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GENETICS OF HOST-CACTUS RESPONSE AND LIFE-HISTORY EVOLUTION AMONG ANCESTRAL AND DERIVED POPULATIONS OF CACTOPHILIC *DROSOPHILA MOJAVENSIS*

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Abstract.—The extent of host-specific genetic variation for two life-history traits, egg to adult developmental time and viability, and one morphological trait closely tied to fitness, adult thorax size, was exposed by employing a nested half-sib/full-sib breeding design with Baja and mainland populations of *Drosophila mojavensis* recently extracted from nature. This study was motivated by the presence of substantial variation in life histories among populations of *D. mojavensis* that use the fermenting tissues of particular species of columnar cacti for feeding and breeding in the Sonoran Desert. Full-sib progeny from all sire-dam crosses were split into cultures of agria cactus, *Stenocereus gummosus,* and organ pipe cactus, *S. thurberi,* to examine patterns of genotype-by-environment interaction for these fitness components. Baja flies expressed shorter egg-to-adult developmental times, higher viabilities, and smaller body sizes than mainland flies consistent with previous studies. Significant sire and dam components of variance were exposed for developmental time and thorax size. Genotype-by-environment interactions were significant at the level of dams for developmental time and nearly significant for viability ($P = 0.09$). Narrow- and broad-sense heritabilities were influenced by host cactus, sex, and population. No strong pattern of genetic correlation emerged among fitness components suggesting that host-range expansion has not been accompanied by formation of coadapted life histories, yet the ability to estimate genetic correlations and their standard errors was compromised by the unbalanced nature of the data set. Genetic correlations in performance across cacti were slightly positive, evidence for ecological generalism among populations explaining the observed pattern of multiple host cactus use within the species range of *D. mojavensis.*

Key words.—Adaptation, cactus, *Drosophila mojavensis,* genetic correlation, heritability, host race, life history, reaction norm, *Stenocereus.*

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Considerable attention has been devoted to the role of antagonistic pleiotropy among fitness components in outbred populations (Williams 1957; Rose 1982; Charlesworth 1984) because it allows for heritable variation in components of fitness as long as the genetic correlations between them are negative (Robertson 1955). There is little doubt that classical notions concerning the erosion of heritable variation in fitness (Fisher 1930) allow for genetic variation in life-history traits in equilibrium populations (Rose 1982; Roff and Mousseau 1987).

If antagonistic pleiotropy explains life-history variation in most organisms, then how do changes in life histories occur that have produced the profuse demographic variation between populations or species so often observed in nature? Empirical tests of hypotheses generated by life-history theory should require detailed field and laboratory analysis if observed live-history variation is to be reliably interpreted as a functional adaptation to environmental complexity. Demographic theory, using both single-locus and polygenic models with age-structured populations and weak selection (Charlesworth 1980; Lande 1982), suggests that in constant environments, population growth rates, "*r*," will be maximized. When environments can vary or selection is stronger, the use of such demographic arguments to predict life-history patterns requires knowledge of a population's age distribution, variance, and covariance among life-history traits of each age class, current and past sensitivity to environmental variability, and information on the genetic architecture of these traits (Orzack and Tuljapurkar 1989; Tuljapurkar 1990). This complexity alone presents a serious challenge to understanding life-history evolution, but more daunting is the general conclusion that life histories may take on many forms, all with similar fitnesses and that "there is considerable potential for neutral evolution with respect to life history" (Orzack and Tuljapurkar 1989, p. 921), that is, several different life histories may evolve in response to the same environmental factors. Reconciling this theory

with earlier ideas and observations seeking to explain the maintenance of fitness variation in natural populations (Cole 1954; Stearns 1976; Lewontin et al. 1981; Etges 1982; Dingle and Hegmann 1982; Istock 1982a,b, 1984; Reznick, 1985) will be possible by determining the functional role of existing life-history variation in natural populations in relation to known environmental factors. If knowledge of potential natural selection on life-history traits is lacking or incomplete, measured genetic variance in life history will be of little help in resolving why evolution might result in one of several potentially "neutral" life-history trajectories.

To this end, analysis of the genetic bases of life histories in cactophilic *Drosophila mojavensis* was undertaken to determine the form of genetic variation and covariation among fitness traits in populations that use different host cacti in nature. The main objective was to assess the effects of cactus substrates on expression of variation in fitness and determine the extent of within-population genetic trade-offs in life-history traits: presence of within-population genetic variation for fitness traits in this species is of direct significance to the functional role of life-history variation in nature because the ecology of feeding and breeding sites has been documented (Fellows and Heed 1972), the pattern of host use has given rise to genetic differences among populations in cactus-associated life histories signifying the presence of host races (Etges and Heed 1987; Etges 1989a, 1990), and physiological mechanisms of adaptation to different host cacti have been studied in detail (Starmer et al. 1977; Etges and Klassen 1989; Etges 1989b).

History of Host Range Expansion in D. mojavensis.—The pattern of genetic variability in life histories among populations of *D. mojavensis* has resulted from historical, genetic, and behavioral factors. Within geographical regions, fermenting tissues of single host cactus species are used almost exclusively, even if other suitable hosts are present (Heed 1978; Ruiz and Heed 1988). In Baja, the flies primarily use agria cactus, *Stenocereus gummosus,* and almost never use organ pipe, *S. thurberi,* even though organ pipe occurs over much of the peninsula (Heed and Mangan 1986; Etges pers. obs.). In most of mainland Sonora, northern Sinaloa, and Arizona, *D. mojavensis* uses organ pipe provided other preferred hosts are absent. It uses agria in a very localized patch in coastal Sonora and *Stenocereus alamosensis* in scattered locations in Sonora and Sinaloa (Ruiz and Heed 1988). Preference for agria over organ pipe rots has been suggested in both field and laboratory choice tests in mainland populations of *D. mojavensis* (Fellows and Heed 1972; Downing 1985), but no genetic evidence for host preference exists. In the Mojave Desert in southern California, *D. mojavensis* uses barrel cactus, *Ferocactus acanthodes,* and a population of *D. mojavensis* has also been found using *Opuntia demissa* on Santa Catalina Island near Los Angeles, California. Thus, host cactus distribution and preference for particular cacti available at particular locations may explain the observed oligophagy among populations of *D. mojavensis.*

The transition from agria in Baja California to organ pipe on the mainland is thought to have occurred as *D. mojavensis* invaded the mainland, which led to subsequent geographic isolation of the derived, mainland populations (Heed 1981, 1989). Since the invasion, there has been considerable evolution of life-history differences (Etges 1990) and formation of premating reproductive isolation between mainland and Baja populations (Wasserman and Koepfer 1977; Krebs and Markow 1989). Baja populations have shorter egg-to-adult developmental times, higher viabilities, shorter thorax sizes, lower lifetime fecundities, and slower maturation rates than mainland populations (Etges and Heed 1987; Etges and Klassen 1989).

