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Evolution of developmental homeostasis in *Drosophila mojavensis*

WILLIAM J. ETGES
Department of Zoology, University of Arkansas, Fayetteville, AR 72701, USA

Summary

Variation in life histories among populations of cactophilic *Drosophila mojavensis* has been hypothesized to be a by-product of a shift to one of two alternate host plants. When cultured on the ancestral and a secondary host cactus, a Baja population expressed shorter development times and smaller thorax sizes than a mainland population, but viability did not differ. Comparisons with all reciprocal F_1 and F_2 crosses between populations revealed that genetic differences in development time and thorax size were largely additive. Homeostasis in these life history traits was population specific, except for viability. Homeostasis in development time was greater in the Baja population than in the other crosses, suggesting dominance for decreased homeostasis in the mainland population. Underdominance in viability homeostasis of the F_1 hybrids suggested some incompatibility between populations. Homeostasis in thorax size was greater in females than in males and differed among parental populations. Maintenance of heritable differences and genetic variation for homeostasis in these traits suggested a role for cactus-specific differences in environmental uncertainty caused by variation in breeding site duration and abundance in nature.

Keywords: Developmental homeostasis; life history traits; *Drosophila*; breeding site variation; cactus; Sonoran desert.

Introduction

Homeostasis refers to the property of the organism to adjust itself to variable conditions, or to the self-regulatory mechanisms of the organism which permit it to stabilize itself in fluctuating inner and outer environments. *Lerner, 1954.*

Developmental homeostasis, an organism's ability to maintain a more buffered series of developmental pathways resulting in increased phenotypic uniformity of individuals in a population, is one aspect of genetic homeostasis. Although Lerner (1954) was primarily interested in the increased buffering of heterozygotes to environmental fluctuations, he recognized the general significance of homeostasis as a mechanism for adaptation resulting from stabilizing selection in the face of environmental unpredictability (Dobzhansky, 1947; Lerner and Dempster, 1948; Schmalhausen, 1949).

The extent to which homeostasis can evolve is a function of the amount of genetic variation in homeostasis within populations and the relationship of homeostasis to fitness. It has been generally assumed that lack of homeostasis, or phenotypic plasticity, can evolve countering the maintenance of genetic variation due to environmental heterogeneity (Thoday, 1953; Lewontin, 1957; Bradshaw, 1965), and in equilibrium populations, genetic variation for plasticity may be eroded (Via and Lande, 1985). While studies of selection in varying environments have shown that genotypes with less variable reproductive rates will increase in frequency (Gillespie, 1973,

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1977), Orzack (1985) has shown that this is not a general rule. Specifically, he concluded that 'the relative advantage of homeostasis depends upon the environmental frequencies, their autocorrelation, the portion of the life history which is subject to variation, and the covariances between vital rates'. Thus, the fate of genotypes more or less homeostatic for traits closely tied to fitness in natural populations depends upon the environmental conditions such genotypes are exposed to, the ecological significance of these traits, and covariation among life history traits.

To evaluate the potential adaptive nature of homeostasis in life history traits, I investigated the genetic basis of homeostasis in egg to adult development time, viability, and adult thorax size in populations of cactophilic *Drosophila mojavensis*. Homeostasis was measured by comparing expression of each trait at high and low larval densities: better-buffered genotypes were expected to show less phenotypic difference across densities. This measure of homeostasis was considered ecologically relevant and captured the essence of developmental homeostasis, such as in classical studies of bilateral asymmetry (Reeve, 1960; Van Valen, 1962).

Populations of *D. mojavensis* carry out their entire life cycle in and around fermenting cactus tissues, 'rots', of several species of columnar cactus in the Sonoran desert. In Baja California and a small coastal region in Sonora, Mexico, *D. mojavensis* uses pitaya agria, *Stenocereus gummosus*, for feeding and breeding. In Arizona and Sonora, organ pipe cactus, *S. thurberi*, is used, and in southern Sonora and Sinoloa, cina, *S. alamosensis*, is a major host (Ruiz and Heed, 1988). Agria is the preferred host plant (Fellows and Heed, 1972) as *D. mojavensis* has been reared infrequently from organ pipe tissues where the cacti are sympatric (Heed and Mangan, 1986).

