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Review

Water loss in insects: An environmental change perspective

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ABSTRACT

In the context of global environmental change much of the focus has been on changing temperatures. However, patterns of rainfall and water availability have also been changing and are expected to continue doing so. In consequence, understanding the responses of insects to water availability is important, especially because it has a pronounced influence on insect activity, distribution patterns, and species richness. Here we therefore provide a critical review of key questions that either are being or need to be addressed in this field. First, an overview of insect behavioural responses to changing humidity conditions and the mechanisms underlying sensing of humidity variation is provided. The primary sensors in insects belong to the temperature receptor protein superfamily of cation channels. Temperature-activated transient receptor potential ion channels, or thermoTRPs, respond to a diverse range of stimuli and may be a primary integrator of sensory information, such as environmental temperature and moisture. Next we touch briefly on the components of water loss, drawing attention to a new, universal model of the water costs of gas exchange and its implications for responses to a warming, and in places drying, world. We also provide an overview of new understanding of the role of the sub-elytral chamber for water conservation, and developments in understanding of the role of cuticular hydrocarbons in preventing water loss. Because of an increasing focus on the molecular basis of responses to dehydration stress we touch briefly on this area, drawing attention to the role of sugars, heat shock proteins, aquaporins, and LEA proteins. Next we consider phenotypic plasticity or acclimation responses in insect water balance after initial exposures to altered humidity, temperature or nutrition. Although beneficial acclimation has been demonstrated in several instances, this is not always the case. Laboratory studies show that responses to selection for enhanced ability to survive water stress do evolve and that genetic variation for traits underlying such responses does exist in many species. However, in others, especially tropical, typically narrowly distributed species, this appears not to be the case. Using the above information we then demonstrate that habitat alteration, climate change, biological invasions, pollution and overexploitation are likely to be having considerable effects on insect populations mediated through physiological responses (or the lack thereof) to water stress, and that these effects may often be non-intuitive.

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'…the modification of one process to meet a particular life-threatening environmental condition may create new problems.'
Karl Erik Zachariassen (1996)

1. Introduction

Regulation of temperature and water balance are primary components of homeostasis in all organisms. The activities and processes associated with such homeostasis can be costly and may therefore divert resources away from other contributors to fitness (Sibly and Calow, 1986; Chown and Nicolson, 2004). In consequence, variation in the traits associated with temperature and water regulation is regularly found among individuals. Where such physiological variation among individuals has a genetic basis and results in performance and ultimately fitness differences, it may lead to differences in the composition of populations and population density. In turn, landscape level variation in population density determines occupancy and ultimately assemblage composition, thus giving rise to spatial and temporal variation in biodiversity (Gaston et al., 2008; Ricklefs, 2008). Understanding the mechanistic basis of physiological variation, the environmental circumstances that favour the evolution of particular forms thereof, and the ecological implications of this variation have therefore long been significant topics in biology (see Prosser, 1986; Spicer and Gaston, 1999; Chown et al., 2004). Growing realization that much of the biodiversity impact of environmental change now underway (Millennium Ecosystem Assessment, 2005), and forecast to accelerate with accelerating environmental change (e.g. Bertler and Barrett, 2010; New et al., 2011), is mediated through physiological responses (Hoffmann et al., 2003; Helmuth et al., 2005; Pörtner and Knust, 2007; Chown and Gaston, 2008; Deutsch et al., 2008; Dillon et al., 2010), and that understanding physiological variation forms an important component of predicting responses to change (Kearney and Porter, 2009; Buckley et al., 2010), has meant rapidly evolving interest in physiological variation and its evolution (Pörtner and Farrell, 2008; Jackson et al., 2009; Hoffmann and Sgrò, 2011).

In the context of global climate change, much of the focus, to date, and particularly for animals, has rightly been on the effects of changing temperatures (Bale et al., 2002; Harvell et al., 2002; Parmesan, 2006; Pörtner and Farrell, 2008; Helmuth et al., 2010). However, changing patterns of rainfall, humidity and water availability deserve similar attention for several reasons. First, variation in precipitation, and particularly extremes thereof, has profound effects on animals (e.g. Jetz and Rubsenstein, 2011) and this is true also of insects (Andrewartha and Birch, 1954; Wolda, 1988; Hawkins and Holyoak, 1998; Tauber et al., 1998; Todd et al., 2002; Seely et al., 2005; Branson, 2008; Benoit, 2010). Second, and perhaps unsurprisingly, water availability is an important determinant (or at least correlate) of the range position of many species (Robinson et al., 1997; Erasmus et al., 2002; Lobo et al., 2006; Steiner et al., 2008; Kearney et al., 2008, 2009; Tingley et al., 2009; Vieites et al., 2009; Roura-Pascual et al., 2011; Yoder et al., in press), and is also a significant correlate of species richness in many areas (Erasmus et al., 2000; Hawkins et al., 2003; Algar et al., 2009; Chown and Klok, 2011). Third, in vertebrate ectotherms, one of the major fitness-influencing components of thermal performance, the thermal optimum, is more strongly related to ambient precipitation than to average ambient temperature (Clusella-Trullas et al., in press), and similar environmental influences may also affect insect thermal preferences and performance (see Bonebrake and Mastrandrea, 2010 for rationale). Fourth, changes in water availability in the case of disease vectors with aquatic larvae relate to alterations to runoff and to the size and distribution of impoundments. Human impacts thereon (e.g. Fung et al., 2011) may have pronounced impacts on vector populations (Kearney et al., 2009; Lafferty, 2009). Finally, much of the current and forecast global change includes very large direct effects on both precipitation and water availability (Fung et al., 2011; Sanderson et al., 2011), and indirect changes may also be effected through habitat modification (Nair et al., 2003; Webb et al., 2005; Makarieva and Gorshkov, 2007). Thus, the physiological mechanisms underlying variation in the ability of insects to cope with varying water availability, the ecological implications of this variation, and the rate at which the components of water balance might evolve are all significant problems that need to be addressed in the context of environmental change. Here we provide a critical review of key questions that either are being or need to be addressed in this area. Our aim is not to review the field of insect water balance. This has been done comprehensively elsewhere (e.g. Hadley, 1994; Chown and Nicolson, 2004; Bradley, 2009; Benoit, 2010; Benoit and Denlinger, 2010). Rather we identify areas that might inform current understanding of species responses to change, and those that require further work, and highlight the significance of recent developments in these areas.

2. Sensing and behaviour

Insects are not passive recipients of the vagaries of environmental variation. Rather, they show a wide range of responses, from behavioural through to physiological change. Moreover, those individuals that mount the most effective response to an environmental challenge may well be those that contribute to the next generation, though sometimes not without cost (e.g. Marshall and Sinclair, 2010). The first, and arguably most critical, step in the series of events leading to organismal responses and homeostasis (see Woods, 2009) is sensing of changes in environmental conditions. However, as is the case in thermal biology (Chown and Terblanche, 2007), investigations of sensing are often decoupled from investigations of behavioural responses and inferences about adaptation to varying conditions of water availability. In consequence, we provide here a short overview of the selection of optimal humidity conditions and the sensory systems that likely underpin this behaviour.

Insects and other terrestrial invertebrates are clearly highly aware of the abiotic conditions they experience at any given time. A host of early observational research showing that alteration of abiotic conditions leads to rapid responses in position, orientation or activity, and if available, the relocation of the insect towards a presumed environmental optimum, supports such a view (e.g. Shelford, 1918; Edney and Barras, 1962; Yu et al., 2010; see reviews in Edney, 1977; Hadley, 1994; Chapman, 1998; Chown and Nicolson, 2004). However, precisely how insects achieve these responses is far from resolved. Studies of behavioural responses to variation in humidity can be categorized as those that typically offer a continuous gradient in humidity conditions (e.g. Walters and Mackay, 2003; Steidle and Reinhard, 2003) and those which provide two or more discrete humidity options (e.g. Prange and Hamilton, 1992; Jian et al., 2005; Yu et al., 2010). The amount of time spent in a particular location or the numbers of insects recorded under a particular set of conditions are then used to infer optima (Thomson, 1938; Dakshinamurty, 1948; Azis, 1957; Arbogast and Carthon, 1972; Prince and Parsons, 1977; Yu et al., 2010). However, whether these two different approaches offer similar results is generally not well explored. Insects can avoid severely desiccating challenges through behavioural means, suggesting that behavioural modifications are a valuable evolutionary strategy for coping with dehydration. Early work focused extensively on Diptera and to a lesser extent Coleoptera, revealing that insects tend to avoid humidity extremes (especially high humidity at high temperatures) (e.g. Thomson, 1938; Dakshinamurty, 1948; Prince and Parsons, 1977; Amos, 1969; Sayeed and

