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Habitat preference: an interaction between genetic variability and the costs of stress

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ABSTRACT. *Habitat preference: an interaction between genetic variability and the costs of stress.*- Exposure to stressful environments is the norm in natural populations. The consequences include elevated additive genetic variability and increased metabolic cost. Preferred habitats should be located in environments corresponding to minimum total energy expenditure, as found for behavioural adaptation of *Drosophila* to variable temperature (and humidity) conditions. Laboratory-based resource-preference studies in *Drosophila* species suggest low genetic variability underbenign conditions, however, habitat preference studies under stressful conditions need to be emphasized in modelling situations in nature.

KEY WORDS. Stress, Metabolic cost, Habitat preference, *Drosophila,* Fitness, Genetic variability,

The universality of stress

Exposure to stressful environments is the norm in natural populations. The evidence is based upon organizational levels ranging from the molecular to the biogeographic. It is now becoming appreciated that the scenario in nature consists of organisms struggling to survive under conditions where there are severe energetic costs from abiotic stresses of climatic origin, together with inadequate nutrition (Boulétreau-Merle et al., 1987; Parsons, 1987; Hoffmann & Parsons, 1991). In this context, stress can cause injurious changes to biological systems with major impacts on many evolutionary and ecological processes. At the limit at species borders, the cost from stress means that reproduction, and hence species continuity, is effectively precluded (Parsons, 1991a). Behavioural consequences of the stress model have received little attention until recently (Parsons, 1993), which is the aim of the present paper emphasizing habitat preference.

Under extreme stress close to where species continuity is threatened, variability is elevated at the mutational level, the chromosomal level measured by recombination, and at the developmental level measured by morphological variability. At the whole organism level, an association between stress intensity and phenotypic and genetic variability has emerged as a plausible relationship (Parsons, 1987). In the context of this discussion, behavioural stress can be used as an example. In mice, Belyaev & Borodin (1982) studied several traits in offspring from a diallel cross involving three inbred strains which had been kept in two types of cages, a normal cage and a smaller cage where crowding occurred. Crowding reduced reproductive fitness, since 14% of inseminated females in the normal cages did not produce any offspring and 29.4% under crowding. Additive genetic variability increased under crowding stress especially for preimplantation mortality, litter size and relative adrenal weight (table I). For preimplantation mortality and litter size non-additive effects increased which is mainly a reflection of heterozygote advantage which became more pronounced under stress.

This and other examples indicate that additive genetic variability can be high under stress (Parsons, 1988). Approached by conventional quantitative techniques, comparisons of variability pose substantial difficulties in interpretation. Even so, extreme stress is an environmental probe increasing genetic variability revealing associations among life-history and stress traits (Hoffmann & Parsons, 1991).

Energy budgets and fitness

At the physiological level, stress places an organism at a disadvantage requiring the continuous expenditure of excess energy. Ultimately, survival is threatened because of irreversible damage irrespective of the density of organisms. An inverse relationship between the favourableness of a habitat and the metabolic cost involved in occupying that habitat is therefore the expectation; the extreme is the species border where the habitat is so unfavourable that the metabolic cost under stress is restrictive for range expansions (Parsons, 1991a). Assuming that a primary affect of generalized stress is at the level of

TABLE I. Results from a diallel cross between three strains of mice held in uncrowded and crowded (stressed) populations. Mean squares are given for the general combining ability (gca) which is a measure of additive genetic variability and specific combining ability (sca) which measures non-additive effects. (After Belyaev & Borodin, 1982 as summarized by Hoffmann & Parsons, 1991.)

[Resultados de un cruce dialelico entre tres líneas de ratones mantenidas en poblaciones hacinadas (estresadas) y no hacinadas. Se presentan los cuadrados de la media para la habilidad de combinación general (gca) que es una medida de la variabilidad genética aditiva y la abilidad de combinación específica (sca) que mide efectos no aditivos.]

	Preimplantation mortality	Litter size	Adrenal weight	Thymus weight
Control population (uncrowded)				
gca	1.1	0.4	6.7	$8432^{\#}$
sca	1.2	$4.4^{\#}$	3.8	878
Error	0.7	0.5	1.9	1543
Stressed population (crowded)				
gca	2.6^{*}	$3.2^{\#}$	$21.7^{\#}$	$7200^{\#}$
sca	4.2^{*}	$6.7^{\#}$	1.7	650
Error	0.4	0.5	0.9	345

* $p<0.05$; $^{\#}$ $p<0.01$

energy carriers (Atkinson, 1977; Hoffmann & Parsons, 1991), and that stress is the norm in nature, those habitats with low stress levels should be preferred. It is now appropriate to consider energy budgets and fitness, and then with this background consider habitats preferred from benign to stressful environments.

