



Rapid effects of humidity acclimation on stress resistance in *Drosophila melanogaster*



Dau Dayal Aggarwal^{a,b,*}, Poonam Ranga^b, Bhawna Kalra^c, Ravi Parkash^b, Eugenia Rashkovetsky^a, Leonidas E. Bantis^d

^a Institute of Evolution, University of Haifa, Haifa, Israel

^b Department of Genetics, Maharshi Dayanand University, Rohtak 124001, India

^c Department of Biology, University of Haifa – Oranim, Tivon 36006, Israel

^d Department of Statistics and Actuarial – Financial Mathematics, University of the Aegean, Samos 83200, Greece

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ABSTRACT

We tested the hypothesis whether developmental acclimation at ecologically relevant humidity regimes (40% and 75% RH) affects desiccation resistance of pre-adults (3rd instar larvae) and adults of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae). Additionally, we untangled whether drought (40% RH) acclimation affects cold-tolerance in the adults of *D. melanogaster*. We observed that low humidity (40% RH) acclimated individuals survived significantly longer (1.6-fold) under lethal levels of desiccation stress (0–5% RH) than their counter-replicates acclimated at 75% RH. In contrast to a faster duration of development of 1st and 2nd instar larvae, 3rd instar larvae showed a delayed development at 40% RH as compared to their counterparts grown at 75% RH. Rearing to low humidity conferred an increase in bulk water, hemolymph content and dehydration tolerance, consistent with increase in desiccation resistance for replicates grown at 40% as compared to their counterparts at 75% RH. Further, we found a trade-off between the levels of carbohydrates and body lipid reserves at 40% and 75% RH. Higher levels of carbohydrates sustained longer survival under desiccation stress for individuals developed at 40% RH than their congeners at 75% RH. However, the rate of carbohydrate utilization did not differ between the individuals reared at these contrasting humidity regimes. Interestingly, our results of accelerated failure time (AFT) models showed substantial decreased death rates at a series of low temperatures (0, –2, or –4 °C) for replicates acclimated at 40% RH as compared to their counter-parts at 75% RH. Therefore, our findings indicate that development to low humidity conditions constrained on multiple physiological mechanisms of water-balance, and conferred cross-tolerance towards desiccation and cold stress in *D. melanogaster*. Finally, we suggest that the ability of generalist *Drosophila* species to tolerate fluctuations in humidity might aid in their existence and abundance under expected changes in moisture level in course of global climate change.

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1. Introduction

For terrestrial arthropods, water conservation is a most crucial issue that affects their survival, distribution and abundance (Hadley, 1994; Chown and Nicolson, 2004). However, wild populations living under drier conditions have evolved genetic mechanisms to adapt in the local environments (Endler, 1986; Hoffmann and Parsons, 1991; Mousseau et al., 2000; Hoffmann and Sgrò, 2011; Kellermann et al., 2012). Several studies have elucidated evolved water balance mechanisms under xeric/drier habitats in drosophilids (Gibbs and Matzkin, 2001; Gibbs et al., 2003; Parkash et al., 2010). In addition to genetic changes, phenotypic plasticity may also confer increased survival

under desiccation stress (Hoffmann, 1990, 1991, 2010, Chown et al., 2011). Temperate *Drosophila* species have shown improved basal desiccation tolerance due to acclimation, whereas tropical species lack such acclimation ability (Hoffmann, 1991; Kellermann et al., 2009). It has been suggested that humidity levels in the field habitats constrain on physiological mechanisms of desiccation-related traits in *Drosophila* (Hoffmann, 1991; Kellermann et al., 2006, 2009; Hoffmann, 2010). However, the arguments whether varying humidity levels in a laboratory condition affect desiccation resistance, have not been tested for any *Drosophila* species so far.