Benzer, 1996; Steidle and Reinhard, 2003). Such experiments can be confounded by the animal's physiological state or condition. For example, some well-hydrated insects may prefer a low humidity, high temperature option to maximise opportunities for evaporative cooling (e.g. Seymour, 1974; Doi and Toh, 1992; Prange and Hamilton, 1992; reviewed in Prange, 1996) but, when dehydrated, may avoid dry areas and maintain low activity levels. In other cases, selection of high humidity microsites allows some species to absorb atmospheric moisture and thereby maintain water balance. However, absorption of atmospheric moisture is not ubiquitous across insects and seems to be the exception rather than the norm (reviewed in Hadley, 1994; Chown and Nicolson, 2004; Benoit, 2010). A classic example of behavioural adaptation to maximise moisture uptake from the environment is fog basking in Namib desert tenebrionid beetles. During a foggy morning in this arid habitat, Onymacris unguicularis can gain up to 34% of its total body weight through head-down posturing, allowing fog droplets formed on the body to run down to the mouthparts for drinking (Hamilton and Seely, 1976). This and other behavioural strategies employed by tenebrionids in the Namib (e.g. trench building) may have important long-term demographic consequences (Seely et al., 2005). Moreover, the head-down posturing behaviour itself is remarkably efficient, and water accumulation does not, apparently, depend on structural adaptations of the cuticle (Norgaard and Dacke, 2010).

Identification of key hygrosensing sites and understanding of sensing ability of insects has typically been through antennal ablation and electrophysiological studies of nerve impulse transmission (e.g. Sayeed and Benzer, 1996; Tichy, 2003, 2007; Merivee et al., 2010; Yu et al., 2010; for an early review see Altner and Prillinger, 1980). These approaches are still frequently employed, and continue to provide important insights into neural integration of environmental humidity information in insects (e.g. Tichy, 2007; Merivee et al., 2010; Yu et al., 2010), with a growing focus on the underlying cellular mechanisms (see below). Hygrosensors are generally located on the antennal arista, and have been reported from numerous taxa, including caterpillars, bees, mosquitoes, locusts, bugs, flies, stick insects, beetles and cockroaches (see Altner and Prillinger, 1980; Tichy and Loftus, 1996; Tichy, 2003, 2007; Merivee et al., 2010). Two types of moisture receptors exist: moist receptors which increase firing rate frequency in response to higher humidity, and dry receptors that increase frequency in response to lowered humidity (see e.g. Waldow, 1970; Yokahari, 1978; Tichy, 2003). Both the moist and dry receptors can be present in the same sensillum and can have markedly different sensing resolution. It has been suggested that the integration of their signals in the CNS may be important for functional responses to altered ambient moisture (reviewed in Altner and Prillinger, 1980; see also Merivee et al., 2010). The benefits of such a dual system for moisture sensing is that it enables insects to differentiate fine changes in environmental humidity, critical for microsite selection, thereby presumably optimising survival (Merivee et al., 2010). Given the range of habitats insects occupy, interspecific variation in hygrosensing abilities is not unexpected. For example, the ground beetle Pterostichus oblongopunctatus is capable of discriminating relative humidity changes of as little as 2% in the dry receptor (Merivee et al., 2010), while perception of humidity change in Periplaneta americana is approximately half the resolution with responses to humidity in the order of 5% at the CNS (Nishino et al., 2003).

The cellular mechanisms of humidity sensing have received far less attention than temperature sensing in insects (Chown and Terblanche, 2007), though it is becoming increasingly apparent that the two senses may be strongly interlinked (Liu et al., 2007; Tichy, 2007; Montell, 2008). The primary sensors in the sensory nerve endings (generally located in antennae, though also legs, gut and mouthparts in some cases, e.g. Rosenzweig et al., 2005) of insects belong to the temperature receptor protein superfamily of cation channels. These proteins are directly involved in the cellular processes that result in nerve depolarization (Voets et al., 2004). Temperature-activated transient receptor potential ion channels, or thermoTRPs, (Viswanath et al., 2003; Rosenzweig et al., 2005) respond to a diverse range of stimuli and may be a primary integrator of sensory information, such as environmental temperature and moisture. A recent, thorough study has provided detailed evidence that hygrosensing in Drosophila requires the TRP channels wtr 'water witch' and nan 'nanchung', TRPV and TRPA channels, respectively (Liu et al., 2007). By contrast, aquaporins and channels encoding solely mechanical stimuli apparently play little role in hygrosensing (Liu et al., 2007). Notably wtr and nan have opposing functions in hygrosensing, with the former sensing dry and the latter moist air. One advantage of temperature sensors providing moisture information is that this may allow insects to differentiate humidity levels at any given temperature and thus improve the overall resolution of the sensory system, although perhaps the disadvantage might be the substantial quantity of information-processing required (Merivee et al., 2010).

So how do insects differentiate between temperature and humidity if TRPs respond to a range of stimuli? Although TRP ion channels respond to a wide range of stimuli, they do not all simply respond in the same way. That is, TRP channels may have multiple gating modes depending on the types and combination of stimuli (e.g. Kohno et al., 2010), allowing them to differentiate signals and transmit appropriate neural responses. This probably allows more efficient signal processing. Moreover, effective CNS integration between TRP channels and their respective signals must exist because several TRP channels typically occur within a single antenna, and sometimes even within a single sensilla, and all can presumably send information simultaneously via neurons to various brain regions continuously. In addition, neurons may end in different brain regions (see e.g. Liu et al., 2007), resulting in further signal differentiation. Liu et al. (2007) speculate that humidity sensing may be mechanical or thermosensory, or that humidity modifies the receptor's function, rather than acting directly as humidity detection. This conclusion was reached on the basis of several lines of evidence, including that the TRP channels were linked to neural projections in brain regions associated with mechanical sensing. Liu et al.'s (2007) results also suggest that two distinct sets of receptors and sensors are required simultaneously for proper neural integration and behavioural responses, and that such a dual mechanism comprising opposing receptors implies that the system is always ready to respond to changes in either direction. In addition, it should allow better precision of sensing than a system measuring only absolute humidity values (Liu et al., 2007). Clearly, there is still much to be learned regarding the cellular mechanisms of humidity sensing, neural processing and integration with whole-animal behavioural responses.

Variation in the expression and temperature-sensitivity of thermoTRPs has led to their categorization into distinct types or families. For insects, two key families, with several forms of thermoTRPs in each subfamily, have been described: the melastatin subfamily and the vanilloid subfamily. Receptors in the melastatin subfamily respond to temperatures in the 17–25 °C range, while the vanilloid receptors are sensitive across the 33–52 °C range (for detailed review of structural and functional variation in insect TRP channel members see e.g. Montell, 2005). Until recently little information was available documenting how, if at all, thermoTRP family composition in sensillae might vary among insect taxa. Indeed, the role of TRP channels in insects had mainly been explored in Drosophila (e.g. Rosenzweig et al., 2005; Viswanath et al., 2003). However, Matsuura et al. (2009) have now shown that TRP channels are well conserved across a range

of insect taxa, *viz.* Diptera – *Drosophila melanogaster*, Lepidoptera – *Bombyx mori*, Coleoptera – *Tribolium castaneum*, Hymenoptera – *Apis mellifera*, *Nasonia vitripennis*, and Phthiraptera – *Pediculus humanus*. All of the species they examined had several TRP channels and the total range of insect TRP family members now stands at 13–14, which is roughly half that of mammalian TRPs (Matsuura et al., 2009). Thus, it appears that single TRP channels may integrate a host of sensory information (see also Montell, 2008). Moreover, it is clear from Matsuura et al.'s (2009) work that among the insects both conservation of TRPs and evolution-ary variation in structure and function can be found (and see Viswanath et al., 2003), particularly for the TRPA sub-family, the latter of which plays a key role in thermotaxis in *Drosophila* (Rosenzweig et al., 2005). For example, *A. mellifera* has several novel TRPs likely used for temperature sensing, but no TRPA1. Thus, honey bees have a fundamentally different thermosensing mechanism to *Drosophila* (and see Kohno et al., 2010). Regardless, key areas for future research in thermoTRPs for insects would be documenting variation in TRP type and function within and among species (e.g. along geographic clines) and relating this to environmental conditions occupied, or with artificial selection for variation in preferred body temperatures (e.g. Good, 1993) or humidity conditions. It would also be useful to know if variation in desiccation resistance or tolerance is coupled to variation in humidity perception among species. A key question in this regard is whether the level of sensitivity in sensing translates into similar sensitivity in terms of physiological plasticity. For example, despite substantial detection abilities for temperature change, it appears that many species of insects show a threshold rather than continuous response to actual environmental variation when it comes to plasticity in response to changing thermal conditions (Marais and Chown, 2008).

