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Direct and indirect effects of development temperature on adult water balance traits of *Eldana saccharina* (Lepidoptera: Pyralidae)

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ABSTRACT

For water balance physiology, prior thermal history may pre-condition individuals to be more sparing in their water consumption at a given temperature upon subsequent exposure, or alternatively, may relax constraints on water economy leading to more frivolous use of water at a later stage. Here we test these two major alternative hypotheses on the adult life stage of *Eldana saccharina* Walker (Lepidoptera: Pyralidae) by exposing them to different rearing temperatures (acclimation treatments) during immature stage development and comparing adult physiological performance (water loss rates, time to death) and water-balance related traits (body size, water content). Developmental acclimation at 20 °C, 25 °C or 30 °C throughout the larval and pupal stage resulted in significant effects on water balance traits of two-day old adult male and female *E. saccharina*. In summary, lower developmental acclimation resulted in a 61% increase in water loss rate (range: 0.78 mg/h) and a 26% reduction in survival time (6.8 h). Initial body water content and initial body mass generally remained similar across male acclimation groups while higher developmental acclimation reduced female body mass significantly. High developmental acclimation resulted in significantly higher (~23%) body water content at death possibly indicating a better overall ability to withstand desiccating conditions, although there was no difference in time to death compared to the intermediate group. The relationship between time to death and body mass was altered from negative at 25 °C and 30 °C acclimation, to positive at 20 °C acclimation. These results show pervasive effects of rearing temperature on adult physiological performance, with low temperature relaxing what appear to be substantial constraints on water economy at higher temperatures for *E. saccharina*. Furthermore, they are significant for understanding the recent range expansion of *E. saccharina* into cooler environments in southern Africa and for management of the species.

1. Introduction

Terrestrial insects may be dramatically influenced by water availability in their environment, in part owing to their small body size and high surface area-to-volume relationship (Hadley, 1994). Environmental water availability, and an insect's ability to manage its water loss rate or withstand losing water, can have a direct impact on population abundances and geographic distribution, through activity and survival times (e.g. Kellermann et al., 2009; Overgaard et al., 2014; reviewed in Hadley, 1994; Benoit et al., 2010; Chown et al., 2011). Death may occur upon exhaustion of either water or lipid reserves from the insect body (Marron et al., 2003; Hoffmann and Harshman, 1999). Essentially survival time under low humidity conditions of an insect is a function of how much body water the insect has, the rate at which it is lost, and how much water it can withstand losing (Hadley, 1994; Chown et al., 2011).

Simulations of forecast climate change, with predictions of increasing frequency and severity of droughts (e.g. Easterling et al., 2000; Fortain et al., 2010), suggest that terrestrial insects could be affected by changes in their evaporative water loss rates and changing environmental moisture availability (Chown et al., 2011). However, climate change is likely to involve concurrent changes in both moisture availability (e.g. relative humidity, precipitation) and ambient temperature, thus emphasizing the need to understand both aspects of these two abiotic variables on insect physiological responses and water balance at various time-scales (Chown et al., 2011; Kleynhans and Terblanche, 2011).

Water loss, as a result of respiration and cuticular transpiration, pose significant challenges to terrestrial insects in novel or changing environments (Woods and Smith, 2010; Chown et al., 2011).

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Furthermore, insect are susceptible to increased respiratory water loss with increasing temperature (e.g. Terblanche et al., 2010) since respiration rates follow an exponential pattern and are generally doubled for every 10 °C increase in temperature. This means that at higher ambient temperatures, even small changes in temperature can result in large differences in metabolic rate, and presumably also respiratory water loss (Dillon et al., 2010; Addo-Bediako et al., 2002; Kearney, 2012). Although the temperature dependence of biological rates is well accepted and typically follows an exponential relationship (e.g. Dell et al., 2011), any general expectation for what the impacts of prior thermal history might be on these rates is far more contentious. It is clear that prior temperature or relative humidity exposure can have a marked effect on subsequent water loss rates in insects via physiological adjustments (Hoffmann et al., 2005; Parkash et al., 2005, but see Terblanche et al., 2005; Gibbs et al., 2003; Bedick et al., 2006; Gray and Bradley, 2005).

The influence of rearing temperature on body size is generally well examined in insects (e.g. Gaston and Chown, 2013). By contrast, the influence of rearing temperature on various traits of insect water balance and related traits associated with body size variation are largely unclear (see reviews and discussion in e.g. Leinaas et al., 2009; Terblanche and Kleynhans, 2009). Two alternative hypotheses can be proposed for responses of water balance physiology to rearing temperature. First, prior thermal history may pre-condition individuals to be more sparing in their water consumption at a given temperature upon subsequent exposure, or alternatively, prior exposure may not be stressful and thus relax constraints on water economy leading to more frivolous use of water at a later stage. Estimates of body water content, and rates of water loss, and to a lesser extent, critical body water contents at time of death (defined as BWC_{CRIT} here), have all enjoyed considerable attention to date (e.g. Hadley, 1994; Addo-Bediako et al., 2001; Bazinet et al., 2010). It is therefore surprising that the influence of rearing temperature on these various components of water balance, and what the net outcome of rearing temperature is for survival under dehydrating conditions, has not been well examined (Leinaas et al., 2009). Regardless, the magnitude and direction of phenotypic plasticity in response to developmental acclimation is important as this forms a critical component of understanding insect population dynamics under variable field conditions (Fallis et al. 2014; Kleynhans et al., 2014b).

