Evolutionary Ecology Research, 2000, **2**: 685–699

Evidence of independent climatic selection for desiccation and starvation tolerance in Indian tropical populations of *Drosophila melanogaster*

Ravi Parkash[1]* and Ashok K. Munjal[2]

[1]*Genetics Research Laboratory, Department of Biosciences, Maharshi Dayanand University, Rohtak 124 001 and* [2]*Department of Bioscience and Biotechnology, Banasthali Vidyapith, Banasthali 304 022, India*

ABSTRACT

On the Indian subcontinent, geographical populations (8.0° to 33.0°) of *Drosophila melanogaster* demonstrate opposite latitudinal clines for desiccation ($r = 0.83$) and starvation ($r = -0.88$). Desiccation tolerance is significantly and positively correlated with body size and abdominal pigmentation, whereas starvation is negatively correlated with body size and life-history characteristics. Analysis of variance and analysis of covariance show a substantial direct effect of body size for both traits. For the Indian geographical populations, both latitudinal and altitudinal variations can explain the observed divergence of these two traits of ecological significance. Regression analysis of climatic variables (i.e. T_{max}, T_{min} and $T_{average}$), which are not significantly correlated with latitude, are positively and significantly associated with starvation and can explain trait variability ($R^2 = 0.78$–0.88). In contrast, T_{CV} ($R^2 = 0.65$), rainfall and precipitation ($R^2 = 0.32$) are significantly but positively associated with desiccation tolerance. The observed negative correlation between climatically selected starvation and desiccation in Indian geographical populations is not in line with the correlated selection response of these traits on the basis of laboratory selection experiments. For south Indian tropical populations, higher starvation tolerance might be selected because of temperature variables (T_{max}, T_{min} and $T_{average}$), higher metabolic stress in relation to smaller body size, greater competition and involve a trade-off for life-history traits. In contrast, significantly higher desiccation tolerance in subtropical (northern) populations might be selected because of T_{CV}, rainfall and precipitation, which reflect seasonal variations. Desiccation and starvation tolerance are independent traits that reveal rapid evolutionary trends in tropical and subtropical climates.

Keywords: climatic selection, *Drosophila melanogaster*, opposite latitudinal clines, starvation and desiccation tolerance, tropical populations.

INTRODUCTION

Most living organisms cope with an array of environmental stresses in their natural habitats (Hoffmann and Parsons, 1991). For environmental stress response traits, there is

* Address all correspondence to Ravi Parkash, U.H.-9, Medical Enclave, Rohtak 124 001 (Haryana), India. e-mail: mdu@mdul.ernet.in

considerable genetic variability on which climatic selection might act directly. Much attention has been paid to stress resistance in different taxa of plants (Levitt, 1980), in aquatic and terrestrial organisms, and other ectothermic and endothermic organisms (Sibley and Calow, 1986). For *Drosophila melanogaster*, laboratory studies have demonstrated genetic variation for resistance to a range of environmental stresses, but there is limited information about the level of genetic variation in field conditions (Coyne *et al*., 1983). Hoffmann and Parsons (1989a,b, 1993) hypothesized that laboratory selection for desiccation tolerance is correlated with starvation tolerance and with a trade-off of early fecundity, but not with changes in body size. At present, it is generally believed that there is a common genetic basis for both traits, which demonstrate high heritability (>0.60), and adaptation to stress involves a reduction of metabolic rate and activity under stressful conditions. Laboratory selection experiments on starvation tolerance and on postponed senescence are characterized by a correlated selection response of other stress response traits (Service *et al*., 1985; Chippindale *et al*., 1996). Such laboratory experiments have used extreme stress conditions for desiccation or starvation, resulting in more than 80% mortality during selection protocols.

Analysis of environmental stress response traits in populations of diverse *Drosophila* species can help to explain the climatic adaptations that are essential for a species' colonizing potential and its distribution and abundance patterns on different continents, which vary widely in their abiotic and biotic conditions. For geographical populations, data on starvation tolerance are limited. However, desiccation tolerance and cold resistance were analysed in three Australian populations of *D. melanogaster* and in some other Australian *Drosophila* species (Stanley and Parsons, 1981) and the results often matched climatic adaptations. In contrast, in an endemic species from Australia, *D. serrata*, no geographical divergence was observed for desiccation or starvation resistance (Blows and Hoffmann, 1993).

D. melanogaster, a cosmopolitan species, is tropical in origin but has colonized both tropical and temperate parts of the world. In the past, this species was considered genetically less diverse because of greater gene flow between populations; this species is now considered highly variable genetically (Lemeunier *et al*., 1986). Investigations of Indian tropical and subtropical populations of *D. melanogaster* are important because of their ancient evolutionary history and much broader latitudinal (8° to 33°) and altitudinal (38 to 2050 m) ranges. In corresponding locations on the African continent, there is the Sahara Desert between northern and equatorial Africa. Our observations match climatic selection trends under wild conditions for stress response traits in Indian populations of *D. melanogaster*.

MATERIALS AND METHODS

D. melanogaster populations were bait-trapped as well as collected by net-sweeping from fruit markets at various sites, which varied latitudinally (from 10.0°N at Ernakulam to 32.74°N at Jammu) and altitudinally (from 38 to 2050 m; Table 1). Pairs of isogroups were established for each geographical population with 30 wild-collected individuals and were analysed for starvation and desiccation for two generations in the laboratory. All experiments were performed at 17°C and 25°C within 2 months of collection. After emergence, adults were lightly etherized and distributed into groups of 10, placed in food vials with corn meal sugar seeded with live yeast and aged for 3 days. Preliminary experiments failed

to show any consistent differences between the sexes; we chose to use males. For the desiccation experiments, adults were introduced in air-tight plastic vials containing silica gel, so that the relative humidity was close to zero. For starvation tolerance, similar vials were used but water on absorbent paper was provided at the bottom of each vial. For each trait, five replicates of 10 flies of each generation were used per population. The vials were inspected for dead flies every 3 h until all flies were dead. Survival was plotted against time and the time to 50% survival was estimated graphically. We tried to show that any variations had a genetic basis by studying two successive generations for each population.