Adaptation to these host plant differences was suggested by Etges and Heed (1987), who found that an agria-inhabiting Baja population was characterized by shorter egg-to-adult development times, higher viabilities, and smaller adult body sizes than a mainland population over a range of larval densities in both agria and organ pipe cultures. They concluded that populations from Baja were able to maintain more constant phenotypic expression of these life history characters than mainland populations with increasing density. In this study, I constructed reciprocal crosses among populations of *D. mojavensis* and cultured them on both species of cacti to verify both the genetic basis of these life history differences and variation in homeostasis for these fitness components. I also measured rates of tissue decomposition of both host plants during fermentation as indicators of breeding site duration in nature.

Materials and methods

Populations of *D. mojavensis* were sampled from nature by aspirating adults from fermenting cactus tissues in the field and by rearing adults from these tissues upon return to the laboratory. Large crossbred laboratory populations were started using wild adults from two localities: Punta Prieta, Baja California Norte (3918 founders) and Santa Rosa Mountains near Tucson, Arizona (352 founders). All flies were cultured in vials on banana–yeast–malt–karo–agar food at room temperature.

Prior to growth on cactus, about 50 mature virgin pairs of adults from each population were placed into each of seven half-pint milk bottles with lab food and allowed to mate and oviposit for 3–4 days. Adult virgins from each of these replicate cultures were collected, aged, and both reciprocal crosses between populations were made with about the same numbers of adults. Reciprocal F_1, F_2 and within-population crosses were produced simultaneously and replicated seven times. About 200 mature males and females from each parental, reciprocal F_1 and F_2 cross were placed in plastic freezer bozes with a 6 cm hole drilled in one side to accommodate a removable petri dish containing oviposition media consisting of 1% agar-rotted agria slurry. Eggs

were collected over 6 hour intervals, held overnight in an incubator at 25°C, and used the next day for culturing on fermenting cactus.

Eggs from each replicate cross were washed in distilled water, surface-sterilized in 70% ethanol for 10 minutes, and washed again with sterile water. These eggs were counted out on to 1 cm^2 pieces of filter paper in lots of 50 or 400. Two replicates of each density were started on fermenting agria and organ pipe tissues. Artificial rots were made with 35 g pieces of fresh cactus placed on 75 g of gravel in half-pint milk bottles sealed with cotton. Only older yellow-brown cactus tissues were used (see later). After autoclaving, each was inoculated with a pectolytic bacterium and seven species of yeast common to natural rots of both cactus species (Starmer, 1982; Fogleman and Starmer, 1985). Yeasts used were: *Pichia cactophila, P. mexicana, P. amethionina* var. *amethionina, Cryptococcus cereanus, Candida valida, C. ingens,* and *Torulopsis sonorensis*. Thus, for each set of six crosses – both parentals and reciprocal F_1s and F_2s — two replicate cultures on two cacti at two densities were started and cultured side by side in a 25°C incubator with a 14:10 LD photoperiod.

Egg-to-adult viability and development time were measured by collecting all eclosed 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. Thus, viability estimates were not biased by differences in egg hatchability. Adult thorax size was measured with an ocular micrometer to the nearest 0.025 mm using aged adults. Three adults per day of development time per sex per replicate were measured for thorax size.

Variation in development time, viability, and thorax size was assayed by analysis of variance using PROC GLM in SAS/STAT (SAS Institute, Inc., 1985). In the Anova model, I considered cactus and density fixed effects, and cross and cross replication random effects using type IV sums-of-squares. All data were tested for normality: viability data were arc sin transformed.

The measure of developmental homeostasis I used was simply the difference between replicate bottles at each density for each cactus for each character measured. For example, development time increased at high densities. Homeostasis in development time was calculated as the difference in development time at high density and low density. Thus, greater homeostasis for each character was indicated by smaller differences across densities. These data were also subjected to analysis of variance and between-generation *t*-tests to evaluate the effects of cactus substrates on homeostasis for each character.

