

Short Review

Desiccation and starvation resistance in *Drosophila*: patterns of variation at the species, population and intrapopulation levels

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A substantial number of *Drosophila* studies have investigated variation in desiccation and starvation resistance, providing an opportunity to test for consistent patterns of direct and correlated responses across studies and across the species and population levels. In general, responses to laboratory selection for these traits in *D. melanogaster* are rapid and indicate abundant genetic variation in populations. However, slower responses to selection for desiccation resistance occur in other species including *D. simulans*. Clines suggest adaptive divergence although specific selection pressures have not been documented empirically. *Drosophila* species differ markedly in desiccation and starvation resistance and there is also marked variation within species for desiccation resistance that may be linked to local climatic conditions. Laboratory selection experiments on starvation resistance in *D. melanogaster* suggest that changes in lipid content are largely responsible for

resistance variation but this factor may be less important in explaining variation among species. For desiccation, lines with increased resistance show reduced rates of water loss but no changes in the minimum water content that flies can tolerate. Changes in life history traits are sometimes associated with altered levels of stress resistance. Increased starvation resistance is associated with longer development time and reduced early age reproduction in different studies. However, other associations are inconsistent between studies as in the case of stress resistance changing following selection for longevity. Multiple mechanisms may underlie genetic variation in stress resistance and future studies should address the evolutionary importance of the different mechanisms at the population and species levels.

Keywords: environmental stress, laboratory selection, life history, trade offs

Introduction

Variation in stress-related traits in insects and other organisms has been widely studied because it underlies the ability of insects to adapt and counter the effects of changing climatic conditions. For instance, in *Drosophila* a high level of desiccation resistance is associated with adaptation to arid habitats while a high level of cold resistance is linked to adaptation to high latitudes (David *et al.*, 1983; Hoffmann & Parsons, 1991; Kimura & Beppu, 1993). To understand these adaptive changes, detailed studies of evolutionary shifts in stress-related traits can be undertaken at different levels: within populations, among populations, and among species. Ultimately, these levels need to be linked to understand how evolutionary processes within populations relate to adaptive divergence among species exposed to different climatic conditions.

Studies of stress-related traits in *Drosophila* are now sufficiently comprehensive to start exploring these linkages. Stress-related traits have been examined extensively by undertaking selection experiments, characterizing mutants and molecular variants, and by comparing populations and species

in laboratory assays. Field studies are still relatively rare although there is a renewed emphasis on field *Drosophila* research for stress resistance (Feder & Hofmann, 1999).

Much of the focus of this *Drosophila* research has been on desiccation and starvation resistance, mechanisms underlying these resistance traits and interactions between resistance and life history variation. This brief review examines findings from the different studies on these traits, mentions areas where results are inconsistent, and raises possible future research directions. We start by examining variation for these traits within populations, and extend to cover geographical and species-level variation. We then consider mechanisms underlying resistance to starvation and desiccation, and the interactions between the stress resistance traits and life history variation.

Variation within populations

There is ample genetic variation for both starvation and desiccation resistance within populations of *D. melanogaster*. This is apparent from the rapid responses to laboratory selection for these traits (Service *et al.*, 1988; Hoffmann & Parsons, 1989a; Chippindale *et al.*, 1996; Harshman & Schmid, 1998). Moreover, high heritability estimates have

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been observed for both traits; estimates near 100% have been obtained for starvation resistance (Service & Rose, 1985) whereas for desiccation resistance estimates are around 60% (Hoffmann & Parsons, 1989a). High levels of genetic variation allow for large shifts in the mean resistance of populations. For instance, Chippindale *et al.* (1996, 1998) increased levels of desiccation and starvation resistance in a population of *D. melanogaster* by 3–4 and 4–6 times, respectively.

Data for other species are more limited. In *D. simulans*, Hoffmann & Parsons (1993a) estimated a heritability of 24% for female desiccation resistance based on the response to early generations of selection, while Ringo & Wood (1984) obtained an estimate of 19%. In an Australian endemic species, *D. serrata*, the realized heritability for desiccation resistance varied between populations and ranged from 1% ($\pm 3\%$) to 24% ($\pm 7\%$) (Blows & Hoffmann, 1993). The high levels of genetic variation observed in *D. melanogaster* might therefore not be typical for *Drosophila* species.