The body weight of males did not vary with age and was measured in five replicates of 10 individuals and the results expressed in mg $\times 10^2$ per fly. Various life-history traits, including number of ovarioles, fecundity per day, percent hatchability and mean duration of development (in hours), were also recorded. The climatic data for the geographical sites were taken from climatological tables. There are significant differences in the range of the coefficient of variation (CV) for mean monthly temperature (T_{CV}), which varies from 3.1% in Ernakulam to 28.1% in Jammu. Some temperature variables do not differ significantly across the Indian subcontinent (T_{max} = 28.8–30.0°C, T_{min} = 18.4–18.7°C, $T_{average}$ = 23.6–24.3°C).

RESULTS

Data for starvation and desiccation tolerance for two successive generations at 17°C and 25°C in 13 Indian geographical populations of *D. melanogaster* are given in Table 1. For two successive generations, the mean (± standard error) value of a trait on the basis of five replicates of 10 individuals for a given population did not differ (Student's *t*-test; data not shown). For each trait (desiccation or starvation tolerance at 25°C), the mean values of generation 1 and generation 2 were significantly correlated ($r = 0.60$ for starvation and 0.72 for desiccation; Fig. 1). A significant correlation between generations suggests stability and repeatability of trait values, thus supporting the genetic basis of both traits.

The relationship between desiccation and starvation tolerance was considered on the basis of correlations within populations as well as for the sample as a whole covering all geographical populations (Table 1). Within each population, the traits were negatively correlated (mean $r = -0.33$). For the complete data set, there was a significant negative correlation ($r = -0.95$) at both temperatures. Correlations between traits at the two temperatures are shown in Fig. 2a. The coefficient of variation, which represents within-population genetic variability, was in the range 5–18%. However, the overall coefficient of variation was higher for desiccation than for starvation tolerance. For starvation and desiccation tolerance at 17°C and 25°C, the mean values demonstrated significant differences between geographical populations. North Indian populations (at a higher altitude and latitude) showed significantly more desiccation tolerance but less starvation tolerance, whereas the reverse was noted for south Indian populations.

The complete data set for both traits was subjected to analysis of variance (ANOVA) and analysis of covariance (ANCOVA), with body size as the covariate. On the basis of ANOVA, there was significant variability between populations ($F = 22.63$, $P < 0.001$ for desiccation; $F = 6.12$, $P < 0.001$ for starvation). There was a significant main effect of temperature ($F = 405.8$, $P < 0.001$ for desiccation; $F = 212.3$, $P < 0.001$ for starvation), but no such effect of generation or of the resulting interactions. Because there were significant

Table 1. Starvation and desiccation tolerance (mean ± standard error, hours; coefficient of variation; and correlation between the traits) at 17°C and 25°C in 13 Indian geographical populations of *D. melanogaster*

Populations (latitude; altitude)	Generation	Starvation tolerance				Desiccation tolerance				Correlations	
		25°C	CV	17°C	CV	25°C	CV	17°C	CV	25°C	17°C
Jammu	G1	101.2 ± 3.46	7.64	130.0 ± 7.20	12.4	23.8 ± 0.30	2.82	36.4 ± 1.59	9.76		
(32°7′N; 366 m)	G2	112.0 ± 10.1	20.1	130.0 ± 10.1	17.4	23.0 ± 0.75	1.86	35.6 ± 1.28	8.04		
	$\bar{x}$	106.6 ± 3.37	9.94	130.0 ± 6.54	15.9	23.4 ± 0.88	11.9	36.0 ± 1.09	11.2	−0.29	−0.31
Manali	G1	92.4 ± 3.92	9.48	111.6 ± 8.98	17.9	28.2 ± 1.75	13.8	41.0 ± 1.71	9.33		
(32°3′N;	G2	90.0 ± 6.79	16.9	123.6 ± 7.12	12.3	28.8 ± 1.63	19.4	39.2 ± 2.02	10.5		
2050 m)	$\bar{x}$	91.2 ± 4.15	14.4	117.6 ± 6.36	17.1	28.5 ± 1.27	14.0	40.1 ± 1.29	10.1	−0.30	−0.27
Shimla	G1	94.4 ± 6.94	16.4	126.4 ± 1.31	2.32	25.6 ± 1.52	13.3	40.2 ± 2.63	14.6		
(31°3′N;	G2	93.6 ± 2.15	5.14	118.4 ± 8.41	15.8	26.8 ± 0.82	6.84	40.4 ± 1.43	7.91		
1950 m)	$\bar{x}$	94.0 ± 3.83	12.9	122.4 ± 3.67	9.50	26.2 ± 0.77	9.31	40.3 ± 1.69	13.3	−0.28	−0.27
Kullu	G1	106.2 ± 4.70	9.89	138.4 ± 6.02	9.73	23.2 ± 1.21	11.7	34.6 ± 1.15	7.43		
(32°0′N;	G2	100.8 ± 2.63	5.77	131.2 ± 5.47	9.32	25.4 ± 1.04	9.76	36.8 ± 2.15	13.1		
1310 m)	$\bar{x}$	103.5 ± 9.98	9.10	134.8 ± 4.45	10.5	24.3 ± 0.92	12.4	35.7 ± 1.33	11.8	−0.32	−0.51
Solan	G1	110.4 ± 3.50	7.09	145.6 ± 6.91	10.6	22.4 ± 0.83	8.28	34.2 ± 1.24	8.11		
(30°8′N;	G2	100.8 ± 11.6	25.2	131.8 ± 9.36	15.9	25.4 ± 0.67	5.89	36.8 ± 1.25	7.59		
1250 m)	$\bar{x}$	105.6 ± 6.65	19.7	138.7 ± 6.55	14.9	23.9 ± 0.75	9.95	35.5 ± 1.02	9.13	−0.22	−0.30
Kalka	G1	111.4 ± 3.48	6.98	146.4 ± 5.72	8.74	22.2 ± 1.45	14.6	30.2 ± 0.85	6.29		
(30°4′N; 600 m)	G2	103.2 ± 4.29	9.29	134.4 ± 4.02	6.69	25.8 ± 0.91	7.89	32.8 ± 0.52	3.54		
	$\bar{x}$	107.3 ± 3.22	9.48	140.4 ± 4.19	9.44	24.0 ± 1.03	13.5	31.6 ± 0.54	5.29	−0.50	−0.28
Rohtak	G1	111.2 ± 2.86	5.25	142.2 ± 6.29	9.89	20.8 ± 0.95	10.2	30.8 ± 2.50	18.2		
(28°9′N; 253 m)	G2	105.6 ± 4.01	8.49	137.6 ± 10.2	16.6	21.6 ± 1.15	11.9	32.8 ± 1.56	10.6		
	$\bar{x}$	108.4 ± 2.76	8.05	139.9 ± 6.37	14.4	21.2 ± 0.79	11.7	31.6 ± 1.58	15.8	−0.23	−0.15

