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Larval Reaction to Alcohol as an Indicator of Resource Utilization Differences between *Drosophila melanogaster* and *D. simulans*

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Summary. Newly hatched larvae of *Drosophila melanogaster* derived from southern Australian populations (37–38° S) have a strong preference for agar containing alcohol, while larvae of sympatric populations of *Drosophila simulans* show no initial preference. The alcohol preference of a more northern *D. melanogaster* population (10° S) is lower due to a high level of variability among isofemale strains. This agree with the general principle of decreasing biological diversity with increasing latitude, and is shown here for a simple behavioural trait with a chemical basis. The results are of application to the ecological biology of resource utilization in the wild.

Introduction

The genus *Drosophila* gained its ascendency by specializing on a diversity of organisms causing fermentation or decay so providing a great variety of substrates in many diverse habitats (Throckmorton, 1975). Even so, the majority of species studied in the laboratory, which include the sibling species *D. melanogaster* and *D. simulans*, are normally attracted to a fermented fruit resource (Parsons, 1973). These two species show a remarkable degree of morphological and genetic homology, and differences between the species are mainly quantitative. Alcohol is an exception, since *D. melanogaster* adults and larvae are more tolerant of alcohol in the environment than *D. simulans* (McKenzie and Parsons, 1972), which provides an explanation for large numbers of *D. melanogaster* in sites such as fermentation areas of wineries (Briscoe et al., 1975).

The larval stage of the *Drosophila* life cycle has been neglected almost totally, even though this is the stage of maximum resource utilization. Any resource utilization differences between the two sibling species are necessarily initially important in niche determination in the wild. Experiments on larval behaviour whereby newly hatched larvae are given the choice of agar with and without ethanol, provide a test system (Parsons and King, 1977), since Melbourne *D. melanogaster* larvae show a clear initial preference for ethanol which *D.*

simulans does not. This result is suggestive of discrete and different microniches for the two species in the wild, even though adults of both species are attracted to fermented fruit baits.

Here, larval alcohol preferences will be considered for three populations where the two species are sympatric, namely two Victorian populations (Melbourne, Australia and the nearby winery at Chateau Tahbilk at latitudes in the 37–38° S range) and Townsville, North Queensland (latitude 20° S). The former localities have a temperate climate with a hot relatively dry summer and cool damp winter, and the latter a subtropical climate with a hot damp summer and warm dry winter. Recent work (Parsons, 1977a) has shown intraspecific differences between the Melbourne and Townsville populations for adult cold-temperature resistance, especially *D. melanogaster*. In the northern hemisphere, latitudinal clines for adult alcohol resistance occur for *D. melanogaster*, whereby alcohol tolerance increases with latitude. The offered interpretation of David and Bocquet (1975) is that this species becomes more linked with human activities such as artificial fruit fermentations with increasing latitude. They suggested that *D. simulans* is independent of alcohol food sources in agreement with the above experiments on larval behaviour.

Methods and Materials

All strains tested were derived from single inseminated females collected in the wild (isofemale strains). The were cultured in the laboratory at 20° C, this being relatively optimal for both species (Parsons, 1975a). Six strains were tested for each population and species except Townsville *D. simulans* where four were tested.

Individual tests consisted of placing ten newly hatched larvae centrally on a Petri dish containing agar. One semicircle of the agar contained 6% alcohol the other being pure agar. The relative numbers on the two sectors were noted after 15, 30, and 60 min. Ten replicates per isofemale strain were scored.

Results

Mean numbers of larvae choosing agar with ethanol up to 60 min from the start of the experiment are given in Figure 1 (*D. melanogaster*) and Figure 2 (*D. simulans*), with the six possible means formed by combining isofemale strains within populations and species in Figure 3.