Cumulative volumes of rot exudate produced after inoculation of fresh tissues were measured by fermenting weighed fresh tissues (as above) and collecting all the liquid produced. Lots of 100 eggs from a Santa Rosa Mountains population of *D. mojavensis* were placed in each of six replicate bottles containing agria and organ pipe tissues. A small funnel was taped to the top of each bottle, and then the bottle was inverted with the funnel inserted into a graduated cylinder and partially sealed with Parafilm. Variation in tissue quality of fresh cactus arms was compared by collecting juice from green tissues that had been removed from the younger growth tips of arms, and from older tissues that were yellow-brown or brown and had been removed from arms near the base of the plants.

Results

Genetic differences in developmental homeostasis

Differences in development time varied among cross types from high to low densities (Table 1). The Baja population was more homeostatic in development time than the mainland population (three-way Anova, $F = 11.48, p = 0.001$; Fig. 1), particularly on organ pipe ($t = 3.50, p = 0.002$, 13 d.f.).

Table 1. Analysis of variance results for homeostasis in development time, viability, and thorax size among population crosses in *Drosophila mojavensis*.

Source[a]	d.f.	Mean-square	*F*-value
Development time homeostasis			
MODEL	17	38.446	16.97 ****
CROSS TYPE	5	7.435	3.28 ***
CROSS REPLICATION	6	7.409	3.27 ***
CACTUS	1	571.136	252.15 ****
CTYPE*CACTUS	5	0.667	0.29 ns
Error	150	2.265	
Arc sin (viability homeostasis)			
MODEL	17	0.074	5.73 ****
CROSS TYPE	5	0.016	1.26 ns
CROSS REPLICATION	6	0.021	1.64 ns
CACTUS	1	1.006	78.46 ****
CTYPE*CACTUS	5	0.006	0.48 ns
Error	150	0.013	
Thorax size homeostasis			
MODEL	24	0.015	10.14 ****
CROSS TYPE	5	0.009	5.59 ****
CROSS REPLICATION	6	0.004	2.90 ***
CACTUS	1	0.168	109.80 ****
SEX	1	0.125	81.84 ****
CTYPE*CACTUS	5	0.001	0.40 ns
CACTUS*SEX	1	0.001	0.11 ns
CTYPE*SEX	5	0.001	0.77 ns
Error	309	0.002	

[a] Cross type refers to parental populations, F_1s and F_2s. Cross replication refers to the seven replicate cross sets. CTYPE is CROSS TYPE.
*** $p < 0.01$, **** $p < 0.0001$, ns not significant.

The Baja population was also more homeostatic in development time than the pooled F_1s ($t = 2.66$, $p = 0.011$, 40 d.f.) and F_2s ($t = 2.14$, $p = 0.039$, 39 d.f.) on organ pipe but not agria (Fig. 1a). The mainland population did not differ from either F_1 or F_2 pooled reciprocal crosses. Thus, differences in homeostasis for development time among populations were genetic and the genes causing decreased homeostasis in the mainland populations exhibited some dominance over the genes causing increased homeostasis in the Baja population.

Homeostasis in egg-to-adult viability did not differ among parental populations ($t = 0.49$, $p = 0.628$), so all intergeneration *t*-tests were performed with pooled data (Fig. 1b). Average homeostasis in viability of the parental populations exceeded that of the F_1s on organ pipe ($t = 2.19$, $p = 0.034$, 27 d.f.) but not agria ($t = 1.60$, $p = 0.115$, 27 d.f.). Thus, hybrids from these interpopulation crosses were less homeostatic than either parental population on one substrate used for breeding and feeding in nature, suggesting some underdominance in the action of genes controlling homeostasis in egg-to-adult viability.