Gwalior	G1	115.2 ± 3.70	7.18	148.0 ± 7.59	11.5	20.6 ± 1.03	11.2	29.4 ± 1.08	8.21		
(26°1′N; 207 m)	G2	100.8 ± 8.03	17.8	145.2 ± 12.5	19.3	22.0 ± 1.17	11.9	27.2 ± 1.93	15.9		
	$\bar{x}$	108.0 ± 5.16	15.1	146.6 ± 7.72	12.9	21.3 ± 0.86	12.9	28.3 ± 1.22	13.6	−0.26	−0.57
Bhopal	G1	116.0 ± 2.99	7.96	147.2 ± 4.33	6.57	20.8 ± 0.95	10.2	29.0 ± 2.06	15.9		
(23°1′N; 207 m)	G2	108.0 ± 5.88	17.8	147.0 ± 7.76	11.8	22.4 ± 1.46	14.6	31.4 ± 1.08	7.69		
	$\bar{x}$	112.0 ± 3.72	10.5	147.1 ± 4.68	10.1	21.6 ± 0.95	13.9	30.2 ± 1.28	13.5	−0.30	−0.21
Nagpur	G1	116.6 ± 4.15	5.76	146.4 ± 2.36	3.60	20.6 ± 0.92	9.58	28.6 ± 1.00	7.82		
(21°1′N; 311 m)	G2	112.8 ± 9.00	12.2	145.6 ± 3.55	5.45	22.8 ± 1.11	10.9	25.4 ± 0.92	8.09		
	$\bar{x}$	114.7 ± 5.27	14.5	146.0 ± 2.25	4.88	21.7 ± 0.84	12.3	27.0 ± 0.89	10.5	−0.68	−0.24
Hyderabad	G1	118.4 ± 3.12	5.89	148.0 ± 16.9	25.5	20.8 ± 0.87	9.35	27.4 ± 0.93	7.59		
(17°2′N; 545 m)	G2	112.4 ± 3.12	6.21	147.8 ± 6.08	9.19	21.2 ± 0.87	9.18	26.2 ± 1.48	12.6		
	$\bar{x}$	115.4 ± 2.53	6.93	147.9 ± 9.49	20.3	20.5 ± 0.67	10.3	26.8 ± 0.94	11.1	−0.33	−0.36
Tirumala	G1	120.2 ± 6.02	11.4	149.8 ± 3.86	5.76	18.2 ± 1.45	17.8	26.8 ± 1.18	9.84		
(13°4′N; 598 m)	G2	117.6 ± 4.02	7.72	148.8 ± 11.5	17.3	21.8 ± 0.52	5.33	28.4 ± 1.12	8.82		
	$\bar{x}$	118.9 ± 3.84	10.2	149.3 ± 6.17	13.1	20.0 ± 1.01	15.9	27.6 ± 1.09	12.3	−0.27	−0.41
Ernakulam	G1	130.0 ± 5.88	9.67	151.2 ± 2.08	3.08	16.4 ± 0.46	6.27	26.4 ± 0.88	7.56		
(10°0′N; 38 m)	G2	126.0 ± 5.54	10.3	154.0 ± 5.54	8.04	16.6 ± 0.67	9.03	25.4 ± 1.12	9.86		
	$\bar{x}$	128.0 ± 5.02	12.4	152.6 ± 3.82	7.91	16.5 ± 0.43	8.18	25.9 ± 0.77	9.34	−0.30	−0.25
Overall mean ± S.E.		109.4 ± 1.50	15.29	138.9 ± 1.79	14.9	22.5 ± 0.34	17.4	32.1 ± 0.53	18.7	−0.96	−0.95
Standard deviation		16.73		20.76		3.91		5.99			
Variance		279.96		431.09		15.31		35.95			

G1 and G2 = first and second generations.

