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Adaptive Strategies in Natural Populations of *Drosophila*

Ethanol Tolerance, Desiccation Resistance, and Development Times in Climatically Optimal and Extreme Environments

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Summary. Adult tolerance of ethanol vapour in a closed system containing 12% ethanol in solution, decreases in a cline from southern to northern Australia. However a Darwin population is more tolerant than predicted from its latitude. Ethanol tolerance races in Australia have almost certainly evolved within the last 100-150 years, because of resource unavailability prior to that time. Within populations, variation among isofemale strains is lowest in the climatically extreme southern Melbourne (37°S) and northern Darwin and Melville I. (11-12°S) populations. This suggests low resource diversity within extreme populations compared with the climatically less extreme Brisbane (28°S) and especially Townsville (19°S) populations. For desiccation resistance, the population rankings are:

Darwin
Melbourne > Townsville > Brisbane
Melville I.

and for development time, rankings are similar:

Darwin
Melbourne < Townsville < Brisbane
Melville I.

Therefore resource utilization heterogeneity is greatest in populations not greatly stressed by desiccation and where development times are extended. In total therefore, the utilization of a diversity of resources is a feature of populations tending somewhat towards a K-strategy; this is emphasized by the relative heterogeneity among isofemale strains of these populations for desiccation resistance and to a lesser extent development times.

The *D. melanogaster* gene pool can be viewed as made up of climate-associated races. Since the ethanol tolerances of adjacent (and climatically similar) Darwin and Melville I. are very different, resource utilization races may occur within climatic races. Such a mosaic of resource utilization races are more likely in climatically extreme than in optimal habitats.

Key words: *Drosophila* – Ethanol – Climatic races – Desiccation – Development times

Introduction

Associations between environmental heterogeneity and genetic differentiation have been reported in plant and animal populations over many years (Andrewartha and Birch 1954; Dobzhansky 1971; Endler 1977; Ford 1971; Jain and Bradshaw 1966). Phenotypic character gradients or clines are often observed and can be explained by environmentally determined fitness gradients. Such studies on *Drosophila* in natural environments are now on the increase. However, it is often difficult to relate the genotypic distributions so found to primary environmental variables. More commonly *Drosophila* populations are studied in artificial laboratory environments where data of potential ecological significance may emerge (Parsons 1973), but the direct study of variables of likely ecological significance is relatively rare. A measurable trait in natural populations with direct ecological significance is ethanol tolerance. In *D. melanogaster*, tolerance clines have been documented at the Chateau Tahbilk winery which are describable in terms of genetic adaptation to ethanol (McKenzie and Parsons 1974a). Ethanol tolerances are higher in the wine cellar population than immediately outside. Furthermore, ethanol tolerance increases with proximity to the cellar during vintage. This latter cline, in particular, is attributable to the direct effects of ethanol-mediated selection, since it is transient, disappearing during non-vintage periods when the concentration of ethanol in the outside environment is much reduced (McKenzie and McKechnie 1978). From this it can be argued that most variations in ethanol tolerances are adaptive. In the northern hemisphere, David and Bocquet (1975) showed that tolerances fall with decreasing latitude towards the equator. As *D. melanogaster* is a cosmopolitan species, parallel tolerance clines may therefore be expected in the two hemispheres. Australia would appear an ideal region for southern hemisphere studies.

Ethanol cannot be regarded just as an environmental stress however, since in a closed system ethanol vapour

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causes a diet-independent increase in *D. melanogaster* longevity up to a threshold where it becomes toxic. This threshold exceeds 9% ethanol in the liquid section of the closed system for a temperate-zone population from Melbourne Australia. Thresholds for sympatric populations of the sibling species *D. simulans*, and the more remotely related species *D. immigrans* are just above 3% and 1.5% respectively (Parsons et al. 1979; Parsons and Spence 1980). The thresholds represent the transition between ethanol as a metabolic benefit being utilized as a resource, and a metabolic cost whereby longevity falls below the control at higher ethanol concentrations. Additional evidence for a diet independent increase of *Drosophila* longevity due to ethanol is given by Starmer et al. (1977) and van Herrewege and David (1974, 1978).

