CHAPTER 2

Direction of Life History Evolution in Drosophila mojavensis

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1. INTRODUCTION

Studies of the genetic basis for life history evolution involving analysis of demographic change in response to patterns of environmental variability have yet to provide a general explanation for the diversity of life histories often observed among species. Part of this problem is due to the lack of information about the forces actually responsible for causing the genetic variation observed in natural populations, without which we cannot evaluate the significance of the variation measured or the precise outcome in long-term life history evolution. Adaptation to environmental variability can lead to different equilibrium life histories all with equivalent fitnesses (Schaffer and Rosenzweig, 1977). The form of life history expected will depend on the pattern of environmental variation and degree of correlation among life history traits (Tuljapurkar, 1988; Orzack and Tuljapurkar, 1989). Only when observed genetic variation and covariation in components of fitness can be associated with the causes in nature responsible for their maintenance will understanding of the microevolutionary processes directing life history evolution be possible (Istock *et al.*, 1976; Reznick and Endler, 1982; Etges, 1989a).

The process of adaptation to different environments leading to life history evolution can also cause reproductive isolation in allopatry arising from pleiotropy or linkage. Genetic differentiation caused by adaptation to new environments may secondarily cause sexual isolation because those genes involved in adaptation may influence sexual isolation (Muller 1939, 1942; Rice, 1987). In concert with genetic drift, adaptive divergence in allopatry may be a potent factor in speciation due to disruptive selection causing fixation of incompatibility genes producing sexual and/or postmating isolation upon secondary contact (Dobzhansky, 1940; Mayr, 1963; Carson,

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1971, 1975, 1982; Nei, 1976; Nei *et al.*, 1983; Kaneshiro, 1980).

The microevolutionary connections between changes in life history and reproductive isolation are central to arguments about species formation. In its most simplistic form, evolution may be viewed as a long process of allelic substitutions at many loci of small effect or frequency changes of alleles at loci controlling regulatory functions or "major genes". At some crucial point, genetic change becomes irreversible (Dobzhansky, 1970) whether reinforced by speciation or not. Such irreversible evolutionary change may be achieved in any number of ways including classical divergence in allopatry (Mayr, 1963; Futuyma and Mayer, 1980) and genetic drift in structured populations (Wright, 1932, 1982; Templeton, 1980; Carson and Templeton, 1984). Since the form of genetic change must at some point be expressed through variation in fitness, genetic analysis of variation in integrated developmental and physiological pathways, i.e., life history traits, will reveal something about the nature of shifts involved in large-scale genetic reorganizations during evolutionary transitions. When functionally related sets of life history traits are reshaped together, the process probably involves many genes and irreversibility may occur quickly (Istock, 1982).

Natural populations of *Drosophila mojavensis* are ideal for the study of causal relationships between adaptive divergence in life histories and incipient speciation. Not only does premating isolation exist among certain geographically isolated populations (Wasserman and Koepfer, 1977; Zouros and D'Entremont, 1980; Markow *et al.*, 1983), but also the origin of this species and history of range expansion, mediated by shifts to alternate host cacti, have been described in detail (Johnson, 1980; Heed, 1982; Heed and Mangan, 1986; Ehrman and Wasserman, 1987; Etges and Heed, 1987; Etges, 1989b). Populations of *D. mojavensis* from Baja California are considered ancestral and invaded mainland Mexico by switching host plants. The Gulf of California now forms a major geographical barrier to gene flow as evidenced by both inversion and allozymic differentiation among mainland and Baja populations (Zouros, 1973; Johnson, 1980). A central-marginal pattern of inversion polymorphism closely follows the distribution of host plants (Johnson, 1980). Polymorphism is mainly restricted to agria cactus, *Stenocereus gummosus*, in Baja California and one small patch in coastal Sonora (Fig. 1). A rare ancestral chromosome is found only in central Baja, and agria is the preferred host plant even when other cacti are present (Heed, 1982). Mainland populations are typically chromosomally monomorphic throughout Sonora, northern Sinaloa, and Southern Arizona and use organ pipe cactus, *S. thurberi*, with occasional use of cina, *S. alamosensis*, a major host plant of *D. arizonensis* in Sonora and Sinaloa (Heed, 1982). In southern California, all populations of *D. mojavensis* are fixed for an alternate gene arrangement where barrel cactus, *Ferocactus acanthodes*, is the sole host plant.

Incipient speciation among Baja and mainland Sonora populations has been suggested in studies of premating isolation