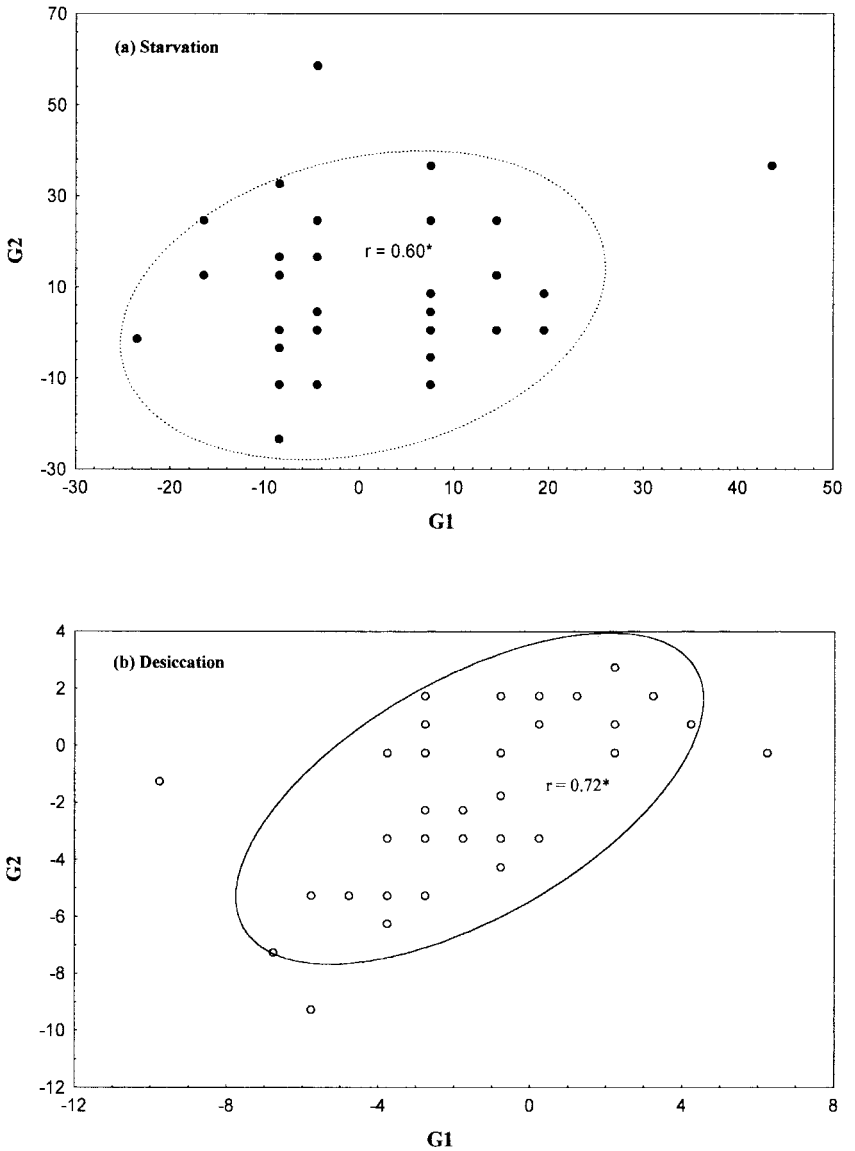

Fig. 1. Correlation between two successive generations (G1 and G2) for starvation and desiccation tolerance in five replicates for each of 13 populations of *D. melanogaster*. There are highly significant correlations between generations based on standardized data. Ellipses = 85% probability.

variations in body size between *D. melanogaster* populations, ANCOVA was used to demonstrate any geographical variability in both traits (Table 2). The *F*-values were lower but still significant for desiccation and starvation.

The mean values for starvation, desiccation and body weight for the different geographical populations were investigated further on the basis of latitudinal correlations

Table 2. Results of ANCOVA, with body size as a covariate, applied to the complete data set for each trait (desiccation tolerance and starvation resistance) to test the variability due to populations, temperatures, generations and their interactions in 13 Indian populations of *D. melanogaster*

	Desiccation		Starvation	
Source of variation	MS	*F*	MS	*F*
Population	94.53	7.30***	688.88	2.18*
Temperature	5976.01	405.76***	59252.40	212.30***
Generation	41.20	3.12	707.85	2.27
Population × temperature	35.10	2.38	173.45	0.62
Population × generation	8.95	0.96	229.77	0.74
Generation × temperature	32.20	4.94*	47.39	0.73
Population × generation × temperature	3.98	0.61	171.56	0.67

*** Significant at $P < 0.001$. * Significant at $P < 0.05$.

and linear regressions (Table 3 and Fig. 2b). Desiccation tolerance was significantly and positively correlated with latitude ($r = 0.83$ at 25°C) and demonstrated a steady increase with a slope of 0.32 h per degree of latitude at 25°C; there was a significantly steeper slope of 0.57 h per degree of latitude at 17°C. Starvation tolerance, on the other hand, exhibited the opposite trend – that is, a decrease of 1.10 h per degree of latitude (Fig. 3a). The slopes were similar at 17°C and 25°C for starvation tolerance. Variation in body weight was positively correlated with desiccation ($r = 0.86$) and negatively correlated with starvation tolerance ($r = -0.88$). The slopes for body weight versus desiccation tolerance were lower compared with those versus starvation resistance. The latitudinal slopes for desiccation were two times higher than those for body size and differed significantly at 17°C and 25°C. Thus, variations in body size have a significant effect on both desiccation and starvation tolerance (Fig. 2b).