The ability to acclimate, and thus alter phenotype-related physiology (Huey et al., 1999), or adapt to environmental change within a short time frame have to be considered and interpreted within the functional and genetic constraints of an insect (Cooper et al., 2010). Acclimation of water balance physiology might thus enhance fitness, but it might also come at a cost or lead to sub-optimal trait responses (see discussions in Hoffmann, 1995; Huey and Berrigan, 1996; Deere and Chown, 2006; Terblanche and Kleynhans, 2009). The consequence of rearing history (developmental plasticity) on the adult life stage is however, not often separated from within-life stage consequences of environmental variability (but see Terblanche and Chown, 2006). Phenotypic plasticity of physiological traits can be beneficial for survival and evolutionary fitness (Piersma and van Gils, 2011; Kleynhans et al., 2014b).

Eldana saccharina Walker 1865 (Lepidoptera: Pyralidae) is an indigenous graminaceous stem borer of economic importance in many African countries due to larval induced crop losses (Bosque-Pérez, 1995; Polaszek, 1998; Mazodze and Conlong, 2003). Depending on temperature and diet, the life-cycle of *E. saccharina* lasts for 2–3 months (Girling, 1978; Way, 1995). Whether the life stages of *E. saccharina* can adjust readily to enhance their water-balance related physiological performance within or across life-stages has not been explored previously. Here we assessed the two major alternative hypotheses for the impacts of rearing temperature on water balance-related traits (e.g. hydration and water economy) on the adult life stage of *E. saccharina* by exposing immature stages of this species to different rearing temperatures both above and below optimum conditions, and then measuring the resultant adult physiological performance (water loss rates, time to death) and water-balance related traits (body size, water content). We also sought to assess what traits varied in response to immature stage rearing temperature, and what the net outcome thereof might be for survival of desiccating conditions as adults.

2. Materials and methods

Developmental acclimation effects of temperature on male and female *E. saccharina* WLR, BWC and time to death were tested individually following larval to adult rearing at constant 20 ± 1 °C, 25 ± 1 °C or 30 ± 1 °C and 76 ± 5% relative humidity (found to be the optimum relative humidity range for laboratory rearing). Humidity was controlled using a saturated sodium chloride salt solution (~360 g NaCl in 1 L distilled water at 20 °C), placed on the bottom of 50 L incubators used during immature stage acclimation (following Winston and Bates, 1960). In the wild, development of *E. saccharina* continues throughout the year, resulting in multivoltine populations. Average temperatures for the warmest quarter (average summer temperatures) of the year were 20.0 °C in the southern Midlands of KwaZulu-Natal of South Africa (29.9°S, 30.6°E), 25.3 °C for Mpumalanga, South Africa (25.5°S, 31.6°E) and 30.1 °C in Kenya (1.5°S, 36.6°E). *E. saccharina* occurs naturally in all these areas, but their biotypes are different (Assefa et al., 2005). We chose three developmental acclimation temperatures representing those experienced by these wild populations during the warmest quarter of the year in their relevant areas. We used long term average temperatures from the WorldClim database (1970–2000 data; Hijmans et al., 2005) to determine the corresponding site- and rearing temperatures.

The effects of immature stage rearing temperature (i.e. acclimation) on water balance-related traits on two-day old adult moths were estimated using gravimetric methods (see description below). We specifically chose this age since activity and mating generally occurs between 24 and 48 h after adult emergence (Dick, 1945), female egg-laying peak on the second and third night after emergence (Dick, 1945; Way, 1994), and most importantly, two-day old male moths are used for sterile insect release programs. Rearing followed the methods outlined in Conlong (1989), Gillespie (1993) and Kleynhans et al. (2014a). In brief, the egg stage developed at 24 ± 2 °C. Larvae that emerged from $N > 1200$ eggs were transferred into nine 500 ml jars, each containing eight 30 ml vials with 10 ml artificial diet medium each (for further information on the artificial diet see Gillespie, 1993). The jars with the larvae were placed at the three respective developmental temperatures (three replicated jars per treatment). After ~260 heat units (see Way, 1995) third instar larvae were transferred individually into 30 ml vials containing 10 ml artificial diet. The vials were returned to the respective acclimation temperatures in their respective incubators. Pupae, when formed, were removed from the vials and placed into individual cells of replicated multi-cell trays within 24 h of pupation. The trays were kept in the same incubators as the larvae, to complete development at the three respective temperatures. Freshly emerged adult moths were removed from the multi-cell trays daily in order to track age (in days) and sex. Moths (at least 30 males and 30 females per developmental temperature) were weighed individually to determine body mass, WLR and BWC. The initial body mass, minus the body mass at time of death, divided by the time to death was used to calculate WLR. Following the measurement of adult body mass at