

11-1-2016

Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures?

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Citation of this paper:

Sinclair, Brent J; Marshall, Katie E; Sewell, Mary A; Levesque, Danielle L; Willett, Christopher S; Slotsbo, Stine; Dong, Yunwei; Harley, Christopher D G; Marshall, David J; Helmuth, Brian S; and Huey, Raymond B, "Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures?" (2016). *Biology Publications*. 92.
<https://ir.lib.uwo.ca/biologypub/92>

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3 1 REVIEWS AND SYNTHESSES
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6 2 **Can we predict ectotherm responses to climate change using thermal**
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9 3 **performance curves and body temperatures?**

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53 24 **Statement of authorship:** BJS and RBH led the writing of the ms, all authors contributed
54
55 25 substantially to the conception and revisions.

56
57 26 **Running Title:** A critique of thermal performance curves

58
59 27 **Keywords:** Climate change, fitness, thermal performance, body temperature, thermal variability

60
28 **Word count:** 171 Abstract; 6274 Main text; 201 Text box 1.

29 **100 References; 7 Figures; 1 Table; 1 Text Box**

1
2
3 30 **Abstract**
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6 31 Thermal performance curves (TPCs), which quantify how an ectotherm's body temperature (T_b)
7
8 32 affects its performance or fitness, are often used in an attempt to predict organismal responses to
9
10 33 climate change. Here we examine the key – but often biologically unreasonable – assumptions
11
12 34 underlying this approach; for example, that physiology and thermal regimes are invariant over
13
14 35 ontogeny, space, and time, and also that TPCs are independent of previously experienced T_b . We
15
16 36 show how a critical consideration of these assumptions can lead to biologically useful
17
18 37 hypotheses and experimental designs. For example, rather than assuming that TPCs are fixed
19
20 38 during ontogeny, one can measure TPCs for each major life stage and incorporate these into
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22 39 stage-specific ecological models to reveal the life stage most likely to be vulnerable to climate
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24 40 change. Our overall goal is to explicitly examine the assumptions underlying the integration of
25
26 41 TPCs with T_b , to develop a framework within which empiricists can place their work within
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28 42 these limitations, and to facilitate the application of thermal physiology to understanding the
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30 43 biological implications of climate change.
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46 **Introduction**

47 Anthropogenic climate change is causing demonstrable and accelerating biological impacts on
48 organisms and ecosystems, and biologists are attempting to understand and predict these impacts
49 (Pacifi *et al.* 2015). Inevitably, these effects are mediated in large part by the behavioral and
50 physiological responses of organisms to changing abiotic variables. Most organisms are
51 ectotherms and thus have body temperatures (T_b – see Box 1 for a glossary of terms) that reflect
52 their environments to varying degrees (Angilletta 2009). Extremely high or low temperatures are
53 lethal, and temperature determines the rate of biochemical and physiological reactions. Indeed,
54 all cellular and physiological functions, including metabolism, development, growth, movement,
55 and reproduction, are temperature-dependent; and this has profound consequences at organismal,
56 community, and ecosystem levels (e.g. Grigaltchik *et al.* 2012). Thus, addressing the impacts of
57 climate change through the lens of ectotherm thermal biology allows us to draw conclusions
58 relevant to almost all of the Earth's species.

59
60 A standard way to evaluate the ecological consequences of temperature involves (1) measuring
61 (or predicting) actual body temperatures of ectotherms in nature and (2) determining how body
62 temperature affects organismal-level performance (generally, the rate at which an organism can
63 perform an ecologically-relevant activity) or fitness (Huey & Slatkin 1976). Then one can either
64 predict instantaneous performances associated with those T_b , or, by integrating over a
65 temperature distribution for a time interval or habitat, estimate the average performance level
66 over a given time or habitat (see Angilletta 2009, and the references therein). More recently, this
67 approach has also been used to predict the ecological consequences of climate warming on
68 performance or fitness (e.g. Deutsch *et al.* 2008; Vasseur *et al.* 2014; Levy *et al.* 2015). This