Within-generation correlations between homeostasis in development time and viability were

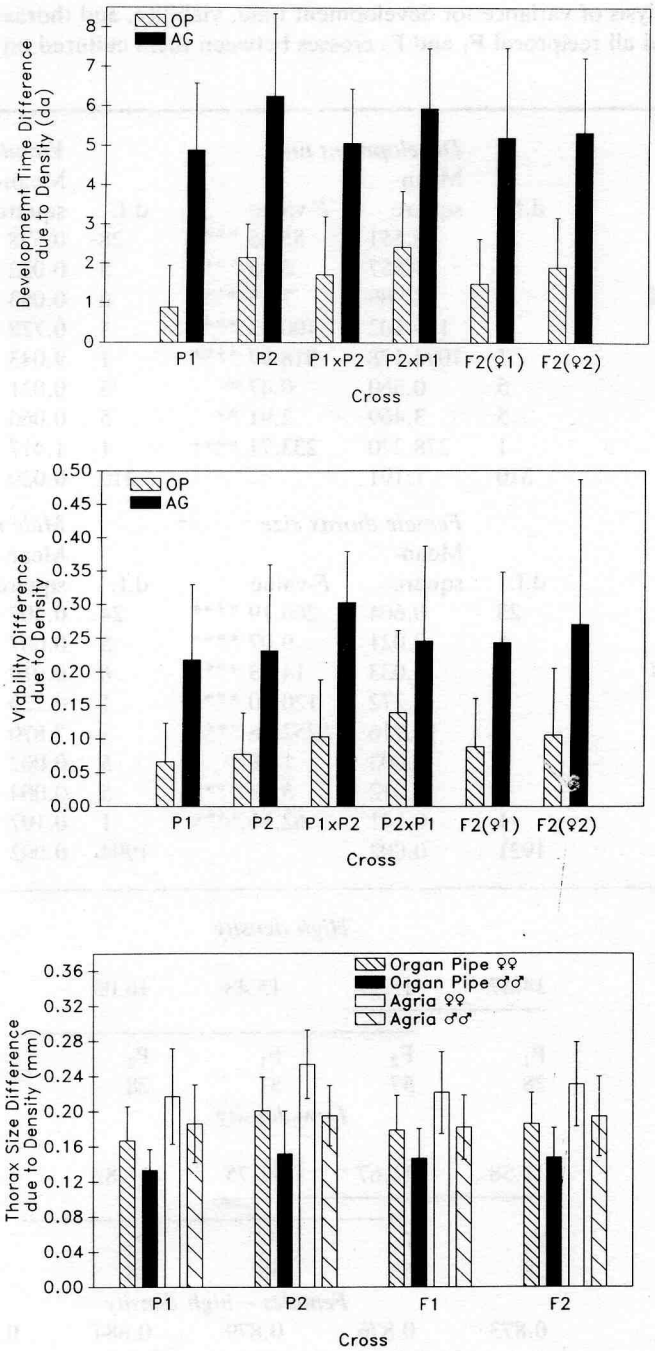

Figure 1. Homeostasis (+1 SE) in (a) development time (observed development time at high density–low density of paired replicates); (b) egg to adult viability (absolute value [observed viability at high density–low density of paired replicates]); (c) thorax size (observed thorax size at high density–low density of paired replicates) among generations on both host cacti. OP refers to organ pipe and AG refers to agria.

Table 2. Results of analysis of variance for development time, viability, and thorax size among Baja and mainland populations and all reciprocal F_1 and F_2 crosses between them cultured on two host cacti at two densities.

	Development time			*Viability*		
Source[a]	d.f.	Mean-square	*F*-value	d.f.	Mean-square	*F*-value
MODEL	28	65.551	55.05 ****	28	0.528	18.23 ****
CROSS TYPE	5	4.557	3.83 ***	5	0.052	1.81 ns
CROSS REPLICATION	6	8.989	7.55 ****	6	0.083	2.86 **
CACTUS	1	119.102	100.03 ****	1	0.728	25.14 ****
DENSITY	1	1094.178	918.97 ****	1	9.043	312.15 ****
CTYPE*CACTUS	5	0.560	0.47 ns	5	0.031	1.07 ns
CTYPE*DENSITY	5	3.469	2.91 **	5	0.066	2.28 *
CACTUS*DENSITY	1	278.270	233.71 ****	1	1.417	48.91 ****
Error	310	1.191		310	0.029	
	Female thorax size			*Male thorax size*		
Source	d.f.	Mean-square	*F*-value	d.f.	Mean-square	*F*-value
MODEL	23	0.604	266.19 ****	24	0.407	253.59 ****
CROSS TYPE	5	0.021	9.07 ****	5	0.007	4.12 ***
CROSS REPLICATION	6	0.033	14.43 ****	6	0.019	11.67 ****
CACTUS	1	0.272	120.00 ****	1	0.223	139.21 ****
DENSITY	1	11.916	5252.76 ****	1	7.870	4907.90 ****
CTYPE*CACTUS	5	0.003	1.48 ns	5	0.002	1.34 ns
CTYPE*DENSITY	5	0.012	5.30 ****	5	0.004	2.41 *
CACTUS*DENSITY	1	0.141	62.11 ****	1	0.107	66.84 ****
Error	1921	0.002		1904	0.002	