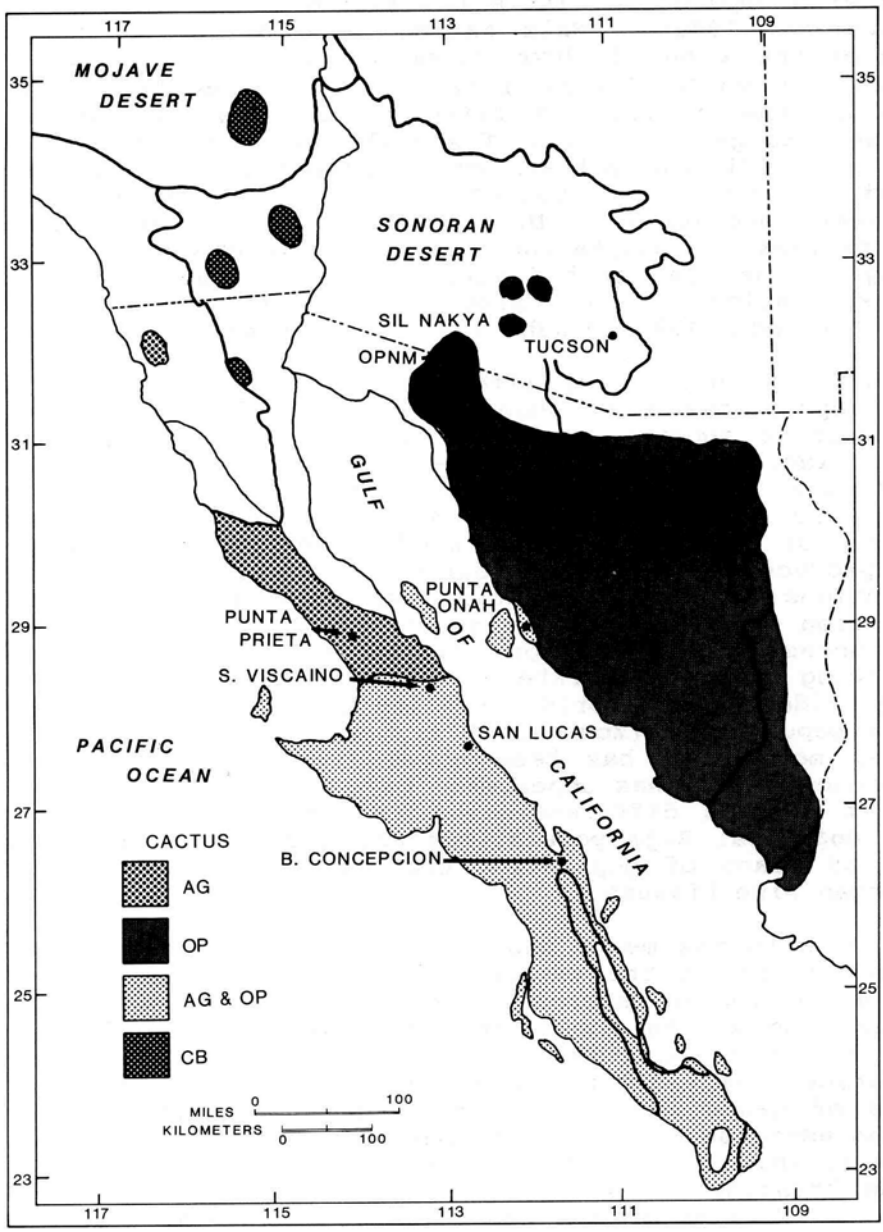

Figure 1. Map of the Sonoran Desert showing the ranges of the major host cacti of *D. mojavensis* and the collecting sites described in the text. Cactus types are: AG, agria; OP, organ pipe; CB, California barrel cactus.

between Sonora females and Baja males (Wasserman and Koepfer, 1977; Zouros and D'Entremont, 1980; Zouros, 1981; Koepfer, 1987a, 1987b). Sonoran females discriminate against Baja males with apparently little postmating isolation (Zouros and D'Entremont, 1980). Male mating behavior is influenced by genes on the X and Y chromosomes and interactions with other chromosomes while female behavior is influenced mainly by genes on the second and fifth chromosomes (Zouros, 1981). Because this genetic basis of sexual isolation does not correlate well with the pattern of inversion polymorphism on the second and third chromosomes, Zouros (1981) concluded that incipient speciation in *D. mojavensis* may not be related to "the process of adaptation to local environments" (p. 716) adding to the view that inversions *per se* have little to do with speciation events (Carson, 1975, 1978, 1982; Craddock, 1974; Paterson, 1981; Walsh, 1983; but see White, 1978).

However, considerable life history variation exists among those populations which show behavioral isolation. Flies from Baja express shorter egg to adult development times, higher viabilities, smaller thorax sizes, lower lifetime fecundities, and slower rates of sexual maturation than mainland flies (Etges and Heed, 1987; Etges and Klassen, 1989). Detailed analysis of the magnitude and kind of genetic transitions that have produced life history differences will be necessary if connections to sexual isolation are to made, as will within-population studies of expression of genetic variances and covariances of life history traits and sexual isolation on fermenting cactus substrates like those used in nature. There is no evidence for hybrid sterility between Baja and mainland Sonora populations (Zouros, 1973), yet some variation in male genital morphology has been noted (Heed, unpublished data). The present study was undertaken to further clarify the magnitude of genetic differentiation in life history now present among ancestral Baja populations and derived mainland populations by means of population crosses cultured on both agria and organ pipe tissues.

Changes in the means and variances among parental, F_1, and F_2 generations in the expression of these fitness components were of particular interest in examining the extent of genetic coadaptation within populations (Vetukhiv 1953, 1954; McFarquhar and Robertson, 1963; Anderson, 1968). Locally adapted populations may exhibit genetic integration or epistasis among groups of genes that have been shaped by natural selection. Crosses among such populations may show heterosis in the F_1s or F_2 breakdown, or loss of fitness in the F_2 generations caused by the breaking up of coadapted gene complexes by recombination. As McFarquhar and Robertson (1963) noted, "differences in co-adaptation should be assessed in terms of fitness with respect to the normal environment". In attempting to measure variation in components of fitness under nearly natural conditions, I assayed the extent of coadaptation in Baja and mainland populations by comparing generation means and variances for the fitness components studied on fermenting cactus substrates.