In this paper, populations from Melbourne (latitude 37°S), Brisbane (28°S), Townsville (19°S) and Darwin/Melville I. (11-12°S) are studied (Fig. 1) for ethanol tolerances. The climatic range is from temperate to tropical (Fig. 2). The possibility of differentiation at a more local level is considered by comparing populations from Darwin and neighbouring Melville I. Following the ethanol tolerance discussions, desiccation resistance will be considered to obtain a direct assay of climatic selection, and also development time which is an important life-history component.

Materials and Methods

Flies were collected by sweeping over fermenting fruits positioned in the shade for high yields. Isofemale strains were set up immediately following the collection of flies and kept at 20°C. Collection dates were: Melbourne (October, 1978), Brisbane (May, 1978), Townsville (August, 1978), Darwin/Melville I. (September, 1978). The experiments were carried out early in 1979, that is not more than 10 generations after flies were introduced into the laboratory. Repeated tests on a number of traits – morphological, physiological and behavioural – have shown that the characteristics of isofemale strains accurately reflect the original populations for considerably longer (Parsons 1975).

The apparatus for testing ethanol tolerance was adapted from that of Starmer et al. (1977). About 1 g of cotton wool was placed in the bottom of an empty 40 ml vial and 10 ml of a test solution of H_2O and 12% ethanol added. Twenty adults aged one day (10 of each sex) were placed together in a second vial which was covered with a terylene cloth. The vial was then inverted, placed on top of the ethanol vial to which it was sealed, so that the