In addition to behavioral avoidance (Benoit et al., 2007; Benoit, 2010), three other major avenues of water balance, (i) storage of higher bulk water, (ii) reduced rate of water loss and (iii) greater dehydration tolerance, confer greater survival under desiccation stress in arthropods (Hadley, 1994; Gibbs et al., 1997; Gibbs and Gefen,

* Corresponding author at: Institute of Evolution, University of Haifa, Haifa, Israel.
E-mail address: ddgenetics@gmail.com (D.D. Aggarwal).

2009; Benoit, 2010). Nevertheless, desiccation stress has not consistently constrained on multiple mechanisms of water balance in *Drosophila* species. For example, laboratory selected desiccation resistant strains of *Drosophila melanogaster* have shown higher bulk water as compared to control (Gibbs et al., 1997; Folk et al., 2001). In contrast, increased desiccation resistance of xeric than mesic *Drosophila* species has been associated with reduced rates of water loss, despite lack of significant differences in other avenues of water balance between them (Gibbs and Matzkin, 2001). Further, arthropods can tolerate ~30–50% loss of body water, but some taxa adapted to drier habitats have evidenced higher dehydration tolerance i.e. ~40–60% body water loss before succumbing to death (Hadley, 1994; Benoit et al., 2005; Benoit, 2010). In *D. melanogaster*, laboratory selected desiccation resistant strains (Gibbs et al., 1997) as well as high altitudinal populations (Parkash et al., 2011) have shown a substantial greater loss of body water content before reaching to death under desiccation stress as compared to their counterparts. However, previous studies on *D. melanogaster* have analyzed evolved genetic adaptations for water balance, despite the fact that mechanistic basis of plastic responses due to fluctuating local environment has not been tested so far.

For arthropods, changes in the storage levels of energy metabolites have been considered among basic mechanisms that alleviate the consequences of desiccation stress (Gibbs, 2002; Chown and Nicolson, 2004). However, there are debates whether carbohydrates or lipids facilitate physiological adaptations under desiccation stress. For example, large sized insects (locusts and tse-tse fly) as well as small sized mosquitoes – *Culex pipiens* – store and use lipids under dehydration stress (Loveridge and Bursell, 1975; Nicolson, 1980; Benoit et al., 2010). Similarly, higher levels of body lipid content have been consistent with increased desiccation resistance for laboratory selected desiccation resistant lines as compared to control (Telonis-Scott et al., 2006). In contrast, several studies have interpreted the role of glycogen contents in enhanced desiccation resistance of desiccation resistant lines of *D. melanogaster* (Graves et al., 1992; Gibbs et al., 1997; Chippindale et al., 1998; Djawdan et al., 1998; Gibbs, 1999; Folk et al., 2001; Gibbs, 2002). Besides elucidating genetic adaptations, only one study has explored the effects of adult desiccation acclimation (pre-treatment at ~0–5% RH) on levels of carbohydrate (glycogen) contents in *D. melanogaster* (Bazinet et al., 2010). However, it is not clear whether developmental acclimation to ecological relevant humidity conditions constrained on levels of energy metabolites, consistent with desiccation resistance in *D. melanogaster*.

Previous studies have revealed a trade-off between faster duration of development and stress (starvation/desiccation) tolerance capacities in *D. melanogaster* (Chippindale et al., 1996, 1998). These studies suggested that a greater acquisition of energy reserves in larval stages due to longer duration of development has conferred higher stress (starvation/desiccation) resistance. Similarly, Gefen and coworkers addressed that desiccation resistant lines of *D. melanogaster* have stored greater glycogen content due to the prolonged development time of 3rd instar larvae as compared with control (Gefen et al., 2006). Further, the reaction norms of duration of development match habitat specific thermal variations in tropical versus temperate populations of *D. melanogaster* (Trotta et al., 2006). Therefore, the outcomes of the previous studies indicate that duration of development has been associated with stress resistance (Chippindale et al., 1996, 1998; Gefen et al., 2006), and showed plastic responses for thermal variables in the laboratory conditions (Trotta et al., 2006). However, we tested whether plastic responses in duration of development due to humidity variations have been associated with stress resistance in *D. melanogaster*.