Thus, behaviour–physiology coupling, i.e. the co-adaptation of hygrosensing, behavioural responses and desiccation physiology, might be widely expected in insects, as is the case for thermal adaptation (Angilletta et al., 2006). If such co-adaptation does indeed occur for hygric responses, it is likely to have intergenera-tional implications, such as in the case of the selection of microclimates by ovipositing females for eggs that are often much more susceptible to water stress than other stages (Pincebourde et al., 2007; Woods, 2010). These areas deserve closer integration with work on landscape-related variation in physiological traits associated with varying water availability.

3. Physiological regulation and the components of water loss

Assuming that behavioural responses do not entirely eliminate the realized physiological effects of environmental change (see Huey et al., 2003 for discussion), insects responding to changes in water availability can do so in a host of different ways. Most typically investigated are changes in initial water content, rates of water loss (desiccation resistance) and tolerance of water loss (desiccation tolerance) (Hadley, 1994; Hoffmann and Harshman, 1999; Chown, 2002; Gibbs et al., 2003; Yoder et al., in press), though changes in water excretion and uptake may also be studied (Woods and Bernays, 2000; Chown and Nicolson, 2004; Benoit and Denlinger, 2010). Variation in these components of insect water economy among species and populations has given rise to the idea that adaptive responses will largely take place via them, although variation in desiccation tolerance is typically less pronounced than variation in the rates of water loss (Hadley, 1994; Addo-Bediako et al., 2001; Benoit and Denlinger, 2010), and in some cases among-population variation may be negligible (Klok and Chown, 1998, 2005).

Much more contentious is the role that modification of respiratory relative to cuticular water loss might play in altering
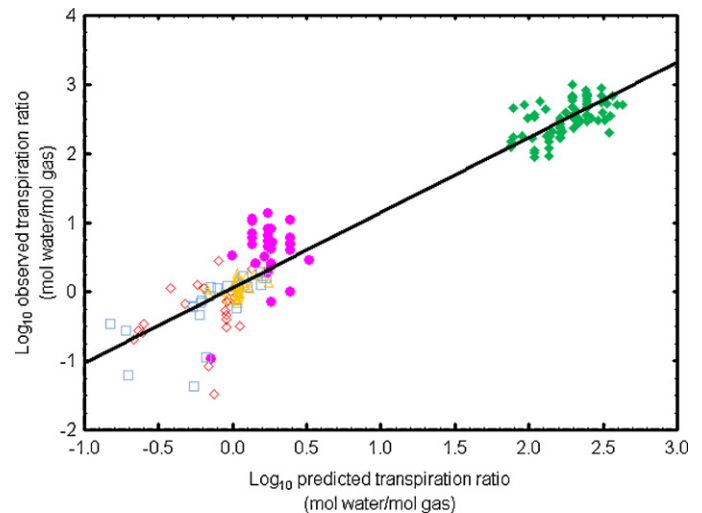

Fig. 1. The observed transpiration ratio (mol water per mol gas) and that predicted by Woods and Smith's (2010) universal model for the water costs of gas exchange, for birds and their eggs (open diamonds and triangles, respectively), mammals (squares), insects (filled circles) and plants (filled diamonds). The solid line is a least-squares best fit. Note that the observed values for insects are much higher than those predicted.
Drawn using the data provided by Woods and Smith (2010).

the water budget, and whether discontinuous gas exchange (Chown et al., 2006) might be significant in effecting water conservation. The early arguments were summarized by Chown (2002), but much theoretical and empirical work has accumulated since then. Perhaps most notable is the universal model of the water costs of gas exchange in terrestrial species (Woods and Smith, 2010). The model shows that water loss is an inevitable, mechanistic consequence of gas exchange and that adult insects appear to be more profligate with their water than other organisms for the same levels of gas exchange (Fig. 1). Moreover, it has several important consequences in the context of previous work on insect water loss, of which two are most notable. First, the model demonstrates that the relationship between gas exchange and water loss is not simply a consequence of variation with a third factor (such as mass) (as argued by Addo-Bediako et al., 2001 for mesic insects). This does not mean that the relationships between gas exchange and water loss might not vary between mesic and xeric species (as originally suggested by Zachariassen et al., 1987), but rather that water loss is a mechanistic consequence of gas exchange, which then somehow has to be compensated for. Second, it appears that insects showing discontinuous gas exchange (two-thirds of those used in the empirical validation of the model) have traded off a higher than expected water loss against ridding themselves of CO_2 while preventing oxidative damage (Woods and Smith, 2010). Alternatively, the water loss could be traded off against substantial energy conservation. Reduction of energy expenditure seems to be the one universal feature of all species showing discontinuous gas exchange (Matthews and White, 2011). Irrespective, the intriguing possibili-ty arises that the strong associations between variation in components of the discontinuous gas exchange cycle and water availability (e.g. Chown and Davis, 2003; Marais et al., 2005; White et al., 2007) may have arisen not because discontinuous gas exchange is an adaptation to save water, but rather because it is a water profligate solution to an energy and oxidative damage problem, and in water poor environments has to be modified (Chown, in press). How discontinuous gas exchange arises mechanistically fits well with these ideas. Downregulation of energy expenditure or of oxygen uptake during low metabolic

demand (see also Moerbitz and Hetz, 2010) means that control by the insect brain (cephalic ganglia) is relinquished to the segmental ganglia, which as a consequence of feedback delays and interacting setpoints, results in spiracle behaviour that alternates between closed, flutter and open states (Förster and Hetz, 2010).

Importantly, the universal model not only allows for substantial variation among species, but also draws attention to the need for explaining this variation (Woods and Smith, 2010). Early interspecific comparative work on insect metabolic rate and water loss (Zachariassen et al., 1987) suggested that, despite evidence to the contrary in other studies (see review in Chown, 2002), alteration of metabolic rate might be an important component of the overall strategy (see also Zachariassen, 1996). While some of these ideas are still perhaps not as widely explored as they could be (especially the role of variation in extracellular and intracellular Na^+ and free amino acid concentrations), evidence is accumulating that metabolic rate may well be downregulated as a water savings mechanism (Chown and Davis, 2003; Marron et al., 2003). For example, in response to acclimation at 25 °C (by comparison with 15 °C and 20 °C), *Scarabaeus spretus* shows both cuticular and respiratory water loss rate reduction, with the latter being associated with a marked depression of metabolic rate (Terblanche et al., 2010) (Fig. 2). Thus, the change in metabolic rate with acclimation appears not to be some form of metabolic cold adaptation, but rather a metabolic response to increasing water loss rates associated with higher temperature. Such an interpretation is supported by the simultaneous reduction in both cuticular and respiratory water loss, so also vindicating previous arguments

that comparison of percentage water losses among these avenues is unlikely to be insightful (Chown, 2002).

