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Reprint of: The effectiveness of common thermo-regulatory behaviours in a cool temperate grasshopper ☆

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ABSTRACT

Behavioural thermoregulation has the potential to alleviate the short-term impacts of climate change on some small ectotherms, without the need for changes to species distributions or genetic adaptation. We illustrate this by measuring the effect of behaviour in a cool temperate species of grasshopper (*Phaulacridium vittatum*) over a range of spatial and temporal scales in laboratory and natural field experiments.

Microhabitat selection at the site scale was tested in free-ranging grasshoppers and related to changing thermal quality over a daily period. Artificial warming experiments were then used to measure the temperature at which common thermoregulatory behaviours are initiated and the subsequent reductions in body temperature. Behavioural means such as timing of activity, choice of substrates with optimum surface temperatures, shade seeking and postural adjustments (e.g. stilting, vertical orientation) were found to be highly effective at maintaining preferred body temperature. The maximum voluntarily tolerated temperature (MVT) was determined to be 44 °C ± 0.4 °C, indicating the upper bounds of thermal flexibility in this species.

Behavioural thermoregulation effectively enables small ectotherms to regulate exposure to changing environmental temperatures and utilize the spatially and temporally heterogeneous environments they occupy. Species such as the wingless grasshopper, although adapted to cool temperate conditions, are likely to be well equipped to respond successfully to coarse scale climate change.

1. Introduction

Behavioural thermoregulation has always been an ectotherm's first line of defence against variable temperatures. Rapid and reversible, it enables an organism to control its exposure to conditions at a small scale and maintain body temperatures that may be substantially different to ambient (May, 1979). The effectiveness of behaviour in regulating body temperatures is therefore an important determinant of the abundance and distribution of a species, particularly in variable environments and under changing climatic conditions (Bonebrake et al., 2014). Rather than being highly sensitive to climate change by virtue of their ectothermy, many insects and other small ectotherms may in fact be tolerant of increasing temperatures, with behaviour having the potential to alleviate the impacts of climate change (Kearney et al., 2009).

Thermoregulation is ultimately dependent on the rate of heat exchange between an animal and its environment, and this is determined not only by the prevailing environmental conditions of radiation, wind, and ambient temperature, but also the degree of melanism, morphology, size and behaviour of the animal (Digby, 1955; Kearney et al., 2009; Pereboom and Biesmeijer, 2003). Behavioural thermoregulation aims to maintain a body temperature within the optimal range, where fecundity and survival is highest and mortality lowest. The preferred temperature, the temperature to which an insect moves if given its choice of a temperature gradient (Deal, 1941), is a measure of thermoregulatory behaviour through habitat selection and as such it incorporates trade-offs between ecological thermal optima and physiological optima. A range of performance measures of insects have been shown to be maximised at the preferred temperature, such as feeding rates and development in grasshoppers (Lactin and Johnson, 1996; Miller et al., 2009) and butterflies (Porter, 1982), reproductive optima in beetles (Deal, 1941), and brood survival and caste

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determination in ants (Brian, 1963, 1965).

Grasshoppers are well known to be very effective thermoregulators, commonly using a range of behavioural adaptations such as postural adjustments, timing of activity and selection of microhabitats to maintain their preferred temperature (Uvarov, 1977). There is an extensive literature showing that body temperatures of live grasshoppers in natural situations differ from ambient temperatures, either with (eg. Anderson et al., 1979; Parker, 1982)) or without (eg.Gillis and Smeigh, 1987; Willott, 1997) relating them to the operative temperature of non-thermoregulating models (Hertz et al., 1993). Field studies on grasshoppers have demonstrated that the proportion of individuals exhibiting behaviours such as basking, stilting or crouching is related to surface temperatures (Chappell, 1983; Gilman et al., 2008; O'Neill and Rolston, 2007; Samietz et al., 2005), but few studies have attempted to measure the change in body temperature accompanying particular behaviours. Basking has been shown to lead to increases in body temperature under exposure to solar radiation, but the effects of passive warming and active thermoregulation are not always distinguished (Carruthers et al., 1992). Stevenson (1985) applied biophysical models to rank the importance of different behaviours in ectotherms of different body sizes. He found that, theoretically, microhabitat selection would have the greatest impact on body temperature, particularly when shuttling between sun and shade or climbing vertically up vegetation.

Most studies have focussed on species from extreme habitats such as deserts (Chappell, 1983; Fraenkel and Gunn, 1961; Parker, 1982; Whitman, 1987; Whitman, 1988) or alpine environments (Chappell, 1983), and ask how grasshoppers have adapted to stay cool in hot environments or warm in cold environments. These studies predominantly concern northern hemisphere species. In contrast to previously studied examples, we test behavioural thermoregulation in a generalist species from cool temperate habitats in the southern hemisphere, the wingless grasshopper (*Phaulacridium vittatum*). The thermal flexibility of a generalist species may be indicative of the upper limits of short-term adaptability to climate change in ectotherms.