Zotin (1990) argued that the most stable state of biological systems corresponds to periods of minimum energy dissipation usually assessed by metabolic rate. For example, metabolic efficiency, measured from the amount of energy required from a *Drosophila melanogaster* female to produce an average egg at various temperatures is higher in the 22-25°C range than at 18°C and 28°C (Arking et al., 1988). At intermediate temperatures, daily egg production, egg hatchability, fecundity and viability are maximal indicating that maximum fitness occurs in the temperature range incorporating the region of minimum energy cost of development. High metabolic rate may occur away from optimal habitats and may be stressful.

TABLE II A comparison of control (desiccation sensitive) and desiccation resistant strains in *D. melanogaster*

[Comparación entre líneas resistentes a la desecación y control en *D. melanogaster*.]

	Control	Resistant
Metabolic rate	High	Low
Starvation	Sensitive	Resistant
Heat	Sensitive	Resistant
Intense radiation	Sensitive	Resistant
Toxic ethanol level	Sensitive	Resistant
Toxic acetic acid level	Sensitive	Resistant
Early fecundity	High	Low
Early behavioural activity (movement)	High	Low
Male longevity	Short	Long

Compiled from data discussed in Hoffmann & Parsons (1991, 1993)

Assuming that the input of resources to organisms is relatively fixed, any shift in allocation to one component of metabolism is at the expense of other components which provides a physiological basis for various trade-off models. Processes with energy costs in insects include maintenance and survival, reproduction, viability of eggs, growth, resistance to stress, and genetic adaptation (De Kruijf, 1991). If the maintenance and survival components cannot be modified, the energetic costs of stress would reduce the energy available for other processes (Parsons, 1992).

An illustration of trade-offs among various metabolic costs comes from an energetic approach to aging and longevity. For example, "shaker" mutants of *D. melanogaster* are characterized by high metabolic rate and behavioural activity level, and reduced longevity and courtship success (Trout & Kaplan, 1970; Burnet et al., 1974). Furthermore, these and other high metabolic rate mutants and strains of *D. melanogaster* are sensitive to environmental stresses including high temperature and desiccation (Homyk et al., 1980). One of the "shaker" mutants, hyperkinetic^1, is sensitive to Los Angeles smog, especially in combination with temperature stress (Trout & Hanson, 1970; Parsons, 1991b). In addition, Barros et al. (1991) found that some of these "shaker" mutants are sensitive to stress from an unsaturated aldehyde, acrolein. High sensitivity to environmental stresses and reduced longevity follows from the cost of the substantial drain of metabolic energy of these strains.

Conversely strains selected for stress-resistance should have low metabolic rate as found in desiccation-resistant *D. melanogaster* (Hoffmann & Parsons, 1991, 1993). In accord with such metabolic arguments, desiccation-resistant strains are resistant to an array of generalized stresses, and have reduced early fecundity, reduced behavioural activity and longer life span than unselected strains (see table II). The model is energetically appealing since trade-offs can be considered in terms of the relative metabolic cost of various processes, and can be integrated with other evolutionary phenomena that can be similarly expressed.

Habitat preferred

In habitat preference studies, the phenotype measured is ecobehavioural but there are few genetical studies. Of these, many are genotypic in approach considering gene (in particular eletrophoretic) and chromosome polymorphisms as primary units of study (Parsons, 1983) This approach is limited to those polymorphisms that can be easily scored, and cannot fully explain the total nature of the underlying genetic variation. The alternative phenotypic approach involves the *a priori* and direct study of quantitative traits important in locating, examining and utilizing habitats. In a few examples, the two approaches converge such as in the determination of the duration of flight in *Colias* butterflies by genotypes of the polymorphism of the phosphoglucose isomerase locus, PGI (Watt, 1991). However, the phenotypic approach has tended to focus upon contrasts between populations, species and higher taxa. The quantitative genetic analysis of variation within populations has received less emphasis even though necessary in explorations of relationships between metabolic rates, fitness, and stress intensity (Parsons, 1991a).