The discussion will refer mainly to the response at 15 min as most indicative of initial preferences, although results for later times are in broad agreement. All *D. melanogaster* strains from Chateau Tahbilk and Melbourne have greater responses to alcohol than all *D. simulans* strains. Both populations within species are very similar since the *D. melanogaster* means are all >7.5 and *D. simulans* 5–6. Clearly, the former species seeks out ethanol as a resource, although by 60 min the *D. melanogaster* means fall below seven (Fig. 3) presumably because other resources (not provided) are being sought at this stage. The slight fall of *D. simulans* larvae on alcoholic agar with time suggests the development

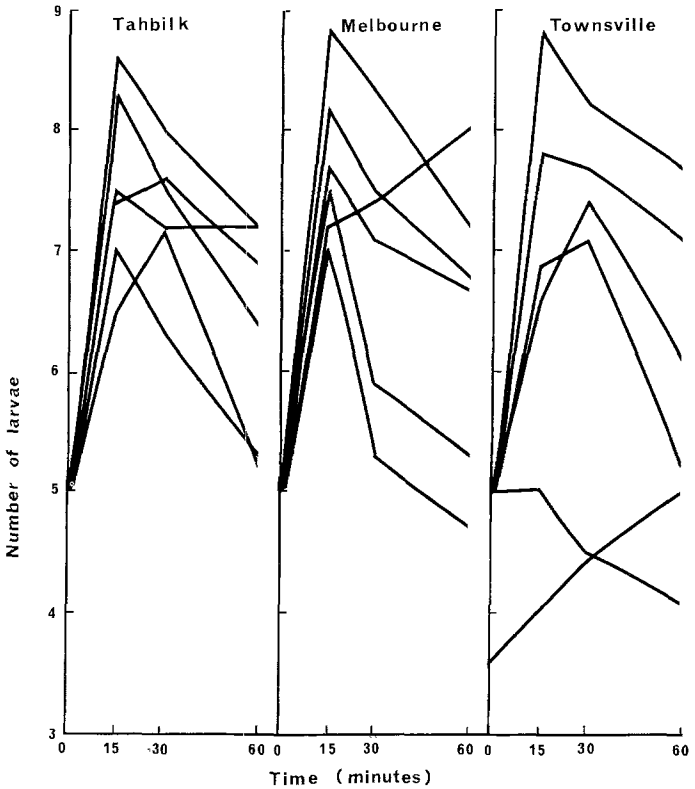

Fig. 1. Mean number of larvae out of ten choosing ethanol containing agar up to 60 min for isofemale strains of the three *D. melanogaster* populations

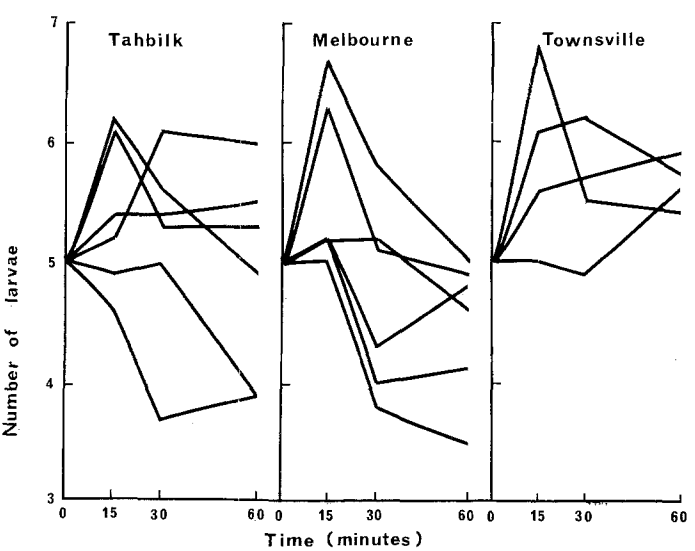

Fig. 2. Mean number of larvae out of ten choosing ethanol containing agar up to 60 min for isofemale strains of the three *D. simulans* populations