Phaulacridium vittatum is widely distributed in open habitats in eastern and southern Australia, from -23° 36' to -43° 06'S latitude (Key 1938). Its preferred temperature ("set-point" temperature) has been determined to be between 22.5 and 25.0 °C in a laboratory thermal gradient. In natural populations across its full distribution, the peak preferred temperature ranges between 27.5–30.0 °C (overall mean 27.04 ± 0.26 °C), with a sharp avoidance of high temperatures above 35–37.5 °C and low temperatures below 15 °C (Harris et al., 2013c). This is low compared to other acridid grasshoppers, which are generally in the range 32–38 °C (Deal, 1941). In Australia, for example, the migratory locust (*L. migratoria)* has a preferred temperature of 38 °C (Miller et al., 2009). While the low preferred temperature of *P.vittatum* reflects its distribution as a cool temperate species, it raises the question of how this temperature is maintained over such a wide range, when it is commonly found in habitats where it is regularly exposed to very high surface temperatures.

In this paper we test the hypothesis that *P.vittatum* is able to regulate its body temperature using behavioural thermoregulation. We use laboratory and natural field experiments to test for thermoregulatory behaviour at different scales. Firstly, we test for microhabitat selection under natural conditions at the site scale. Then we measure the efficiency of particular behaviours in individuals in artificial warming experiments. Specifically, we test the following predictions:

i. grasshoppers are not randomly distributed across a habitat, but are found on different substrates that reflect the thermal quality of the microhabitat at different times of the day;
ii. grasshoppers will exhibit thermoregulatory behaviours when exposed to high temperatures that will cause measurable changes to their body temperatures; and
iii. these behaviours will be effective up to a point, the Maximum Voluntarily Tolerated temperature (MVT), above which grasshoppers can no longer maintain the preferred body temperature.

2. Methods

Phaulacridium vittatum is a small grasshopper, ranging from 10–20 mm in length (Key, 1992). It exhibits variability in colour, ranging from light through to dark brown and black (and rarely, green). Approximately 5% of both sexes have two white longitudinal stripes on the dorsal surface (Baker, 2005). The range of colour morphs can be present within the same population, and is set for an individual once it reaches the adult stage (Key, 1992). The majority of adults have short, undeveloped wings, and are unable to fly, but a small proportion has wings and is capable of considerable wind-assisted flight (referred to here as "wingless" and "winged" respectively). These forms occur together in almost all populations of *P. vittatum* (Key, 1992). The wingless form is most abundant in pastures, while in areas dominated by shrubs, strips along forest margins, and in gardens, the winged is the more abundant form (Clark, 1967).

Melanism, the occurrence of darker pigmentation in individuals, is an important determinant of body temperature in this species, as has been shown in other ectotherms (Clusella-Trullas et al., 2007). Darker unstriped grasshoppers warm more rapidly and reach a higher equilibrium body temperature than lighter grasshoppers (Harris et al., 2013a), and this is reflected in both the body temperatures and preferred temperatures of grasshoppers in natural situations. The darkest unstriped grasshoppers have a higher preferred temperature and maintain higher body temperatures compared to the lightest (Harris et al., 2013b).

We assessed behaviour in the wingless grasshopper using two approaches. Firstly, we measured microhabitat selection and timing of activity in field populations, to assess mechanisms that may be used under natural conditions to maintain body temperatures within the preferred temperature range. Secondly, we exposed individual grasshoppers to warming experiments in the laboratory to identify common thermoregulatory behaviours and measure their efficiency at maintaining preferred body temperature.

2.1. Microhabitat selection and timing of activity in natural populations

We investigated microhabitat selection in free-ranging grasshoppers at two sites in southern Tasmania, Australia, which represented the range of temperatures at which this species is found. One site was at high altitude, >900 m above sea level (asl.), near Old Man's Head (-42° 11' 16.0"S, 147° 13' 26.5"E), in recently logged *Eucalyptus* forest with trees ranging from 15 m to seedlings and an open ground cover. The other site was at low altitude (<10 m asl.) at Snug (-43° 04' 24.39"S, 147° 15' 27.92"E) in grassy pasture surrounded by remnant *Eucalyptus* trees and bracken fern (*Pteridium esculentum*) within an agricultural landscape.

Measurements were taken during the period 27th March–7th May, 2007. The monthly mean maximum temperature for April was 13.5 °C in the high altitude area and 18.2 °C in the low altitude area. The monthly mean minimum temperatures were 1.4 °C and 5.4 °C for the high and low altitude sites respectively (Australian Bureau of Meteorology, Liawenee and Grove weather stations).

To test the prediction that grasshoppers are not randomly distributed across a site, but utilise different substrates at different