The role of the sub-elytral chamber in reducing respiratory water loss has also turned out to be quite different to that originally proposed. In the dung beetle *Circellium bacchus*, little gas exchange at rest takes place via the abdominal spiracles within the sub-elytral chamber. Rather, gas exchange during the large, open phase of discontinuous gas exchange is almost entirely dominated by tidal airflow through the right mesothoracic spiracle (Duncan and Byrne, 2002). Thus, airflow is not retrograde with water loss being restricted by the humid sub-elytral chamber as originally thought. Rather, it appears that gas exchange through a single spiracle, equipped with a sieve plate, reduces cross-sectional area over which exchange takes place, thus lowering water loss, and that airflow is either anterograde or tidal. Nonetheless, pressure measurements taken from the tracheal system and sub-elytral chamber (Duncan et al., 2010) and little evidence of water loss from the chamber (Duncan, 2002) suggest that during interburst periods oxygen may enter the tracheal system from the sub-elytral chamber, with little water loss owing to michrotrichial sealing of the chamber (Duncan et al., 2010). Increasing use of the mesothoracic spiracles for gas exchange at rest appears to be a graded response to aridity. Work on dung beetles again highlights this point. In the mesic *Pachylomerus femoralis* the largest contribution to gas exchange is made by the abdominal spiracles (88%), while in *Pachysoma gariepinum* and *Pachysoma striatum* from more xeric environments, the contribution made by the mesothoracic spiracles increases substantially (20% and 46%,
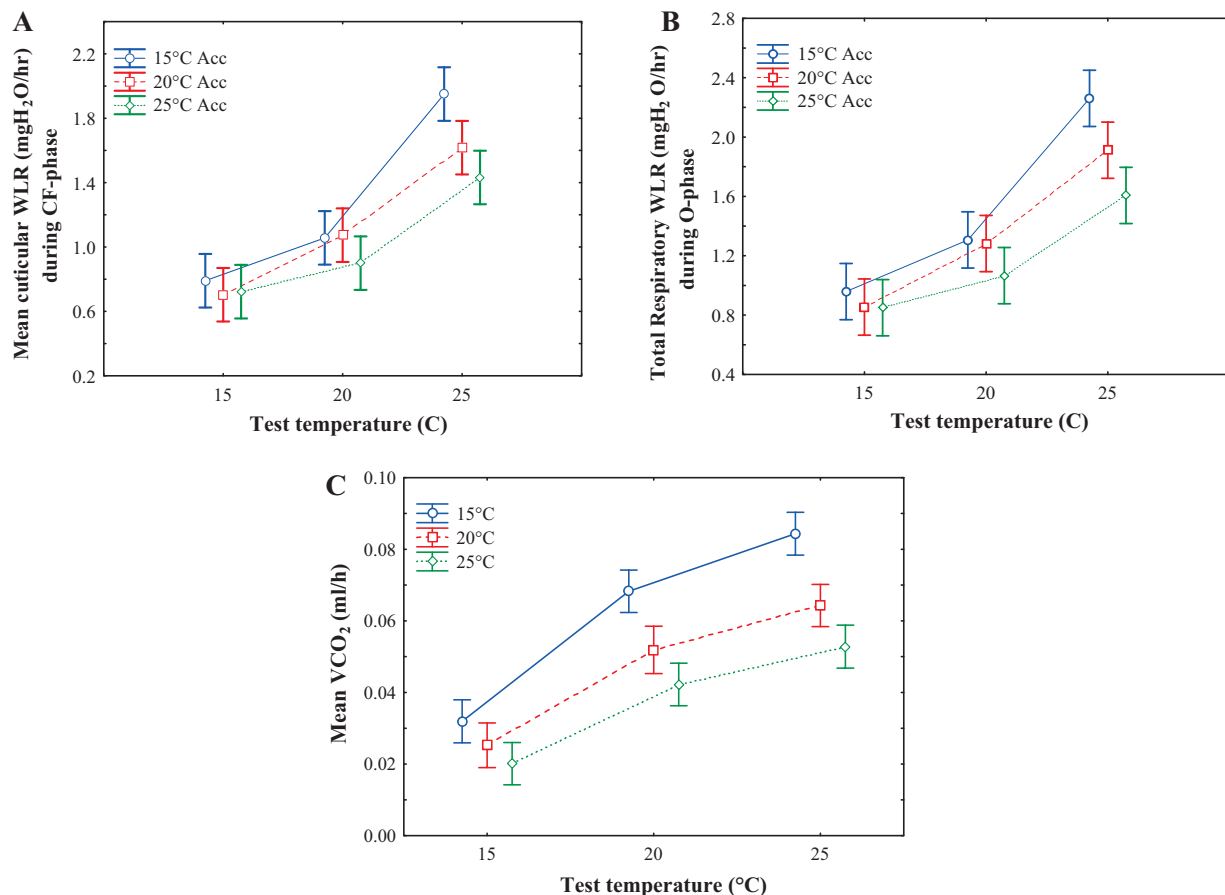
Fig. 2. The effects of acclimation and test temperature on (A) mean cuticular water loss rate (in mg H_2O/h, ±95% CLs); (B) respiratory water loss rate (in mg/h) (means ± 95% CLs) during the O phase of discontinuous gas exchange; (C) mean resting metabolic rate (least-squares VCO_2 means, ±95% CLs) after correcting for body mass (ANCOVA) during rest, in the dung beetle *Scarabaeus spretus*. 15 °C acclimation, circles with solid line; 20 °C acclimation, squares with dashed line; 25 °C acclimation, diamonds with stippled line. Redrawn from Terblanche et al. (2010).

respectively) (Duncan and Byrne, 2005). In *C. bacchus* the contribution is 79%. Predominant use of the mesothoracic spiracles during gas exchange at rest has also been demonstrated in three species of flightless desert tenebrionids (Duncan, 2003; Duncan and Dickman, 2009), providing generality for the idea that water savings is effected by reduction of cross-sectional area over which water can be lost (see Kestler, 1985; Schilman et al., 2008; Woods and Smith, 2010). Thus, the role of the sub-elytral chamber is much more complex than previously thought.

Perhaps one of the most significant features of modern comparative work on water loss is that, by and large, it has been restricted to the adult stages. Nonetheless, the immature stages, and especially of holometabolous species, may be much more vulnerable to dry conditions than are the adults (Klok and Chown, 1998, 1999; Woods and Bernays, 2000; Woods and Harrison, 2001; Woods, 2010). Although an argument may be made that vulnerable immature stages (i.e. not desiccation tolerant eggs) tend only to be present under favourable conditions, extreme events can still have effects on these stages. These events may take several forms, such as anomalous high temperatures, which might increase ambient saturation deficit or reduce water availability in host plants, or biotically induced incidents, such as defoliation of an area during outbreak conditions, so limiting water available from host plants (Klok and Chown, 1999). Moreover, neonatal herbivorous insects may be exposed routinely to desiccating conditions as a consequence of host plant responses which may be geared to enhance desiccation stress to their benefit, but at a cost to the herbivores (the neonate desiccation hypothesis – Woods, 2010). In the context of changing water regimes forecast under global climate change, and especially increasing variation in rainfall (Fung et al., 2011; New et al., 2011; Sanderson et al., 2011), all of these topics, as well as the significance of the oxygen-water tradeoff in eggs and the role of microclimates and their change in affecting water loss, require further investigation (Woods, 2010).

Despite these complexities, much work has demonstrated that water loss rate is the main factor accounting for variation in insect desiccation resistance, and that cuticular loss forms its main component (Chown and Nicolson, 2004; Benoit, 2010). The primary mechanisms underlying variation in cuticular permeability are the amount and composition of the water proofing components of the epicuticle lipids, mainly cuticular hydrocarbons (CHCs) (Edney, 1977). Increased compactness (amount), linearity and length (composition), and saturation of CHCs result in greater water retention properties. These characteristics vary both among species and within species exposed to varying conditions (an excellent recent review is provided by Benoit, 2010).

However, in spite of these general patterns, variation in CHCs does not always conform to adaptive expectations, and may not solely serve a function for water conservation. In *D. melanogaster* and *Drosophila simulans*, although CHC length varies in a seemingly adaptive fashion, the absolute amount of cuticular lipids is generally not variable among geographical strains. In *D. melanogaster*, CHC composition varies adaptively with breeding temperature while *D. simulans* shows the opposite response (Rouault et al., 2004). The sexes in *D. melanogaster* also show marked differences in the composition of CHCs while the genders of *D. simulans* are much more alike. Among multiple species of *Drosophila* (Gibbs et al., 2003) and among populations of *Glossina pallidipes* (Jurenka et al., 2007) the absolute amount and composition of CHCs vary inconsistently with environmental conditions.

One reason for the seemingly inconsistent variation in CHC profile is the function these molecules also serve as pheromones, which may be used for mate, species, and nest recognition. Such variation has been found in ants (Martin and Drijfhout, 2009), Lepidoptera (Lienard et al., 2008), and in *Drosophila* (Takahashi et al., 2001; Chertemps et al., 2006; Foley et al., 2007) (see also the

general review by Howard and Blomquist, 2005). Thus, selection for pheromonal functions could be interfering with selection for desiccation resistance. Furthermore, CHC profiles are also affected by feeding status in ticks (*Hyalomma dromedarii* and *Ornithodoros savignyi*) (Hafez et al., 1970), by age in the Queensland fruit fly *Bactrocera tryoni* (Weldon and Taylor, 2010), and by mating status in the desert harvester ant, *Pogonomyrmex barbatus* (Johnson and Gibbs, 2004). Mating status-related variation has also been found in *Drosophila* and is possibly due to mechanical transfer of cuticular lipids between the sexes during copulation (Everaerts et al., 2010). The significance for desiccation resistance of these changes is not well known.