Table I
Collection records of *D. mojavensis* used for this study. Cactus refers to the host plant from which imagoes were reared, and record ID refers to the collection numbers of William B. Heed at the University of Arizona

Location[a]	Record ID	Cactus	# Rots	# Emerged
Baja California				
Punta Prieta (P)	A916	Agria	11	3918[b]
South Viscaino (V)	A917	Agria	4	1699[c]
		Organ Pipe	3	14
South of Bahia Concepcion (B)	A918	Agria	3	107
San Lucas (L)	A920	Agria	2	217
Mainland Sonora and Arizona				
Punta Onah (O)	FOG2	Agria	2	200[d]
Organ Pipe National Monument, AZ (M)	OPNM	Organ Pipe	1	1074
Santa Rosa Mountains, AZ(S)	A911	Organ Pipe	2	155

[a]Abbreviated population designation in parentheses.
[b]Includes 233 adults aspirated from rots in the field.
[c]Includes 38 adults aspirated from rots in the field.
[d]Estimated number.

2. MATERIALS AND METHODS

2.1. Origin of Stocks

Seven populations of *D. mojavensis* were sampled from nature 3-5 generations prior to the start of the first set of crosses (Table I). In addition to adults aspirated from rots in the field, all adults eclosing from rots returned to the lab were used to start laboratory populations. All flies were reared in mass culture in large numbers on banana-yeast-malt-Karo-agar food in shell vials until crosses were made.

2.2. Cactus Rearing Conditions

Artificial rots were made with 25 g pieces of fresh cactus placed on 75 g of sand in half-pint milk bottles sealed with cotton. After autoclaving, each was inoculated with a pectinolytic bacterium 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. mexi-*

cana, P. amethionina var. *amethionina, Cryptococcus cereanus, Candida valida, C. ingens* and *C. sonorensis*.

2.3. Population Crosses - I

For each cross, about 200 virgin adults of each sex were placed in polyethylene freezer boxes with a hole on one side large enough for a removable petri dish containing an oviposition medium (1% agar-agria rot juice). First, four crosses were made: both parental populations and both reciprocal F_1 crosses. Four second generation crosses included one parental population, F_1 backcrosses to each parental population, and an F_2 population made by intercrossing half of the adults from each reciprocal. Combinations of populations were chosen for crossing to represent a variety of genetic differences within and among geographical regions in the species range of *D. mojavensis*.

2.4. Population Crosses - II

In order to assess the degree to which experimental error due to rearing generations at different times may have influenced the expression of life history variation, a second set of crosses using populations A924, a more recently collected Santa Rosa Mountains stock, and A916 were performed in the same fashion as above, but all replicated generations were cultured side-by-side (Etges, 1989c). Replicates of 50 or 400 eggs per 35 g cactus tissue were started for these crosses to determine how larval competition might influence gene expression of life history traits.

For both sets of population crosses, eggs were collected from small petri dishes on each population cage over 6 hr intervals, surface sterilized by washing in sterile water, 70 % ethanol and again in sterile water. Groups of 100, or 50 and 400 eggs for the second experiment, were counted out onto sterile filter paper strips and placed on freshly inoculated agria or organ pipe cactus. For each generation, eggs from each cross were counted onto 3 (2 replicates for the second experiment) replicates of each cactus species each day. All cultures were grown at 25°C in a 14:10 LD photoperiod.

Egg to adult viability and development time were measured by collecting eclosing adults every day. The number of unhatched eggs was recorded after removing the filter paper strips from the culture bottles and subtracted from the total number of eggs. Adult thorax size was measured with an ocular micrometer on aged adults. Three adults per replicate per day of development time per sex were scored for thorax size.

2.5. Statistical Analysis

Development time data were rescaled by log transformation, viability data were arc sin transformed, and thorax length

Table II

Nested ANOVA results for all parental, control populations cultured in this study on both host cacti after reclassifying each population as either Baja or mainland depending upon geographical origin. Means for each variable (1 SE) showing significant Cactus x Region interaction terms are shown

Source of variation	df	TYPE IV SS	F	P
Egg to Adult Development Time				
Region	1	0.0265	164.83	0.0001
Population(Region)[a]	32	0.0272	5.29	0.0001
Cactus	1	0.0080	49.95	0.0001
Cactus x Region	1	0.0027	16.97	0.0001
Cactus x Pop(Region)[b]	32	0.0173	3.36	0.0001
Error	136	0.0219		

	Baja	n[c]	Mainland	n
Organ Pipe	12.29[d] (0.077)	54	12.74 (0.101)	48
Agria	11.78 (0.039)	54	12.59 (0.061)	48