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3 69 examination of T_b through the lens of physiological (or physiologically-mediated) responses
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5 70 sometimes yields counter-intuitive surprises: for example, several studies have predicted that
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8 71 climate warming will have relatively large and negative effects on tropical ectotherms, even
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10 72 though the rate of warming is slower in the tropics than at higher latitudes (Deutsch *et al.* 2008;
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12 73 Dillon *et al.* 2010; Thomas *et al.* 2012; Sunday *et al.* 2014).
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17 75 Measuring instantaneous physiological rates ('performance') across temperature generally yields
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19 76 a curve where performance (assumed to be a proxy for fitness) rises slowly with temperature up
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21 77 to a maximum level (T_{opt}), and then drops rapidly (Fig. 1). These Thermal Performance Curves
22
23 78 (TPCs) describe how T_b affects an ectotherm's performance or fitness (Huey & Stevenson 1979)
24
25 79 over the range of T_b for which performance is positive (i.e. between the critical thermal
26
27 80 minimum and maximum, CT_{min} and CT_{max}). In studies with ecological applications, TPCs
28
29 81 typically quantify whole-organism performance (e.g., speed, stamina, feeding rate, or growth) or
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31 82 sometimes fitness proxies (e.g. reproductive output), because such integrative, higher-level, traits
32
33 83 are more directly related to ecological performance than are lower-level ones such as enzyme
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35 84 activity.
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38
39 86 Mapping T_b onto performance provides an intuitive heuristic model of impacts of temperature or
40
41 87 temperature change on organism physiology and ecology. This mapping is not, however, without
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43 88 hazards. Here we explore assumptions and complications associated both with quantifying T_b
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45 89 and TPCs, and specifically when integrating them to predict impacts of climate change. These
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47 90 factors can fundamentally alter predictions of the likely impacts of climate change, but our initial
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49 91 goal is to identify the assumptions underlying TPC-based models, and to encourage analyses of
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3 92 how sensitive the models are to those assumptions. Our central conclusion is that the TPC- T_b
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5 93 approach – despite many limitations – remains a useful exploratory tool for evaluating responses
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8 94 to climate change.
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96 **Using TPCs to predict the consequences of climate change**

97 In principle, TPCs and T_b distributions can be used to predict the performance or fitness
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17 98 consequences of an organism's thermal environment. First, one empirically estimates how
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20 99 fitness, w , changes instantaneously with T_b , giving $w(T_b)$. Next, one estimates the frequency
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22 100 distribution of body temperatures, $p(T_b)$, experienced by the animal during some time period.
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24 101 The total fitness (W) in a given environment can then be integrated via Eqn. 1, which is, in effect,
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27 102 a rate summation of fitness over T_b (Huey & Slatkin 1976; Deutsch *et al.* 2008; Vasseur *et al.*
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29 103 2014):

$$31 \quad 104 \quad W \sim \int_{CT_{\min}}^{CT_{\max}} [w(T_b) \cdot p(T_b)] dT_b \quad (1)$$