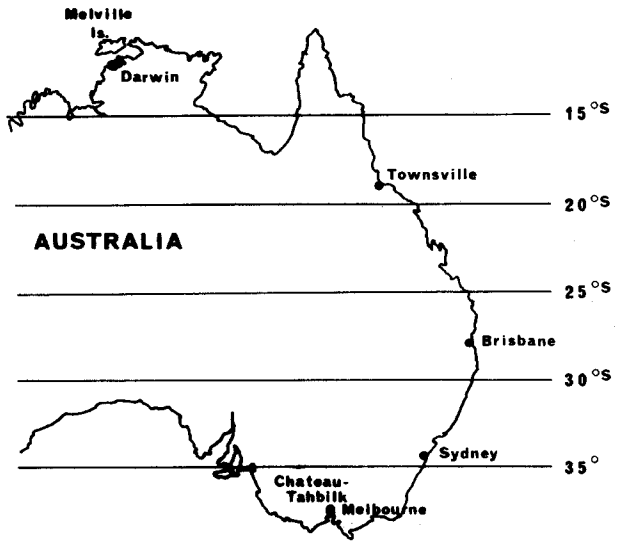

Fig. 1. Map of Australia showing the localities of populations sampled

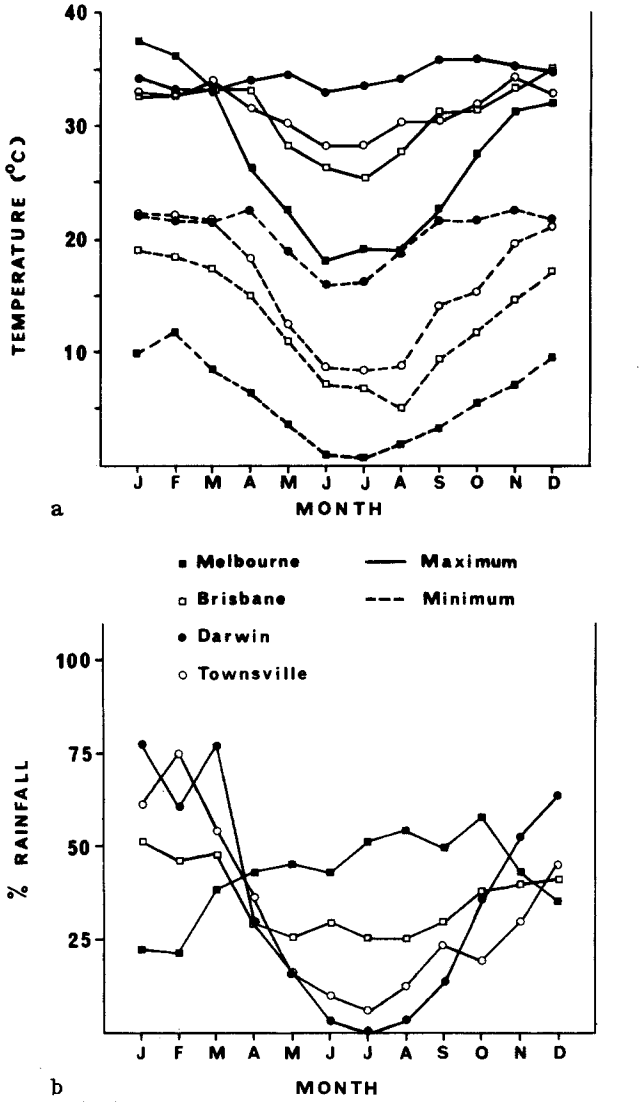

Fig. 2a and b. Mean highest and lowest temperatures (a) for each month for the years 1973-5 together with the percentage of days with rain (b) – from meteorological records for Melbourne, Brisbane, Townsville and Darwin (Melville I. readings are almost identical to those from Darwin)

system was essentially closed. Adults were therefore exposed to atmospheric ethanol and water vapour derived from the liquid phase in the lower vial. The controls contained water and water vapour only. Five replicates were exposed to ethanol together with one control, for eight to ten isofemale strains per population. In this way variation could be monitored within and among populations. Rearing and testing was carried out at 20°C. Adult survivorship was expressed as the number alive after various time intervals, and LT_{50}'s expressed as the number of hours at which 50% of flies had died were calculated by linear interpolation.

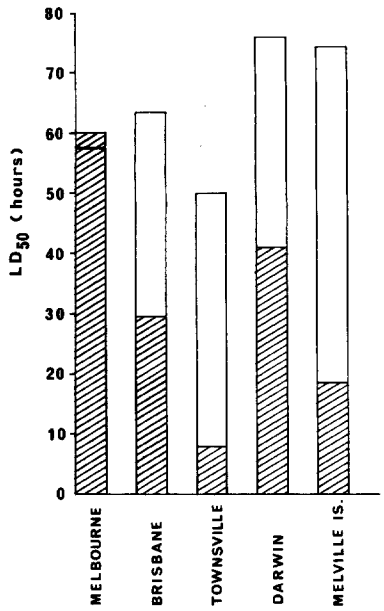

Fig. 3. LT_{50} values (hours) for means for the Melbourne, Brisbane, Townsville, Darwin and Melville I. populations. Shaded regions are on 12% ethanol and the controls are unshaded; in the case of the Melbourne population, the mean longevity on 12% ethanol just exceeded the control as indicated by a line in the shaded section

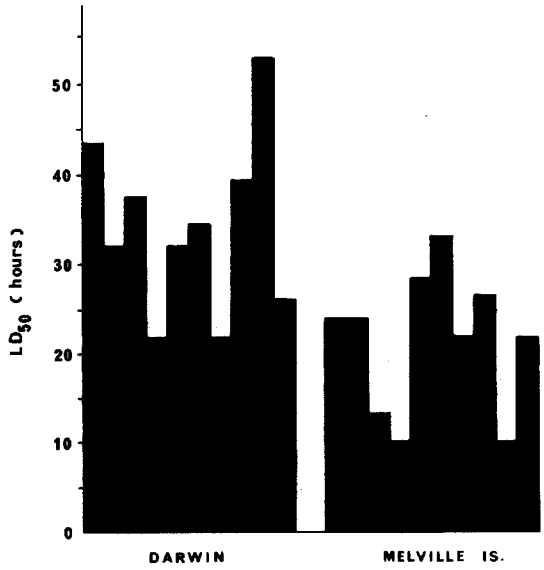

Fig. 4. LT_{50} values (hours) on 12% ethanol for 10 isofemale strains from the Darwin and Melville I. populations

Desiccation resistance was assayed by exposing five replicates of 25 virgin flies per sex per isofemale strain to 0% RH at 25°C in a desiccator with silica-gel as the desiccant. Sexes were tested separately at three days of age. Development times were assayed as percentage of flies emerging at day 11 and day 12 from 1st instar larvae to adult emergence. Five replicates of 25 larvae were set up for each isofemale strain at 20°C.