	High density			
Mean development[b] time (da)	14.47	15.27	15.48	16.03
Cross type[c]	P_1	F_2	F_1	P_2
N[d]	28	57	57	28
	Low density			
Mean development time (da)	11.58	11.67	11.75	11.82
Cross type	P_1	F_1	F_2	P_2
N	28	55	58	28

	Females – high density					
Thorax size (mm)	0.873	0.876	0.879	0.884	0.885	0.905
Cross type[b]	P_1	F_2–2	F_1–2	P_2	F_2–1	F_1–1
N	243	281	286	289	270	248

			Males – high density			
Thorax size (mm)	0.821	0.825	0.827	0.828	0.833	0.844
Cross type	F_2–2	P_1	F_1–2	P_2	F_2–1	F_1–1
N	274	233	287	289	268	251
			Females – low density			
Thorax size (mm)	1.077	1.092	1.101	1.103	1.109	1.122
Cross type	P_1	F_2–1	F_2–2	F_1–1	F_1–2	P_2
N	57	64	52	53	49	54
			Males – low density			
Thorax size (mm)	0.996	1.002	1.006	1.011	1.013	1.015
Cross type	P_1	F_2–2	F_1–1	F_2–1	F_1–2	P_2
N	57	54	50	64	53	49

[a] Treatment effects are defined in Table 1.
[b] Means connected by a line are not significantly different by Duncan's multiple range test ($p < 0.05$).
[c] Cross types include P_1, the Baja population, P_2, the mainland population; F_1–2 refers to F_1s with mainland mothers, and F_2–2 refers to F_2s whose mothers were F_1–2 and *vice versa*.
[d] *N* is the number of cultures. For thorax sizes, *N* is the number of thorax size means for each day of development time.
* $p < 0.05$, ** $p < 0.025$, *** $p < 0.01$, **** $p < 0.0001$, [ns] not significant.

all positive across cacti, but only significant for the pooled F_1s and F_2s on organ pipe ($r = 0.674$, $p < 0.0001$, $n = 28$ and $r = 0.546$, $n = 27$, $p = 0.0032$, respectively). This covariation resulted from the loss of homeostasis for both traits in the F_1s and F_2s.

Baja females were more homeostatic for thorax length than mainland females on organ pipe ($t = 2.34$, $p = 0.027$) and marginally so on agria ($t = 2.03$, $p = 0.053$), but males were not (Fig. 1c). All reciprocals were pooled, as none differed significantly. No other significant differences among crosses were found even though a total of 10 827 adults were measured, but in all cases females were more homeostatic for thorax size than males were (Table 1).

Population-cross differences

The Baja population expressed shorter development times than the mainland population on organ pipe (12.07 vs 12.81 days, $t = 2.56$, $p = 0.014$) and agria (13.98 vs 15.03 days, $t = 1.22$, not significant; Table 2). Maternal effects were absent, thus reciprocals were pooled. Genes influencing differences in development time acted additively at low densities: the F_1s and F_2s tended to be intermediate relative to the parentals. At high densities, some dominance for long development time was evident, as indicated by the ranking of F_1s and F_2s (Table 2). Thus, expression of genes influencing development time was dependent on the degree of larval competition, and hence nutrition.