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37 106 Fitness will approach a maximum if most T_b match the optimal T_b (T_{opt} , see Fig. 2), which should
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39 107 (theoretically) be the preferred temperature (but see Martin & Huey 2008). A shift in the mean
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42 108 of $p(T_b)$ – caused by behavior, seasonality, habitat selection, or climate change – can increase,
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44 109 have no impact, or decrease total fitness, depending on the magnitude, direction, and position of
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47 110 the shift relative to T_{opt} (Huey 1991). Similarly, a shift in the variance or skewness of $p(T_b)$ will
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49 111 also have positive or negative effects on W , again depending on the magnitude and position of
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52 112 the shift relative to T_{opt} and to the degree of thermal specialization versus generalization
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54 113 (Angilletta 2009; Vasseur *et al.* 2014), in part as a consequence of Jensen's inequality (discussed
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56 114 below).
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6 116 Equation 1 evaluates fitness as a function of the T_b experienced by an ectotherm during some
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8 117 time period, but T_b can sometimes reach or exceed the CT_{max} – for example, if temperatures
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10 118 warm, or if the animal moves into the sun – with deleterious and potentially lethal consequences.
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12 119 Because the TPC is asymmetric, T_{opt} is much closer to the CT_{max} than it is to the CT_{min} (Fig. 1). A
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14 120 risk-avoidance hypothesis (Martin & Huey 2008) proposes that ectotherms should avoid T_b that
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16 121 approach CT_{max} : thus they should maintain an ample “thermal safety margin (TSM).” [Note:
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18 122 TSM has been defined in several ways. In Fig. 1 and Box 1, we use the distance between the
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20 123 optimal T_b and the CT_{max}]. The smaller the thermal safety margin in a given environment, the
21
22 124 greater the likelihood that an organism will overheat (and possibly die) as climate warms.
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24 125 Because among-species variation in CT_{max} is relatively small, tropical species – assumed to
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26 126 experience relatively stable, warm, temperatures (Janzen 1967) – should have very small TSMs
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28 127 and therefore be disproportionately affected by small increases in mean temperature with climate
29
30 128 change (Deutsch *et al.* 2008). Parallel arguments have extended this concept to other
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32 129 stenotherms, for example polar fishes (Peck *et al.* 2010). Importantly, CT_{min} and CT_{max} bound
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34 130 the TPC, but are not necessarily survival limits, especially during short-term exposures. For
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36 131 example, freeze-tolerant sub-Antarctic *Pringleophaga marioni* caterpillars stop moving at around
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38 132 -0.6 °C, but only die at temperatures below c. -7.5 °C (Klok & Chown 1997). Some intertidal
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40 133 gastropods lose mobility at CT_{max} , but still survive brief exposures to higher temperatures (e.g.
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42 134 Marshall *et al.* 2015).
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53 136 The curvilinear relationship between performance and temperature over much of the TPC (Fig.
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55 137 1) means that the effects of small changes in temperature can be small, negligible, or large,
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3 138 depending on where on the TPC those changes occur (Jensen's inequality – see Ruel & Ayres
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5 139 1999). Jensen's inequality has two significant implications for ectotherms under climate change.
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8 140 First, thermal variability becomes a central determinant of ectotherms' responses to
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10 141 environmental change independent of changes in mean temperature (e.g. Helmuth *et al.* 2014;
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12 142 Vasseur *et al.* 2014; Colinet *et al.* 2015). Second, because metabolic rates increase exponentially
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14 143 with temperature below the inflection point, for a given shift in temperature the metabolic rates
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16 144 of ectotherms in regions with high mean temperatures (i.e. the tropics) may increase more than
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18 145 those of ectotherms in regions with a relatively low mean temperature (e.g. terrestrial Arctic
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20 146 habitats), even though temperature increases in the tropics have been relatively small (Dillon *et*
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22 147 *al.* 2010). By contrast, Kingsolver *et al.* (2013) and Vasseur *et al.* (2014) argued that temperate
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24 148 species may be more vulnerable to climate warming than are tropical species because of higher
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26 149 thermal variability in temperate zones, which increases the incidence of lethal temperatures,
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28 150 despite lower mean temperatures. Variability can be important even at non-lethal temperatures in
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30 151 temperate species; for example, driving evolution of metabolic suppression in butterflies
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32 152 (Williams *et al.* 2012).
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41 154 **Do TPCs really estimate fitness?**