Baja California is considered to be the likely ancestral range of *D. mojavensis* where, in allopatry, this species arose from a mainland ancestor (Ehrman and Wasserman 1987; Ruiz et al. 1990). Both extant sibling species, *D. arizonae* and *D. navojoa,* have mainland distributions (Heed 1982). Baja California populations are considered older than mainland Sonora and Arizona populations of *D. mojavensis* because of the presence of considerable inversion polymorphism and extensive population structuring (all seven described gene arrangements can be found there), discovery of a complex ancestral gene arrangement containing three inversions not found elsewhere, widespread availability of the preferred host cactus (agria) there and not elsewhere, and the presence of most secondary host cacti used by *D. mojavensis* outside of Baja (Johnson 1980; Heed 1982). Mainland populations are nearly chromosomally monomorphic leading toward a classical central-marginal pattern (Johnson 1980).

The specific objective of this study was to measure the within-population genetic vari-

ance/covariance structure of life-history traits using half-sib/full-sib analysis of variance within and between populations of *D. mojavensis* cultured on agria and organ pipe cacti. A split-plot design was used to determine the extent of genotype-by-environment interactions indicated by the reaction norms of sire and dam family groups on both agria and organ pipe cacti for those life-history characters that have shown evolutionary change between populations. Great care was taken to simulate natural conditions in the laboratory (cf. Istock et al. 1976; Gould 1979; Rausher 1984; Via 1984a) because the estimation of genetic effects under natural conditions has yet to be performed (cf. Clausen et al. 1940; Perrins and Jones 1974; Berven 1982; Jaenike 1986; Mitchell-Olds 1986; Shaw 1986; Newman 1988; Prout and Barker 1989; Via 1991). I was most interested in demonstrating the potential for short-term life-history evolution within populations (Via 1984a, 1990; Via and Lande 1985) by assessing environment-dependent expression of life histories that have evolved since the host shift from agria to organ pipe when *D. mojavensis* invaded mainland Sonora from Baja California.

Materials and Methods

Natural populations of *Drosophila mojavensis* were sampled from Punta Prieta, Baja California Norte (BCN) and Punta Onah in the Desemboque region of Sonora, Mexico in March 1989. Wild adults were aspirated directly from agria rots located by searching over several thousand plants (Mangan 1982) and combined with all adults that emerged from rots brought back to the lab. This sampling scheme insured that these collections were large, outbred population samples from nature, even though single-rot demes are probably not inbred (Quezada-Diaz et al. 1992). The Baja stock was founded with 800 adults aspirated from 16 rots plus 5042 adults that emerged from 12 agria rots, and the mainland stock was founded with 210 adults aspirated from 8 agria rots plus 196 adults that emerged from 3 agria rots. Though collected from agria, flies from Punta Onah were selected as representatives of a mainland population because they share genetic, morphological, and behavioral attributes with other mainland populations, and are located at nearly the same latitude as Punta Prieta, BCN, diminishing documented latitudinal effects on these life-history traits (Etges 1990). Agria and organ pipe cacti are sympatric at Punta Onah, yet the flies do not use organ pipe here. Outside this patch of agria, large contiguous populations of organ pipe cacti are present, particularly to the north of the Desemboque area, allowing for gene flow between *D. mojavensis* in Punta Onah and other mainland demes. There is no evidence for adaptation to agria by *D. mojavensis* in Punta Onah (Etges 1990). Both populations were maintained in shell vials using banana-Karo-malt-brewer's yeast-agar food with proprionic acid added as a mold inhibitor (Etges and Heed 1987) and were increased in size for two to three generations to remove any effects of host experience before the start of the experiment.

Large (12,720 cm^3) plexiglass mating chambers were established with approximately 5000 adults from each of the vial-maintained populations. Flies within each mating chamber were allowed to age for 10 to 14 days and fed banana food in screw-on cups. Eggs were collected from six cups per chamber over 24-h intervals and placed in 8–10 half-pint milk bottles per population containing banana food to minimize nutritionally induced maternal/environmental effects on sires and dams resulting from mass culture of the parental stocks in vials. The bottle cultures were grown at medium larval densities and maintained in an incubator with a 14:10 LD photoperiod that cycled from 27° to 17°C. All emerging adults were separated by sex and aged for a week.

Within populations, single sires were mated with two virgin females. After 4–5 days, dams were separated into individual oviposition chambers. Each chamber consisted of a 1-dram shell vial glued into one well of a 24-well microtiter plate with the open end of the vial closed by a snap cap with a hole covered with nylon netting. Eggs were collected over 6-h intervals from each group of 24 dams by inverting the plate onto a flat of 4% ethanol-enriched lab food: the females fed and oviposited through the nylon mesh covering each vial. Each day, eggs were collected from two sets of 12 sire-dam combinations from each population. Eggs from each dam were vigorously washed in sterile water, 70% ethanol, and again in sterile water. Ten eggs were counted onto a 1-cm square of filter paper and placed onto fermenting cactus tissue in 8-dram shell vials.

Cactus Food.—Live agria and organ pipe stems were collected and fresh frozen. Variation in tissue quality among arms of each species was re-

duced by mixing subsamples from several arms. These cactus tissues were homogenized in a blender into a pourable slurry that was then heated with deionized water and agar in the following proportions: 1000 g fresh cactus: 510 cc water: 5.2 g agar. Only older, brown cactus tissues were used (Etges 1989a). This mixture was then autoclaved and cooled, and 20 cc of this food was dispensed into 8-dram shell vials containing 10 g of sterile aquarium gravel and plugged with cotton. Vials were slanted before cooling, maximizing the food surface area within vials and then frozen in sealed containers. Three batches of each type of cactus food were prepared during the experiment. For daily use, vials were allowed to reach room temperature and inoculated with 0.1 cc of a suspension of a pectolytic bacterium and 0.1 cc of a suspension of seven yeast species common to agria and organ pipe rots in nature (Starmer 1982; Fogleman and Starmer 1985); *Pichia cactophila, P. mexicana, P. amethionina* var. *amethionina, Cryptococcus cereanus, Candida valida, Candida ingens,* and *Torulopsis sonorensis.* These artificial "rots" were thus standardized for microbial conditions much like natural rots at the early stages of fermentation (Fogleman and Starmer 1985).

Cactus cultures were maintained in an incubator programmed as described above. All cultures were grown together in trays rotated to different shelves inside an incubator every few days to avoid the effects of temperature stratification. After 3 to 4 days, the filter paper squares were removed and the number of unhatched eggs was counted. Egg-to-adult developmental time and viability (corrected for egg hatching) were scored by counting the number of emerging adults daily. Adults were aged for about one week and then frozen. Thorax length (the distance from the anterior margin of the thorax to the posterior tip of the scutellum in lateral view), a trait correlated with ovariole number and dispersal ability, was measured to the nearest 0.0001 mm at 25× using the JAVA® video image analysis system (Jandel Scientific, Corte Madera, Calif.) after the experiment was over. The entire experimental design was replicated three times (blocks).