Viability was not significantly different among cross types. Even though mainland populations tend to be less viable than Baja populations (Etges and Heed, 1987; Etges, 1989), this difference was not apparent here.

Baja adults were smaller than mainland adults, particularly at low densities (Table 2). Thorax sizes of reciprocal F_1s and F_2s were not always homogeneous, indicating maternal effects on adult size. Therefore, comparisons were made with unpooled data at each density level because there was no cross type × cactus interaction (Table 2). Female and male F_1s with Baja female parents

were larger than all other crosses at high densities, but mainland adults were consistently larger than all other crosses at low densities. Thus, there was some indication of dominance for large thorax size at low densities, particularly among females.

Rot juice accumulation experiment

After 22 days, fluid volumes collected from fermenting tissues differed considerably between cactus types (one-way Anova, $f = 18.03$, $p < 0.0001$; Fig. 2). Older, yellow-brown agria tissues produced 0.55 cc of fluid per gram of fresh tissue during this interval versus 0.04 cc per gram produced by older, yellow-brown organ pipe tissues. Green agria tissues produced about the same volume of liquid as green organ pipe tissues (Duncan's multiple range test, $p < 0.05$), 0.31 vs 0.25 cc per g, respectively. Thus, older yellow-brown tissues of agria and organ pipe, like those found in nature that ferment to provide active feeding and breeding sites for *D. mojavensis*, differ considerably in rates of decomposition during microbial degradation.

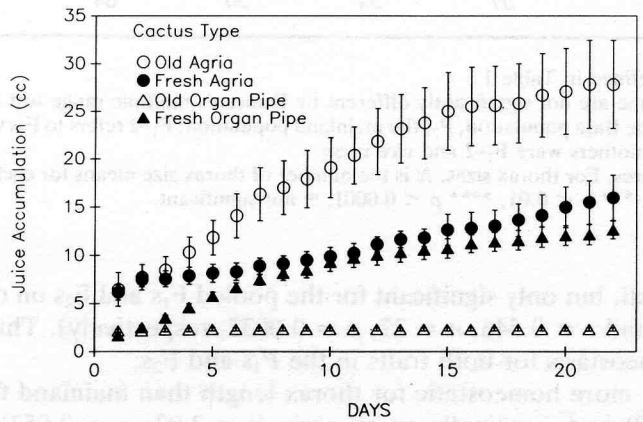

Figure 2. Plot of the host cactus differences, young vs old tissues, in amounts of cactus juice (±1 SE) produced during microbial fermentation.

Discussion

The greater ability of the Baja population to maintain a more constant expression of phenotypes directly related to fitness has a genetic basis. The mainland population has lost homeostasis in development time while retaining homeostasis in viability, so it is likely that these two traits are under independent genetic control. The observed underdominance in viability homeostasis is evidence for genetic incompatibility between geographically separated populations of *D. mojavensis* if such homeostasis is correlated with increased fitness in nature. Association of shorter development time and increased homeostasis in development time in the Baja population versus the mainland population implies some selection, past and/or present, for lower averages and variances in development time. Such genetic variation is relevant to the differences in ecological and growth characters of the resources upon which *D. mojavensis* are totally dependent throughout their life cycle: agria and organ pipe cacti (Mangan 1978, 1982; Heed 1981; Heed and Mangan, 1986; Etges and Heed, 1987; Etges, in press; Etges and Klassen, 1989).

Agria and organ pipe rots differ considerably in abundance, distribution, and size (Heed, 1981; Mangan, 1982; Etges and Heed, 1987; Ruiz and Heed, 1988). Breeding site duration is assumed