Egg to Adult Viability				
Region	1	0.5595	19.80	0.0001
Population(Region)	32	5.4715	6.05	0.0001
Cactus	1	0.3676	13.01	0.0004
Cactus x Region	1	0.0000	0.00	0.9769
Cactus x Pop(Region)	32	1.9415	2.15	0.0013
Error	136	3.8419		
Female Thorax Size				
Region	1	1.3306	124.19	0.0001
Population(Region)	32	0.7505	2.19	0.0010
Cactus	1	0.0000	0.00	0.9622
Cactus x Region	1	0.0234	2.19	0.1413
Cactus x Pop(Region)	32	0.2858	0.83	0.7201
Error	139	1.4893		
Male Thorax Size				
Region	1	0.6249	138.50	0.0001
Population(Region)	32	0.6530	4.52	0.0001
Cactus	1	0.0004	0.09	0.7621
Cactus x Region	1	0.0479	10.61	0.0014
Cactus x Pop(Region)	32	0.2192	1.52	0.0524
Error	139	0.6272		

	Baja	n	Mainland	n
Organ Pipe				
(females)	4.21[e] (0.013)	57	4.38 (0.013)	48
(males)	3.87 (0.010)	57	3.99 (0.010)	48
Agria				
(females)	4.18 (0.003)	58	4.38 (0.017)	47
(males)	3.86 (0.014)	57	4.02 (0.011)	48

[a]Population(Region) = populations nested within geographical region.
[b]Cactus x Pop(Region) = interaction of cactus with populations nested within geographical region.
[c]n refers to the total number of cultures per cactus for each region. The number of cultures for each parental population were: S- 9, M- 21, O- 18, P- 15, V- 18, L- 15, and B- 6. Population abbreviations are given in Table I.
[d]Development time in days.
[e]Thorax size in micrometer units X 10.

data were rescaled to ocular micrometer units x 10 (4 units =1 mm). Maternal effects were assessed by t-tests of the means of the reciprocal crosses. Differences between pooled Baja and mainland populations for each trait were assayed with nested ANOVA. Differences among mid-parent and F_1 ($MP-F_1$) means, mid-parent and F_2 ($MP-F_2$) means, and F_1 and F_2 (F_1-F_2) means were subjected to t-tests.

3. RESULTS

3.1. Life History Differences between Baja and Mainland Populations

With a few exceptions, development times were shorter, viabilities were higher, and thorax sizes were smaller for the Baja populations than for the mainland populations (Fig. 2). Development times of Baja populations were shorter on agria than on organ pipe cactus accounting for a significant Cactus x Population interaction (Table II). Thus, Baja *D. mojavensis* developed faster on their resident host cactus signifying regional adaptation to agria in Baja California. Egg to adult viability differed among mainland and Baja populations, but no host plant adaptation was evident because there was no Cactus x Region interaction; however, different populations within regions expressed differences in viability due to cactus substrates suggesting geographical variation in egg to adult viability (Table II). Mainland adults were larger than Baja adults on both cacti, but Baja males were smaller on agria generating another Region x Cactus interaction (Table II).

Discriminant function analyses were performed with the replicated parental populations using the four fitness components as variables. On agria and organ pipe, these life history differences significantly discriminated among Baja and mainland populations (agria - Wilk's Lambda = 0.318, χ^2 = 115.58, P > 0.0001, df =4; organ pipe - Wilk's Lambda = 0.620, χ^2 = 48.26, P > 0.0001, df = 4). Thus, significant differences exist between Baja and mainland populations in these life history traits.

Latitudinal clines in development time and thorax size, but not viability, were evident among populations. The total number of replicates cultured for each parental population was averaged and regressed on latitude, so only seven data points were analyzed for each character. Development time on agria ($r = 0.726$, $P = 0.065$), female thorax size on organ pipe ($r = 0.725$, $P = 0.065$), female thorax size on agria ($r = 0.754$, $P = 0.05$), male thorax size on organ pipe ($r = 0.770$, $P = 0.043$), and male thorax size on agria ($r = 0.812$, $P = 0.026$) were all positively associated with increasing latitude. Such clines suggest that climatic variation in addition to host plant variation may have influenced development time and thorax size; however, life history differences characterizing Baja and mainland populations were particularly evident in the Punta Prieta (Baja) and Punta Onah (mainland) populations that are located at similar latitudes (Figs 1, 2). Further analy-