Besides latitudinal variations, the sites also differ in terms of altitude (from 38 to 2050 m). Thus, multiple-regression, as a simultaneous function of latitude and altitude, was used to analyse the complete data set at 17°C and 25°C for both traits (Table 4). When both geographical parameters are considered, 89–92% and 85–92% of trait variability can be explained at 17°C and 25°C respectively. The slopes do not differ significantly between the two temperatures (17°C *vs* 25°C) for either trait. However, the slopes do differ significantly between traits (desiccation *vs* starvation tolerance) at both temperatures. The y-intercept (a) shows predicted trait values at the equator. Starvation decreases with slope (0.69 and 0.58 h per degree of latitude at 17°C and 25°C respectively), whereas desiccation increases (0.18 and 0.32 h per degree of latitude at 17°C and 25°C respectively). However, variability in trait values owing to altitude exhibited a decrease of 7 h per 1000 m at 17°C and 9 h per 1000 m at 25°C for starvation. The altitudinal slope values for desiccation tolerance were 2.5 h and 3.6 h per 1000 m at 17°C and 25°C respectively. Such an analysis offers predictive values for desiccation and starvation tolerance if the geographical location of a population in terms of altitude and latitude is known.

Because desiccation and starvation tolerance are significantly correlated with latitude and altitude, although in opposite directions, regression analysis based on the climatic variables of temperature, rainfall, relative humidity and precipitation was used to help explain

Table 3. Correlation and linear regression between characters at 17°C and 25°C in 13 Indian populations of *D. melanogaster* (mean ± standard error)

	Correlation (*r*)	Slope (*b*)	y-intercept (*a*)	Correlation (*r*)	Slope (*b*)	y-intercept (*a*)
Traits		25°C			17°C	
Desiccation/lat.	0.83 ± 0.17*	0.32 ± 0.06	14.41 ± 1.70	0.85 ± 0.16*	0.57 ± 0.11	18.01 ± 2.85
Starvation/lat.	–0.88 ± 0.15*	–1.09 ± 0.18	136.20 ± 4.76	–0.78 ± 0.19*	–1.10 ± 0.26	167.37 ± 6.89
BW *vs* desiccation	0.86 ± 0.16*	0.16 ± 0.03	2.93 ± 3.62	0.87 ± 0.15*	0.28 ± 0.05	–2.51 ± 5.97
BW *vs* starvation	–0.88 ± 0.14*	–0.53 ± 0.08	173.83 ± 10.5	–0.84 ± 0.16*	–0.56 ± 0.11	209.07 ± 13.84
OV *vs* desiccation	0.81 ± 0.18*	0.66 ± 0.14	–1.57 ± 5.26	0.84 ± 0.16*	1.20 ± 0.23	–11.35 ± 8.46
OV *vs* starvation	–0.89 ± 0.14*	–2.31 ± 0.36	193.47 ± 13.4	–0.82 ± 0.17*	–2.40 ± 0.51	227.51 ± 18.78

* Significant at $P < 0.05$. BW = body weight, OV = number of ovarioles.

Table 4. Multiple regression analysis of starvation and desiccation tolerance at 17°C and 25°C as a simultaneous function of latitude and altitude ($y = a + b_1$ lat $+ b_2$ alt) and R^2 values in Indian geographical populations of *D. melanogaster* (mean ± standard error)

Resource	Temperature	a	b_1 lat	b_2 alt	R^2
Starvation (a)	17°C	131.37 ± 3.07	–0.69 ± 0.14*	–0.007 ± 0.001*	0.92
	25°C	161.06 ± 5.34	–0.58 ± 0.24*	–0.009 ± 0.002*	0.82
Desiccation (b)	17°C	16.15 ± 1.11	0.18 ± 0.05*	0.0025 ± 0.0006*	0.89
	25°C	20.48 ± 2.32	0.32 ± 0.09*	0.0036 ± 0.0012*	0.85
Comparisons of slopes (a *vs* b)	17°C	—	3.90*	5.63*	—
	25°C	—	2.91*	3.37*	—

* Significant at $P < 0.05$.

Table 5. Regression analysis of starvation and desiccation with different variables of temperature and rainfall for 13 Indian populations of *D. melanogaster* (values are partial regression coefficients and R^2 in parentheses)

	Starvation		Desiccation	
	25°C (R^2)	17°C (R^2)	25°C (R^2)	17°C (R^2)
Latitude	–0.88* (0.76)	–0.78* (0.61)	0.83* (0.69)	0.85* (0.71)
Altitude	–0.86* (0.74)	–0.84* (0.71)	0.84* (0.76)	0.82* (0.67)
Longitude	–0.18 (–0.03)	–0.15 (–0.02)	0.08 (–0.06)	0.39 (0.08)
T_{max}	0.88* (0.78)	0.89* (0.81)	–0.88* (0.78)	–0.89* (0.78)
T_{min}	0.94* (0.88)	0.86* (0.74)	–0.91* (0.62)	–0.88* (0.78)
$T_{average}$	0.92* (0.86)	0.91* (0.82)	–0.90* (0.81)	–0.88* (0.77)
T_{CV}	–0.91* (0.88)	–0.85* (0.72)	0.81* (0.65)	0.84* (0.69)
Relative humidity	–0.03 (–0.001)	–0.34 (0.12)	0.15 (–0.02)	0.12 (–0.01)
Rainfall	–0.75* (0.57)	–0.77* (0.59)	0.75* (0.54)	0.65* (0.42)
Precipitation	–0.56* (0.31)	–0.60* (0.36)	0.56* (0.32)	0.49 (0.24)
T_{CV} &	–0.71*	–0.61*	0.58*	0.68*
Precipitation	–0.36* (0.92)	–0.44* (0.86)	0.42* (0.77)	0.27 (0.75)

* Significant at $P < 0.05$.

climatic selection of trait variability (Table 5). There were no effects of longitude (75.0–77.9°E), since the populations did not vary significantly on this geographical parameter. Furthermore, latitude was not significantly correlated with T_{max}, T_{min} or $T_{average}$. Whereas these three temperature variables demonstrated significant and positive regression coefficients with starvation ($R^2 = 0.78$–0.88 at 25°C), we recorded significant but negative regression coefficients with T_{CV}, rainfall and precipitation. Rainfall and precipitation were able to account for starvation variability to a limited extent, whereas relative humidity had no effect. For desiccation tolerance, T_{CV}, rainfall and precipitation demonstrated significant