Results

Ethanol Tolerances

Except for the Melbourne population, exposure to 12% ethanol reduced longevity compared with the controls indicating toxic effects which imply a metabolic cost (Fig. 3). On average the Melbourne population obtained a slight metabolic benefit from the ethanol, although some isofemale strains suffered a metabolic cost. A south-north transect of the east coast of Australia for the Melbourne, Brisbane, and Townsville populations, shows a cline of decreasing ethanol tolerance as the equator is approached indicating broad agreement with the northern hemisphere latitudinal cline in accordance with expectation (David and Bocquet 1975).

However, the Darwin and Melville I. populations being to the north (and considerably to the west) of Townsville are exceptional since tolerances were higher than the Townsville population. This applies to the Darwin population in particular. The plot of isofemale strain means in Figure 4 shows the clear distinction between these two neighbouring populations, which is confirmed by a two-way analysis of variance (Table 1) showing that they differ significantly ($P < 0.001$).

The variation among populations for mean ethanol tolerances is extremely striking. Although the history of the introduction of *D. melanogaster* into Australia is not known, this species is only found in urban/orchard regions which did not exist before white settlement. Therefore, the evolution of ethanol tolerance races has almost certainly occurred within the last 100-150 years. On the

Table 1. Hierarchical analysis of variance of LT_{50} values in hours for the ten isofemale strains of the Darwin and Melville I. populations

Source of variation	d.f.	m.s.	F.
Between populations	1	3803.19	17.42[a]
Between isofemale strains within populations	18	218.38	7.93[a]
Between replicates within isofemale strains	80	27.53	

[a] $P < 0.001$

other hand Chateau Tahbilk winery studies show the evolution of ethanol tolerance races over very short time intervals consequent upon genetic adaptation to an ethanol associated resource (McKenzie and Parsons 1974a; McKenzie 1975). It can therefore be argued that rapid adaptation to various ethanol levels occurs in nature in direct response to resources available. If this is so, a likely situation is a mosaic of local ethanol tolerance races. The large and significant difference between the Darwin and Melville I. populations can perhaps be explained in this way, although detailed studies on resources utilized in the two localities are needed. However, the Darwin flies were collected over fallen mangoes in a suburban garden, and the Melville I. flies over fallen mangoes in a cleared region surrounded by native vegetation suggestive of ecological differences at least. The possibility of local resource races is given support by Stalker's (1976) observation of genetic heterogeneity in *D. melanogaster* reared from oranges and grapefruit. Indeed Gould and Johnston (1972) consider that selection is the prime cause of ordering most geographic variation within species over long and short distances. Ehrlich and Raven (1969) consider this to be likely even when organisms are reasonably mobile as the Chateau Tahbilk results show (McKenzie 1975).

As well as population means it is important to assess relative intrapopulation variabilities. Using analyses of variance, variability among isofemale strains is tested in Table 2. Since there are some minor differences in control longevities across populations (Fig. 3), the analyses are given for both the LT_{50} on 12% ethanol, and the ratio of LT_{50} on 12% ethanol: the control LT_{50} on 0% ethanol. The results are in substantial agreement, showing that variation in control longevities is not of great importance. Even so, it is appropriate to base further discussions on analyses of the ratios. In all cases variation among isofemale strains is significant as McKenzie and Parsons (1974a) found from studies at the Chateau Tahbilk winery. The level of variability in the Townsville population is extremely high, and that of Brisbane somewhat greater than the other three populations. Another way of looking at the data is by computing the estimated between-strain variance, V, which is the mean square between strains – mean square within strains divided by the number of replicates. These are given in Table 2 for the LT_{50} ratios, and show no particular pattern. However, a quantity $\sqrt{V}/\bar{x}$ where $\bar{x}$ is the population mean, being analogous to the coefficient of variation, does show the same trend of increasing variability towards the equator with the variability of the Townsville population again being particularly high. Since in these and subsequent tables, the means between populations are highly variable, it is therefore felt that the 'dimensionless' F test (in terms of means) is an appropriate method of handling the data. Even so, variability arguments should be treated with caution because of the highly variable means among populations.