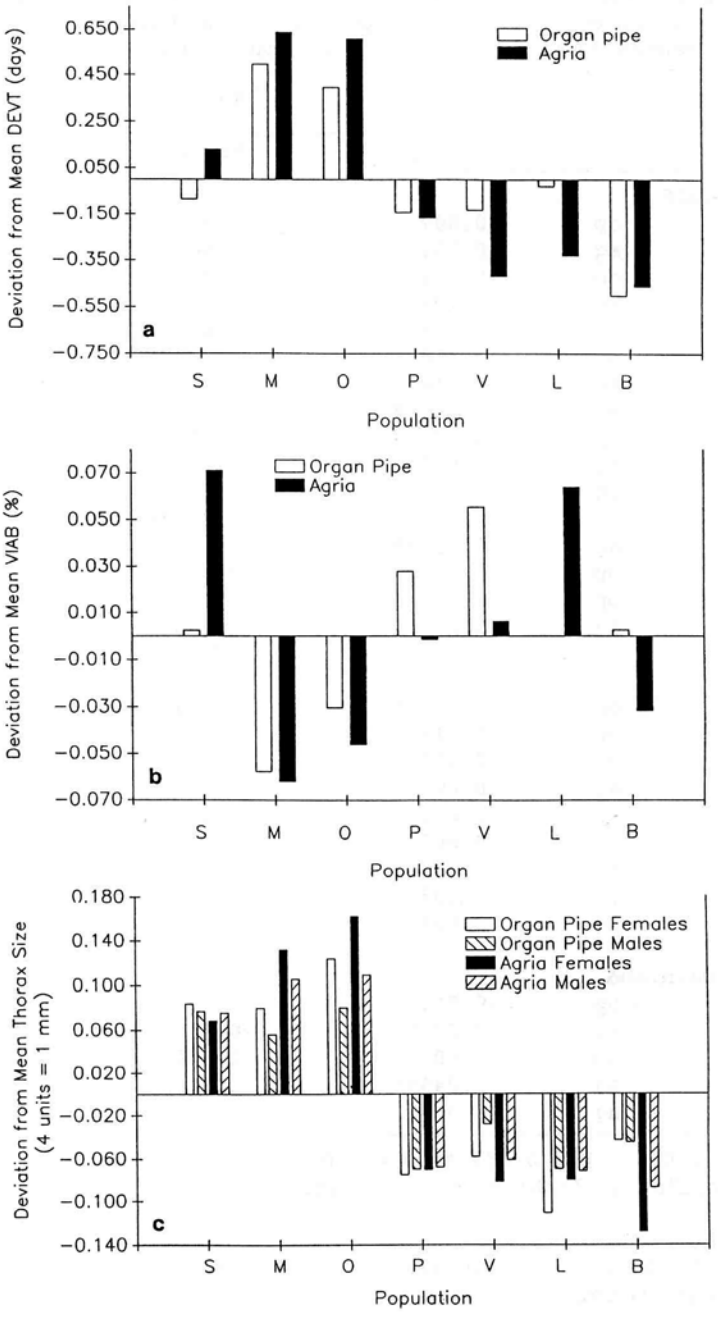

Figure 2. Comparisons of (a) egg to adult development time, (b) viability, and (c) adult thorax size among the 7 populations used in this study. Differences are expressed as deviations from the overall mean of all populations for each trait. Populations are arrayed from north to south (see Fig. 1). Population labels are defined in Table I.

Table III

Differences in $\log_{10}$ (egg to adult development time) among populations for Baja California and mainland populations and their crosses[a] of *D. mojavensis* cultured on organ pipe (op) and agria (ag) cacti

Cross		Contrast		
		MP-F_1	MP-F_2	F_1-F_2
Across the Gulf				
PS and SP	op	-0.007	0.006	0.014
	ag	-0.002	-0.002	0.000
PM and MP	op	-0.001	0.001	0.002
	ag	0.002	0.018*	0.020**
PO	op	0.013	-0.013	-0.026*
OP	op	-0.010	-	-0.003
PO	ag	0.014	-0.012	-0.025+
OP	ag	-0.031**	-	0.019
VO and OV	op	-0.029	0.004	0.033*
VO	ag	-0.014	0.007	0.021*
OV	ag	0.008	-	-0.001
LM and ML	op	-0.019+	-0.037**	-0.018
	ag	-0.033**	-0.012	0.022*
LO	op	-0.003	-0.005	-0.002
OL	op	0.006	-	-0.011*
LO and OL	ag	-0.004	0.014	0.017*
Within Baja				
VP	op	-0.050**	-0.009	0.041+
PV	op	0.013	-	-0.022
VP	ag	-0.018*	0.000	0.018*
PV	ag	0.004	-	-0.004
LV and VL	op	0.008	0.004	-0.005
	ag	-0.002	0.013	0.015*
BL and LB	op	0.022*	0.015	-0.007
BL	ag	-0.033*	0.017*	0.050*
LB	ag	-0.002	-	0.018*
Within the mainland				
OM and MO	op	-0.010	-0.004	0.021
	ag	0.022**	-0.003	-0.025*
SM and MS	op	0.005	-0.009+	-0.014
SM	ag	-0.045**	-0.010	0.035*
MS	ag	0.008	-	-0.018

+ $0.1 < P < 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[a]Maternal population label precedes paternal label.

sis of more Baja and mainland populations from similar latitudes is warranted.

3.2. Population Crosses

Eleven crosses were performed among populations: six involved populations on either side of the Gulf of California, with three within-Baja crosses and two within-mainland

crosses. Means of the F_1 and F_2 generation crosses were adjusted for the differences between the parental populations cultured with them to remove the average effects of variations among cactus tissue quality that can influence larval growth and development (Etges, unpublished data). When differences among reciprocal crosses were significant, replicates were not pooled. Contrasts among generation means were constructed including mid-parent-F_1 differences as indicators of overdominance or underdominance and mid-parent-F_2 comparisons as indicators of F_2 breakdown.

Considering all crosses, development time of the F_1s tended to be greater than that of the mid-parents with little indication of a cactus effect; maternal influences were significant in some cases (Table III). A majority of these significant differences involved within-region crosses indicating as much, or more, genetic differentiation within Baja and the mainland as between regions. Few differences were significant among mid-parent-F_2 comparisons, but development time was significantly greater in a majority of the F_1s than in the F_2s. Recombination of genotypic arrays influencing development time in these populations thus caused decreases in development time.

Egg to adult viability increased in those F_1s showing significant differences, suggesting some heterosis (Table IV). More evidence of maternal effects were found than with development time. However, a majority of the F_2 comparisons were negative, clearly showing increases in F_2 viability or lack of coadaptation.