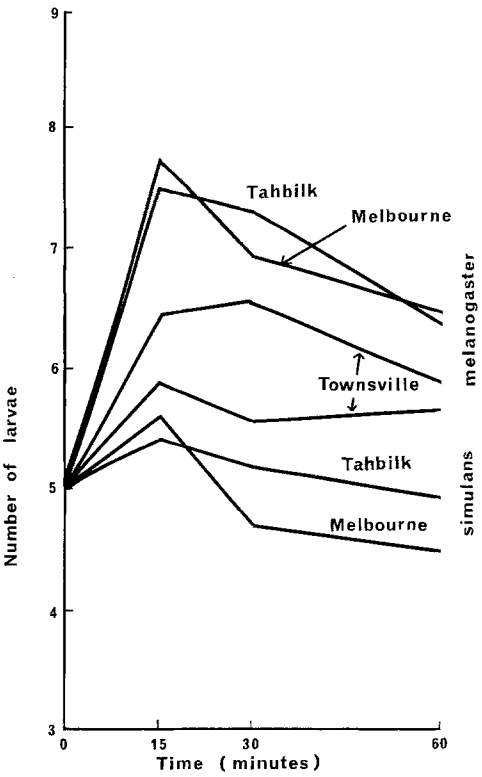

Fig. 3. Mean number of larvae out of ten choosing ethanol containing agar for the three populations of the two sibling species

of an avoidance reaction with time so that both means are just < 5 at 60 min. The results are in broad agreement with cited published data on adult and larval survival.

Only two of six *D. melanogaster* strains from Townsville have a greater response at 15 min than all four *D. simulans* strains and, indeed, one *D. melanogaster* strain shows alcohol avoidance. Four of the six *D. melanogaster* strains are in the range of the Chateau Tahbilk and Melbourne strains, the other two being far lower. Another way of assessing the data is from the 15 min ranges of the six strains at Chateau Tahbilk, Melbourne, and Townsville, which are 6.5–8.8, 7.0–8.8, and 3.6–8.8 or 2.3, 1.8 and 5.2. In view of the enormous Townsville range, the lower Townsville mean is to be expected.

By contrast, the *D. simulans* Townsville population shows a slight overall alcohol preference, so that the difference between the two species are small in Townsville (Fig. 3). The 15 min *D. simulans* ranges are 1.6, 1.5, and 1.8, which are all smaller than for the corresponding three *D. melanogaster* populations listed above, especially Townsville.

Discussion

As for adult tolerance, the differences between the two species for larval alcohol preference are lower closer to the equator. Studies on southern hemisphere

strains even closer to the equator would be of interest, since at latitudes 0–10° N, the two species are almost indistinguishable for adult alcohol tolerance, the difference becoming clear at latitudes to the north of 20° N (David and Bocquet, 1975). The clear differentiation between the two species at 37–38° S for larval reaction to alcohol, and larval and adult mortalities, is in good agreement with corresponding northern hemisphere adult mortality data. David and Bocquet (1975) have data as far north as 50° N. Comparable data are, unfortunately, unobtainable in Australia, as the most southerly land mass is at 43°38'S.

The high range of variability among isofemale strains for the Townsville *D. melanogaster* populations, being in excess of twice the other *D. melanogaster* populations and all the *D. simulans* populations based on 15 min responses, indicates a high level of polymorphism for larval response in this population. From this, it can be argued that as *D. melanogaster* spread south there was a premium on selection for alcohol resource exploitation. This can be presumed to be a process of selection among isofemale strains. [In addition it shows that a likely effective way of obtaining a rapid response to selection in the laboratory for this trait is to base selection on the extreme strains as advocated and demonstrated by Parsons (1975b) for scutellar chaeta number in *D. melanogaster*.]