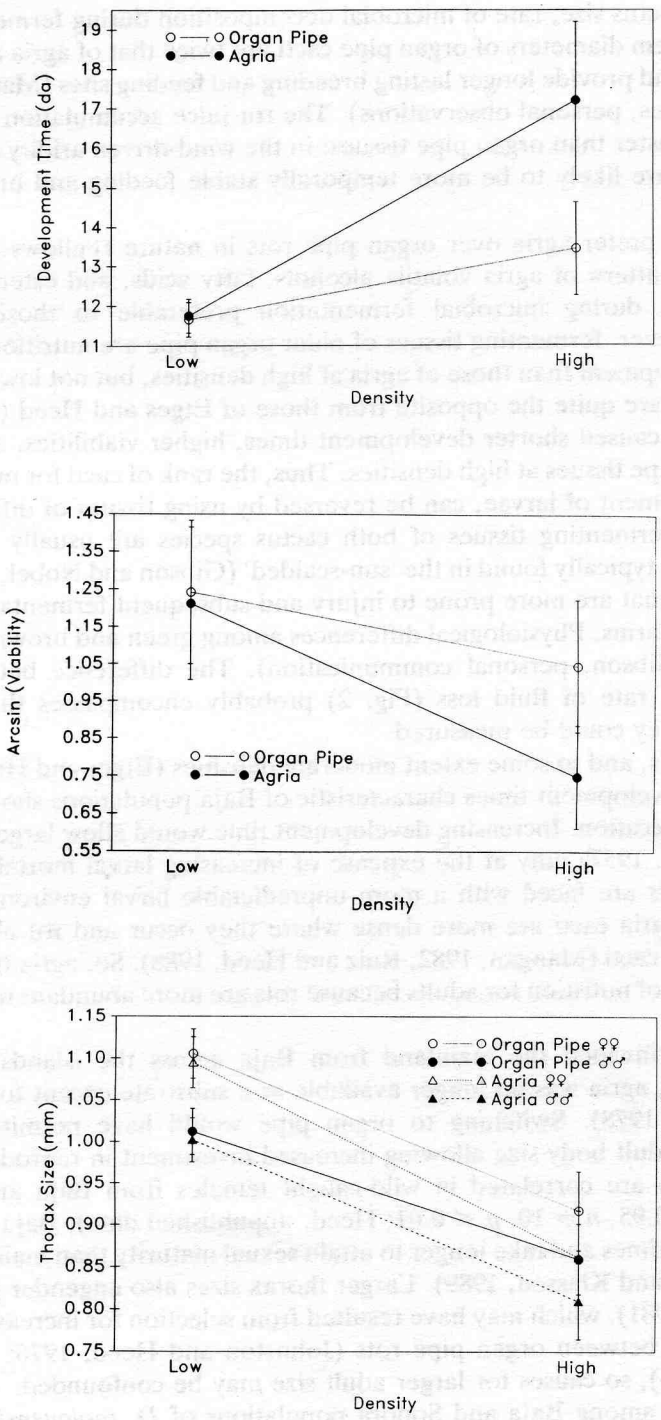

Figure 3. Density-caused variation (±1 SE) in (a) egg to adult development time, (b) viability, and (c) thorax size due to the kind of cactus used for culture across all generations in this experiment.

to be proportional to cactus size, rate of microbial decomposition during fermentation, and rate of tissue desiccation. Stem diameters of organ pipe cacti are twice that of agria and so organ pipe rots are usually larger and provide longer lasting breeding and feeding sites (Mangan, 1982; Heed and Mangan, 1986; Etges, personal observations). The rot juice accumulation results show that older agria tissues rot faster than organ pipe tissues: in the wind-driven aridity of the desert, the larger organ pipe rots are likely to be more temporally stable feeding and breeding sites than agria.

Adult *D. mojavensis* prefer agria over organ pipe rots in nature (Fellows and Heed, 1972) because they find the pattern of agria volatile alcohols, fatty acids, and esters (Fogleman and Heed, 1989) produced during microbial fermentation preferable to those of organ pipe (Downing, 1985). However, fermenting tissues of older organ pipe are nutritionally superior for larval growth and development than those of agria at high densities, but not low densities (Fig. 3, Table 2). These results are quite the opposite from those of Etges and Heed (1987) who found that green agria tissues caused shorter development times, higher viabilities, and larger thorax sizes than green organ pipe tissues at high densities. Thus, the rank of cacti for nutritional quality, i.e. growth and development of larvae, can be reversed by using tissues of different quality.