Maternal effects were not apparent for female or male thorax size nor was there much evidence for heterosis in the F_1s (Table V). Of the 17 significant differences between mid-parent means and F_2s, seven were positive, and six of these seven were from within region crosses. Most F_2s from across the gulf crosses were larger than the mid-parents, but there was no trend in comparisons of F_1s and F_2s. Little evidence for coadaptation was thus apparent for thorax size, except for the results from the within-region crosses.

Virtually no evidence for either decreased variance among the F_1s or increased variance among the F_2s was found in comparisons of pooled within-bottle variances among generations (Table VI). Some increased variance within the parental mainland populations was suspected, which could have obscured comparisons among generations, but this was significant in only two of eight cases (Table VI). Similar results were obtained from a separate set of independent crosses using high and low larval densities on both host cacti (Etges, 1989c; Table VII). Variability in development time was greater in the Arizona population at high densities and the F_2s were more variable than the F_1s, but only on organ pipe. Increased variability among F_2s was consistent with coadaptation within populations, but expression of such genetic variation depended upon breeding substrates. Variation in thorax size did not provide strong evidence for coadaptation of genes influencing

Table IV
Differences in arcsin (egg to adult viability) among populations for Baja California and mainland populations and their crosses[a] of *D. mojavensis* cultured on organ pipe (op) and agria (ag) cacti

Cross		Contrast		
		$MP-F_1$	$MP-F_2$	F_1-F_2
Across the Gulf				
PS	op	0.123	-0.087+	-0.230*
SP	op	-0.106	-	0.019
PS	ag	-0.081	-0.141	-0.059
SP	ag	0.020	-	-0.160
PM	op	-0.045	0.123	0.167
MP	op	-0.050	-	0.073
PM and MP	ag	-0.049	0.110	0.061
PO	op	-0.393+	-0.106	0.286*
OP	op	0.102	-	-0.208
PO and OP	ag	-0.250+	-0.203	0.047
VO and OV	op	0.171	0.067	-0.103
	ag	0.042	-0.117+	-0.158
LM	op	-0.209*	-0.159	-0.368+
ML	op	0.393*	-	-0.552+
LM and ML	ag	0.301*	-0.159	-0.460*
LO and OL	op	-0.140+	-0.438**	-0.298*
LO	ag	0.007	-0.102	-0.108
OL	ag	-0.390*	-0.102	0.090
Within Baja				
VP	op	0.113	-0.157*	-0.270**
PV	op	-0.235+	-	0.078
VP	ag	0.180+	-0.323*	-0.511*
PV	ag	-0.080	-	-0.243+
LV and VL	op	-0.110	0.207+	0.317*
	ag	0.011	-0.116	-0.127
BL and LB	op	-0.477**	-0.087	0.390*
	ag	-0.044	0.134	0.179
Within the mainland				
OM and MO	op	0.006	0.047	0.005
OM	ag	-0.107	-0.019	0.087
MO	ag	0.134	-	-0.153*
SM and MS	op	-0.191*	-0.049	0.142
SM	ag	-0.096	-0.270**	-0.173
MS	ag	-0.181	-	-0.089

+ $0.1 < P < 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[a]See footnote - Table III.

Table V

Differences in thorax size (1 unit = 0.25 mm) among populations for Baja California and mainland populations and their crosses (see footnote - Table III) of *D. mojavensis* cultured on organ pipe (op) and agria (ag) cacti

		Contrast					
		$MP-F_1$		$MP-F_2$		F_1-F_2	
Cross		Females	Males	Females	Males	Females	Males
Across the Gulf							
PS and SP	op	0.090+	0.060	0.105	-0.235***	0.015	-0.195**
	ag	0.022	-0.006	-0.092	-0.142**	-0.114	-0.136*
PM and MP	op	0.055	0.065	0.063	0.007	0.118*	0.072
	ag	0.065	0.064	-0.022	-0.047	0.043	0.017
PO and OP	op	-0.022	-0.019	0.047	-0.012	0.069	0.007
	ag	-0.090	-0.044	0.129	-0.056	0.220**	-0.013
VO and OV	op	0.088	0.020	-0.054	0.008	-0.142	-0.012
	ag	-0.006	-0.036	-0.221**	-0.159*	-0.216**	-0.123*
LM and ML	op	-0.087	-0.041	-0.216**	0.027	-0.128+	0.069
	ag	0.006	-0.022	-0.157+	-0.120+	-0.163	-0.098
LO and OL	op	-0.051	-0.073+	0.081	0.161**	0.132*	0.234***
	ag	0.000	-0.013	0.036	-0.049	0.036	-0.036
Within Baja							
VP and PV	op	-0.070	0.002	-0.184*	-0.215*	-0.115	-0.217*
	ag	-0.100	-0.084	-0.458**	0.233**	-0.358**	0.317**
LV and VL	op	-0.005	0.078*	-0.028	-0.009	-0.024	-0.087*
	ag	0.172*	0.025	0.067+	0.198**	-0.105	0.172*
BL and LB	op	0.065	0.025	-0.080	0.000	-0.145	-0.026
	ag	-0.001	-0.080+	0.214+	0.046	0.215+	0.126*
Within the mainland							
OM and MO	op	-0.015	0.005	0.105*	0.026	0.121*	-0.156***
	ag	-0.020	0.018	0.090	0.025	0.110**	0.007
SM and MS	op	-0.033	-0.036	-0.048	-0.037	-0.014	0.000
	ag	0.102	0.067	0.121+	0.015	0.019	-0.052

+ $0.1 < P < 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

body size (Table V). Overall, recombination did not generally increase variability among the F_2s from interpopulation crosses of *D. mojavensis*.