Across the insect orders, CHCs show a remarkably large molecular variation within and among species (van Wilgenburg et al., in press). For example, a response to selection in *Drosophila* mate recognition pheromones is found in *D. melanogaster* (Takahashi et al., 2001), as is large within-population variation in the expression of CHCs (Foley et al., 2007). The latter study also found strong sexual dimorphism and low inter-sex correlation suggesting, at least partly, independent genetic control of CHC composition among genders probably owing to their role as contact pheromones in males. Much is known about the molecular pathways involved in the formation and modification of the CHCs. Genes identified as involved in producing variation in CHCs in *Drosophila* include *Desat 2* (Fang et al., 2002), *smoq* (Ferveur and Jallon, 1996), *FatP, DesatF* and *sept* and several others (Foley and Telonis-Scott, 2011). The variation in CHC profile within a *D. melanogaster* population was investigated by Foley and Telonis-Scott (2011). This study showed much genetic variation for CHCs which is associated with desiccation tolerance in this population. This large variation suggests that ample genetic variation is available for selection, thus, allowing adaptive divergence in CHCs given selection. However, such work has primarily taken a 'pheromone perspective' and the role of these genes for variation in desiccation resistance is largely unknown, although several of these candidate genes co-localize with desiccation quantitative trait loci (Foley and Telonis-Scott, 2011).

4. Molecular responses and candidate genes for desiccation (and cold) tolerance

Some understanding of the molecular adaptations by which insects achieve cold and desiccation resistance and tolerance has, nonetheless, been achieved. These molecular components serve different roles and thus also occur in different proportions in species using different desiccation strategies. The molecular mechanisms connected to plastic responses to desiccation are related to different levels of individual water balance. First, a group of mechanisms serve to avoid desiccation, i.e. provide desiccation resistance. These include the CHCs and osmoregulation, which relate to barriers to water loss. A second set of mechanisms concerns the cellular boundary, the movement of water within animals, and the ability to tolerate unbalances here, i.e. desiccation tolerance. Finally, some mechanisms are related to preventing and handling the damage induced by extensive water loss. These latter two groups will be discussed shortly below.

A variety of molecules acting as cryoprotectants, thermal hysteresis proteins, and molecular chaperones, or molecular changes affecting membrane lipid changes and membrane-bound proteins are involved in tolerance, resistance and responses to desiccation. These molecules are in many cases also related to tolerance to cold and thus might functionally explain the connection among these two traits (Chown and Nicolson, 2004; Bennett et al., 2005; Holmstrup et al., 2010). In many terrestrial insects, both desiccation and low temperature stimulate the production of glycerol or trehalose (Chown and Nicolson, 2004;

Yoder et al., 2006; Holmstrup et al., 2010). Trehalose (and a range of other sugars or polyols) is known to provide protection against the deleterious effects of cellular dehydration on membrane and protein integrity (Crowe et al., 1992; Kikawada et al., 2007) and the accumulated amount is correlated with desiccation and cold tolerance in insects, e.g. in *Anthonomus pomorum* (Koštál and Simek, 1996).

The mechanisms promoting desiccation tolerance, i.e. cryo- and desiccation protectants, are often accumulated in advance of a low temperature stressor, as preparation for seasonally climatic changes (seasonal acclimatization). Such responses have long been considered adaptive, and Franca et al. (2007) and Lopez-Martinez et al. (2009) bear out these views, arguing that deleterious effects of dehydration are better managed by preventing damage (active and early responses) than by repairing them. Thus, induction of the *Trehalose-6-Phosphate Synthase* (*TPS*) gene and the accumulation of trehalose could be considered such an active protective system induced to prevent damaging effects.

The accumulation of cryoprotectants and desiccation protectants is often investigated in strongly cold and desiccation exposed species, e.g. *Belgica antarctica* and *Polypedilum vanderplanki*. In larvae of the Antarctic midge, *B. antarctica*, dehydration-induced trehalose is found at levels proportional to the severity of the dehydration. Accumulation of trehalose is correlated with desiccation, but also with cold and heat resistance (Benoit et al., 2009). This species also accumulates glycerol and erythritol during desiccation, while freezing induces the same polyols in addition to mannitol. Thus, these molecules might functionally link resistance in these traits (Michaud et al., 2008). During desiccation, larvae of the sleeping chironomid, *P. vanderplanki* accumulate trehalose up to 18% of dry body mass after two days (Watanabe et al., 2002). These species are both extremely cold and desiccation resistant. However, many species show similar patterns of sugar and polyol induction in response to adverse environmental condition or as preparation for seasonal variation (overwintering) (Denlinger and Lee, 2010).

Aquaporins provide a further example of molecules playing a role in desiccation tolerance. These proteins serve as channels for water and small solutes to pass through the cell membrane (Campbell et al., 2008), and thus, genes encoding aquaporins are relevant because water movement across cellular membranes must be drastically increased during both dehydration and rehydration to maintain osmotic balance and to avoid uncontrollable cell shrinkage or swelling. Some studies have shown that aquaporins may have a significant role in the cold and desiccation tolerance of freeze tolerant insects (Izumi et al., 2006; Philip et al., 2008). Thus, in freeze-tolerant larvae of the goldenrod gall fly, *Eurosta solidaginis*, aquaporin expression patterns vary with temperature and desiccation acclimation, while experimentally blocking aquaporins decreases freeze tolerance of several (but not all) tissues (Philip et al., 2008). One of two different aquaporin genes identified in larvae of the sleeping chironomid, *P. vanderplanki*, is also induced by dehydration (Kikawada et al., 2008), while transcript levels of a homolog thereof in the Antarctic midge *B. antarctica* were not altered in response to dehydration (Goto et al., in press). When cloned and expressed in *Xenopus* oocytes these genes were shown to be involved in water transport. However, little is known of the significance of aquaporins for dehydration of other anhydrobiotic or strongly desiccation tolerant insects where they could be assumed to be important (Campbell et al., 2008).

The potential role of Late Embryonic Abundant (LEA) proteins in invertebrates is a recent discovery and little is still known of the functional role and regulation of these proteins. However, the LEA proteins have been shown to be induced by desiccation and associated with desiccation tolerance of an increasing range of invertebrates, of which several are anhydrobiotic invertebrate species (animals tolerating an almost complete desiccation) (Hand et al., 2011). This protein family has previously been found in desiccation tolerant seeds and pollen of plants (Browne et al., 2002). *In vitro* studies have shown that LEA proteins help prevent aggregation and maintain enzymatic activity during drought stress in human cells (Chakrabortee et al., 2007). Other studies have suggested that LEA proteins can act as a "molecular shield" that forms a transient barrier between biomolecules, or to preserve membrane integrity presumably in connection with different sugars, e.g. trehalose (Hand et al., 2011). Thus, even though LEA proteins are only known to be induced by dehydration in one insect species, the nearly anhydrobiotic chironomid, *P. vanderplanki*, these proteins are likely present and play important roles for several strongly desiccation tolerant species (Kikawada et al., 2006).

Heat shock protein 70 (Hsp70) is thought to be important for survival of insects under a range of environmentally stressful conditions, including cold e.g. in *Pyrrhocoris apterus* (Koštál and Tollarová-Borovanská, 2009) and desiccation. Desiccation-induced Hsp70 expression has been found in the mosquito species *Aedes aegypti*, *Anopheles gambiae* and *Culex pipiens* (Benoit et al., 2010a). Interfering with expression of *hsp70* (83% reduction) by RNAi in *A. aegypti* females did not alter water content or water loss rates, but decreased dehydration tolerance from 36% to 28%, being lethal and suggesting a critical role of Hsp70 for survival of dehydration (Benoit et al., 2010a). *Sarcophaga crassipalpis* non-diapausing pupae express Hsp70 and Hsp23 in response to both dehydration and rehydration (Hayward et al., 2004). In contrast, diapausing pupae constitutively upregulate these proteins entering diapause with no further upregulation by dehydration (Hayward et al., 2005). During re-hydration, both Hsp90 and Hsc70 (a constitutively expressed form) are upregulated in both types of pupae, in a response very similar to the one induced by cold. In *Drosophila*, desiccation does not seem to induce Hsp70, which otherwise responds to a diverse range of stress factors (Goto et al., 1998; Sørensen et al., 2003; Sinclair et al., 2007). Thus, responses to desiccation seemingly involve partly different sets of genes in different organisms. The basis for this disparity is not understood and requires further investigations. Some molecular chaperones are induced in connection to programmed acclimation e.g. diapause, and thus might function by preventing desiccation-induced damage together with sugar or polyol protectants, aquaporins and LEA proteins. However, the induction of Hsp70 should be interpreted as a repair response to damage that occurs when desiccation becomes so severe that the presence of protectants and other mechanisms cannot prevent it.

