



## Behavioural thermoregulation alters microhabitat utilization and demographic rates in ectothermic invertebrates

Gang Ma<sup>a, b</sup>, Chun-Ming Bai<sup>a</sup>, Xue-Jing Wang<sup>a</sup>, Muhammad Z. Majeed<sup>a</sup>,  
Chun-Sen Ma<sup>a, b, \*</sup>

<sup>a</sup> Climate Change Biology Research Group, State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, China

<sup>b</sup> Scientific Observing and Experimental Station of Crop Pests, Ministry of Agriculture, Guilin, China

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Thermoregulatory behaviours are of great importance for ectotherms buffering against the impact of temperature extremes. Such behaviours bring not only benefits but also organism level costs such as decreased food availability and foraging efficiency and thus lead to energetic costs and metabolic consequences. However, there remains an important gap in our knowledge to link thermoregulatory behaviour to population level ecological consequences. Aphids, as ectothermic invertebrates, can escape from thermal extremes by either dropping off the plant they are on or moving to suitable microclimates. Here we used the English grain aphid, *Sitobion avenae*, as a model system to test the hypothesis that aphids may behaviourally avoid heat stress while also altering their microhabitat utilization leading to demographic consequences. We found that heat stress drove the aphids to leave their host plant; this reduction in host plant residence was associated with increasing leaf temperatures indicating that aphids exhibit thermoregulatory behaviour to escape heat stress. Specifically, we found that behavioural thermoregulation made the aphids disperse and redistribute themselves within different microclimates and thus led to changes in microhabitat utilization. We also discovered that leaving the host plant during behavioural thermoregulation resulted in a considerable decrease in aphids' survival probability due to their inefficient relocation to other plants and increased risk of starvation. Finally, we found that the aphids' thermoregulatory behaviour prevented heat stress while concurrently resulting in decreased survival and reproduction. Together, these findings support our hypothesis that behavioural thermoregulation alters microhabitat utilization and demographic rates in aphids. This study highlights the importance of behavioural thermoregulation and its ecological consequences and has important implications for understanding population responses in the context of current climate change.

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Climate change is predicted to lead to substantial increases in global mean temperatures as well as in amplitude, frequency and duration of extreme temperature events (Easterling et al., 2000; IPCC, 2013; Meehl & Tebaldi, 2004). Climate warming is expected to push organisms to or even exceed their upper physiological thermal thresholds (Neuheimer, Thresher, Lyle, & Semmens, 2011; Parmesan, Root, & Willig, 2000; Reyer et al., 2013; Vasseur et al., 2014) and has already caused a series of severe impacts on species, communities and ecosystems (Ma, Rudolf, & Ma, 2015; Scheffers et al., 2016; Wernberg et al., 2013). Since ectotherms have limited ability and plasticity to increase their upper thermal limits (Heerwaarden, Kellermann, & Sgrò, 2016; Hoffmann, Chown, & Clusella-Trullas, 2013), behavioural mechanisms play important

roles in adapting to the ongoing climate warming (Huey et al., 2012; Kearney, Shine, & Porter, 2009; Sunday et al., 2014).

Despite changes in large-scale geographical distribution to track cooler climates in some species (Bebber, Ramotowski, & Gurr, 2013; Umina, Weeks, Kearney, McKechnie, & Hoffmann, 2005), heterogeneous microhabitat utilization is a more realistic way to deal with frequent summer temperature extremes (Bonebrake, Boggs, Stamberger, Deutsch, & Ehrlich, 2014; Chapperon & Seuront, 2011a, b; Prinzing, 2005). Since microhabitat complexity and diel temperature fluctuation lead to spatiotemporal variability in microclimates (Bonebrake et al., 2014; Chapperon & Seuront, 2011; Pincebourde, Sinoquet, Combes, & Casas, 2007), animals can reduce their exposure to temperature extremes behaviourally (Scheffers, Edwards, Diesmos, Williams, & Evans, 2014; Woods, Dillon, & Pincebourde, 2015). Behavioural thermoregulation is thus an important strategy in buffering against the impact of

\* Correspondence: Chun-Sen Ma, No. 2, Yuanmingyuan West Road, Haidian District, 100193 Beijing, China.

E-mail address: [machunsen@caas.cn](mailto:machunsen@caas.cn) (C.-S. Ma).

temperature variation (Huey, Hertz, & Sinervo, 2003; Marais & Chown, 2008), and particularly in coping with extreme high temperatures in the context of climate warming (Scheffers et al., 2014; Woods et al., 2015).

Behavioural thermoregulation can undoubtedly improve the survival of animals encountering extreme heat stress (Buckley, Ehrenberger, & Angilletta, 2015; Mason, 2017; Sears et al., 2016). Nevertheless, it brings not only benefits but also a series of costs such as reduced availability of suitable habitat (Kleckova, Konvicka, & Klecka, 2014) and food, decreased foraging efficiency (Du Plessis, Martin, Hockey, Cunningham, & Ridley, 2012) and thus energy acquisition, and in turn increased energy requirements (Levy, Borchert, Rusch, Buckley, & Angilletta, 2017; Sears & Angilletta, 2015). Previous studies have established important relationships between behavioural thermoregulation and both energetic costs and metabolic consequences at the individual level. However, these studies mainly focused on endotherms (Du Plessis et al., 2012; Rezende & Bacigalupe, 2015) and ectothermic vertebrates (Busch, Kirillin, & Mehner, 2012; Levy et al., 2017; Ruiz-Aravena et al., 2014) rather than terrestrial arthropods which are important for biodiversity and ecosystem stability under global warming (Isbell et al., 2015).