4. DISCUSSION

The expansion of the geographical range of *D. mojavensis* has involved shifts to alternate host cacti and genetic changes in life history. An historical explanation for this pattern involves geographic isolation in Baja California and subsequent divergence from a mainland form, now the sibling species, *D. arizonensis* (Ehrman and Wasserman, 1987). Gastil *et al.* (1975) have postulated that tectonic drift transported the Baja peninsula from its connection to mainland Mexico to its present location, effectively isolating *D. mojavensis*. Following migration across the islands of the Gulf of California, *D. mojavensis* invaded the mainland by switching to organ pipe in Sonora and Arizona, and cina in southern Sonora and Sinaloa. Origins of the southern California barrel cactus-breeding and Santa Catalina Island *Opuntia*-breeding populations are discussed elsewhere (Johnson, 1980; Heed, 1982).

Table VI

Ratios of pooled within-group variances for parental, F_1, and F_2 generations from all crosses in this study cultured on both organ pipe, op, and agria, ag, cacti for egg to adult development time, DEVT, female thorax size, THFM, and male thorax size, THML. F ratios for egg to adult viability were formed using replicate averages

Generations Compared	Cactus	df	MS Ratio	F
1. P_2/P_1				
DEVT	op	2052	0.4264	0.784
		2917	0.5440	
	ag	2232	0.6232	1.872 ***
		3092	0.3329	
VIAB	op	97	0.0516	0.671
		64	0.0769	
	ag	97	0.0505	1.208
		65	0.0418	
THFM	op	215	0.0273	1.270 +
		282	0.0215	
	ag	215	0.0203	0.832
		253	0.0244	
THML	op	216	0.0195	1.224
		293	0.0159	
	ag	243	0.0152	1.076
		266	0.0141	
2. Mid-Parents/F_1				
DEVT	op	4969	0.5697	0.908
		4303	0.6271	
	ag	5324	0.4546	0.857
		4869	0.5305	
VIAB	op	97	0.0516	0.671
		64	0.0769	
	ag	97	0.0505	0.208
		65	0.0418	
THFM	op	497	0.0240	1.087
		427	0.0221	
	ag	468	0.0225	0.842
		413	0.0267	
THML	op	509	0.0175	0.951
		437	0.0184	
	ag	509	0.0146	1.139
		444	0.0128	
3. F_2/F_1				
DEVT	op	2297	0.4058	0.647
		4303	0.6271	
	ag	2392	0.4064	0.766
		4869	0.5305	
VIAB	op	33	0.0637	0.828
		66	0.0769	
	ag	33	0.0581	1.390
		68	0.0418	
THFM	op	76	0.0172	0.779
		427	0.0221	
	ag	206	0.0172	0.644
		413	0.0267	
THML	op	180	0.0172	0.935
		437	0.0184	
	ag	203	0.0142	1.108
		444	0.0128	
4. F_2/Mid-Parents				
DEVT	op	2468	0.4252	1.270 *
		2151	0.3349	
	ag	2588	0.4234	0.689
		2118	0.6146	
VIAB	op	33	0.0637	1.234
		102	0.0516	
	ag	33	0.0581	1.151
		101	0.0505	
THFM	op	196	0.0166	0.926
		177	0.0179	
	ag	226	0.0173	1.033
		182	0.0168	
THML	op	204	0.0164	1.089
		169	0.0151	
	ag	225	0.0137	0.950
		215	0.0144	

+ $0.1 < P < 0.05$, * $P < 0.05$, *** $P < 0.001$.

Table VII
Across generation F ratios of pooled within-bottle variances of egg to adult development time and thorax size in *D. mojavensis*

a. Development time

Variance Ratio[a]	Density[b]	Organ Pipe F	Organ Pipe df	Agria F	Agria df
1. P_2/P_1	L	0.630	618/631	0.854	614/640
	H	2.314***	4915/4833	1.285*	4979/4942
2. Mid-parents/F_1	L	1.173	1249/1165	1.154	1254/1202
	H	1.133	9748/9842	0.943	9921/10339
3. F_2/Mid-parents	L	1.171	1181/1249	0.903	1367/1254
	H	1.035	9784/9748	1.145	10203/9921
4. F_2/F_1	L	1.374**	1181/1165	1.041	1367/1202
	H	3.122***	9784/9842	1.080	10203/10339

b. Thorax Size

Variance Ratio	Sex	Density	F	df	F	df
1. P_2/P_1	F	L	1.312	78/75	0.593	71/78
	F	H	1.127	319/243	0.996	475/423
	M	L	0.834	70/73	0.950	67/72
	M	H	1.205	325/228	0.956	489/422
2. Mid-parents/F_1	F	L	1.128	153/138	0.957	149/148
	F	H	0.948	562/576	1.103	898/933
	M	L	1.914***	143/144	1.238	139/144
	M	H	1.134	553/585	0.874	911/942
3. F_2/Mid-parents	F	L	0.839	159/153	1.138	161/149
	F	H	1.191	606/562	1.073	915/898
	M	L	0.725	164/143	1.425**	164/139
	M	H	0.972	599/553	1.049	941/911
4. F_2/F_1	F	L	0.947	159/138	1.090	161/148
	F	H	1.129	606/576	1.184	915/933
	M	L	1.387*	164/144	1.764***	164/144
	M	H	0.943	599/585	0.960	941/942

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[a]Generation designations are defined in the text.
[b]L = low density, H = high density.