Given the levels of genetic variation demonstrated in laboratory studies, these traits should respond rapidly to selection in natural populations exposed to changing environmental conditions. Only one study (McKenzie & Parsons, 1974) has tested for short-term changes in desiccation resistance in a natural population. This study showed that in a temperate population of *D. simulans*, resistance to desiccation was highest in the warmest months and declined as the temperature decreased. This pattern suggests seasonal selection associated with the higher desiccation stress of the summer months. No such changes were evident in *D. melanogaster*, which has a high heritability for the trait (Hoffmann

& Parsons, 1989a). Given the genetic potential to respond to selection, why was *D. melanogaster* less influenced by presumably comparable ecological variation? Another relevant study (Nevo *et al.*, 1998) demonstrated differences in desiccation resistance of *D. melanogaster* isofemale lines collected from two slopes of a canyon. However the adaptive significance of this difference was unclear because lines from the dry south-facing slope survived more poorly under dry conditions than lines from the wetter north-facing slope at one of the two temperatures tested.

Variation between populations

There is evidence for variation among natural populations for both stress traits. The level of resistance to desiccation tends to be relatively higher in populations from temperate areas compared to tropical ones, whereas the reverse pattern is evident for starvation resistance (Table 1). This trend is most clearly demonstrated on the Indian subcontinent (Karan *et al.*, 1998), where parallel clines have been observed in three drosophilids (*D. melanogaster*, *D. ananassae*, *Zaprionus indianus*).

Deviation from clinal patterns suggests local adaptation. For instance, Stanley & Parsons (1981) and Parsons (1980) showed that the desiccation resistance of *D. melanogaster* was higher in temperate Melbourne compared to a subtropical and tropical location along the east coast of Australia. There was also a relatively high level of desiccation resistance in two other tropical populations exposed to extremely dry conditions in winter. Thus differences among populations appeared adaptive even though they did not form clines. In the same vein, Da

Table 1 Geographical variation among populations of *Drosophila* species for the strength of desiccation and starvation resistance

| Species | Number of populations | Desiccation pattern | Starvation pattern | Reference |
|-------------------------|-----------------------|-----------------------------------|----------------------|------------------------------|
| <i>D. ananassae</i> | 5 | temperate > tropical | tropical > temperate | Karan <i>et al.</i> , 1998; |
| <i>D. bipectinata</i> | 3 | temperate > tropical | tropical > temperate | Parkash <i>et al.</i> (1994) |
| <i>D. kikkawai</i> | 7 | temperate > tropical | tropical > temperate | Karan & Parkash (1998) |
| <i>D. malerkotliana</i> | 3 | temperate > tropical | tropical > temperate | Parkash <i>et al.</i> (1994) |
| <i>D. melanogaster</i> | 5 | temperate > tropical ¹ | | Parsons (1980) |
| <i>D. melanogaster</i> | 5 | temperate > tropical ² | | Stanley & Parsons (1981) |
| <i>D. melanogaster</i> | 3 | temperate = tropical ³ | tropical > temperate | Da Lage <i>et al.</i> (1990) |
| <i>D. melanogaster</i> | 2 | temperate > tropical | | Hoffmann (1991) |
| <i>D. melanogaster</i> | 9 | temperate > tropical | tropical > temperate | Karan <i>et al.</i> (1998) |
| <i>D. pseudoobscura</i> | 7 | no pattern ⁴ | | Coyne <i>et al.</i> (1983) |
| <i>D. serrata</i> | 2 | no pattern | | Hoffmann (1991) |
| <i>D. serrata</i> | 4 | no pattern | | Blows & Hoffmann (1993) |
| <i>D. simulans</i> | 3 | temperate > tropical | | Parsons (1980) |
| <i>D. simulans</i> | 2 | temperate > tropical | | Hoffmann (1991) |
| <i>Z. indianus</i> | 5 | temperate > tropical | tropical > temperate | Karan <i>et al.</i> (1998) |

¹ Higher desiccation resistance observed in Darwin and Melville Island than in the other tropical location consistent with a low rainfall between April and October.