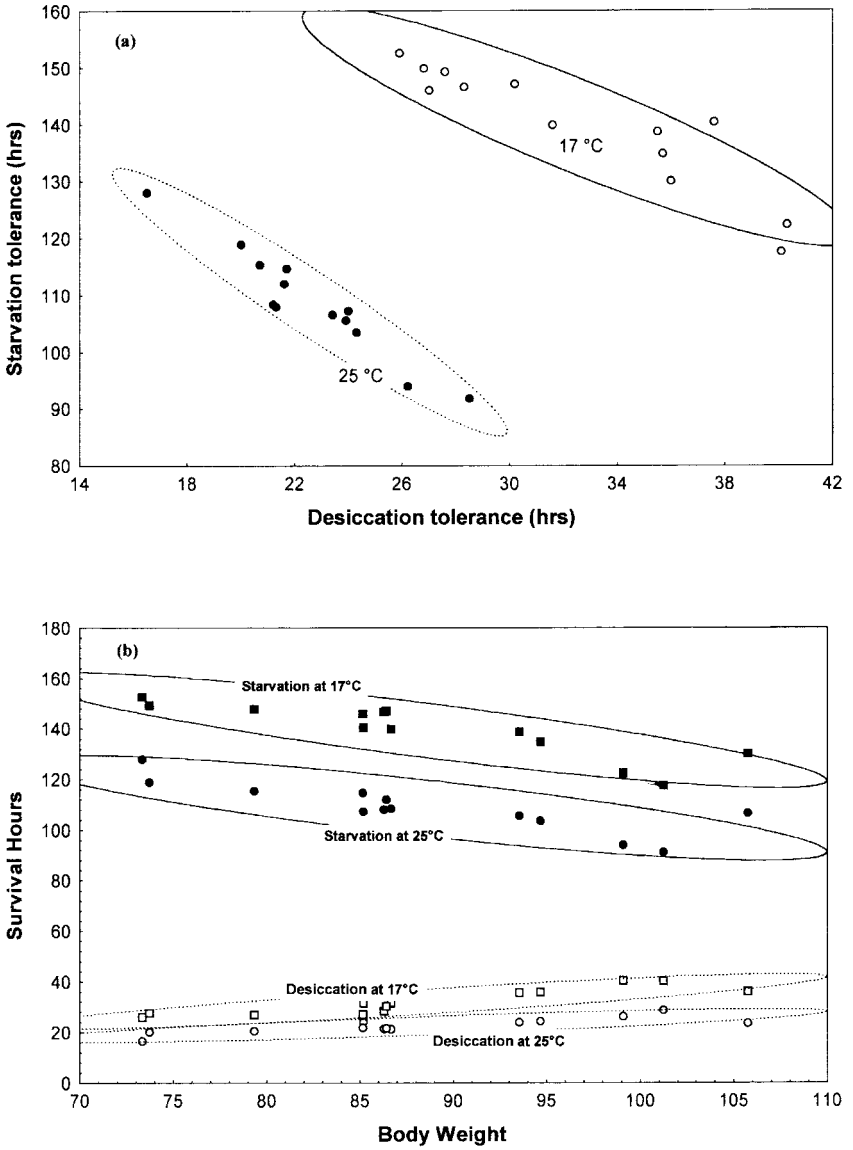

Fig. 2. (a) Correlation between starvation and desiccation (hours of survival) at 17°C and 25°C for 13 populations of *D. melanogaster*. (b) Relationship between body weight and starvation, and between body weight and desiccation tolerance, at 17°C and 25°C for 13 populations of *D. melanogaster*.

and positive regression coefficients. The geographical variability in desiccation tolerance can be explained in the main by T_{CV} ($R^2 = 0.65$ at 25°C) and precipitation ($R^2 = 0.32$). The relationship between T_{CV} and starvation is shown in Fig. 3b.

Since body size has a considerable impact on the observed variability in starvation and desiccation tolerance, other related life-history traits were considered for six geographical

