations reared from agria correspond to density levels of 200–400 eggs per 25 g agria in the present study, suggesting that agria can support higher

population densities of larval *D. mojavensis* than organ pipe. Greater body sizes of organ pipe breeders suggest that larval densities in nature are lower than in agria. These conclusions must be interpreted with caution because of the large effects of temperature on body size in *Drosophila* species. Because adult body size in *Drosophila* is partly determined by larval nutrition (Sang 1956), adjustment to a poorer nutritional environment may have also been accomplished by increasing development time (Table 2).

The host plant shift from agria to organ pipe cactus represents an expansion of possible breeding and feeding sites which has shaped the population structure of *D. mojavensis* and the life history differences between populations. Both 'central' and 'marginal' populations exhibit higher relative preadult fitness on the preferred host plant, agria, suggesting that the organ pipe-breeding populations of *D. mojavensis* have apparently not evolved sufficiently to have overcome their ancestral agria habitat requirements. Lack of any population by environment interactions in preadult fitness characters (Table 3) suggests that allopatric host cactus use among populations has not produced true host races (sensu Futuyma and Mayer 1980; Futuyma and Peterson 1985; Jaenike 1981; Jermy 1984). Oviposition preference for agria was demonstrated in organ pipe forests where no agria grow (Fellows and Heed 1972) and shown to be heritable in laboratory choice tests (Lofdahl 1985). Thus, *D. mojavensis* is a polytypic species that has diverged into less favorable environments yet to have caused genetic changes leading to greater adaptation in preadult fitness characters or postmating reproductive isolation (Zouros 1973).

However, evaluation of the role of adaptation to agria and organ pipe cacti must take into account all life history stages. Cactus specific differences influencing adult survival need also be considered. The present study suggests that body sizes of organ pipe breeders are larger than those of agria breeders (Table 3). Selection for increased dispersal ability, and hence greater body sizes, may explain these differences in body size because of the greater distances between potential breeding sites in organ pipe populations (Mangan 1978). Thus organ pipe populations may be better adapted for longer flight. This may represent an intraspecific example of the positive correlation between thorax size and host cactus stem diameter found among all Sonoran desert *Drosophila* (Heed and Mangan 1986), emphasizing the role of breeding site geometry and rot duration in the evolution of cactophilic *Drosophila*.

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