Statistical Analysis.—All data analyses were performed using SAS, Release 6.06.01 (SAS Institute 1985). The data were checked for normality with the UNIVARIATE procedure; normality of developmental time data was improved with log transformation and viability data were arcsin transformed. Block effects were detected because of a malfunctioning incubator during the third block where temperatures dropped by about 4–5°C.

Within each block, the 24 sires each mated to 2 dams for each population formed the experimental design: two replicate groups of 10 eggs from each dam were counted out into agria and organ pipe food vials. This half-sib/full-sib design allowed for estimation of additive genetic variance components based on variation due to male half-sib families and variation among full-sib families nested within sires leading to the estimation of dominance variance, maternal effects, and environmental variance combined (Falconer 1981). Because replicates were nested within cactus in this design, it was possible to estimate genotype-by-environment interactions by estimating Sire-by-Cactus and Dam-by-Cactus interactions within populations, indicative of the effect of cactus substrates on half-sib and full-sib families (Via 1984a).

Because female *D. mojavensis* are cyclical egg layers (Etges and Heed 1992), obtaining enough eggs from each dam was difficult at times. Missing replicates forced the use of the GLM procedure, which is appropriate for unbalanced data. Sex was considered a fixed effect, whereas Cactus, Population, Sire, and Dam were included as random effects; Type IV sums of squares were used throughout. GLM is preferable to other algorithms in a mixed model hierarchical two-way ANOVA (Ayres and Thomas 1990) because it provides exact calculation of expected mean squares with unbalanced data (Goodnight and Speed 1978), and the assumption that covariances of dependent variables for family members experiencing different cacti are equal is met (Scheffé 1959).

Variance components were estimated for each level in the model for each fitness component by the VARCOMP procedure with Sex included as a fixed effect with the MIVQUE0 method (Hartley et al. 1978). Causal components of variance were computed directly from the estimated variance components for a two-environment design (Falconer 1981; Groeters 1988). When negative variance components were generated, the causal components were calculated with these included and by setting them to zero (Searle 1971; Via 1984a). Heritabilities of the fitness components within populations and cactus were estimated by

$$h_s^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_d^2 + \sigma_w^2}$$

and

$$h_d^2 = \frac{4\sigma_d^2}{\sigma_s^2 + \sigma_d^2 + \sigma_w^2}.$$

h_s^2 is the "narrow-sense" heritability based upon the sire component of variance σ_s^2, where h_d^2 is the "broad-sense" heritability (Falconer 1981) that includes four times the maternal effects, dominance variance, etc. in the numerator (Becker 1984). σ_d^2 is the dam (full-sib) component of variance and the within full-sib family variance is

$$\sigma_w^2 = \sigma_r^2 - (3\sigma_d^2 - \sigma_s^2),$$

where σ_r^2 is the residual variance.

Genetic correlations among life-history traits were estimated in several ways (Via 1984b). For development time and thorax size, the NESTED procedure was used with the data sorted by sex and cactus, with sires, dams, and replicates nested within populations. This provided estimates of additive and nonadditive genetic variances and covariances for both sexes within cactus environments. Additive genetic correlations were also approximated by correlation of half-sib family means and full-sib family means. Viability data were based on family means by definition, so it was possible to include these data at this level of the analysis. Phenotypic correlations were also calculated for comparison. Standard errors of genetic correlations were calculated according to the formula in Becker (1984, p. 124) and used to test the hypothesis that $r = 0$ by substituting in the equation $t = r/\mathrm{SE}(r)$ (Ostle and Mensing 1975). Resampling procedures such as the jackknife (Arveson and Schmitz 1970) or bootstrapping for calculation of confidence intervals were not used because of the size of the data set.

Genetic correlations across cacti using half-sib and full-sib family means were also calculated as indices of trade-offs in performance in different environments for all characters. Cross-environment genetic correlations estimate average genetic effects expressed in both environments and illustrate the nature of the genotype-by-environment interaction variance (Robertson 1959). Parametric correlations were used because of their known statistical properties, even though they may underestimate the true correlation (Yamada 1962; Via 1984b).

Results

A total of 146 sires and 253 dams from both populations produced 7124 progeny cultured across cacti. Some of the dams failed to produce eggs when they were separated from sires, primarily because fecundity of *Drosophila mojavensis* females is dependent on frequent remating (Markow 1982; Etges and Heed 1992) resulting in unbalanced data. Significant differences among blocks were revealed by ANOVA for each character, so all data were corrected for block effects before analysis. Several of the main effects showed interactions with blocks, but these terms were small relative to the variation caused by the main effects (Appendix). Removal of the block effect in the ANOVAs was necessary to reduce the considerable computer memory allocation required for analyses of developmental time, viability, and thorax size using the GLM procedure.

Population, Cactus, and Sex Differences in Life History.—Overall, the Baja population expressed shorter egg-to-adult developmental times, higher viabilities, and smaller thorax sizes than the mainland population (fig. 1). Population differences accounted for 35%–38% of the total variance in developmental time and thorax size (table 1). Egg-to-adult viability was marginally different between populations ($P = 0.085$), consistent with earlier studies (Etges and Heed 1987; Etges 1990). Female *D. mojavensis* tended to eclose faster and were larger as adults than males (fig. 1A,B).

Effects on larval growth of agria versus organ pipe substrates were small. Cactus differences accounted for only 2.8%–5.8% of the variances in all three fitness components (table 1). Although the Cactus-by-Population interaction term for thorax size was significant in the ANOVA ($P = 0.0467$), this level accounted for less than 1% of the total variance in expression of this trait. Given the variation among blocks for the effects of cactus (Appendix), variation in cactus tissue quality was certainly a causal factor. Inspection of figure 1A reinforces this conclusion: sex and population differences in thorax size were greater than those due to cactus in these two populations.

Genetic Basis of Host Cactus Response.—Significant sire effects were detected for development time and thorax size, but not viability (table 1). Additive genetic variation accounted for 10%–15% of the total variance for the former two traits. Nonadditive genetic/maternal effects, estimated by the variance among dams nested within sires, were significant for all three traits. Although the variance component for thorax size was negative, dam effects accounted for 5.1% of the variance in developmental time and 15.7%

of the variance in viability. Much of this variation was probably due to maternal effects for developmental time and viability as shown in results of interpopulation reciprocal crosses (Etges 1990). Taking these kinds of genetic variation together, additive and nonadditive genetic/maternal effect components of variance accounted for approximately 15%–20% of the phenotypic variation in these traits.