² Higher desiccation resistance observed in Darwin and Thursday Island than in the other tropical location consistent with a low rainfall between April and October.

³ Highest desiccation resistance in a North African population from an oasis in Tunisia where desiccation stress likely to be extremely high.

⁴ Weak association detected between desiccation resistance of males from the populations and likely stress experienced in the field.

Lage *et al.* (1990) found that *D. melanogaster* from a tropical African population was more resistant to desiccation than a temperate European population, but flies from a geographically intermediate location (a Tunisian oasis) exhibited the highest level of resistance.

In some cases, the evidence for adaptation is mixed. Coyne *et al.* (1983) considered the association between desiccation resistance and potential measures of desiccation stress in seven populations of *D. pseudoobscura*. They found that the variation in desiccation resistance of the females did not follow adaptive predictions although the male data provided some support for the predictions.

To further interpret variation among populations, ecological data are needed on the stresses likely to be encountered by the different *Drosophila* species under field conditions. There is also a need to undertake detailed studies of genetic variation in populations along the lines of McKenzie & Parsons (1974) who compared levels of resistance at different times within populations. This type of study should ideally consider stress responses in adults and in other life cycle stages.

Interspecific variation

Desiccation and starvation resistance vary markedly among *Drosophila* species. The most extensive comparison has considered resistance in 22 species and related differences among species to their tropical/temperate origins and to their cosmopolitan/endemic status (Van Herrewege & David, 1997). For desiccation resistance at 25°C, survival varied from a mean of 61 h (*D. arizonensis*) to only 9 h (*D. teissieri* and *D. kikkawai*). In general, tropical species are less resistant to desiccation stress than temperate species but there are no clear patterns for endemism. Tropical species are also less resistant to starvation, which varied (at 25°C) from 171 h (*D. buzzatii*) to only 25 h (*D. sechellia*).

Comparisons among species can be confounded by variation within species. Sampling one or a few populations may not be representative of the species. For instance, *D. repleta* was one of the most sensitive species to desiccation in the survey by Van Herrewege & David (1997), whereas in Parsons (1982) this species was one of the most resistant species. In addition, tropical and temperate populations of both *D. melanogaster* and *D. simulans* can differ markedly in resistance, particularly for starvation resistance (Da Lage *et al.*, 1990; Van Herrewege & David, 1997). This raises the issue of whether resistance levels of species dictate their distributions, or instead whether resistance levels are a consequence of distributions.

Van Herrewege & David (1997) also considered correlations among traits although a phylogenetic correction was not undertaken to control relatedness among species. They found a positive correlation between desiccation and starvation resistance among temperate species but not tropical ones. Water content (aqueous proportion of body weight) was not correlated with desiccation resistance for either group of species. As might be expected, starvation resistance was correlated with the lipid energy reserves of the flies but only among temperate species. The range of starvation resistance levels was narrower among tropical species and this may help to explain the

absence of a correlation between these traits in the tropical group.

Finally, species differences raise questions about the nature of the clinal selection (Table 1). *Drosophila ananassae* is particularly sensitive to desiccation stress. The most resistant populations of this species along the Indian cline are more sensitive to desiccation and starvation stress than the least resistant populations of *D. melanogaster* from the same region (Karan *et al.*, 1998). If selection is determining the cline in *D. ananassae*, why is a similar cline evident in *D. melanogaster* where the baseline resistance is much greater? Would one expect a shallower cline over the same distance in the more resistant species? It is possible that the less resistant species experiences lower stress levels because of behavioural evasion. Ultimately laboratory assays are limited by the artificial environments used to test and rear the flies and further detailed ecological studies are needed to answer these questions.