Considering the phenotypic approach, females seeking oviposition sites in *Drosophila* should prefer benign (i.e. non-stressful) physical conditions because animals early in development cannot tolerate extreme and metabolically costly conditions. It can be difficult to find the natural substrates on which *Drosophila* females lay their eggs. However, Jones *et al.*, (1987) indirectly assessed whether oviposition-site preference might reflect thermoregulatory preference in *D. melanogaster* using a temperature-sensitive eye mutant in which adult eye colour depends upon developmental temperatures in early pupae. At Beltsville, U.S.A. (40 m elevation) the mean temperature experienced by pupae was 22.0±0.26°C and at Shenandoah (1000 m elevation) 20.7±0.19°C. While the difference, 1.3±0.32°C, is highly significant, it is considerably less than the 4.5±0.23°C difference in mean air temperature at the two sites. The likely interpretation is behavioural flexibility whereby the geographic effects of temperature were ameliorated in the habitats preferred. Such behavioural flexibility would dampen down the energetic costs of temperature extremes and so would be favoured in an evolutionary context.

Laboratory-based *Drosophila* studies typically involve generalist species attracted to fermented-fruit baits. In Australia there is a *Drosophila* fauna, principally subgenus *Scaptodrosophila*, not attracted to such baits. For commoner species such as *D. inornata*, microhabitats where adults are located can readily be determined. Adults of *D. inornata* often rest on the fronds of tree ferns in rainforests. Over a series of collections deep inside rainforests, fern fronds where flies were collected were in the 15 20°C range with a mean of 17.7±2.0°C, while the ambient temperatures at the edge of these rain forest sites were in the 16 - 27°C range with a mean of 20.0±3.4°C (Parsons, 1975, 1983). Behavioural responses to microenvironments are involved since collections within rainforests at different times during the day show that flies migrate among microhabitats selecting those with optimal temperature/humidity conditions. Therefore flies exert a preference for microhabitats based upon temperatures optimal to their adaptive requirements, and in so doing select habitats of low physical stress.

Comparing benign and stressful situations

Comparisons of habitat preference under benign and stressful conditions are rare. Hoffmann and Turelli (1985) investigated the effect of starvation on the distribution of *D. melanogaster* on alternative resources (apple bait, orange bait) in orchard sites and in the laboratory. Longevity tests indicated that the apple medium was the better food resource for both sexes. They found that flies caught in the poorer of the two habitats may be preferentially recaptured there because they are stressed and less discriminating than flies from the better habitat. Behaviour was therefore altered environmentally. Assuming that stress is the norm in natural populations, flies may be less discriminating in response to resources than is the norm under more benign laboratory conditions.

The utilization of less than optimal resources implies a metabolic cost and lowered fitness as the environment becomes stressful. Since these are conditions under which increased genetic variability is likely, concentrating solely upon laboratory paradigms may be restrictive. On the one hand, a laboratory environment may be so artificial as to be stressful as is common in the process of domestication (Parsons, 1988), or alternatively it may be so benign that natural conditions are not modelled.

These issues are illustrated in Henderson's (1981) studies of infant mice that have limited visual and auditory sensitivity and poor locomotory activity. Placing young mice in a totally new environment is necessarily stressful, and there was substantial additive genetic variation. However, moving young mice away from the nest but with access to it is less stressful since the highly efficient maternal retrieval response of mice becomes effective, and there was low heritability and dominance towards low activity. Therefore the genetic architecture of activity depends upon habitat defined by the location of young mice in relation to the maternal nest. This situation affords the possibility of studying genetic architectures under a gradation from non-stressful to stressful situations.

Hoffmann & O'Donnell (1990) found resource-related heritable variation in behaviour (resource response) and performance (the ability of flies to utilize a resource as a breeding site) in field collected *D. melanogaster* and *D. simulans* tested in the laboratory. However, the genetic differences between flies for these resources are relatively small, perhaps because these fruit resources are very similar given the dependence of these species on fermentation products. Even so, the number of examples of habitat preference for resources is now increasing rapidly especially in arthropods and molluscs (Jaenike & Holt, 1991). A recent example comes from a multivoltine whitefly, *Siphoninus phillyreae*, where in four of seven species tested, there was an association between ovipositional preference and survival (Leddy *et al.*, 1993).

In the field there are examples of major evolutionary shifts associated with resource heterogeneity. In the evolution of a race of *Rhagoletis pomonella* to use the introduced domestic apple, the resource shift from its native host hawthorn appears associated with a period of selection involving climatic stress (Bush & Howard, 1986; Feder et al., 1988), and in the cactophilic *D. mulleri* species complex a switch in host plant from *Opuntia* to columnar cactus is associated with an increase in temperature and aridity (Ruiz & Heed, 1988). Consistent directional climatic stress may therefore be associated with a resource shift when high genetic variability of ecologically important phenotypes is likely (Parsons, 1991a). Following the initial switch based upon an ecological window of opportunity, oviposition and development would tend to become associated with the resources, temperature, and other climatic features of the new habitat. This could take some time since a temperature change affects many reactions with a concomitant metabolic cost (Parsons, 1989).