The decline in heterogeneity in the southern *D. melanogaster* populations compared with the Townsville population agrees with the general principle of declining biological diversity as latitude increases (Emlen, 1973). In this case, the result is based upon variations in the utilization of a simple chemically defined resource. Most studies measure biological diversity by species diversities within a genus or higher taxa. For example, considering endemic Australian *Drosophila*, species diversities are highest in the rain forests of North Queensland where over 50 species are known, while south of 42° S in Tasmania only six species are known (Bock, 1976; Parsons and Bock, 1977). In addition, the niches utilized fall going south, since the three major collection methods of sweeping, fermented fruit and mushroom baiting are effective in North Queensland, but sweeping only in southern regions. Since, as a genus, *Drosophila* utilizes fermentation products of plants for resources, a fall in species diversity going south is predictable as plant diversity too falls dramatically.

In *D. simulans*, as expected, no latitudinal change in heterogeneity for larval alcohol preference occurs. Clearly, these heterogeneity conclusions for both species would not have been possible without considering variability among isofemale strains, an approach in need of more emphasis in the study of traits of ecological and behavioural significance in natural populations (Parsons, 1977b). The lack of heterogeneity in *D. simulans* is consistent with the observation that, generally, *D. melanogaster* shows more chromosomal, enzyme, and protein polymorphism than *D. simulans* and in addition, can exist under more diverse temperatures and light conditions than the latter species (Parsons, 1975a).

In conclusion, this paper discusses differences in larval use of alcohol as a resource within and between species. The comparative study of resource utilization by larvae of different *Drosophila* species, however, remains an open field. Detailed investigations of sibling species in particular may yield information of interest concerning evolutionary divergence. This is necessarily a conclusion

applying to many potential resources, of which an enormous variety may be relevant in a genus as diverse as *Drosophila*, considering its dependence upon the microbial degradation products of plants.

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References

Bock, I.R.: Drosophilidae of Australia. I. *Drosophila* (Insecta: Diptera). Aust. J. Zool. Suppl. Ser. No. **40**, 1–105 (1976)

Briscoe, D.A., Robertson, A., Malpica, J.-M.: Dominance at *Adh* locus in response to adult *Drosophila melanogaster* to environmental alcohol. Nat. **225**, 148–149 (1975)

David, J., Bocquet, C.: Similarities and differences in latitudinal adaptation of two *Drosophila* sibling species. Nat. **257**, 588–590 (1975)

Emlen, J.M.: Ecology: An evolutionary approach. Reading, Massachusetts: Addison-Wesley 1973

McKenzie, J.A., Parsons, P.A.: Alcohol tolerance: an ecological parameter in the relative success of *Drosophila melanogaster* and *Drosophila simulans*. Oecologia (Berl.) **10**, 373–388 (1972)

Parsons, P.A.: Behavioural and Ecological genetics: A study in *Drosophila*. Oxford: Clarendon Press 1973

Parsons, P.A.: The compapative evolutionary biology of the sibling species, *Drosophila melanogaster* and *Drosophila simulans*. Quart. Rev. Biol. **50**, 151–169 (1975a)

Parsons, P.A.: Quantitative variation in natural populations. Genet. **79**, 127–136 (1975b)

Parsons, P.A.: Resistance to cold temperature stress in populations of *Drosophila melanogaster* and *D. simulans*. Aust. J. Zool. (1977a, in press)

Parsons, P.A.: Genes, behavior, and evolutionary processes: The genus *Drosophila*. Advances in Genetics **24**, 1–32 (1977b)

Parsons, P.A., Bock, I.R.: Australian endemic *Drosophila*. I. Tasmania and Victoria, including descriptions of two new species. Aust. J. Zool. **25**, 249–268 (1977)

Parsons, P.A., King, S.B.: Ethanol: larval discrimination between two *Drosophila* sibling species. Experientia (1977, in press)

Throckmorton, L.J.: The phylogeny, ecology and geography of *Drosophila*. In: Handbook of genetics, Vol. 3 (R.C. King, ed.), pp. 421–469. New York: Plenum Press 1975

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