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43 155 The relationships between T_b and fitness in Eqn. 1 are simple and appealing. If one knows the
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45 156 TPC and how climate change will affect $p(T_b)$, one can predict the fitness consequences of
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47 157 climate change for an ectotherm. However, fitness is notoriously hard to define, let alone to
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49 158 measure. Classical life history measures of fitness (e.g., net reproductive rate, R_0 ; intrinsic rate
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51 159 of population growth, r) must be measured at least over an organism's lifespan (Huey &
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53 160 Berrigan 2001; Thomas *et al.* 2012). Not surprisingly, actual measurements of the thermal
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3 161 dependence of fitness have generally been limited to short-lived taxa in the laboratory or to
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5 162 organisms studied by – possibly hypothetical – biologists with long careers and reliable funding.
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8 163 Such data exist as life tables (age-specific table of survival and reproduction) primarily of
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10 164 economically-important insects raised at multiple temperatures (Huey & Berrigan 2001).
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12 165 Importantly, TPCs for r and R_0 have different shapes, even when based on the same life table,
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15 166 because r is inversely related to generation time, which in turn decreases at high temperatures:
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17 167 consequently, T_{opt} for r is often higher than that for R_0 (Huey & Berrigan 2001), and analyses
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20 168 using r vs. R_0 can yield conflicting predictions (Deutsch *et al.* 2008; Kingsolver *et al.* 2011).
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22 169 These life table studies also require exposing animals throughout their lives to fixed temperatures
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24 170 (see Assumption 9 in Table 1). Two problems arise here. First, fixed temperature exposures are
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26 171 inappropriate if life stages live in different micro-environments and thus experience different
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28 172 body temperatures in nature, which is true for insects and many other taxa (Kingsolver *et al.*
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30 173 2011; Colinet *et al.* 2015; Levy *et al.* 2015). Second, long exposure to fixed temperatures may
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32 174 induce pathologies, especially at high temperature (Kingsolver & Woods 2016).
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38 176 Because of the above issues, an instantaneous measure of performance, such as locomotor speed
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40 177 or feeding rate, is often used as a proxy for $w(T_b)$ (Assumption 1, Table 1; Figures 3, 4, 5). Often
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42 178 the choice of performance traits for TPC analyses is driven by expediency, rather than by
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44 179 validated links to fitness. Importantly, TPCs estimated for different traits can differ markedly
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46 180 even in a single species (Fig. 3), which means that contrasting conclusions about fitness could
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48 181 easily be derived from TPCs for different traits acquired on the same organism. Maximal sprint
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50 182 speed has been measured across the most taxa, but its relationship to fitness is rarely established
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52 183 (Miles 2004). Feeding rate can determine an organism's ability to meet and exceed metabolic
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3 184 demands but, above some threshold, mechanical limits to food processing or physiological limits
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6 185 to absorption mean that additional food does not necessarily increase fitness (Riisgard 2001), and
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8 186 it is unclear where this threshold occurs relative to T_{opt} . Trait differences may arise from
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11 187 physical constraints or evolutionary and behavioral selection of different thermal regimes that
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13 188 mean they have been optimized for specific $p(T_b)$; for example locusts enhance digestion by
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15 189 selecting high temperatures after a meal, but choose cooler regimes to reduce energetic costs
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18 190 when starved (Clissold *et al.* 2013). TPCs can also shift with food resources (Fig. 6a; Brett
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20 191 1971), and are not, as Eqn. 1 implies, fixed. One approach to resolve this issue may be to
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22 192 integrate a composite panel of TPCs that use different $w(T_b)$ relationships for different activities,
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24 193 habitats, or times of day.
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29 195 Finally, some temperature-dependent traits may be poor proxies for fitness. For example,
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31 196 although resting or standard metabolic rates increase with temperature, higher rates indicate
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33 197 higher energetic expenditures as well as higher activity, and may not therefore translate to higher
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35 198 fitness, particularly during non-feeding life stages (Clarke 1991). Thus, identifying the most
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37 199 relevant fitness proxies is necessary when parsing contrasting – or even contradictory – signals
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39 200 from different traits (e.g. Fig. 3).
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46 202 **Breaking down $w(T_b)$: What are the implicit and explicit assumptions of using TPCs to**
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48 203 **predict fitness?**
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50 204 Equation 1 provides a simple way to conceptualize how organismal thermal sensitivity (TPC)
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52 205 and body temperature map to organismal fitness (W). However, doing so makes a number of
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54 206 assumptions about the relationship between temperature and fitness. In particular, biologists
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3 207 tend to assume that their chosen trait reflects fitness (Assumption 1 in Table 1), that TPCs are
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5 208 evolutionarily fixed (Assumptions 2-5 in Table 1), that the well-documented physiological
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8 209 adjustments to temperature can be ignored (Assumptions 6-9 in Table 1), and that temperature is
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10 210 the primary driver of fitness (Assumptions 10 & 11 in Table 1). Below we critically address
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12 211 each assumption.