Heritabilities of developmental time and thorax size were influenced by both cactus and sex (table 2). Standard errors of heritability estimates from unbalanced data are unknown and thus were not included. Additive genetic variance in developmental time was expressed in organ pipe cultures for both populations, but not in agria cultures. Therefore, potential response to selection for egg-to-adult developmental time was host-specific. This result suggests that mainland populations may still respond to natural selection for this trait throughout most of their range where organ pipe is available for feeding and breeding. Broad-sense heritabilities in developmental time were significant for Baja flies only. This suggests that more of the genetic variation in developmental time is due to dominance, epistasis, maternal effects, etc., in Baja, irrespective of cactus. Additive genetic variance in thorax size was not influenced by cactus, but was expressed in a sex-specific fashion in each population.

Additive and nonadditive genotype-by-environment interactions were represented by the Cactus-by-Sire within population and Cactus-by-Dam within Sire within population interaction terms, respectively. A significant genotype-by-environment interaction at the level of dams was evident for developmental time, accounting for 38%–40% of the total variance in this trait, slightly more than the main effect of population. Those genotypes influencing shorter developmental times on agria therefore caused relatively longer developmental times on organ pipe in both populations and vice versa. Crossing of the lines in plots of two-environment reaction norms (Gupta and Lewontin 1982; Parker 1984) shows the nature of these interactions (fig. 2). I plotted the sire means across cacti rather than the dam means because the large number of dams made the plots difficult to interpret. The most obvious genotype-by-environment interactions were apparent for viability (fig. 2). These were marginally significant at the sire level ($P = 0.087$), explaining 15%–21% of the phenotypic variation (table 1).

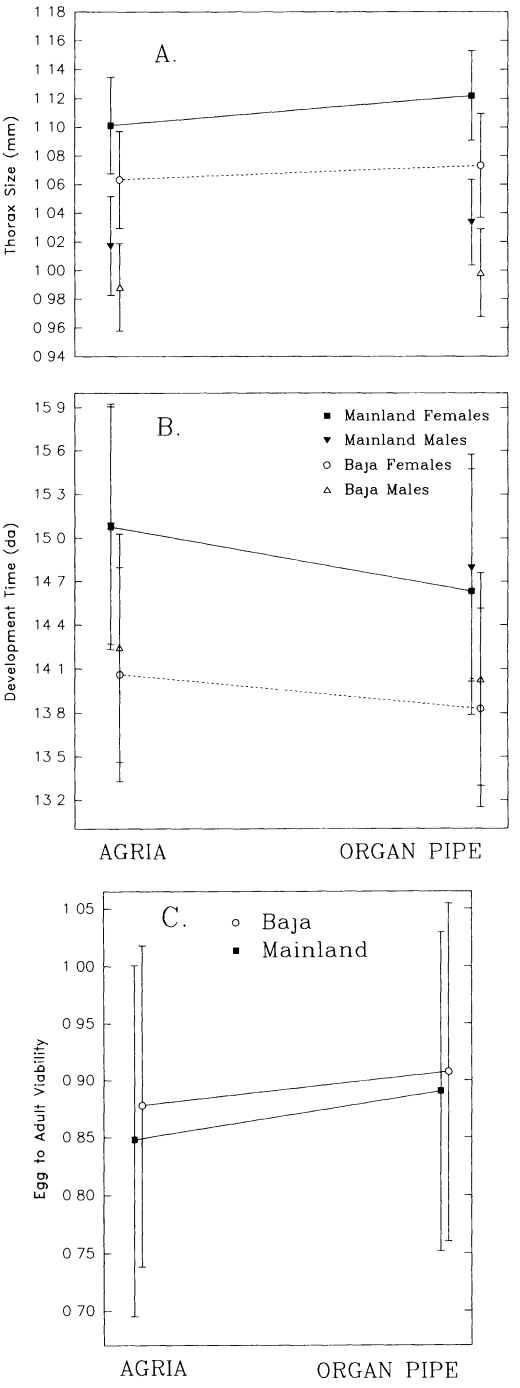

FIG. 1. Average (± 1 SD) response of mainland and Baja populations to agria and organ pipe cactus for the three life-history characters measured in this study: A, thorax size; B, egg-to-adult developmental time; and C, viability.

TABLE 1. Nested ANOVA results for (A) developmental time, (B) thorax size, and (C) viability for Baja and mainland populations of *Drosophila mojavensis* cultured on organ pipe and agria cactus.

Source of variation	df	Type IV sums of squares	Mean square ratio*	*F* value	*P*	Observed variance component†	Causal components (%): Negative components added	Causal components (%): Negative components = 0
A. $\log_{10}$(egg-to-adult developmental time)								
1. Model	874	3724.949		12.36	0.0001			
2. Sex	1	43.376	2/11	125.80	0.0001			
3. Cactus	1	101.295	3/7	13.53	0.1690	0.374	4.047	3.848
4. Population	1	979.660	4/5	220.23	0.0001	3.497	37.864	35.999
5. Sire(pop.)‡	145	645.006	5/6	1.37	0.0436	0.257	11.122	10.574
6. Dam(pop. sire)§	105	340.676	6/9	1.49	0.0273	0.382	5.418	5.151
7. Pop. × cactus	1	7.487	7/8	3.18	0.0765	−0.020	−0.212	0
8. Cactus × sire(pop.)‖	140	329.190	8/9	1.08	0.3553	0.166	7.167	6.815
9. Cactus × dam(pop. sire)#	90	196.542	9/10	1.47	0.0071	1.079	39.563	37.614
10. Rep(pop. cact. sire dam)**	389	577.728	10/11	4.31	0.0001			
11. Error	6004	2070.196				3.501	−4.970	0
							V_p = 9.236	V_p = 9.714
B. Thorax size								
1. Model	873	17.427		9.68	0.0001			
2. Sex	1	9.411	2/11	4561.29	0.0001			
3. Cactus	1	0.237	3/7	17.53	0.1492	1.085	5.845	5.701
4. Population	1	1.744	4/5	200.33	0.0001	6.715	36.193	35.298
5. Sire(pop.)	145	1.262	5/6	2.07	0.0001	0.672	14.481	14.123
6. Dam(pop. sire)	105	0.441	6/9	1.55	0.0165	0.559	−2.440	0
7. Pop. × cactus	1	0.014	7/8	4.03	0.0467	1.500	0.808	0.789
8. Cactus × sire(pop.)	140	0.469	8/9	1.24	0.1374	0.000	−0.095	0
9. Cactus × dam(pop. sire)	90	0.244	9/10	1.08	0.3030	1.206	26.099	25.454
10. Rep(pop. cact. sire dam)	388	0.970	10/11	1.21	0.0036			
11. Error	5869	12.109				8.172	19.109	18.637
							V_p = 18.554	V_p = 19.025
C. Arcsin (egg-to-adult viability)								
1. Model	473	62.936		1.27	0.0056			
2. Cactus	1	2.035	2/6	80.45	0.0707	46.47	3.789	2.800
3. Population	1	0.473	3/4	3.00	0.0852	14.78	1.205	0.890

TABLE 1. Continued.