Life history evolution can thus be attributed, at least partly, to the shift to different host cacti along with the morphological, cytological, behavioral, and genic differentiation among populations that has prompted description of geographical subspecies, races, and subraces of *D. mojavensis* (Mettler, 1963; Zouros, 1973; Zouros and D'Entremont, 1980).

Regional differences in development time and viability can be considered adaptations to the host cacti used. Baja populations express shorter development times and smaller thorax sizes on their resident host plant, agria, than do mainland populations on their host plant, organ pipe cactus. Unraveling the causes for the smaller adult size of Baja flies and the larger adult sizes of the mainland flies will require field studies of dispersal and estimation of genetic correlations with other traits, particularly development time. If smaller thorax size is genetically correlated with shorter development time, small thorax size may not be adaptive.

The characteristics of agria and organ pipe rots that have been implicated with these life history shifts concern rot duration, abundance, and dispersion. Agria cactus is considered a more predictable resource for adult feeding and oviposition, but unpredictable for larval survivorship because stem diameters are smaller and tissues decompose faster leading to faster rot desiccation than organ pipe (Johnson, 1980; Heed, 1981; Etges and Heed, 1987; Etges, 1989c). Thus, agria is a more ephemeral breeding substrate but more abundant as a feeding site than organ pipe, and those populations that use agria are more viable, develop faster, and are smaller as adults.

Invasion of mainland Sonora and Arizona was possible because of the presence of organ pipe, and to the south, cina and organ pipe. Little is known of the ecology or genetics of the cina-breeding populations, except that they sometimes coexist with *D. arizonensis* (Ruiz and Heed, 1988). In Sonora and Arizona, organ pipe-breeding *D. mojavensis* populations are faced with greater trophic unpredictability for adults because organ pipe rots are less frequent (rots per plant per hectare) and further apart (Johnson, 1980; Mangan, 1982; Heed and Mangan, 1986; Ruiz and Heed, 1988). However, organ pipe rots are usually much larger than agria rots because stem diameters are larger providing temporally more stable breeding sites. Longer lasting rots could have allowed increases in larval development time and adult body size in organ pipe-breeding populations of *D. mojavensis* with a corresponding increase in ovariole numbers (Heed, unpublished data) and lifetime fecundity (Etges and Klassen, 1989). Dispersal ability must be greater in organ pipe-breeding populations because of the greater distance between rots than in agria-breeding populations (Mangan, 1982), which may also explain the body size increases. Thorax size is known to be correlated with dispersal ability (Roff, 1981) and rot-to-rot distances among all Sonoran Desert Drosophila (Johnston and Heed, 1976; Heed and Mangan, 1986).

Despite adaptation to such very different breeding and feeding environments, little reorganization of the gene pool

influencing life history differences among populations has occurred since invasion of the mainland. Most of the genetic differences among populations are additive or nearly so (Etges, 1989c). The lack of coadaptation among population crosses suggests that new epistatic gene complexes did not evolve in the face of considerable gene frequency change. Wright (1977) predicted that microevolutionary divergence would be most rapid when small populations or demes were separated in space or time, gene flow was reduced or absent, and demes were exposed to differing environments. It is unlikely that the lack of genetic restructuring or incompatibility is due to gene flow with the ancestral Baja populations given the degree of allozymic differentiation and the abrupt loss of inversion polymorphism outside of the small agria patch in coastal Sonora (Heed, 1978; Johnson, 1980). The mainland populations have clearly begun a new evolutionary trajectory, yet no postmating reproductive barriers have yet evolved.

Thus, the mainland populations have not undergone irreversible genetic changes in life history traits and only the one-way sexual isolation between mainland females and Baja males suggests any evolution of reproductive isolation. Further study of the quantitative genetic basis of within-population variation and covariation of life history traits and premating isolation may provide insight into the genetic processes of species formation before isolation is complete.

5. SUMMARY

Baja California and mainland populations of *D. mojavensis* exhibit geographic differences in components of fitness, egg to adult development time, viability, and adult thorax size that are genetically based. These regional differences are consistent, and are greater between regions than within regions. The expression of life history variation was influenced by the type cactus used for larval growth and development. Baja populations of *D. mojavensis* exhibited shorter development times and smaller thorax sizes on their resident cactus, agria, than the mainland populations did on their host plant, organ pipe cactus, suggesting host plant adaptation. Smaller thorax sizes of Baja adults may not be adaptive if thorax size is genetically correlated with development time. Results of population crosses within and between Baja and mainland populations for these life history characters showed few instances of overdominance in the F_1s or F_2 breakdown, and many cases of maternal effects for development time and viability. The lack of coadaptation suggests that selection has not produced epistatic gene complexes in spite of considerable gene frequency change since *D. mojavensis* shifted to new host cacti. Since Baja and mainland populations are fully interfertile and exhibit only one-way premating isolation, further genetic analysis of the population differences in life history should yield insight into the process of incipient speciation.

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