Trait associations

These interspecific comparisons raise the issue of associations among resistance traits and potential underlying mechanisms and associations with life history traits. Studies at the intraspecific level have also tackled this issue, mostly by investigating correlated responses in selection experiments (Table 2). Desiccation and starvation resistance have normally been selected directly although selection on a low-quality resource (lemons) was also used to select for starvation in one study (Harshman *et al.*, 1999a). Have any consistent patterns emerged?

Starvation resistance mechanisms

For starvation, there is good evidence that an increase in the lipid content of adults underlies increased resistance to starvation. Some data suggest that this trait accounts for almost all the variation in starvation resistance. For instance, Chippindale *et al.* (1996) scored lipid and starvation levels in different sets of lines selected for starvation or changes in life history traits. They found a correlation close to one between starvation and lipid levels when all lines were considered. The lipid association has also been documented from a set of starvation-selection lines derived from a different base population (Harshman *et al.*, 1999a), in comparisons of allozyme genotypes (Oudman *et al.*, 1994), and the way in which lipid levels and starvation change with age (Service, 1987). Similar experiments have not been conducted in other species of *Drosophila*, although at the species level there is a correlation between these traits, as already noted (Van Herrewege & David, 1997).

Other factors may contribute to starvation resistance although their general importance is uncertain. An increase in body weight has been associated with resistance in some studies (Table 2), and body weight may reflect the total reserves of energy storage compounds carried by organisms. However, a reduced rate of respiration could underlie starvation resistance; there was no correlated change in respiration rate in lines selected for female starvation resistance

Table 2 Genetic associations between traits involved in desiccation resistance and starvation resistance in *D. melanogaster* and other *Drosophila* species

| Resistance | Correlated trait | Patterns | Techniques ¹ | Other species ² | References ³ |
|------------------------|---|------------------------------|-------------------------|---|---|
| Desiccation | Water loss rate (live flies) | +, +, +, +, + | S,S,S,S,M | <i>simulans</i> (×2) | HP93a, Gibbs97, Ringo84, Kimura85 |
| | Water loss rate in dead flies (cuticle) | =, + | S,S,M | | HP89a, Graves92, Kimura85 |
| | Metabolic rate | -, -, - ⁴ | S,S,S | <i>serrata</i> | BH93, HP89a, HP89b, Dwaj97 |
| | Wet weight | =, =, =, +, +, +, + | S,S,S,S,S,L,L | <i>simulans</i> , <i>serrata</i> , <i>pseudoobscura</i> | HP93a, BH93, Gibbs97, Chipp98, Par70, Thom71 |
| | Dry weight | -, =, =, +, + | S,S,S,S,L | <i>simulans</i> | HP93a, Gibbs97, Chipp98, Par70 |
| | Glycogen/carbohydrate | =, +, + | S,S,S | <i>serrata</i> | BH93, Djaw98, Chipp98 |
| | Lipid level | =, =, = | S,S,S | <i>serrata</i> | BH93, Djaw98, HP89b |
| | Activity | -, - | S,S | <i>simulans</i> | HP93 |
| | Water content | =, =, =, + | S,S,S,S | <i>simulans</i> | HP93, Gibbs97, Chipp98 |
| | Basal water level tolerated | =, = | S,S | <i>simulans</i> | HP93 |
| | Cuticular lipids amount | =, = | S,S | | Graves92, Gibbs97 |
| | Length of cuticular hydrocarbons | + | S | | Gibbs97 |
| | Viability | -, + | S,S | | Chipp98, HP93b |
| | Development time | +, = | S,S | | Chipp98, HP93b |
| | Early fecundity | -, = | S,S | | HP89a, Ser88 |
| | Longevity | +, +, +, (+) ⁵ | S,S,S | | HP93b, Rose92, Ser85, Force95 |
| | Starvation | Lipid level | +, +, +, +, + | S,S,S,S,L | |
| Wet weight | | +, + | S,S | | Chipp96, Harsh99 |
| Dry weight | | + | S | | Chipp96 |
| Metabolic rate | | -, -, =, = ⁴ | S,S,S,L | | Djaw97, Djaw98, Harsh98, Harsh99, Oud94 |
| Carbohydrate | | + | S | | Djaw98 |
| Utilization efficiency | | = | S | | Chipp96 |
| Viability | | - | S | | Chipp96 |
| Development time | | +, + | S,S | | Chipp96, Harsh99 |
| Early fecundity | | -, - | O,S | | Ser85b, Ser88 |
| Longevity | | =, =, +, +, + | S,S,S,S,M | | Force95, Harshunp, Rose92, Ser85a, Zwaan95, Lin98 |
| Desiccation | | +, +, +, +, (+) ⁶ | S,S,S,S,S | <i>simulans</i> , <i>serrata</i> | HP93, BH93, Harsh99, Rose92 |

