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# Has behavioural thermoregulation evolved solely to stay alive in insects, nothing more?

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1 FE Spotlights [1002 words]

2 Commentary on the article FE-2023-01052: Thermoregulation enhances survival but not  
3 reproduction in a plant-feeding insect, by Noah T. Leith, Em A. Miller and Kasey D. Fowler-  
4 Finn.

5

6 Has behavioural thermoregulation evolved solely to stay alive in  
7 insects, nothing more?

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12 Conflict of interest: none

13

14 Has behavioural thermoregulation evolved solely to stay alive in  
15 insects, nothing more?

16 Temperature is probably the most influential abiotic variable as it drives nearly all  
17 physiological rates. Temperature is both easy to measure, especially with our technological  
18 level, and complex to apprehend, because it varies widely across temporal and spatial scales.  
19 The mere question of what temperature a given ectotherm experiences at the level of its cells  
20 and enzymes (ie, body temperature) has generated tons of excellent works since a century  
21 (Gates, 1980; Angilletta, 2009; Clarke, 2017). The process of behavioural thermoregulation is  
22 a key tenet in these studies because it bridges organismal performance and temperature  
23 heterogeneity. In its broad definition, behavioural thermoregulation is the use of locomotion  
24 or behavioural adjustments to meet permissive temperatures in the environment (Lahondère,  
25 2024). For thermal ecologists, behavioural thermoregulation is a stimulating topic as it  
26 involves several disciplines including behaviour, physiology, biometeorology and biophysics  
27 (Gates, 1980; Helmuth, 1998; Kearney & Porter, 2004; Pincebourde & Woods, 2012).

28 Behavioural thermoregulation occurs in various ectotherm taxa. Amazingly, studies on  
29 reptiles' thermoregulation largely focused on their ability to find the optimal temperature for  
30 their performance (eg, locomotion, activity window) while works on insects mostly  
31 investigated their capacity to avoid overheating and improve survival under extreme heat.  
32 However, in both cases, the picture is only partial, and only few studies so far have analysed  
33 behavioural choices in the context of thermoregulation to both avoid lethal temperatures and  
34 maximise performance by selecting the optimal temperature. This is precisely the aim of the  
35 study by Leith et al. (2024). In a small herbivore insect, Leith and colleagues assess if  
36 behavioural thermoregulation both improves survival and maximise reproduction  
37 performance within the mosaic of thermal microenvironments of the host plant.

38 In an open-air mesocosm, Leith et al. (2024) surveyed body and operative temperatures of  
39 treehoppers across different plant structures using infrared imaging. The operative  
40 temperature (ie, the body temperature at a given position without any thermoregulatory effect)  
41 was inferred using judicious 3D printed models with colour, size and shape matching the  
42 treehopper body. Operative temperatures are used to describe the available microclimates.  
43 Among the most astonishing results, Leith et al. reports high heterogeneity of operative  
44 temperatures within and across plant individuals at any point in time, by up to almost 20°C.  
45 The variability in actual body temperatures is lower, suggesting that the insect actively  
46 thermoregulate to some extent, especially to avoid the most stressful temperatures above  
47 ~36°C that elicit the rapid heat escape behaviour. However, the thermal preference range  
48 remains wide, and the insect is unlikely to select directly its microclimate within this range to  
49 optimize mating activity. Indeed, the thermal preference of the treehopper does not vary with  
50 sex and mating status (as inferred by playing playbacks of acoustic courtship primers during  
51 thermal preference assays), suggesting that mating behaviours do not modify thermal biology  
52 metrics.

53 Finally, the core of this study consists in analysing the effects of thermal quality (ie, if lethal  
54 temperatures are present within the plant) and variability (ie, the temperature range present  
55 across the plant) on the thermoregulation accuracy. The relationship between  
56 thermoregulation metrics unambiguously demonstrates that the cost-benefit conceptual model  
57 applies in this system: the insect actively select body temperature within its thermal  
58 preference range mostly when lethal temperature are present somewhere in the plant, and  
59 thermoregulation is even more accurate in a highly heterogeneous thermal environment.  
60 Indeed, thermoregulation was mostly effective under high ambient air temperature and when  
61 the insect is on a leaf, which are the conditions with higher probability to meet lethal  
62 temperatures. Otherwise, the insect mostly thermoconforms suggesting that the treehopper

63 does not thermoregulate behaviourally to meet the narrow range of body temperatures that  
64 maximise mating activity.

65 The study of Leith et al. is highly significant for the field of thermal ecology. Conceptually,  
66 studies that allow to partition between the cost-benefit and the inhibited-movement models of  
67 thermoregulation remain exceptional. Indeed, the thermal heterogeneity at fine scale is such  
68 that it may become unpredictable for the insect which should spend a huge amount of energy  
69 to search and exploit body temperatures near optimum for mating – in other words the cost  
70 outweighs the benefits of being precise. This cost-benefit model certainly applies to numerous  
71 arthropod species that display similar heat escape behaviours such as aphids (Ma et al., 2018).  
72 The rapid heat escape behavior to avoid exposure to lethal temperature is not without  
73 consequences, however. Insects that fall on the ground to escape overheating at the leaf  
74 surface are suddenly exposed to soil predators and are at risk of starvation before they relocate  
75 themselves on the plant (Ma et al., 2018). An important trade-off should exist therefore  
76 between heat avoidance, predation exposure, and feeding constraint which complexifies the  
77 picture. Comparative analyses across species differing in behaviour are necessary to better  
78 comprehend the drivers of this compromise.

79 Although survival is improved by behavioural thermoregulation, the population level  
80 performance may still be challenged under elevated atmospheric temperatures because most  
81 individuals remain at suboptimal temperatures for reproduction. Thus, this study provides  
82 mechanistic understanding of recent works reporting that the thermal sensitivity of  
83 reproduction more accurately predicts species distributions and vulnerability to climate  
84 change (Parratt et al., 2021; van Heerwaarden & Sgrò, 2021). Since a decade or so, we have  
85 seen a resurgence of macroecological studies considering microclimates (air temperature) as a  
86 potential buffer of species vulnerability to climate change (Zellweger et al., 2020) – this is not  
87 enough as neglecting body temperatures within fine scales misses the actual level of exposure

88 to limiting temperatures. This is particularly true in ecosystems where organisms are exposed  
89 to solar radiation which generate strong levels of thermal heterogeneity within fine scales  
90 (Saudreau et al., 2017; Pincebourde & Suppo, 2016), by contrast to the understorey of forests  
91 which are shielded from radiation and display homogeneous thermal environments (Zellweger  
92 et al., 2020). Training on heat transfer processes certainly is key to comprehend the  
93 mechanisms generating thermal heterogeneity and to adjust appropriate designs (Briscoe et  
94 al., 2023). Ecologists working in this area should develop their own “biophysical intuition” to  
95 better anticipate the amplitude of body temperature gradients within fine spatial scales.

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