Source of variation	df	Type IV sums of squares	Mean square ratio*	F value	P	Observed variance component†	Causal components (%) Negative components added	Negative components = 0
4. Sire(pop.)	141	22.218	4/5	1.22	0.1385	15.03	4.903	3.623
5. Dam(pop. sire)	106	13.665	5/8	1.41	0.0505	63.18	15.704	11.604
6. Pop. × cactus	1	0.025	6/7	0.21	0.6469	−4.79	−0.391	0
7. Cactus × sire(pop.)	138	16.569	7/8	1.32	0.0868	64.66	21.092	15.584
8. Cactus × dam(pop. sire)	83	7.572	8/9	0.87	0.7722	−42.49	−34.953	0
9. Error	418	43.666				1069.44		
							V_p = 1226.27	V_p = 1659.68

* Mean-square ratios (numbers correspond to levels in the model under "Source of variation") used for calculating the F ratio.
† × 10^{-4} Error variance components included replicate and residual variation.
‡ Sires nested within populations.
§ Dams nested within sires within populations.
‖ Interaction between cactus and sires nested within populations.
Interaction between cactus and dams nested within sires nested within populations.
** Replicates nested within all levels.

Genetic Correlations within and across Environments.—Despite the large differences in developmental time and thorax size between the sexes, developmental time was positively correlated among males and females, as was thorax size, with $0.64 \leq r \leq 0.78$ (table 3). None of the 95% confidence intervals of these z-transformed correlation coefficients included zero or one; therefore, developmental time and thorax size are partially independent among males and females, suggesting the potential for further sexual dimorphism. The range of coefficients of determination, $0.41 \leq r^2 \leq 0.61$, suggests that roughly half of the covariation between the sexes for these fitness components has been explained. These between-sex correlations were insensitive to cactus and have been conserved since *D. mojavensis* invaded the mainland from Baja (table 3).

Variance component correlations between developmental time and thorax size were calculated within each combination of population and sex because of the large differences in these traits revealed by ANOVA, and with the data grouped by cactus. Few of the genetic correlations between developmental time and thorax size were significantly different from zero (table 3). Those that were different from zero were negative in sign, suggesting positive pleiotropy for these components of fitness. Here, a trade-off among components of fitness would be indicated by a positive correlation; longer developmental times covary with larger thorax sizes and vice versa. The only indication of a life-history trade-off in which significant additive genetic variances were detected for both traits (table 2) was the additive genetic correlation among mainland, female development time, and thorax size on agria, r = 0.402, SE = 0.608. The magnitudes of standard errors for this and all the other correlation estimates were large because of variation in family size, missing dams (Falconer 1981), and a less than optimal number of families assayed per population required to detect significance (Klein 1974).

The degree to which genotypes ranked equivalently in agria and organ pipe cultures was also estimated by calculating genetic correlations across environments. For both developmental time and thorax size, cross-cactus correlations based on sire and dam means were significantly positive, but small in both populations (table 4). For egg-to-adult viability, all correlations except those based on dam means for Baja flies were close to zero. Negative correlations between

TABLE 2. Heritabilities (narrow sense, top row, and broad sense, bottom row), for egg-to-adult developmental time, adult thorax size, and viability for both populations of *Drosophila mojavensis* cultured on agria and organ pipe cactus in this study. Methods for calculating heritabilities are described in the text. Significance levels are based on mean-square ratios.

	Mainland		Baja	
	Females	Males	Females	Males
Developmental time				
Agria	0.353	0.378	0.118	0
	0.337	1.238*	1.621***	1.378***
Organ pipe	2.002***	1.061**	0.355†	0.106
	0.182	0.118	1.144***	0.848*
Thorax size				
Agria	0.803**	0.199	0.064	0.515***
	0.479†	0.478*	0.911***	0
Organ pipe	1.560***	0.241	0.198	0.391*
	0.971*	1.759**	1.287***	0.601*
Viability				
Agria	0.219		0.099	
	0.173		0	
Organ pipe	0.120		0.577	
	0		0.947*	

† $0.1 < P < 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

components of fitness across host plants are expected if genetic specialization on one or a few favored hosts has been accompanied by tradeoffs in performance on other hosts (Rausher 1984; Via 1984b). Most of the correlations between traits measured across cacti were also zero indicating the influence of different sets of genes across environments and fitness components. Because all the correlations were significantly different from one, different sets of genes must be operating in agria and organ pipe environments consistent with the genotype-by-environment interactions revealed by ANOVA (table 1). Thus, there is no evidence for trade-offs in fitness across two of the major host cacti used by *D. mojavensis* for these two populations, and the low positive genetic correlations suggest a genetic mechanism underlying the past colonization of secondary host plants throughout the species range. In both populations, there are high fitness genotypes that perform well on primary and secondary host cacti.

DISCUSSION

The evolution of resource use among ancestral and derived populations of *Drosophila mojavensis* has played a major role in the causes for life-history variation among populations. The absence of strong negative genetic correlations in life-history traits across cacti suggests that *D. mojavensis* is an ecological generalist able to switch to alternative hosts, documenting an absence of host-plant specialization within populations (Rausher 1984; Via 1984a; Futuyma and Philippi 1987; James et al. 1988; Jaenike 1989). The extent of genotype-by-environment interaction and low, but positive genetic correlations across cacti demonstrate the degree to which agria and organ pipe cacti are experienced as different environments by both Baja and mainland populations of *D. mojavensis*. The degree of population differentiation in relation to the genotype-by-environment interactions suggests that divergence onto secondary hosts from the ancestral agria cactus is ongoing and has produced the observed geographic variation in life histories. Over a broader scale of populations distributed within regions, differences between four Baja and three mainland populations in these components of fitness were greater than among-population/within-region differences (Etges 1990). Baja flies, particularly males, tended to be smaller and developed faster when cultured on agria. Mainland flies were correspondingly larger with longer developmental times on organ pipe, leading to significant Population-by-Cactus interactions (Etges 1990). Such interaction terms are considered statistical evidence for the presence of population-level host-plant specialization, or host races (Jaenike 1981; Futuyma and Mayer 1980). Therefore, life history evolution has pro-