Further, an association between physiological adaptations for desiccation and cold tolerance has been evidenced in many invertebrate species, including nematodes (Forge and Macguidwian, 1992), earthworms (Holmstrup and Zachariassen, 1996), tardigrades (Sømme, 1996), arctic collembolans (Holmstrup and Sømme, 1998), and several other insects (Ring and Danks, 1994, 1998; Danks, 2005). For

cold-hardy arthropods, several studies have explored the link between drought acclimation and subsequent tolerance to desiccation and cold stress. Drought acclimation facilitates improved survival after subsequent exposure to cold and desiccation stress in *Folsomia candida* (Bayley et al., 2001; Sjørnsen et al., 2001; Holmstrup et al., 2002), in antarctic collembolan *Cryptopygus antarcticus* (Elnitsky et al., 2008) and for *Belgica antarctica* (Hayward et al., 2007; Benoit et al., 2009; Benoit, 2010). Metabolites profiling indicates that low humidity as well as low temperature promotes trehalose and glycerol levels to confer enhanced tolerance against desiccation and cold stress (Holmstrup et al., 2001; Yoder et al., 2006; Elnitsky et al., 2008; Benoit et al., 2009; Benoit, 2010; Holmstrup et al., 2010). However, such possible connection in non-cold hardy arthropods, including *D. melanogaster* has not been examined so far. Thus, it is interesting to test whether ecologically relevant drought acclimation elicits cross-tolerance for cold and desiccation stress in *D. melanogaster*.

Traditionally, eco-physiologists have assessed the role of temperature in inducing plastic responses for stress-related traits (Chown and Nicolson, 2004; Chown and Terblanche, 2007; Angilletta, 2009) but such consensus for humidity variations has not been tested so far. In the present study, we tested whether rearing at two different ecologically relevant humidity conditions (40% and 75% RH) may result in rapid changes in desiccation resistance. Further, we examined possible physiological mechanisms of water balance that might contribute to plastic responses, consistent with evolved differences in desiccation resistance at two humidity regimes i.e. 40% and 75% RH. Finally, we examined whether drought acclimation facilitates improved cold tolerance i.e. plastic responses for desiccation resistance and cold tolerance follow similar physiological pathways in *D. melanogaster*.

2. Materials and methods

2.1. Collections and cultures

Wild occurring *D. melanogaster* flies (200–250 individuals) were collected in July and October 2010 by net-sweeping method from a highland montane locality (Baridhar) of the Western Himalayas (geographical variables: latitude 30°33' N, longitude 77°51' E, altitude 2140 m). In October, mean monthly temperature (T_{ave}) and relative humidity (RH %) were lower as compared to those in July (Table 1). Daylight period differs ~1 h between July and October (July: 13 h and 57 min, October: 12 h and 40 min, Table 1). Differences in relative humidity were relatively more pronounced than the differences in monthly temperature and day length between July and October. Flies collected in July and October were used to examine differences in desiccation resistance. We used isofemale line ($n = 20$ IF lines) approach to assess induced developmental plasticity by varying relative humidities (40% versus 75% RH) in laboratory conditions for

Table 1

Data on climatic variables (temperature and humidity), and day-light (photo) periods in July and October, 2010 (Baridhar, Western Himalayas).

| Climatic variables | July | October |
|-----------------------|-------|---------|
| T_{min} (°C) | 16.3 | 14.8 |
| T_{max} (°C) | 28.8 | 26.3 |
| T_{ave} (°C) | 22.4 | 20.5 |
| RH _{min} (%) | 67.9 | 30.2 |
| RH _{max} (%) | 81.1 | 50.7 |
| RH _{ave} (%) | 74.5 | 40.4 |
| Sun-rise time (am) | 5.21 | 6.15 |
| Sun-set time (pm) | 7.12 | 6.50 |
| Day-light period (h) | 13.51 | 12.40 |

T_{min} – minimum value of temperature; T_{max} – maximum value of temperature; T_{ave} – average temperature; RH (%) – relative humidity.

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