¹ Techniques include selection (S), line comparisons (L), parent-offspring comparisons (O) and mutant isolation (M).

² Species in addition to *D. melanogaster*.

³ Reference abbreviations: BH93 — Blows & Hoffmann (1993); Chipp98 — Chippindale *et al.* (1998); Chipp96 — Chippindale *et al.* (1996); Djaw97 — Djawdan *et al.*, 1997; Djaw98 — Djawdan *et al.* (1998); Force95 — Force *et al.* (1995); Gibbs97 — Gibbs *et al.* (1997); Graves92 — Graves *et al.* (1992); Harsh98 — Harshman & Schmid (1998); Harsh99 — Harshman *et al.* (1999a); Harshunp — Harshman *et al.* (unpublished); HP89a — Hoffmann & Parsons (1989a); HP89b — Hoffmann & Parsons (1989b); HP93a — Hoffmann & Parsons (1993a); HP93b — Hoffmann & Parsons (1993b); Kimura95 — Kimura *et al.* (1985); Lin98 — Lin & Benzer (1998); Oud94 — Oudman *et al.* (1994); Par70 — Parsons (1970); Ringo84 — Ringo & Wood (1984); Rose92 — Rose *et al.* (1992); Ser85a — Service *et al.* (1985); Ser85b — Service & Rose (1985); Ser88 — Service *et al.* (1988); Thom71 — Thomson (1971); Zwaan95 — Zwaan *et al.* (1995).

⁴ These associations are for mass-specific metabolic rate. Once the amount of non-metabolizing mass is controlled, a negative association between metabolic rate and resistance was no longer evident in two of the desiccation comparisons and one of the starvation comparisons.

⁵ In one study only a weak desiccation – longevity association was detected (Force *et al.*, 1995).

⁶ In one study (Rose *et al.*, 1992), selection for desiccation resistance increased starvation resistance but not *vice versa*.

(Harshman & Schmid, 1998). There is some evidence for an association between starvation resistance and carbohydrate metabolic reserves, particularly as the association between starvation and energy reserves is strongest when both carbohydrate and lipid components of these reserves are considered (Djawdan *et al.*, 1998).

Desiccation resistance mechanisms

For desiccation, laboratory selection experiments provide evidence that rates of water loss in *D. melanogaster* are closely associated with resistance (Table 2: Hoffmann & Parsons, 1993a; Gibbs *et al.*, 1997). Moreover, *D. melanogaster* genotypes at the adipose locus (Clark & Doane, 1983) and a desiccation-resistant mutant (Kimura *et al.*, 1985) also show this relationship. In *D. simulans* two studies have provided evidence for an association between diminished rate of water loss and desiccation resistance (Ringo & Wood, 1984; Hoffmann & Parsons, 1993a).

Water loss may occur through the spiracles or the cuticle. If loss through the spiracles is important, there may be an association between resistance and a lower metabolic rate which could enable flies to keep spiracles closed for longer. Desiccation resistance has been associated with changes in patterns of CO₂ release via spiracles but the effect of these patterns on water loss rate was unclear (Williams & Bradley, 1998). In desert species of *Drosophila*, there was no correlation between the rate of CO₂ release and desiccation resistance (Gibbs, 1999). Selection on desiccation resistance appeared to decrease mass-specific metabolic rate (Hoffmann & Parsons, 1989a; Blows & Hoffmann, 1993; Djawdan *et al.*, 1997). However, this association may disappear once the mass of stored lipid and carbohydrates is factored out of the measurement of metabolic rate, as recommended by Djawdan *et al.* (1997). Moreover, Service (1987) found no association between age-specific metabolic rate and desiccation resistance.