The trend of increasing variability towards the tropics

Table 2. Analyses of variance for variation within and between isofemale strains for the Melbourne, Brisbane, Townsville, Darwin and Melville I. populations

	Based on LT_{50} over 12% ethanol			Based on ratio of LT_{50} over 12% ethanol: LT_{50} over water			
	d.f.[a]	ms	F	ms	F	Between-line variance, V.	$\frac{\sqrt{V}}{\bar{x}}$
Melbourne							
between	7	344.06	9.77[b]	0.0838	8.30[b]	0.0147	0.11
within	32	35.20		0.0101			
Brisbane							
between	8	104.96	9.71[b]	0.0253	12.04[b]	0.0046	0.12
within	36	10.81		0.0021			
Townsville							
between	8	177.49	54.21[b]	0.0902	70.75[b]	0.0178	0.78
within	36	3.27		0.0013			
Darwin							
between	9	225.35	9.56[b]	0.0691	8.23[b]	0.0121	0.20
within	40	23.57		0.0084			
Melville I.							
between	9	168.36	6.57[b]	0.0559	6.73[b]	0.0095	0.39
within	40	25.62		0.0083			

[a] Number of isofemale strains = d.f. + 1
[b] $P < 0.001$

could be a reflection of the utilization of a greater diversity of fermented-fruits in tropical compared with temperate-zone populations. The low southern heterogeneity agrees with the general principle of declining biological diversity as latitude increases (MacArthur 1972), and in the field would reflect a decline in the variety of suitable microhabitats. At the interspecific level there are parallel results for the genus *Drosophila*, since species diversities fall markedly towards temperate regions associated with a corresponding drop in definable resources (Parsons and Bock 1979a). Since ethanol tolerances provide a measure of resource utilization, it is felt that arguments on comparative diversities within and between species are valid, and do not present the problems of interpretation which occur for chromosomal and allozyme frequency data (Carson 1965; Parsons 1973; Lewontin 1974). Another way of obtaining an indication of resource utilization is via larval reaction to ethanol (and other metabolites) based on the argument that the larval stage is when maximum feeding occurs. Using the choice of agar containing 6% ethanol and plain agar, the Melbourne population was found to be strongly ethanol preferring and relatively homogeneous, while the Townsville population was less ethanol preferring and extremely heterogeneous (Parsons 1977) with isofemale strains ranging from strongly ethanol preferring as in the Melbourne population to showing no preference at all. This result therefore also shows a premium on ethanol utilization in southern populations.

By contrast with Townsville, within the Darwin and Melville I. populations, ethanol tolerances are more homogeneous even though they are from tropical regions. The Darwin and Melville I. climate is, however, very extreme for *Drosophila* in terms of high temperature and desiccation stresses (Fig. 2). Indeed *D. simulans* has not been found in Darwin or Melville I. probably because of the extreme climate (McKenzie and Parsons 1974b). Parsons (1979a) considered resistances of the sibling species *melanogaster* and *simulans* to high temperatures in relation to humidities from which it is clear that the Darwin summer would be stressful for both species but more so for *D. simulans*; the only redeeming feature (for *Drosophila*) is that the high summer temperatures tend to be associated with high humidities (Fig. 2). Generally *Drosophila* species diversities are low (unpub. data) as would be expected in climatically extreme habitats. Such climatic extremes presumably mean the utilization of a lesser diversity of resources compared with more optimal habitats, and consequently a relatively uniform level of ethanol tolerance/resource utilization within populations, even though mean tolerances differ from the relatively homogeneous temperate-zone Melbourne population.