In addition to the genes known to be involved in responses to desiccation, genome wide studies, using e.g. microarrays or related techniques, are likely to identify new candidate genes and molecular pathways for desiccation tolerance in insects (Sørensen et al., 2007). However, in spite of demonstrated desiccation-induced gene expression, it is still not fully known how the regulation of the gene expression levels confers desiccation resistance on animals or how general such genes might be. For example, Sarup et al. (2011) demonstrated that the detection of candidate genes using *Drosophila* microarrays is strongly influenced by the genetic background of the experimental flies. Kawano et al. (2010) provide an example of a verified new desiccation induced gene, *Desiccate*, contributing to desiccation tolerance in *D. melanogaster* larvae. Such investigations are likely to become increasingly common in the future for both model and non-model organisms, which will help to clarify the molecular mechanisms underpinning responses to water stress. Nonetheless, while the mechanisms and genes involved in responses to water stress are being increasingly elucidated, little is still known about the costs of

inducing these changes and the amount and rates of evolutionary change possible. Thus, whether changes in these mechanisms are a viable avenue for adapting to future climate change is not well known and needs further attention.

5. Plasticity and evolutionary change

In response to changing environmental conditions, insects may either show the production of an alternative phenotype from a given genotype, or may show some other form of reaction to the environmental input. Such phenotypic plasticity has been widely discussed generally and in insects specifically (see West-Eberhard, 2003; DeWitt and Scheiner, 2004; Chown et al., 2008; Whitman and Ananthakrishnan, 2009). It may promote or retard adaptation (or intergenerational change, see Endler, 1986), and may itself evolve (Ghalambor et al., 2007). For the purposes of the current discussion, behavioural change (which may also be considered a form of plasticity – West-Eberhard, 2003) will not be dealt with, nor will emigration or other responses which entail movement to a different patch on the part of the organisms involved. These are clearly significant components of the response of organisms to change, and have an influence on the extent to which plastic vs. fixed responses will evolve. However, they have been dealt with extensively elsewhere (e.g. Chown and Terblanche, 2007; Whitman and Ananthakrishnan, 2009; Chevin et al., 2010; Hoffmann and Sgrò, 2011), and, at least in the latter context, are not especially well understood as far as water balance is concerned. Therefore, the focus here will rather be on plastic responses of the components of water loss to changing humidity and temperature regimes, and the extent to which the components of water loss might evolve in response to changing conditions.

Insects exposed to desiccating conditions tend to have lower water loss rates on a subsequent exposure (e.g. Appel and Rust, 1985; Hoffmann, 1990, 1991; Woods and Harrison, 2001; Terblanche and Kleynhans, 2009) and hence survive for longer under dry conditions (e.g. Hoffmann, 1990). For example, rearing *Manduca sexta* larvae on a low water content diet, reduces cuticular water loss rates, rather than altering body water content, excretion rates, faecal water content or other avenues of water balance (Woods and Harrison, 2001). A similar outcome has been found in the cockroach *Periplaneta fuliginosa* (Appel and Rust, 1985), which responded to the treatment by reducing cuticular permeability and faecal water content. In another cockroach species, *Nauphoeta cinerea*, chronic exposure (five weeks) to low humidity conditions results in a *ca*. 10-fold reduction in rates of mass loss, accompanied by a reduction in duration of the discontinuous gas exchange cycle (Fig. 3) (Schimpf et al., 2009). While cuticular and respiratory water losses were not distinguished in the study, it seems likely from the data presented that water loss through both avenues is reduced. Recently, Bazinet et al. (2010) also demonstrated that rapid responses to desiccation in *D. melanogaster* are likely affected by reductions in cuticular water loss rates and not changes in respiratory water loss.

Responses to altered humidity levels can take place rapidly and are clearly reversible in the few instances where time-courses have been examined. A prior non-lethal period of exposure to low humidity of only a few hours markedly improves desiccation resistance (LT50 increases from <16 h to >19 h) in *D. melanogaster* (Hoffmann, 1990). These responses develop rapidly (within 2 h) and persist for more than a day after a 9 h exposure period. Moreover, genetic variation for acclimation ability to humidity also seems plausible, because desiccation-selected lines show weaker acclimation responses than unselected lines. Variation in these acclimation responses to desiccation has also been investigated in several *Drosophila* species and populations from different environmental moisture regimes (Hoffmann, 1991). Acclimation
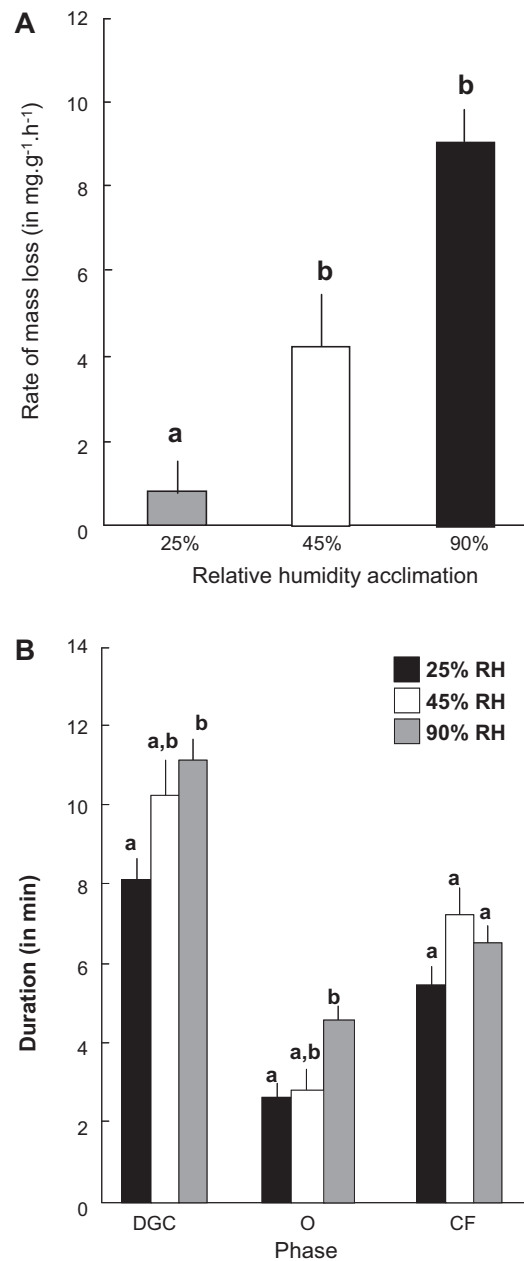

Fig. 3. (A) Mean rates of mass loss at three different humidities in the cockroach *Nauphoeta cinerea*. (B) Adjusted least-squares means of the total discontinuous gas exchange duration, as well as duration of each of the component phases thereof. Different letters indicate significant differences among treatments. Redrawn from Schimpf et al. (2009).

responses to humidity are limited in a rainforest species, *Drosophila birchii*, while other, more widespread species (*D. simulans*, *Drosophila immigrans* and *Drosophila serrata*) are readily capable of acclimating to low humidity. However, *D. serrata* populations from different environments have similar acclimation responses and Hoffmann (1991) therefore suggested limited geographic variation in acclimation ability exists in this species (see also Hoffmann et al., 2003).