Evidence for an association between desiccation resistance and motor activity has been found in *D. melanogaster* and *D. simulans* (Hoffmann & Parsons, 1989b; Hoffmann & Parsons, 1993a). This suggests that the active metabolic rate of flies may be altered by selection for desiccation resistance. However, it is not known to what extent this factor accounts for variation in resistance, and conditions that inhibit activity do not appear to increase desiccation resistance (Hoffmann & Parsons, 1993a).

Cuticular lipid could influence water loss rates through the cuticle. However, changes in cuticular composition due to exposure to different temperatures do not influence water loss rates in *D. mojavensis* (Gibbs *et al.*, 1998). Rates of water loss through the cuticle rather than spiracles can be investigated by killing flies with ether, which causes spiracles to remain open. Ether-killed *D. melanogaster* from desiccation-resistant selected lines do not lose water faster than dead flies from control lines (Hoffmann & Parsons, 1989a). However, a *D. melanogaster* mutant that is sensitive to desiccation and lines selected for postponed senescence did show an increased rate of water loss through the cuticle (Kimura *et al.*, 1985; Graves *et al.*, 1992).

Differential amounts of stored water could underlie desiccation resistance. Compared to control lines, there was relatively more water in some desiccation-selected lines of *D. melanogaster* (Gibbs *et al.*, 1997; Chippindale *et al.*, 1998) but not in others (Hoffmann & Parsons, 1989a) and not in selected lines of *D. simulans* (Hoffmann & Parsons, 1989a; Hoffmann & Parsons, 1993a). Bulk water may be associated with glycogen or be retained in some other manner. Glycogen levels may be related to desiccation resistance. There is evidence that this association holds in some *D. melanogaster* lines (Graves *et al.*, 1992; Chippindale *et al.*, 1998), but not in others (Blows & Hoffmann, 1993), nor in hybrid lines derived from crosses between *D. serrata* and *D. birchii*, two species differing in desiccation levels (Hercus & Hoffmann, 1999).

It is possible that the minimal amount of water tolerated might be a cause of desiccation resistance. However, there is no supporting evidence in selected lines of *D. melanogaster* (Hoffmann & Parsons, 1989a; Gibbs *et al.*, 1997) and for a range of *Drosophila* species the minimum level of water tolerated is invariant despite variation in desiccation resistance (Van Herrewege & David, 1997).

Finally, one might expect an association between desiccation resistance and size because larger flies have a smaller surface area for water loss relative to their weight. A size-resistance relationship was evident in comparisons of hybrid lines generated from crosses between *D. serrata* and *D. birchii* (Hercus & Hoffmann, 1999) and in a comparison of *D. melanogaster* isofemale lines (Parsons, 1970). However, there was no correlated change in body size when lines were selected for increased resistance to desiccation in *D. melanogaster* (Hoffmann & Parsons, 1989a; Hoffmann & Parsons, 1993a) and in *D. simulans* (Hoffmann & Parsons, 1993a).

In summary, the laboratory results suggest that increased desiccation resistance is consistently associated with a decreased rate of water loss, but less consistently with changes in glycogen levels, wet weight and other potential mechanisms (Table 2). This suggests that increased desiccation resistance can develop through multiple evolutionary pathways. It remains to be seen if different *Drosophila* populations and species have evolved similar levels of resistance through different pathways.