Table 3. Percentage of flies alive after exposure to 0% RH at 25°C for various time intervals

	Assessment time (hours)	% Survivorship	
		Males	Females
Melbourne	21	31.6	82.4
Brisbane	19	25.9	66.1
Townsville	19	54.3	82.1
Darwin[a]	21	23.4	74.2
Melville I.[a]	21	31.2	80.4

The two assessment times reflect effectively 0% death rates in all populations except Brisbane and Townsville at 19 hrs

[a] Five isofemale strains were tested for each of these populations. They were selected randomly from the 10 tested for ethanol tolerances (Table 2)

Desiccation Resistance and Development Times

The effect of high temperatures on natural populations can be assayed in the laboratory using desiccation tolerance at 25°C as an indicator (Parsons 1970, 1980). As shown in Table 3 the Darwin, Melville I. and Melbourne populations are the most desiccation resistant giving a ranking of:

Darwin
Melbourne > Townsville > Brisbane
Melville I

The Darwin and Melville I. populations do not differ significantly which appears to indicate that ethanol resource utilization races may occur at a more local level than the climatic races which are a feature of certain widespread *Drosophila* species (Dobzhansky 1948; Dubinin and Tiniakov 1947; McKenzie and Parsons 1974c; Parsons 1980; Stalker and Carson 1947, 1948). The temperate-zone Melbourne population is more desiccation-resistant than those from less tropical habitats (Townsville, Brisbane), presumably a consequence of more extreme summer maximum temperatures in Melbourne (Fig. 2).

The general importance of climatic selection is emphasized by parallel climatic races in *D. melanogaster* and *D. simulans* for cold and heat stresses (Parsons 1980). Indeed, it is a result relatable to the basic similarities of the life histories of the two species. It can be predicted that other species with similar life histories would show similar trends. An example is the Queensland fruit fly *Dacus tryoni* (Tephritidae) which is endemic to tropical rain forest fruits. With the introduction of cultivated fruits it has spread to greater latitudes and altitudes, associated with the development of climatic races for enhanced tolerances to physiological extremes in marginal habitats (Lewontin and Birch 1966). In other words, as in *D. melanogaster* in Australia, natural selection has over the last 100 years or so built up genetically differentiated races for physiologi-

cal tolerances to climatic extremes. Other Australian candidates for parallel studies include certain *coracina* group species of subgenus *Scaptodrosophila* which are tending to spread (Parsons and Bock 1979b).

Turning to development times, it would be expected that areas of climatic extremes would tend to be those where an r-strategy situation is most strongly favoured (Pianka 1970; Southwood 1977). This would be manifested by rapid development times because of a lower level of predictable resource availability and/or rapid resource deterioration throughout the breeding season, as compared with less extreme habitats. This prediction is confirmed since a ranking of:-

Darwin
Melbourne < Townsville < Brisbane
Melville I.

is apparent from Table 4, which is the same as that of Table 3. (For simplicity the three most rapidly emerging populations are combined even though at day 11, the Darwin and Melville I. populations are just significantly different at $P < 0.05$).

As for resistance to desiccation stress, parallel races would be expected in other species with similar life histories. Birch et al. (1963) reported on life-histories in the reasonably widespread species of subtropical-tropical Australia and New Guinea, *D. birchii* and *D. serrata*. However, no significant emergence time differences according to race were found, which may be a reflection of the high sensitivity of such species to environmental extremes (Parsons and McDonald 1978). Indeed races in the genus *Drosophila* which are demonstrably relatable to climatic variables are mainly found in cosmopolitan species, or those widespread species restricted to temperate-zones or even cooler habitats (Parsons and Stanley 1980). Birch et al. (1963) did, however, find differences in the innate capacities for increase r_m (Andrewartha and Birch 1954) of *D. serrata* and *D. birchii*, which are difficult to relate directly

Table 4. Percentage of flies emerged at day 11 and day 12, representing the duration of development from 1st instar larvae to adult emergence

	Day 11	Day 12
Melbourne	64.9	84.7
Brisbane	4.1	43,9[a]
Townsville	4.6	82.9
Darwin	53.0	83.7
Melville I.	69.6	85.9

[a] Day 13, 80.1%
See footnote, Table 3

Table 5. Analyses of variance for variation within and between isofemale strains for mortalities after desiccation at the assessment times in Table 3, and for emergence percentages in Table 4. Analyses were carried out after applying the angular transformation to the raw data