Tests of the extent to which alterations in water loss responses to changing humidity might be beneficial have recently been undertaken for tsetse pupae of species from mesic and xeric environments (Terblanche and Kleynhans, 2009). In this study, several major alternatives to the beneficial acclimation hypothesis (see Leroi et al., 1994; Deere and Chown, 2006) were proposed and
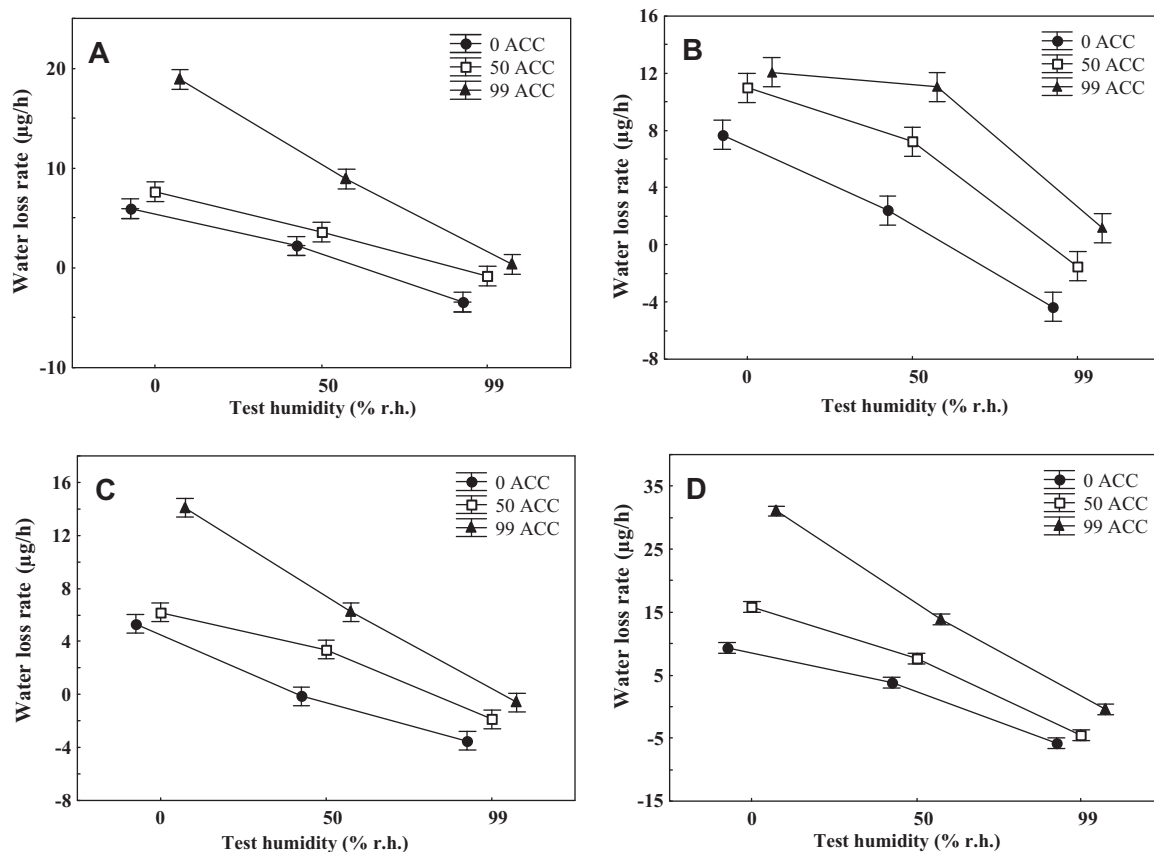
Fig. 4. Mean water loss rate (in μg/h ± 95% confidence limits) of (A) mesic *Glossina palpalis*, (B) xeric *G. morsitans*, (C) mesic *G. austeni* and (D) xeric *G. pallidipes* after 10 days acclimation at 0, 50 and 99% relative humidity. Water loss rate was estimated under test conditions of 0, 50 and 99% relative humidity over four days for each acclimation group. Different acclimation humidity treatments are indicated by different symbols in the legend. Note the *y*-axes differ among species plots for clarity and that negative water loss rates indicate atmospheric water absorption.
Redrawn from Terblanche and Kleynhans (2009).

tested. Holding puparia of any of the species at low humidity (*ca.* 0%) for 10 days generally reduces water loss rates, typically by as much as 4-fold compared with saturated conditions (Fig. 4). Nonetheless, the outcomes also showed several subtleties. For example, in the mesic *Glossina palpalis*, the deleterious acclimation hypothesis could not be rejected – the low humidity acclimation results in higher water loss rates on subsequent testing at low humidity (interpreted in this case as poorer performance). By contrast, in the xeric-adapted *Glossina morsitans* the 'drier is better' hypothesis could not be rejected. In the remaining species the optimal acclimation hypothesis (or possibly the beneficial acclimation hypothesis) and the drier is better hypotheses could not be rejected, suggesting that water balance responses to low humidity are adaptive across the entire genus (and see discussion in Bursell, 1959; Kleynhans and Terblanche, 2009) or perhaps that the classification of 'mesic' is confounded in some way.

In several species, water loss rates also respond to changes in temperature. For example, in *D. melanogaster*, summer-like acclimation conditions improve desiccation resistance (Hoffmann et al., 2005). Similar increases in desiccation resistance with exposure to elevated temperatures have been found in *G. pallidipes*, following acclimation of pupae or adults or a combination thereof (Terblanche and Chown, 2006), and in the dung beetle *S. spretus*, with both cuticular and respiratory components contributing to the acclimation response (Fig. 2). By contrast, some studies have found little indication of acclimation responses with changing temperature. For example, in a desert-dwelling *Drosophila* species, high temperature acclimation does not alter desiccation rates although cuticular hydrocarbon chain length increases (Gibbs

et al., 1998). Likewise, in the chrysomelid *Chirodica chalcoptera*, temperature acclimation has no significant effect on rates of water loss (Terblanche et al., 2005).

Although less comprehensively investigated, it appears that diet also has a pronounced effect on responses to water stress. In *C. pipiens*, adult females provided with access to sugar water survive for longer following repeated exposures to dehydration than do females that are allowed to rehydrate only, likely owing to an inability to replenish carbohydrate and lipid stores (Benoit et al., 2010b). When *D. melanogaster* larvae are reared on a protein enriched diet, both male and female flies survive for longer following exposure to low humidity (0–5%) than do flies which have been fed a carbohydrate enriched diet (Andersen et al., 2010). The reason for the difference in desiccation tolerance is not yet clear.

5.1. Evolutionary change

Substantial variation in desiccation resistance and survival time among insect species living in different habitats, and intraspecific variation among populations shown likely to have a genetic basis (e.g. Edney, 1977; Chown et al., 1999; Hoffmann and Harshman, 1999; Addo-Bediako et al., 2001; Gibbs et al., 2003; Parkash et al., 2005; Terblanche et al., 2006; Benoit, 2010; Hoffmann, 2010; Chown and Klok, 2011), provide ample evidence of the fact that insects adapt to variation in water availability. However, how rapidly particular populations respond to change in the environment (i.e. the extent of responses to selection) and the form of these responses have been examined most commonly in *Drosophi-*

la. Early work on *D. melanogaster* demonstrated that laboratory populations respond rapidly to selection, such that increased resistance to dry conditions can be detected within ten generations (Hoffmann and Parsons, 1989; Hoffmann and Harshman, 1999; Gibbs, 2002). Typically, both increased water content and lowered water loss rates evolve in laboratory populations, while an increased ability to tolerate dehydration stress does not (Gibbs et al., 1997; Gibbs, 2002). By contrast, in a different set of lines of the same species, a 2-fold increase in female survival is associated with enhanced dehydration tolerance, lower water loss rates, and little evidence of increased water content (Telonis-Scott et al., 2006, who also summarize responses to selection in *D. melanogaster*).

The work on *D. melanogaster*, and similar studies on other, widespread, typically temperate species of *Drosophila* have revealed that heritability for desiccation resistance is high and that strong responses to selection are found (Hoffmann and Parsons, 1989; Kellermann et al., 2009). By contrast, in tropical, range-restricted species heritability is low, and these species have much lower tolerance for dry conditions than their temperate counterparts. Moreover, responses to selection are also reduced (Hoffmann et al., 2003). Such variation likely accounts for strong relationships between distributions and physiological traits such as desiccation resistance in *Drosophila* (Hoffmann, 2010). It also suggests that tropical species are unlikely to be able to mount a strong response to environmental change which involves substantial drying, as much of it is likely to (Breshears et al., 2005). Why the tropical *Drosophila* species should show low variation and therefore be unable to respond to selection has not been explored in detail. Nonetheless, it seems likely that reasons may include DNA decay (Hoffmann and Willi, 2008), or some form of trade-off (Kellermann et al., 2009). Lack of responses to selection in other species might also be a consequence of demographic factors, trait and gene interactions (such as might be associated with responses to sexual selection – Foley et al., 2007), or asymmetric gene flow (Willi and Hoffmann, 2009; Hoffmann, 2010).