Wcislo (1989) discussed the proposition that innovation is likely during periods of stress with reference to behavioural traits. For example, some parasitoids oviposit on alternative, otherwise rejected, hosts if they are stressed by being deprived of access to the preferred host. Such switching behaviour has been induced experimentally in the genus *Dacus* (Tephritidae) for the generalist species *D. tryoni* for propensity for oviposition on fruits outside its normal host range (Fitt, 1986). Similarly in *Drosophila*, habitat preference experiments utilizing resources that are outside normal host ranges would be a useful approach. For *D. melanogaster* and *D. simulans*, a possible candidate would be lemons, since adults avoid lemons and larval survival is low, especially for *D. simulans* (Prince & Parsons, 1980). Responses of these two species in wind tunnel experiments tend in the same direction (Hoffmann, 1985).

The stressful scenario provides a reference point for experimental behavioural genetics. Extending considerations beyond habitat preferences, in comparative studies of alcohol dehydrogenase genotypes of *D. melanogaster* at 15, 20, 25 and 29°C, Kohane & Parsons (1987) found more variability among genotypes for survival and development time than for mating ability. This is because mating ability should be subject to intense directional selection irrespective of habitat because of its importance as a component of fitness. Experiments within the *D. melanogaster* subgroup of species show that mating occurs to the limits of survival since fertility occurred under temperature extremes causing high mortality (Parsons, 1992). Following the establishment of fertility, the next step in ensuring population continuity is the selection of preferred habitats for oviposition. These habitats are within more restrictive abiotic conditions than the much briefer process of mating. This calls for studies of habitat preference using behaviour genetic procedures considering a range of stress levels.

Taking temperature as a critical environmental factor, there is a need for habitat preference studies under a range of temperatures with stressed and unstressed flies involving optimal and suboptimal resources. It should be possible to devise a stress regime close to threatening species continuity where additive genetic variability is high and conducive to rapid evolutionary change. It should then be feasible to evolve races associated with particular resource/temperature regimes to model evolutionary shifts in the wild. By adopting an ecobehavioural approach the behaviour geneticist could contribute to investigations of habitat preference applicable to natural populations.

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Summary

Exposure to stressful environments is the norm in natural populations. The evidence is based upon organizational levels from the molecular to the biogeographic. The consequences include (1) elevated additive genetic variability as shown for a range of traits, including behavioural, and (2) elevated metabolic costs. Preferred habitats should therefore be located in optimum environments corresponding to minimum total energy expenditure. This tendency occurs in the field for behavioural adaptation of *Drosophila* to variable temperature (and humidity) conditions. In this way the energetic

costs of temperature extremes are dampened down. Laboratory-based resource-preference studies in *Drosophila* species suggest low genetic variability under benign conditions. However, under more stressful field conditions genetic variability should be higher. Habitat preference studies under stressful conditions therefore need to be emphasized in modelling situations in nature. By adopting such an ecobehavioural approach, the behaviour geneticist can contribute to investigations of habitat preference which have the potential to be applicable to nature.

Resumen

Preferencia de hábitat: una interacción entre la variabilidad genética y los costos del estres.

En las poblaciones naturales la norma es la exposición a medios estresantes. La evidencia se basa en los niveles de organización, desde el molecular hasta el biogeográfico. Las consecuencias incluyen (1) variabilidad genética aditiva elevada, como se ha mostrado para una serie de caracteres incluyendo comportamentales, y (2) costos metabólicos elevados. Los hábitats preferidos deberían, de esta forma, localizarse en medios óptimos que se corresponden a mínimos en el total del gasto energético. Esta tendencia aparece en la naturaleza para adaptaciones comportamentales de *Drosophila* a condiciones variables de temperatura (y humedad). De este modo, se amortiguan los costos energéticos a temperaturas extremas. Estudios en laboratorio sobre preferencias de recursos en especies de *Drosophila* sugieren una baja variabilidad genética en condiciones benignas. Sin embargo, en condiciones de campo mas estresantes, la variabilidad genética deberá ser alta. Por tanto, se necesita hacer énfasis en situaciones modelo en la naturaleza sobre estudios de preferencia de hábitat bajo condiciones estresantes. Adoptando un enfoque ecoetológico los genéticos del comportamiento pueden contribuir a las investigaciones de preferencia de hábitat, que tienen la posibilidad de aplicarse en la naturaleza.

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