		Mortalities after desiccation				Percentage emergence times			
		Males		Females		Day 11		Day 12	
		ms	F	ms	F	ms	F	ms	F
Melbourne									
between	7	141.66	5.09[b]	15.24	0.24	532.83	6.52[c]	176.00	2.86[a]
within	32	88.70		63.89		81.76		61.50	
Brisbane									
between	8	1615.10	12.79[c]	1054.82	14.13[c]	250.35	6.77[c]	654.88	9.45[c]
within	36	126.31		74.63		36.96		69.34	
Townsville									
between	8	730.10	9.59[c]	481.97	7.89[c]	144.35	3.00[b]	288.89	4.89[b]
within	36	76.83		61.08		48.09		58.09	
Darwin									
between	4	32.48	0.32	97.76	1.91	251.73	4.29[a]	120.22	1.11
within	16	102.25		51.33		58.66		108.07	
Melville I.									
between	4	174.04	1.51	374.05	2.41	95.12	1.67	268.23	2.18
within	16	115.28		154.99		58.81		123.06	

[a] $P < 0.05$
[b] $P < 0.01$
[c] $P < 0.001$

to climate since r_m tended to increase from north to south in the former, and to decrease in the latter species. The need for further study of life-history characteristics, including r_m, is evident in the *D. melanogaster* populations being considered.

The final prediction comes from variability considerations, since as in Table 2, the Darwin, Melville I. and Melbourne populations would be expected to show less variability among isofemale strains for both desiccation resistance and development times than those from Townsville and Brisbane. Table 5 confirms this prediction for Darwin and Melville I. populations compared with Brisbane and Townsville populations for both traits. The Melbourne population shows reasonably low variability for desiccation resistance, but development times are as variable as in the Brisbane and Townsville populations. The Melbourne climate, however, is almost certainly such that selection for rapid development times would be less at a premium than in Darwin and Melville I. In the latter localities, the extreme and continuous high temperature/desiccation stresses would mean that resources would normally be very short-lived throughout the entire year.

Discussion

Greater resource utilization heterogeneity may therefore occur within populations not greatly stressed by desiccation in association with longer development times, as compared with populations under greater stress where development times are rapid (Table 6). The utilization of a diversity of resources within populations is apparently a feature of a population tending towards a K-strategy life-history. Even so, as a species *D. melanogaster* can be regarded as mainly subject to r-selection on the r-K continuum of MacArthur and Wilson (1967). Indeed species further from the r-strategy extreme on this continuum may be expected to show less clear results than in Table 6, especially when interspecific competition for resources becomes of importance. In more extreme habitats characterized by intense r-selection however, local but relatively homogeneous resource races may be likely to develop, as shown by the differing ethanol tolerances of the Darwin and Melville I. populations. The intensity of r-selection is also shown by the relative homogeneity among isofemale strains within the three extreme populations compared with the Townsville and Brisbane populations for extreme desiccation resistance and to a lesser extent rapid development times. It would additionally be of interest to look comparatively at variables such as the ovarian state of these wild populations, given Boulétreau's (1978) conclusion that wild flies give priority to individual survival rather than to reproductive effort as measured by fecundity in the field.

The concomitant study of possible resources/metabolites additional to ethanol is needed, especially as geographic differences in both adult and larval responses to acetic acid, ethyl acetate and lactic acid occur in *D. melanogaster* (Fuyama 1976; Parsons 1979b). Acetic acid may be of particular interest, since in the field it occurs to high concentrations in association with high ethanol concentrations in winery wastes (McKenzie and McKechnie 1979). In addition, in those habitats where *D. simulans* occurs sympatrically, the associated resources utilized by this species may be important. The same applies in Darwin and Melville I. where the tropical cosmopolitan species *D. ananassae* occurs sympatrically with *D. melanogaster*. In the case of the sibling species *D. melanogaster* and *D. simulans*, field evidence indicates that the larvae are sympatric in winery wastes to an ethanol concentration of about 3%, while only *D. melanogaster* occurs at higher concentrations as would be expected from comparative ethanol resource utilization thresholds for the two species (Parsons et al. 1979). Assuming that the fermented-fruit baited *Drosophila* species are in positions on the r-K continuum where interspecific competition is unlikely to be important at the population level, then the greatest diversity of resources utilized by *D. melanogaster* is likely to occur when there is a maximal assemblage of fermented-fruit baited species, which in itself is presumably a mani-

Table 6. A comparison of the adaptive strategies of the Darwin, Melville I., and Melbourne populations compared with the Townsville and Brisbane populations