Starvation and desiccation resistance

The experiments undertaken to date suggest a robust association between starvation and desiccation resistance (Table 2), and therefore common mechanisms underlying some of the variation in these traits. This has been demonstrated in *D. serrata* as well as in independently selected lines of *D. melanogaster* (Blows & Hoffmann, 1993; Hoffmann & Parsons, 1993a; Harshman *et al.*, 1999a). It has also been observed in comparisons of isofemale lines of *D. melanogaster* (Hoffmann, unpubl. obs.). This association may stem partly from the contribution of glycogen to both traits (Rose & Archer, 1996). As mentioned before, a comparison of *Drosophila* species (Van Herrewege & David, 1997) also indicates a positive correlation between these traits. However, the association can be decoupled and is unlikely to be an evolutionary constraint, given the opposing clines for these traits in different

drosophilids (see above) and the fact that different mechanisms are partly responsible for variation in these traits in some selection lines (Djawdan *et al.*, 1998). This raises the issue of whether associations at the level of variation among species generally reflect similar patterns at the geographical and intrapopulation levels.

Associations between resistance and life history traits

There is evidence for a relationship between stress resistance and longevity. The relevant *Drosophila* data are based almost exclusively on *D. melanogaster*. Long-lived selection lines of this species are often relatively more resistant to starvation and desiccation stress (Rose & Archer, 1996). In addition, long-lived mutants tend to be stress resistant (Lin & Benzer, 1998) and selection for stress resistance can increase longevity (Rose *et al.*, 1992; Hoffmann & Parsons, 1993b). However, while these results are fairly consistent (Table 2), there are exceptions. One set of *D. melanogaster* lines selected for increased resistance to starvation, and showing increased resistance to a diversity of stresses, did not show a correlated change in longevity (Harshman *et al.*, 1999a). Moreover, one set of long-lived lines did not show a substantial increase in desiccation and starvation resistance (Force *et al.*, 1995), and in another set of lines there was a correlated change in stress resistance under selection for reduced longevity but not increased longevity (Zwaan *et al.*, 1995).

Selection for desiccation and starvation resistance can alter patterns of early fecundity, as well as changing larval viability and development time. Lines selected for desiccation resistance had a lower level of early reproduction (Hoffmann & Parsons, 1989a). However, selection for early reproduction led to a correlated response in starvation resistance but not desiccation resistance (Service *et al.*, 1988). Chippindale *et al.* (1996) showed that lines with an increased level of starvation resistance had a slower development time and lower viability. The correlated response in development was also found by Harshman *et al.* (1999a). Chippindale *et al.* (1998) showed that lines selected for increased desiccation resistance had decreased pre-adult viability and slower development time. However, Hoffmann & Parsons (1993b) found that desiccation resistant lines had an increase in viability at a high larval density and no change in development time.

It has been proposed that lipid and glycogen levels underlying starvation and desiccation resistance also influence reproductive output and longevity (Djawdan *et al.*, 1996). Energy reserves may be used for reproduction, or used to foster survival including viability under stress conditions, suggesting the basis for a tradeoff. However, the absence of consistent correlated responses (Tower, 1996) raises questions about the robustness of inferred relationship between energy storage compounds and reproductive output or longevity.

Concluding remarks

Research on variation in desiccation and starvation resistance in *Drosophila* has provided insights into mechanisms underlying genetic variation in stress resistance and on potential life-history tradeoffs, as well as on problems in extrapolating

findings across species, geographical and population levels. Studies have also shown how variation in stress resistance among populations and species appears to be directly or indirectly under selection. An important next step is to investigate the population differences in more detail by linking these to laboratory studies on populations and to field studies on selection (cf. Feder *et al.*, 1997). In particular, can direct selection on adults for increased resistance be demonstrated, or do population differences reflect selection on correlated traits? Do clinal patterns in different species (and the absence of them) reflect variation in levels of genetic variation and can inherent species differences in resistance be linked to them?

The correlated responses associated with selection for desiccation and starvation resistance suggest that different evolutionary outcomes can arise from the same selection pressures. The challenge now is to test whether these different outcomes also occur in natural populations or whether all populations tend to follow the same evolutionary path. One concern in extrapolating from these results is that laboratory conditions may predispose some types of correlated changes, particularly those associated with resource acquisition (Harshman & Hoffmann, 2000). Rigorous comparative analyses among populations and species are needed to address if heterogeneous outcomes are common and also whether correlations between stress resistance traits and life history characters act as evolutionary constraints.

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