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17 213 *Are TPCs invariant in space and time?*

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19 214 Macrophysiological analyses generally assume that the TPC of a species (or sometimes of an
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21 Order or Class) can be adequately described by a single curve. This is valid only if numerous –
22 215 and unlikely – conditions are met (Assumptions 2-11 in Table 1). The shape, maximum, limits,
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24 216 and breadth of TPCs can vary with habitat, nutritional state, developmental stage, and
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26 217 acclimation history (Figures 4, 5, 6). In addition, individuals within a population may differ
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28 218 significantly, due to both genetic and non-genetic causes (Kingsolver *et al.* 2011; Logan *et al.*
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30 219 2014; Assumption 10 in Table 1).

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36 222 The use of ‘one species, one TPC’ also assumes that the TPC is invariant over both geographical
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38 223 range and evolutionary time (Assumptions 3 and 4 in Table 1). In fact, the thermal sensitivity of
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40 224 ectotherms sometimes varies markedly across their range, often in concert with local conditions.
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42 225 This variation can alter predictions of population dynamics at range edges under climate change
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44 226 (Pearson *et al.* 2009). For example, thermal tolerance of barnacles is higher in subpopulations
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46 227 that experience more extreme temperatures (Schmidt *et al.* 2000), and thermal tolerances can
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48 228 vary widely among insect populations (reviewed by Sinclair *et al.* 2012). This local adaptation
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50 229 illustrates the evolutionary potential of thermal biology to shift over relatively short time scales –
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3 230 less than a century in the case of the cabbage white butterfly, *Pieris rapae*, in North America
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5 231 (Kingsolver *et al.* 2007). Thus, natural selection might conceivably alter $w(T_b)$ for species with
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7
8 232 short life cycles by the 2050 and 2100 dates used for most climate change projections.
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12 234 The capacity for $w(T_b)$ to evolve in this timeframe will vary among taxa, habitats, and traits
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14 235 (Hoffmann & Sgrò 2011), and will also depend on the extent to which climate change affects
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16 236 $p(T_b)$ – see below. The importance of evolution in altering responses to climate change is widely
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18 237 acknowledged (Munday *et al.* 2013), but unfortunately the sensitivity of predicted outcomes to
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20 238 either evolution or plasticity has rarely been incorporated into models (but see Dowd *et al.* 2015
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22 239 for an example). Sensitivity analyses will be required to develop ‘rules’ about how robust
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24 240 predictions are to evolutionary change and (conversely) how much evolutionary capacity or
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26 241 plasticity is necessary to offset climate change impacts.
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34 243 *Do TPCs reflect the realities of the thermal environment?*

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36 244 TPCs for fitness traits are typically constructed using exposure to fixed temperatures, but
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38 245 extrapolating TPCs to field conditions can be complicated by thermal environments that are
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40 246 often highly heterogeneous in space and time, affecting $p(T_b)$ (see below). Thus, both $w(T_b)$ and
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42 247 the experiments we use to derive TPCs carry important assumptions that must be accounted for
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44 248 when using TPCs to derive predictions about the thermal performance of ectotherms in nature.
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50 250 Importantly, temperature exposures in nature vary in duration, and the duration of exposure to a
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52 251 given temperature can determine performance and fitness. For example, a 30-min exposure to 36
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54 252 °C initiates a protective molecular cascade (the ‘heat shock response’) in *Drosophila*
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3 253 *melanogaster*, but exposure to 29 °C for more than a few hours renders flies sterile (David *et al.*
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5 254 2005). These duration effects are particularly significant at high temperatures, where
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8 255 performance usually declines with exposure time (Rezende *et al.* 2014). Even so, mortality and
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10 256 damage accumulation can also result from long exposure to low temperatures (Nedvěd *et al.*
11
12 257 1998; Rezende *et al.* 2014). Such duration effects imply that TPCs are temporally dynamic, but
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14 258 this has been generally ignored in models (Assumptions 6, 7, 11 in Table 1; but see Kingsolver
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17 259 & Woods 2016).