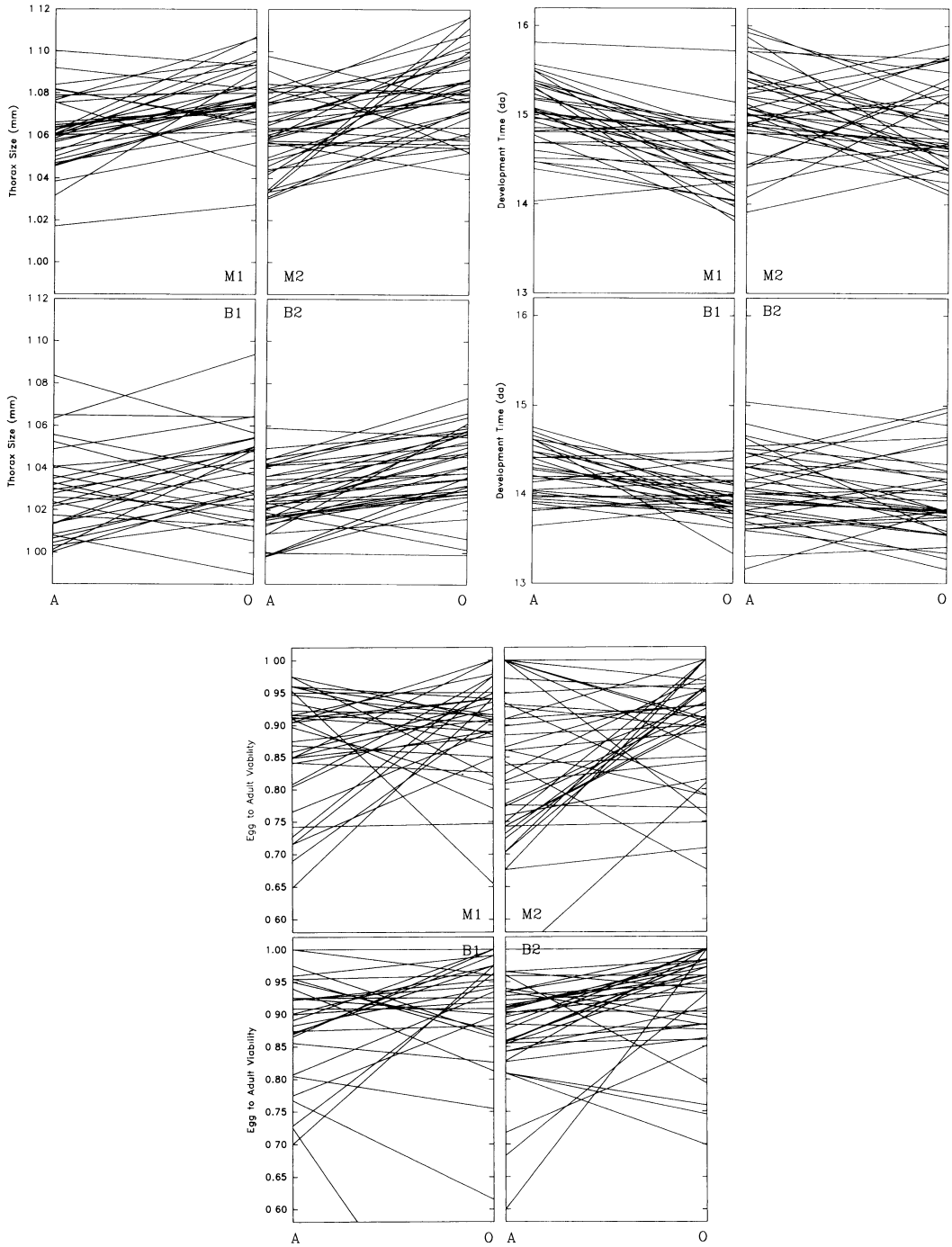

FIG. 2. Reaction norms of mainland (M1 and M2) and Baja (B1 and B2) half-sib families to agria (A) and organ pipe (O) cactus for thorax size, egg-to-adult developmental time, and viability. Two plots, 1 and 2, each comprising about half of the half-sib families were created for each population, M and B, because of the many families in each population. Male and female data were combined.

TABLE 3. Correlations between female development time (FMDVT), female thorax length (FMTHX), male development time (MLDVT), and male thorax length (MLTHX) calculated with phenotypic data (Pheno), sire means (Sire), dam means (Dam), sire variance and covariance components (S covar), and dam variance and covariance components (D covar). Values above the diagonal refer to the mainland population and below the diagonal to the Baja population. The top lines of each set of rows are the correlations based on flies reared on agria cactus and the bottom set from organ pipe cultures. Sample sizes are given in parentheses, as well as the z-transformed 95% confidence intervals of the correlations based on sire means, and standard errors of the variance component correlations.

	FMDVT	FMTHX	MLDVT	MLTHX
FMDVT				
Agria				
Pheno	—	−0.085** (831)	0.734**** (74)	0.005 (74)
Sire	—	−0.224† (75)	(0.608, 0.821)	
Dam	—	−0.180* (123)		
S covar	—	0.402 (75) (0.608)		
D covar	—	−0.558 (123) (0.709)		
Organ pipe				
Pheno	—	0.064 (910)		
Sire	—	−0.326** (76)	0.777**** (73) (0.666, 0.854)	0.109 (73)
Dam	—	−0.158† (125)		
S covar	—	−0.205 (76) (0.271)		
D covar	—	−0.366 (125) (1.21)		
FMTHX				
Agria				
Pheno	0.085** (886)	—		
Sire	0.072 (69)	—	−0.111 (74)	0.635**** (74) (0.475, 0.754)
Dam	0.129 (117)	—		
S covar	0.734 (67) (2.71)	—		
D covar	0.153 (117) (0.207)	—		
Organ pipe				
Pheno	0.030 (920)	—		
Sire	0.114 (68)	—	−0.049 (73)	0.742**** (73) (0.618, 0.831)
Dam	0.067 (117)	—		
S covar	−0.154 (68) (0.830)	—		
D covar	0.133 (117) (0.191)	—		
MLDVT				
Agria				
Pheno			—	−0.207*** (780)
Sire	0.755*** (69) (0.631, 0.843)	−0.064 (69)	—	−0.149 (74)
Dam			—	0.020 (122)
S covar			—	−0.540 (73) (1.08)
D covar			—	−0.067 (112) (0.422)

TABLE 3. Continued.

	FMDVT	FMTHX	MLDVT	MLTHX
Organ pipe				
Pheno			—	0.101*** (833)
Sire	0.708**** (68) (0.565, 0.808)	0.024 (68)	—	−0.055 (75)
Dam			—	−0.053 (125)
S covar			—	0.097 (75) (0.548)
D covar			—	−1.694 (125)
MLTHX				
Agria				
Pheno			−0.057*** (868)	—
Sire	0.110 (69)	0.717**** (69) (0.587, 0.814)	−0.050 (69)	—
Dam			−0.053 (117)	—
S covar			0 (69)	—
D covar			0 (117)	—
Organ pipe				
Pheno			0.041 (833)	—
Sire	0.016 (68)	0.702**** (68) (0.557, 0.804)	−0.029 (68)	—
Dam			−0.041 (117)	—
S covar			−1.030 (68) (1.93)	—
D covar			−0.046 (117) (0.312)	—

† $0.1 < P < 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$; **** $P < 0.0001$.

ceeded long enough that mainland populations have become adapted to organ pipe from the ancestral agria habit, but within-population genetic variance persists in performance across cacti in both populations.