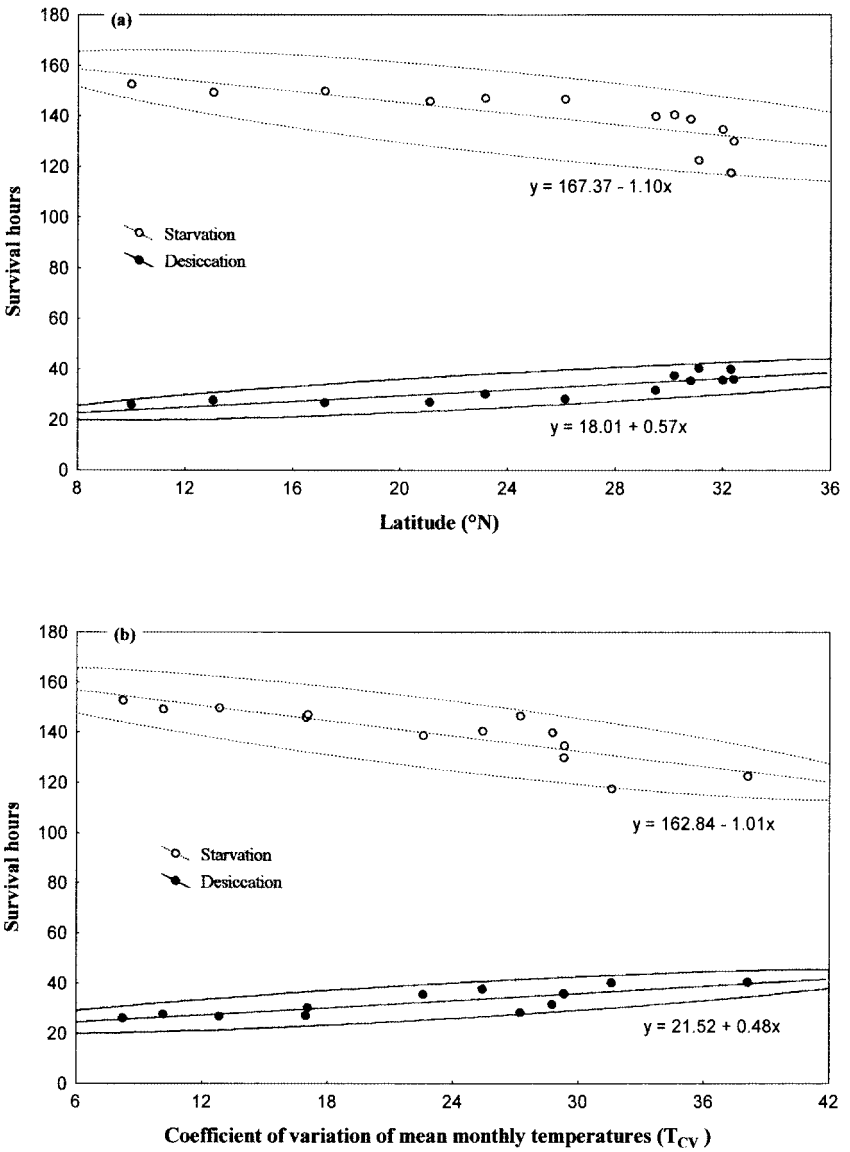

Fig. 3. (a) Latitudinal relationship of starvation and desiccation (hours of survival at 17°C) for 13 populations of *D. melanogaster*. (b) Relationship between starvation and the coefficient of variation of mean monthly temperatures (T_{CV}), and between desiccation tolerance and T_{CV}, at the sites of origin of each population.

populations of *D. melanogaster* (Table 6). There was similar latitudinal variation for desiccation tolerance, life-history variables and abdominal pigmentation, but such highly significant correlations might not reflect a true inter-relationship. For starvation tolerance, the results appear more convincing, because body size and related life-history traits

Table 6. Body weight, four life-history characteristics, abdominal pigmentation (sum of 5th and 7th segment), and their correlation with starvation and desiccation tolerance at 25°C for six Indian latitudinal populations of *D. melanogaster* (mean ± standard error)

	Sex	Ernakulam 10°0′N	Hyderabad 17°2′N	Nagpur 21°1′N	Bhopal 23°1′N	Rohtak 28°9′N	Jammu 32°7′N	Correlation with: Starvation	Desiccation
Body weight (mg × 10^2)	Male	73.7 ± 1.5	79.3 ± 2.4	85.1 ± 1.2	86.4 ± 1.2	86.6 ± 2.4	105.7 ± 5.8	–0.82*	0.85*
	Female	95.2 ± 2.7	105.3 ± 1.2	117.0 ± 2.5	119.0 ± 5.7	126.2 ± 4.9	142.3 ± 3.2	–0.91*	0.89*
Ovariole number	Female	29.0 ± 0.8	30.4 ± 1.21	33.9 ± 1.36	34.4 ± 1.14	37.6 ± 0.78	39.7 ± 0.83	–0.89*	0.84*
Fecundity per day		32.0 ± 1.0	33.6 ± 0.94	35.8 ± 0.93	35.2 ± 0.59	36.4 ± 1.41	38.3 ± 1.15	–0.91*	0.92*
Percent hatchability		60.0	65.50	71.60	75.60	83.46	88.80	–0.91*	0.84*
Duration of development (h)	Male	205.3 ± 1.86	206.5 ± 2.04	215.7 ± 2.57	216.2 ± 2.42	219.5 ± 1.73	222.1 ± 1.87	–0.87*	0.84*
	Female	201.7 ± 1.30	203.5 ± 1.86	209.1 ± 2.10	209.1 ± 2.09	212.7 ± 1.34	219.5 ± 1.73	–0.85*	0.84*
Abdominal pigmentation	Female	7.05 ± 0.14	7.20 ± 0.13	8.48 ± 0.16	8.71 ± 0.16	9.47 ± 0.15	10.60 ± 0.21	–0.85*	0.81*

(fecundity, hatchability and duration of development) demonstrated significant negative correlations. Such relationships can be attributed to a possible trade-off between starvation tolerance and other fitness-related life-history traits.

DISCUSSION

Geographical variations in the two ecological traits are ordered into opposite clines – that is, for Indian populations of *D. melanogaster*, desiccation is positively correlated with latitude, whereas starvation tolerance is negatively correlated with latitude. Such trends should be adaptive and reflect independent climatic selection. The ecological, physiological and climatological conditions of tropical and subtropical *Drosophila* species and populations are significantly different from those of temperate *Drosophila*. The present results demonstrate that desiccation and starvation tolerance are fast evolving traits based on variable climatic conditions on the Indian subcontinent. In the north Indian subtropics, the conditions for desiccation are optimal in the summer months of April, May and June, when the temperature often exceeds 35°C and *Drosophila* individuals are more likely to die from desiccation. In contrast, in the humid tropics of south India, selection for desiccation is minimal and starvation stress might result because of a larger population size and competition under favourable climatic conditions. Such arguments are in line with the *r–K* selection continuum of MacArthur and Wilson (1967). This continuum represents selection in relation to density-dependent resource availability, where *K* represents a population near its equilibrium density in which competition is potentially important under environmental stability, as is the case with south Indian tropical populations of *D. melanogaster*. In contrast, *r* represents a population in a disturbed habitat (seasonally variable environmental stresses) and not at equilibrium, in which a high reproductive rate is generally favoured, as is the case with north Indian subtropical populations of *D. melanogaster*. The present results on environmental stress response traits (desiccation and starvation tolerance) in north versus south Indian populations of *D. melanogaster* match the expectations of such a hypothesis.