Populations	Melbourne Darwin Melville I.	Brisbane and especially Townsville
Overall strategies	Tending towards r-strategy	Tending towards K-strategy
Ethanol tolerances	Relatively homogeneous	Relatively heterogeneous
Desiccation resistance	High with low variability	Low with high variability
Development times	Fast with low[a] variability	Slow with high variability

[a]Except for the Melbourne population (see text)

festation of heterogeneous available resources. For the populations under discussion, the number of species commonly attracted to fermented-fruit baits are Townsville 6, Brisbane 4, Melbourne 3, and Darwin/Melville I. 2 (Bock 1977; Parsons 1978a and unpub. data).

Environmental ethanol has direct effects on the gene pool of populations as demonstrated at Chateau Tahbilk and inferred from the data presented here, although indirect effects can never be excluded. The relationship is certainly far more direct in an adaptive sense than using alleles at the alcohol dehydrogenase, ADH, locus as the variable, since at the Chateau Tahbilk winery little or no relationship between ethanol-tolerance and ADH phenotypes was found (McKenzie and Parsons 1974a; McKenzie and McKechnie 1978). McDonald and Ayala (1978) found genes for ADH activity not adjacent to the ADH locus, with associated variation in natural populations as found by McKenzie and McKechnie (1978) for ethanol tolerance. Even though there are latitudinal clines for the Adh^F allele which increases in frequency away from the tropics (Vigue and Johnson 1973) and with increasing altitude (Pipkin et al. 1976), it would appear that at the population or isofemale strain level, associations are likely to be weak to non-existent. The relationship between the ADH locus and the direct effects of environmental ethanol clearly needs further investigation even though Clarke (1975) reported convincing evidence for ethanol-mediated natural selection at the ADH locus. Indeed the situation may be complex, since there is no reason why all populations should adapt similarly to ethanol in the environment, especially if selection is regarded as acting more upon integrated metabolic phenotypes rather than single loci (Johnson 1974). Since, however, ethanol itself is both a resource and an environmental stress according to its concentration, with thresholds between the two aspects being apparently subject to natural selection, then a greater understanding of ADH locus variants and ADH enzyme activity in natural populations may well come from studying the direct effects of ethanol.

The results suggest that the gene pool of *D. melanogaster* is divided into climate-associated races. Within regions showing little or no climatic differentiation, resource utilization races may occur to form a mosaic of genotypes differentially favoured according to available resources. These resource races may be most likely to develop in regions of temperature/desiccation extremes where resource heterogeneity within populations is lower than in more central populations. On the other hand, ecologically central (and heterogeneous) regions may be characterized by seasonal shifts in favoured genotypes according to resources ripening at different times of the year, but this needs to be tested. In extreme regions, however, seasonal shifts are more likely to occur in traits reflecting the direct effects of climatic selection as McKenzie and Parsons (1974c) have shown for desiccation in Melbourne populations of *D. simulans*. In addition, allozyme (and inversion) frequency clines are likely to be associated with climate or climate associated variables (Parsons and Stanley 1980). Conversely the development of integrated metabolic phenotypes at a local level may make direct associations of allozymes (and inversions) with resources difficult to detect. On the other hand, since habitat selection at a local level within populations in *Drosophila* may occur (Taylor and Powell 1978; Parsons 1978b), the latter possibility cannot be excluded. This is because any form of habitat selection necessarily emphasizes the role of the local interbreeding population as the unit of evolution.

Because of the then lack of a real understanding of the ecology of *Drosophila*, Lewontin (1967) appeared not to hold out great hopes for *Drosophila* when he wrote 'what we require is the study of comparative variation in species whose life history and ecological niche in the community are well understood and easily studied'. While this problem still remains, developments in the last decade as presented here and elsewhere (for example Johnston and Heed 1976; Kaneshiro et al. 1973; Richardson and Johnston 1975) allow some cautious optimism that *Drosophila* may indeed provide meaningful models for the study of variability in natural populations of both cosmopolitan and ecologically more restricted species. In addition, the parallel climatic races in *Drosophila* and *Dacus* show that ecological genetic studies on *Drosophila* may provide models for insects of economic importance having similar life histories.

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