Comparisons of *single* populations collected from particular hosts in nature may not necessarily be representative of the overall patterns of host response for widespread species (but see Jaenike 1989). Experiments designed to assess host plant specialization or host race formation should perhaps involve at least several populations known to use each host (cf. Hsaio 1978; Hare and Kennedy 1986). Use of the terms "Baja" and "mainland" in reference to the two populations studied here does not imply that these populations were representative of all populations in those regions, yet the degree of genetic differentiation between Baja and mainland populations in life histories (Etges 1990) suggests that geographical isolation and restricted gene flow caused by the Gulf of California, indicated by near fixation of different alleles at the *Adh-2* locus (Starmer et al. 1977), will continue to influence host-specific life-history evolution.

Host quality can also influence the outcome of experiments designed to assess host response. This may be particularly important in plant-herbivore experiments where host plants are greenhouse reared and not representative of hosts grown under natural conditions (Via 1990). The condition of cactus tissue used in fermenting cultures has a profound effect on the growth and development of *D. mojavensis* larvae (Etges 1989a). As both agria and organ pipe plants age, cactus arms undergo shifts in tissue color, presumably because of physiological changes that occur as arms senesce. Younger, green, photosynthetically active tissues are typically found at the tips of growing arms. The tissues of older, basal arms are yellow-brown in color. Naturally occurring rots are found almost exclusively in these yellow-brown tissues suggesting they are more prone to injury and microbial degradation. Virtually nothing is known about the metabolic consequences of tissue aging (Gibson and Nobel 1986), other than the large effects tissues of different ages have on growth and development of *D. mojavensis* larvae (Etges 1989a). Although these field collected, yellow-brown tissues have

TABLE 4. Cross-cactus product moment correlations within the Baja and mainland populations of *Drosophila mojavensis* in this study based on sire means (above diagonal) and dam means (below diagonal). Life-history traits expressed in agria and organ pipe environments are preceded with AG or OP, respectively. The traits are egg-to-adult developmental time, DVT; thorax size, THX; and viability, VIB. Ninety-five percent confidence intervals of z-transformed correlation coefficients for large sample sizes (Sokal and Rohlf 1981) are in parentheses below each estimate.

	AGDVT	AGTHX	OPDVT	OPTHX	AGVIB	OPVIB
AGDVT						
Mainland	1	.074 (−.156, .296)	.268** (.042, .468)	.241* (.013, .445)	.095 (−.136, .317)	.044 (−.186, .270)
Baja	1	−.001 (−.236, .236)	.457**** (.245, .627)	−.054 (−.289, .187)	.301** (.069, .502)	−.133 (−.360, .109)
AGTHX						
Mainland	.030 (−.144, .206)	1	−.005 (−.234, .224)	.271** (.045, .470)	−.143 (−.360, .089)	−.185 (−.397, .045)
Baja	−.027 (−.207, .155)	1	.011 (−.229, .249)	.420*** (.201, .603)	−.189 (−.408, .050)	−.400**** (−.583, −.178)
OPDVT						
Mainland	.172† (−.012, .345)	−.128 (−.305, .057)	1	−.078 (−.296, .147)	.084 (−.147, .307)	−.027 (−.254, .202)
Baja	.362**** (.192, .511)	.015 (−.168, .197)	1	.079 (−.163, .311)	−.137 (−.364, .105)	−.129 (−.356, .114)
OPTHX						
Mainland	.101 (−.085, .281)	.262*** (.082, .425)	−.086 (−.256, .090)	1	.182 (−.049, .394	−.026 (−.253, .204)
Baja	−.142 (−.318, .042)	.391**** (.224, .536)	−.065 (−.243, .118)	1	−.059 (−.294, .182)	−.149 (−.374, .093)
AGVIB						
Mainland	.089 (−.093, .265)	−.038 (−.217, .143)	−.041 (−.225, .145)	.209* (.024, .379)	1	.019 (−.211, .246)
Baja	.169† (−.013, .341)	−.050 (−.229, .133)	−.034 (−.217, .151)	−.151 (−.326, .034)	1	.199 (−.041, .418)
OPVIB						
Mainland	−.006 (−.191, .179)	−.144 (−.320, .042)	−.097 (−.270, .082)	−.047 (−.223, .131)	.021 (−.166, .207)	1
Baja	−.059 (−.242, .128)	−.319*** (−.477, −.142)	−.050 (−.232, .134)	−.227* (−.394, −.045)	.192* (.007, .364)	1

† $0.1 < P < 0.05$; * $P < 0.05$; ** $P < 0.025$; *** $P < 0.005$; **** $P < 0.0001$.

been used in several host-response experiments with *D. mojavensis* (except Etges and Heed 1987 and Ruiz and Heed 1988), a major problem remains in that there is no objective way to classify tissue quality other than on the basis of color. Small variations in tissue quality from arm to arm increased environmental variation, as shown by the block interactions (Appendix), and obfuscated estimation of genetic sources of variability.

Host Effects on Life History Evolution.—Potential sources of selection on life histories have been inferred from the contrasting effects of host cacti on *D. mojavensis* life cycles (Heed 1981; Etges and Heed 1987). Resource availability and distribution have been suspected as leading factors shaping the patterns in life history. Agria is used preferentially even when other hosts are present. Host preference for agria is therefore uncorrelated with host performance (fig. 1; Etges 1989a), but choice-performance relationships with other secondary hosts remain to be tested. Agria stems are smaller in diameter and decompose faster during fermentation than organ pipe (Etges 1989a), providing a more unpredictable resource for the offspring of ovipositing females in agria patches. However, because agria plants reproduce clonally and grow as large "thickets" composed of many individual arms, whereas organ pipe reproduce sexually by setting seeds, agria cacti are more densely distributed than organ pipe where they occur. Furthermore, agria tissues are more prone to injury, accounting for the observation that agria rots are 40 times more abundant than organ pipe (Mangan 1982). Therefore, agria patches provide a more predictable source of nutrition for adults, but not for larvae because of decomposition rates and subsequent desiccation. Organ pipe rots are larger because their greater stem size provides a more predictable source of larval nutrition, but their scarcity makes them more unpredictable for adults searching for new feeding and oviposition sites. Such contrasting patterns of trophic unpredictability are concordant with the shorter developmental times, higher viabilities, and lack of significant additive genetic variance in developmental time of Baja populations using agria, and longer developmental times, larger body sizes, correlated with dispersal ability, and additive genetic variance in developmental time in organ pipe cultures in mainland populations.