On the Indian subcontinent, seasonal variations in temperature are characterized by a coefficient of variation of monthly averages (T_{CV}) that ranges from 3.1% in Ernakulam in the south to 28.1% in Jammu in the north. Thus, seasonal variations increase progressively and significantly from south to north. Such a diversity of climates provides spatial opportunities for environmental stress-related traits. It is well known that most *Drosophila* species and populations face some degree of starvation stress in the wild and are characterized by a shorter life-span in their natural habitat (Rosewell and Shorrocks, 1987). Starvation stress implies limited food resources under extreme unfavourable climatic conditions in the temperate zone, or considerable competition exerted by large population size under more favourable conditions in the tropics. The extent of starvation stress in the tropics could increase as a result of a higher metabolic rate (under higher ambient temperature) per unit of body weight. Since rate of metabolism is negatively correlated with body size, smaller body size in southern (tropical) populations might result in higher starvation stress. Regression analysis of the climatic data showed that T_{max}, T_{min} and $T_{average}$ are positively and significantly associated with starvation tolerance, whereas seasonal thermal amplitude (T_{CV}), rainfall and precipitation contribute to selection for desiccation tolerance. Note that the climatic variables T_{max}, T_{min} and $T_{average}$ did not correlate significantly with latitude and account in part for starvation variability ($R^2 = 0.78–0.88$). There was a negative correlation between starvation tolerance and body size, and the observed trade-off (negative

correlation) with life-history traits concurs with the results of laboratory selection experiments. Thus, the present results do not favour a reduction in metabolic rate for the evolution of starvation tolerance in tropical populations of *D. melanogaster* from India. For desiccation tolerance, there was a positive correlation with latitude, and one might expect significant correlations with other traits exhibiting positive latitudinal trends. Body size, life-history characteristics and abdominal pigmentation were significantly correlated with latitude as well as desiccation tolerance. However, based on ANCOVA, there is evidence for a direct effect of body size variations on between-population variability in desiccation and starvation tolerance.

Regression analysis of the climatic data demonstrated that T_{CV} (the coefficient of variation of mean monthly temperature), rainfall and precipitation are significantly and positively associated with variability in desiccation. Furthermore, climatic parameters that are positively correlated with either desiccation or starvation tolerance are mutually exclusive (Table 5). Thus, there is independent climatic selection of desiccation and starvation tolerance under wild conditions. Our results provide further support for the argument that desiccation and starvation tolerance are independent traits.

ACKNOWLEDGEMENTS

We gratefully acknowledge the financial assistance of IFCPAR, New Delhi, Project No. 1103-1. We are also grateful for the helpful comments of Professor Bryan Shorrocks.

REFERENCES

Blows, M.W. and Hoffmann, A.A. 1993. The genetics of central and marginal populations of *Drosophila serrata*: 1. Genetic variation for stress resistance and species borders. *Evolution*, **47**: 1255–1270.

Chippindale, A.K., Terence, J.F.C. and Rose, M.R. 1996. Complex trade-offs and the evolution of starvation resistance in *Drosophila melanogaster*. *Evolution*, **50**: 753–766.

Coyne, J.A., Bundgaard, J. and Prout, T. 1983. Geographic variation of tolerance to environmental stress in *Drosophila pseudoobscura*. *Am. Nat*., **122**: 474–488.

Hoffmann, A.A. and Parsons, P.A. 1989a. Selection for increased desiccation resistance in *D. melanogaster*: Additive genetic control and correlated response for other stress. *Genetics*, **122**: 837–845.

Hoffmann, A.A. and Parsons, P.A. 1989b. An integrated approach to environmental stress tolerance and life history variation: Desiccation tolerance in *Drosophila*. *Biol. J. Linn. Soc*., **37**: 117–136.

Hoffmann, A.A. and Parsons, P.A. 1991. *Evolutionary Genetics and Environmental Stress*. Oxford: Oxford University Press.

Hoffmann, A.A. and Parsons, P.A. 1993. Selection for adult desiccation resistance in *Drosophila melanogaster*: Fitness components, larval resistance, and stress correlations. *Biol. J. Linn. Soc*., **48**: 43–54.

Lemeunier, F., David, J.R., Tsacas, L. and Ashburner, M. 1986. The *melanogaster* species group. In *The Genetics and Biology of* Drosophila, Vol. 3e (M. Ashburner, H.L. Carson and J.N. Thompson, Jr., eds), pp. 147–256. London: Academic Press.

Levitt, J. 1980. *Responses of Plants to Environmental Stress*. New York: Academic Press.

MacArthur, R.H. and Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Parsons, P.A. 1983. *The Evolutionary Biology of Colonising Species*. Cambridge: Cambridge University Press.

Rosewell, J. and Shorrocks, B. 1987. The implications of survival rates in natural populations of *Drosophila*: Capture–recapture experiments on domestic species. *Biol. J. Linn. Soc*., **32**: 373–384.

Service, P.M., Hutchinson, E.W., Mackinley, M.D. and Rose, M.R. 1985. Resistance to environmental stress in *Drosophila melanogaster* selected for postponed senescence. *Physiol. Zool*., **58**: 321–326.

Stanley, S.M. and Parsons, P.A. 1981. The response of the cosmopolitan species, *Drosophila melanogaster*, to ecological gradients. *Proc. Ecol. Soc. Australia*, **11**: 121–130.

Sibly, R.M. and Calow, P. 1989. *Physiological Ecology of Animals: An Evolutionary Approach*. Oxford: Blackwell Scientific.