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22 261 Animals in nature usually experience temperatures in a certain order; a change in T_b from
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24 262 temperature x to temperature $x+3$ necessarily involves exposure to temperatures $x+1$ and $x+2$.
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27 263 Thus, thermal regimes usually do not shift suddenly, except in instances where the animal moves
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29 264 from shade to sun or air to water, or in subtidal environments subject to strong tidal currents,
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31 265 which all can lead to abrupt changes in T_b (Leichter *et al.* 2006). In experiments where
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34 266 performance of individual animals is measured at multiple temperatures, the sequence of body
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36 267 temperatures is usually randomized (although the highest temperature often comes last to avoid
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38 268 any heat shock response affecting performance at other temperatures; e.g. Williams *et al.* 2012).
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40 269 These randomized protocols have some empirical support: for example, thermal sensitivity of
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43 270 instantaneous cricket metabolic rate calculated from ramped, ordered or randomized temperature
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46 271 did not significantly differ (Lake *et al.* 2013). Nevertheless, animals in nature have had prior
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48 272 thermal experience that is largely unaccounted for in TPCs (Assumption 6 in Table 1).

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53 274 Prior thermal experience can modify the TPC directly. For example, acclimation responses can
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55 275 substantially modify the shape and position of the entire TPC (e.g. Fig. 5), including thermal
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3 276 limits (Angilletta 2009). Although the broad physiological and biochemical mechanisms
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5 277 underlying these changes are reasonably well-understood, predicting how TPCs will shift is
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8 278 challenging, even in broad geographic comparisons (Somero 2010). Tropical *Drosophila* appear
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10 279 to have sufficient plasticity to maintain an adequate thermal safety margin (Overgaard *et al.*
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12 280 2011), whereas porcelain crabs do not (Stillman 2003). Predicting TPCs is made even more
13
14 281 complicated by cross-generation effects on TPCs. For example, female blow flies exposed to
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16 282 relatively warm autumn temperatures produce larvae with reduced cold hardiness, which likely
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18 283 reduces overwinter survival (Coleman *et al.* 2014). The capacity for plastic responses to
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20 284 changing temperatures can also depend on the rate of temperature change: emerald ash borer
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22 285 prepupae have relatively high heat tolerance when shifted slowly to a high temperature, because
23
24 286 slow warming allows them to mount a heat shock response (Sobek *et al.* 2011). Whether or not
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26 287 acclimatization is an effective strategy in nature will thus depend on how temporally
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28 288 autocorrelated thermal regimes are over the scale of days, i.e. whether preparing for an extended
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30 289 heat wave or cold snap is an effective use of physiological resources.
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39 291 Both the order of thermal exposure and the rate of temperature change can affect $w(T_b)$, but
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41 292 neither is usually accounted for in models (Assumptions 6 and 8 in Table 1), even though both
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43 293 vary in nature. Plastic responses to temperature fluctuations will likely bear costs and elicit
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45 294 trade-offs, not just as simple shifts in the instantaneous value of $w(T_b)$, but in terms of long-
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47 295 lasting accumulation of fitness. This will particularly be the case when organisms are exposed to
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49 296 temperature extremes. For example, the heat shock response requires energy for the synthesis
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51 297 and ATP-dependent activity of heat shock proteins (Feder & Hofmann 1999), and recovery from
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3 298 being cooled to below the CT_{\min} has a measurable metabolic cost in insects (MacMillan *et al.*
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5 299 2012).