If such differences among tropical and temperate species are more widespread in the insects, then substantial risks to tropical species via changing temperatures (Deutsch et al., 2008; Dillon et al., 2010) might be substantially exacerbated (see also below). Irrespective, the extent to which various stages can mount a response, either within or among generations, to changing environmental conditions has important implications not only for understanding responses to change, but also for forecasting them. For example, when the evolution of desiccation resistance in *A. aegyptii* eggs is included in mechanistic niche modelling, it is clear that much potential exists for the expansion of this species range into northern Australia as climates change (Kearney et al., 2009). The inclusion of realistic evolutionary scenarios into mechanistic and environmental niche modelling is sorely needed (Chown et al., 2010; Hoffmann and Sgrò, 2011).

6. Realized and expected responses to environmental change

Environmental change is clearly proceeding at a rapid, and in many respects, accelerating pace (Chown and Gaston, 2008; Ellis and Ramankutty, 2008; Bertler and Barrett, 2010; Sanderson et al., 2011). How the major forms thereof, notably habitat alteration, climate change, biological invasions, pollution and overexploitation are likely to influence insects via effects on water balance is clear in some instances (such as lack of adaptive responses to dry conditions in restricted, tropical species – see above), but certainly has not been fully explored in others. While in the previous sections we dealt with the likely components of responses, and their propensity for change both within and between generations,

here we indicate how the various forms of change might affect insect populations via their interactions with water balance.

Responses to climate change have been the focus of much of the previous section, and therefore, here, less attention is given to them. However, two areas deserve further consideration. First, based on an assessment of metabolic rate–temperature relationships, and changes in ambient temperatures that have already taken place, it appears that relative metabolic rates in tropical to temperate organisms have increased anywhere from 5 to 12% (Dillon et al., 2010). Presuming that respiratory water loss is a necessary consequence of gas exchange (Woods and Smith, 2010), and that it makes a significant, and in xeric species perhaps considerable, contribution to total water loss (Zachariassen et al., 1987; Zachariassen, 1996; Addo-Bediako et al., 2001), then water loss must also have increased in most ectotherms. Thus, not only are these organisms likely to be faced with increasing energy demand, but also with elevated water loss. The combination may prove especially problematic in species where climate change not only means elevated temperatures but also associated drought (Breshears et al., 2005). Such circumstances may arise in areas just outside the tropics where ambient and maximum temperatures can be very high and rainfall low (Clusella-Trullas et al., in press), but may also arise more locally owing to changes in water availability because of habitat alteration (Webb et al., 2005; Makarieva and Gorshkov, 2007). The inability of tropical species to mount an effective evolutionary response to such change, as suggested by work on *Drosophila* (Hoffmann et al., 2003; Kellermann et al., 2009), is especially concerning. Second, human responses to water shortages, driven both by human demographics and climate change (Fung et al., 2011), include various landscape-level interventions such as the construction of further impoundments and changes to irrigation techniques, and perhaps also an increasing tendency to live in urban areas. Behavioural responses of this kind can substantially alter the landscape for vector species. Many of the responses may prove difficult to predict. For example, an increase in the number of impoundments could improve the availability (both in space and time) of oviposition sites for vector species with aquatic immature stages, so minimizing risks of desiccation stress (see e.g. Kearney et al., 2009) and increasing vector populations. Alternatively, more permanent water could lead to larger aquatic predator populations, so reducing outbreak potential, but increasing the likelihood of outbreaks if the impoundments dry out under extreme conditions (see Chase and Knight, 2003). Similarly, changing ambient conditions in urban areas may favour some species while harming others, so altering vector assemblage characteristics and disease risk, as well as the interventions required to manage the latter (Rogers and Randolph, 2002; Lafferty, 2009).

Differential responses of species to changing ambient conditions could alter assemblage membership in other ways. In particular, concern exists that invasive species might be better able to respond to warming and drying conditions in temperate areas than are species indigenous to the area (Hobbs and Mooney, 2005). For the most part this idea has remained untested in insects. However, for springtails, at least one study, including both physiological work and field experiments, has demonstrated that invasive species respond to high temperature acclimation by lowering water loss rates, but that the opposite is true in the indigenous species, favouring the former in field trials mimicking increase temperature and drought (Chown et al., 2007). Such interactions between climate change drivers are typically not widely explored (Brook, 2008; Brook et al., 2008), and especially not the role that water balance characteristics might play in mediating them. Nonetheless, this may be one of two major ways in which understanding water balance characteristics may assist in forecasting future impacts of invasive species. The second way is in

understanding the extent to which changing transport and food production systems might promote survival of pests and non-indigenous species during the first stage of invasion, which is human-mediated dispersal (Hulme, 2009; Gray, 2010).

Further interactions between change drivers may come in the form of changing body size precipitated by increasing temperatures (see Chown and Gaston, 2010 for review). How this change in size might then affect water balance characteristics, which are strongly related to size (Hadley, 1994; Gibbs et al., 2003; Telonis-Scott et al., 2006; Chown and Klok, 2011), is difficult to tell, but it may also have an indirect impact on the adults of aquatic species via changing temperature and oxygen availability in the water (Harrison et al., 2010). Likewise, changing nutrient availability, as a consequence of nutrient deposition (a major form of pollution: Phoenix et al., 2006; Chown and Gaston, 2008), and changing stoichiometry (Woods et al., 2003) may also have pronounced impacts on herbivore water balance. Much recent work has demonstrated that all organisms seek to balance particular nutrient targets and the extent of water availability plays a role here too (Simpson et al., 2010). Moreover, nutrient availability may affect substantially the ability of insects to survive dry conditions. For example, in *C. pipiens*, mosquitoes without access to carbohydrate resources (sugar) survived repeated bouts of dehydration far more poorly than those with such access, largely owing to a depletion of reserves (Benoit et al., 2010b). To date, this remains one of the only studies highlighting the significance of repeated drought exposures for insect survival, despite the fact that repeated drought stress within an individual's lifetime may be quite common. For insects, much remains to be done to understand these interactions, and recent experimental work showing how temperature preferences may change in response to nutrient availability (e.g. Coggan et al., in press) also suggest how this might be done.

In the case of habitat alteration, the direct effects on insect populations are far the most likely causes of changes to their abundance and distribution. Nonetheless, landscape alteration may also have more subtle effects that may well be mediated through water balance. As noted previously, habitat change can alter substantially the extent of water availability, especially in the case of deforestation (Webb et al., 2005). Afforestation may have the converse effect, though again, the direct consequences thereof, such as changes to host plant availability, are likely to be most significant. Nonetheless, alterations of distance between favourable environments may substantially change the likelihood of successful dispersal because of the water that is lost during flight (boundary layers are disrupted and increasing metabolic rate means increasing water loss – as Lehmann, 2001 showed with matches between spiracular opening and metabolic demand in *Drosophila*). Even if metabolic water is produced during flight as a consequence of carbohydrate and lipid consumption (see discussion in Hadley, 1994; Harrison and Roberts, 2000), ultimately either energy or water shortages may compel an organism to seek resources in an unfamiliar environment where they might not be available, or might mean elevated mortality risks. The significance of flight capability for dealing with habitat alteration has been explored in insects (e.g. Warren et al., 2001; Thomas et al., 2001), but how water balance might play a role here is less well understood.

7. Conclusions

Although much is known about insect water balance and the components thereof, the field continues to develop rapidly. These developments clearly have considerable relevance to understanding of the impacts of environmental change. The inevitability of respiratory water loss, and its likely increase given increased metabolic rates over the last several decades (Dillon et al., 2010; Woods and Smith, 2010) provide an example of the significance of recent work. Other areas also remain comparatively under explored, and particularly interactions between climate change drivers and how these might play out. Likewise, despite a call more than a decade ago for better understanding of the role of rainfall and humidity in diapause induction and termination (Tauber et al., 1998), these topics remain relatively poorly investigated, especially from a mechanistic perspective for insects from habitats that experience seasonal drought (but see examples and discussion in Danforth, 1999; Danks, 2000; Pires et al., 2000; Seymour and Jones, 2000; Moriyama and Numata, 2006; Pappas et al., 2008; Benoit, 2010; Benoit et al., 2010c; Vinod and Sabu, 2010). Moreover, the mechanistic underpinnings of many of the responses continue to provide substantial evidence of cross tolerance or at least the similarity of responses to desiccation and other stresses (Chown and Terblanche, 2007; Denlinger and Lee, 2010; Sørensen and Holmstrup, in press). Investigations thereof may provide considerable insight into what the relative costs and benefits of given responses might be. As Zachariassen (1996) pointed out, and as reproduced at the start of this paper, insect responses have both costs and benefits, and understanding their interaction will continue to form an important component of understanding the significance of water balance physiology in an environmental change context.

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