The differences among mainland and Baja populations in life histories have therefore evolved without producing large within-population genetic correlations between developmental time and thorax size. Even if these correlations were undetectably low, they may still influence future evolution over longer time intervals. The sensitivity of the genetic variances to cactus (table 2) should promote host-specific evolutionary pathways for these fitness components, i.e., additive genetic variances were greater in organ pipe cultures than in agria cultures. Further information is needed about population structure and dispersal, which can influence deme size and rates of inbreeding, and thus the sign and magnitude of genetic correlations (Rose 1984; Charlesworth 1990). Inbreeding and local extinctions may be more common in mainland, organ pipe-dwelling populations because of low rot densities and large inter-rot distances (Mangan 1982). Unless dispersal rates among mainland *D. mojavensis* are high enough to compensate for the scarcity of rots, newly discovered rots may be colonized by only a few founders engendering local inbreeding and increases in population subdivision. Because large body size is thought to allow for greater flight capability in *Drosophila* (Roff 1977; Johnston and Heed 1976; Johnston 1977; Mangan 1982), the consistently larger thorax sizes of mainland populations (Etges 1990) suggest that dispersal rates may indeed be higher than in Baja populations.

Long-term reorganization of life histories should be faster when strong negative correlations between different traits or between traits expressed in different environments are absent (Via and Lande 1985). Factors leading to positive genetic correlations, that is recurrent mutation (Simmons and Crow 1977; Charlesworth 1990), polygenic recombination (Lande 1980), departure from equilibrium conditions, altered patterns of resource allocation (Van Noordwijk and De Jong 1986; de Laguerie et al. 1991), underlying functional constraints on the genes involved (Houle 1991), and expression of quantitative variation in "novel" environments (Service and Rose 1985; Holloway et al. 1990) provide the opportunity for reshaped life histories. The latter factor is not likely to have influenced the present study unless the experimental rots were quite different from those in nature. Thus, the potential for further life-history evolution exists in both populations.

Once positive, the genetic correlations and thus the additive genetic variances for each trait should be eliminated by natural selection. New genetic

variances and covariances may then be reformed in response to mutation-selection balance and environmental heterogeneity. This phase in the transition from one life-history set to another deserves further scrutiny as this period is likely to provide insight into how particular life-history patterns evolve. The process of host switching in *D. mojavensis* has caused evolutionary changes in life history because of the contrasting environments of different host cacti. Populations that use organ pipe cactus have begun a different life-history trajectory. Although many "neutral" life histories may have been possible, life-history evolution has been constrained to only a few directions because relatively few hosts are used by this species. The association between *D. mojavensis* and its host cacti may be an exemplary system with which to pursue an empirical understanding of how particular life histories originate (Orzack and Tuljapurkar 1989).

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Appendix

Analysis of variation in egg-to-adult developmental time, viability, and adult thorax size revealed significant block effects that were removed before running the entire model with PROC GLM. A posteriori analysis of the data corrected for the main effects of block revealed interactions with the main effects of sex, population, and cactus with blocks (table A1). Because these interaction terms could not be merged into the complete experimental design because of the extreme computer memory requirements of GLM, estimates of the nested effects in the complete ANOVAs contain these block effects. Graphs of these block effects (Fig. A1) revealed no strong indication of interactions relative to the large differences between populations and cactus, except for viability. Sex-by-block interactions were of less concern because sex was not included as a crossed effect in the complete ANOVA. Variation in cactus tissue quality is probably the cause for variation among blocks. Even though the food used in this experiment was a blend of several different cactus arms each time food was prepared, the many cultures required more cactus arms than could be used in a single batch of food. Thus, the block-by-cactus interaction resulted from uncontrolled variation in cactus tissue quality across batches of food. Such variation must also exist in nature, but may be exaggereated here because small pieces of cactus were used in each batch of food. Whole cactus arms serve as breeding sites in natural populations.

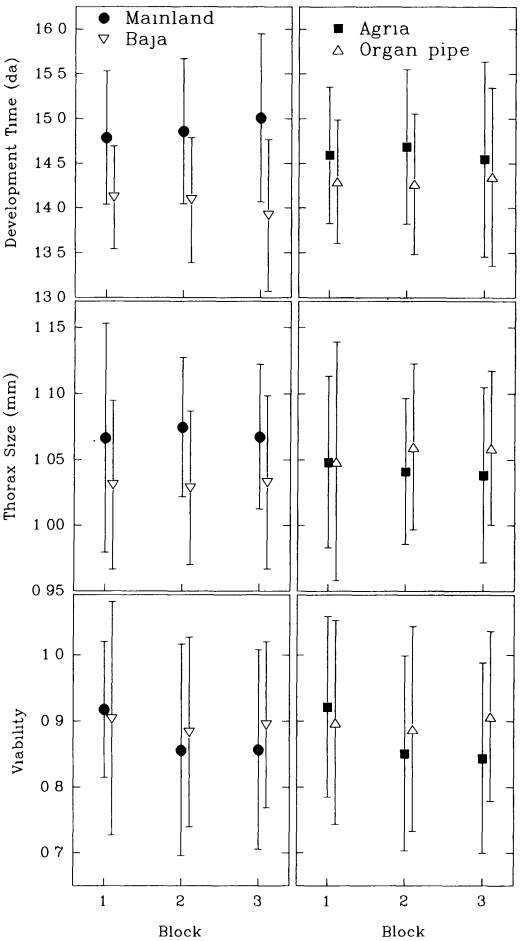

FIG. A1. Graphs of dependent variable means (± 1 SD) for showing variation for population (left three panels) and cactus (right three panels) effects across blocks in this experiment.

TABLE A1. ANOVAs for the three dependent variables in this study with the main effects and crossed effects of block variation included.

	Developmental time			Thorax size			Viability		
Source	df	Type IV sums of squares	*F*	df	Type IV sums of squares	*F*	df	Type IV sums of squares	*F*
Model	11	1594.59	237.32***	11	13.58	532.41***	8	4.82	5.22***
Block	2	1.55	1.27 NS	2	0.03	5.69*	2	0.00	0.00 NS
Sex	1	29.95	49.04***	1	10.18	4357.78***			
Population	1	1147.66	1878.86***	1	2.20	941.37***	1	0.40	3.51 NS
Cactus	1	161.54	264.46***	1	0.24	100.84***	1	0.98	8.50**
Block × sex	2	5.09	4.17*	2	0.01	1.95 NS			
Block × pop.	2	51.87	42.46***	2	0.02	3.77*	2	0.31	1.34 NS
Block × cactus	2	15.62	12.79***	2	0.09	18.62***	2	1.74	7.53**
Error	6782	4135.94		6649	15.51		891	101.79	

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.0001$; NS, not significant.