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10 301 Finally, thermal regimes in nature often repeat themselves (but see above for exceptions); for
11
12 302 most habitats, diel thermal cycles mean that an ectotherm that lives for more than a few hours
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14 303 will be exposed to repeated warm-cold fluctuations (Colinet *et al.* 2015). Given that prior
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16 304 experience can modify the TPC, the degree to which TPCs remain constant across multiple
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18 305 thermal cycles will depend in part on the temporal autocorrelation of the environment, which
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20 306 may be modified with climate change (Assumption 6 in Table 1). Fitness can decline because of
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22 307 repeated exposure to deleterious temperatures – in insects and lizards, this effect may be more
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24 308 important than the duration or intensity of exposure to extreme temperatures (Kearney *et al.*
25
26 309 2012; Marshall & Sinclair 2015). Conversely, thermal cycles under permissive temperatures
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28 310 often increase growth rates (and presumably fitness; Colinet *et al.* 2015). Overall, a predictive
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30 311 understanding of how thermal fluctuations affect ectotherm fitness is still elusive (Kingsolver *et*
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32 312 *al.* 2013; Vasseur *et al.* 2014; Colinet *et al.* 2015), and empirical responses might well prove
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34 313 idiosyncratic.

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39 315 Thus, in reality, $w(T_b)$ is not a fixed curve but a shifting multi-dimensional envelope with an
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41 316 explicit temporal history. Estimates may need to incorporate threshold-crossing events plus
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43 317 duration and frequency of exposure to stressful temperatures (Assumptions 7 and 9 in Table 1).
44
45 318 The consequences of exposure to temperature extremes have been included in models in several
46
47 319 ways. Deutsch *et al.* (2008) assumed that fitness was temporarily zero when $T_b > CT_{\max}$ (or
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49 320 $< CT_{\min}$), Kingsolver *et al.* (2011) assumed that individuals died under these same conditions, and
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3 321 Buckley and Huey (2016) assumed that survival declined exponentially to zero between the
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5 322 CT_{\max} and 60°C. Roitberg and Mangel (in press) have proposed splitting the TPC in two, with
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8 323 fitness costs accumulating (and the $w(T_b)$ curve modified) after exceeding CT_{\max} , but not the
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10 324 CT_{\min} . This latter approach reflects modifications to the TPC by the heat shock response (Feder
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12 & Hofmann 1999), and perhaps provides a template for how other thermal-history-based
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15 326 modifications to the TPC can be modelled. Alternatively, perhaps we need to shift entirely from
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17 327 a TPC approach to a time series model that reflects the time \times sequence \times duration \times temperature
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20 328 interaction implicit in thermal biology in nature – Woodin et al. (2013) begin to take this
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22 329 approach by applying a time component when $T_b > CT_{\max}$. In the short term, determining the
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25 330 relative importance of these components could allow the key drivers of the $w(T_b)$ relationship to
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27 331 be identified and incorporated. For example, the number of cold exposures has a bigger effect on
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29 332 fitness than either the duration or intensity of those exposures in overwintering spruce budworm:
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32 333 thus, a term quantifying exposure-number could account for most effects of thermal variability
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34 334 on this species (Marshall & Sinclair 2015).

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38 336 *Beyond temperature: TPCs in a multi-stressor world*