Importantly, despite recent progress, there remains a sizable gap in our knowledge of the relationship between behavioural thermoregulation and the population level ecological consequences, especially in insects which are the world's most species-rich taxa and play important roles in ecosystem functioning. Insects can rapidly sense even small fluctuations in their ambient temperatures (Garrity, Goodman, Samuel, & Sengupta, 2010; Ni et al., 2013) and behaviourally exploit diverse thermal microhabitats to reduce exposure to heat stress (Lactin & Johnson, 1996; Ma & Ma, 2012b; May, 1979; Pincebourde & Woods, 2012; Woods et al., 2015). Consequently, thermoregulatory behaviours alter insect distribution within habitats and thus thermal microhabitat use for subsequent activities (Caillon, Suppo, Casas, Arthur Woods, & Pincebourde, 2014; Kührt, Samietz, & Dorn, 2005; Pincebourde et al., 2007). However, it remains unclear whether such behaviours affect important fitness components especially in the sap-sucking insects which spend most of their life ingesting plant phloem to obtain sufficient nutrition (Dixon, 1977; Kingsolver & Daniel, 1995).

Aphids, as ectothermic invertebrates, can escape from thermal extremes by either dropping off the plant they are on or moving to a more suitable microclimate (Ma & Ma, 2012a, b; Ma, Hau, & Poehling, 2004; Nguyen, Michaud, & Cloutier, 2009). Here we used the English grain aphid, *Sitobion avenae*, an important agricultural sap-sucking pest worldwide, as a model system. In nature, grain aphids prefer inhabiting and feeding on the top spikes of cereals as these are highly nutritious (Dixon, 1977). Plant canopies and solar radiation often result in a vertical temperature gradient within the plant, with high temperatures at the top (sometimes even exceeding the aphids' upper thermal limit) and lower temperatures at the bottom (Inagaki & Nachit, 2008; Pararajasingham & Hunt, 1991). The temperature gradient provides various thermal microhabitats and the aphids may thus avoid lethal temperature extremes via behavioural thermoregulation. Here we hypothesized that aphids can behaviourally escape from heat stress but that this thermoregulatory behaviour may alter their microhabitat utilization and have certain demographic consequences. We conducted a series of experiments to test the hypothesis and address the following questions. (1) Do aphids leave their initial foraging sites, that is, stop feeding, to avoid heat stress when ambient temperature starts rising? (2) If so, how would thermoregulatory behaviour affect aphids' dispersal and distribution within their microhabitats? (3) Does the process of relocating to other host plants reduce the aphids' time spent feeding and thus increase their risk of starvation? (4) How does behavioural

thermoregulation affect aphids' important fitness components such as survival and reproduction under heat stress?

## METHODS

### Study Insects

We collected the aphids *S. avenae* from a winter wheat field near Beijing (39°48'N, 116°28'E) during May 2010, and then reared them on 5–20 cm high winter wheat seedlings in screen cages (60 × 60 × 60 cm) at 22 ± 0.5 °C, 50–60% relative humidity (RH) under a photoperiod of 16:8 h light:dark. We transferred them to new seedlings weekly. We selected healthy and active fourth-instar nymphs and wingless adults from the rearing stocks as test aphids.

### Host Plant Residence Under Heat Stress

The purpose of this experiment was to assess whether rise in ambient temperature (heat stress) can trigger aphids' thermoregulatory behaviour, that is, make them leave their current sites to avoid extreme high temperatures. We conducted a factorial experiment with three factors to test how temperature treatment (heat stress and control), surface soil moisture (dry and moist) and exposure time (0, 10, 20, 30, 40, 50 and 60 min) would affect aphids' heat avoidance behaviour, as determined by the number of adults and nymphs staying on the wheat seedlings. Moist soil in a pot generated a temperature gradient between the leaves and the soil surface of the pot, and thus provided the aphids with moderate microclimates.

To mimic aphids' feeding in nature, we made a leaf card (see Ma & Ma, 2012a) by fixing freshly cut wheat leaves on one side of a plastic card (diameter = 4 cm) to provide the test aphids with adequate food and habitat conditions. Then we transferred 10 fourth-instar nymphs (or 10 adults) onto the leaf card and suspended it with a thin fibre string inside a climate chamber (PQX, Laifu Ltd., Ningbo, China; accuracy: 1 °C). We maintained the temperature within the chamber at 25 °C with constant light. We placed a plastic pot (diameter = 20 cm, height = 20 cm) filled with dry or moist soil about 50 cm under the leaf card. After allowing the test aphids to settle down for 30 min, we turned on the climate chambers and increased temperature linearly from 25 °C to 40 °C within 60 min. During this period, we counted test aphids on the leaf card every 10 min. We did the test nine times for nymphs and adults in each treatment. To investigate how increases in ambient temperatures affect leaf temperatures, we conducted a similar test without aphids and measured the temperatures of wheat leaves on the sheet by using a thermocouple.

### Microhabitat Shift and Distribution

To understand whether and how behavioural thermoregulation affects microhabitat utilization, we tested the effects of heat stress on microhabitat selection behaviour and relative distribution of adults and nymphs. We used potted wheat plants with moist soil to generate various thermal microhabitats for the test aphids. We defined three types of microhabitats with different thermal conditions: (1) the top microhabitat included the spike (and also spikelets) which are usually the aphids' favourite plant part to live and feed on (Dixon, 1977), (2) the middle microhabitat consisted of three upper leaves and the stem between these leaves, and (3) the bottom microhabitat was the moist soil surface where the aphids could inhabit a cooler microclimate. To simulate aphids' microhabitat shift and distribution, we placed 10 test aphids in groups of five onto the top and the middle parts. Then we placed the potted plant along with the test aphids into a climate chamber. After 30 min, the temperature in the climate chamber started to increase from 25 °C to

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