Naturally occurring fermenting tissues of both cactus species are usually yellow-brown to brown in color. Rots are typically found in the 'sun-scalded' (Gibson and Nobel, 1986) basal arms which are older tissues that are more prone to injury and subsequent fermentation than are the younger, growing green arms. Physiological differences among green and brown tissues have not been studied (A. C. Gibson, personal communication). The difference between green and yellow-brown tissues in rate of fluid loss (Fig. 2) probably encompasses the range of rates occurring in nature if they could be measured.

At high larval densities, and to some extent moderate densities (Etges and Heed, 1987; Etges, in press), the shorter development times characteristic of Baja populations should reduce larval mortality due to rot desiccation. Increasing development time would allow larger adult body size (Sang, 1956; Robertson, 1957) only at the expense of increasing larval mortality. Thus, agria-inhabiting *D. mojavensis* are faced with a more unpredictable larval environment due to rot desiccation; however, agria cacti are more dense where they occur and rot about 40 times as frequently as organ pipe cacti (Mangan, 1982; Ruiz and Heed, 1988). So, agria thickets provide a more predictable source of nutrition for adults because rots are more abundant within stands than organ pipe.

Once *D. mojavensis* invaded the mainland from Baja across the islands in the Gulf of California (Heed, 1982), agria was no longer available as a substrate except for a small area in coastal Sonora (Heed, 1978). Switching to organ pipe would have permitted increases in development time and adult body size allowing increased investment in reproduction. Ovariole number and thorax size are correlated in wild-caught females from Baja and the mainland (among population $r = 0.95$, $n = 10$, $p < 0.01$; Heed, unpublished data). Baja females also lay fewer eggs over their lifetimes and take longer to attain sexual maturity than mainland females on cactus substrates (Etges and Klassen, 1989). Larger thorax sizes also engender greater dispersal capability (Roff, 1977, 1981), which may have resulted from selection for increased dispersal due to the greater distances between organ pipe rots (Johnston and Heed, 1976; Johnston, 1977; Heed and Mangan, 1986), so causes for larger adult size may be confounded.

Life history evolution among Baja and Sonora populations of *D. mojavensis* seems to have been influenced by the contrasting patterns of environmental uncertainty due to the rot characteristics of the host cacti. Shorter development times and increased homeostasis in development time of Baja populations suggest that plasticity for this trait is not adaptive (Smith-Gill, 1983) on agria and that directional selection has maintained shorter development times. The

evolutionary transition to organ pipe involved a decrease in homeostasis in the mainland populations. Dominance in the action of genes decreasing homeostasis, i.e. increasing plasticity, suggests that plasticity in development time has increased since *D. mojavensis* invaded the mainland by switching to organ pipe.

Whether this plasticity is adaptive or will evolve further requires estimation of genetic correlations across cactus substrates of each life history character (Via and Lande, 1985). However, increased developmental plasticity in mainland populations is consistent with the ecology of their major host plant. Organ pipe tissues ferment more slowly (Fig. 2), and although naturally occurring organ pipe and agria rots contain similar numbers of yeast species, means and variances of yeast cell density are lower in organ pipe (Fogleman and Starmer, 1985) resulting in lower concentrations of volatiles (Fogleman, 1982; Fogleman and Heed, 1989). So, mainland flies may experience rots which are nutritionally poorer and on average less attractive (Fellows and Heed, 1972). Therefore, increased plasticity in development time of the mainland flies is related to lower food availability for larvae. Because larvae must complete development in the rot in which they were placed by their mothers or perish, i.e. adults, and not larvae, can move from rot to rot, increased developmental plasticity may have resulted from the greater uncertainty the adults must face in finding rots for oviposition that are in appropriate stages of decomposition.

The genetic architecture of life history traits will also play a role in the evolution of patterns of homeostasis (Orzack, 1985) as well as the autocorrelation of environmental changes, so further study is needed to assay genetic correlations among life history traits, rot durations in nature, and fly population densities. At the population level, the influences of environmental uncertainty and the history of population differentiation due to the host cacti used by *D. mojavensis* have provided a background for elucidating the evolution of life histories and homeostasis in components of fitness.

Acknowledgments

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