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41 337 Environmental physiology of ectotherms often focuses on temperature as a “master variable” that
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43 338 dominates the performance, survival, and fitness of organisms (Assumption 11, Table 1).
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46 339 Nevertheless, interactions involving numerous other environmental and biological factors can
47
48 340 alter the shape of an organism’s TPC and thus how an organism relates to its thermal
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50 341 environment (e.g. Fig. 4; Denny *et al.* 2009; Todgham & Stillman 2013; Gunderson *et al.* 2016).
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53 342 Furthermore, performance curves can just as readily be constructed with respect to other
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55 343 environmental variables such as salinity, pH, and water vapor deficit, and to other anthropogenic
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3 344 stressors, such as pollutants, each of which can modify the effect of temperature on performance
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5 345 (Gunderson *et al.* 2016). Some of these abiotic factors are themselves temperature-dependent;
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7 346 for example, oxygen saturation and $p\text{CO}_2$ for aquatic organisms (Deutsch *et al.* 2015; Gunderson
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10 347 *et al.* 2016). When such interactions occur, the combined effect of two variables usually cannot
11
12 348 be predicted merely by summing the individual effects from single parameter experiments. Non-
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14 349 additive (synergistic) or even antagonistic outcomes in multiple stressor scenarios appear to be
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16 350 the norm, and varying a larger number of environmental parameters yields more substantial
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18 351 effects (Denny *et al.* 2009; Todgham & Stillman 2013; Brennan & Collins 2015; Deutsch *et al.*
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20 352 2015). Fractional factorial designs may be required to deal with multiple factors (Porter *et al.*
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22 353 1984).
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29 355 In most cases, the physiological mechanisms underlying non-additive outcomes in multi-stressor
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31 356 scenarios are not yet fully understood. However, one proposed mechanism linking two stressors
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33 357 in a predictive fashion is oxygen and capacity limited thermal tolerance (OCLTT), which relates
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35 358 performance both to temperature and to the supply of oxygen to the tissues, and therefore to
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37 359 aerobic scope (Pörtner 2010). The generality of OCLTT is debated (e.g. Verberk *et al.* 2016). For
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39 360 example, in contrast to the OCLTT, where extreme temperatures reduce the capacity to deal with
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41 361 a second stressor (reduced oxygen), exposure to thermal extremes can also increase tolerance to
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43 362 other stressors, including hypoxia and hyperoxia, leading to cross-tolerance among multiple
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45 363 stressors (Todgham & Stillman 2013). Nevertheless, the OCLTT approach is an excellent
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47 364 example of a mechanism-based integration of two interacting stressors, and has been used to
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49 365 generate global-level predictions about responses of some aquatic species to climate change
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51 366 (Deutsch *et al.* 2015)..
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368 *Biotic interactions and TPCs*

369 Because of high interspecific variability in thermal performance, climate change is expected to
370 result in “winners” and “losers” (Somero 2010). When performance differs among ecologically-
371 important species such as structuring species, ecosystem engineers, and keystone predators,
372 differential vulnerability among interacting species can translate into differential vulnerability of
373 entire assemblages (Monaco & Helmuth 2011; Dell *et al.* 2014). Similarly, TPCs can be
374 modified by interactions among species: shifts in food abundance (e.g. via predator-prey
375 interactions, or competition) can modify the TPC (Figure 6); non-consumptive effects (‘fear of
376 being eaten’) can reduce foraging success and efficiency, or elicit other physiological costs
377 (Rovero *et al.* 1999; Nelson *et al.* 2004); and parasites and pathogens can induce direct
378 physiological costs (Vernberg & Vernberg 1963) that might modify the TPC. Community
379 interactions can themselves be determined by temperature, creating feedback loops between
380 TPCs and interspecific interactions. For example, elevated temperatures can increase or decrease
381 foraging rates of predators, depending on whether temperature increases occur below or above an
382 organism's T_{opt} (Monaco & Helmuth 2011).

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384 Animals carry with them communities of microbes that can affect behavioral and physiological
385 phenotypes (McFall-Ngai 2015). Although the effect of symbionts on TPCs has not, to our
386 knowledge, been directly explored, there is substantial evidence that symbionts can modify
387 thermal limits. For example, mutations in endosymbiotic *Buchnera* determine the thermal
388 tolerance of their aphid hosts (Dunbar *et al.* 2007), and thermally-tolerant strains of
389 endosymbiotic *Symbiodinium* increase the thermal tolerance of their host corals by more than

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3 390 1°C (Berkelmans & van Oppen 2006). Interactions between immunity and pathogens will also
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6 391 help to shape the TPC; for example, crickets deactivate low temperature immunity during cold
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8 392 acclimation in a trade-off with other physiological activities that contribute to $w(T_b)$ (Ferguson *et*
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10 393 *al.* 2016). Thus, $w(T_b)$ and $p(T_b)$ can be altered by numerous interactions involving hosts and
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12 394 symbiotic or pathogenic microbiota.
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17 396 **Breaking down $p(T_b)$**

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20 397 Global models of ectotherm responses to climate change depend on the relationship between
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22 398 fitness and T_b , and thus the distribution of T_b animals experience, $p(T_b)$. Although T_b has been
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24 399 extensively measured and modelled for animals, empirical T_b distributions are seldom
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27 400 incorporated in global-scale analyses, which tend to substitute large-scale meteorological air- or
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29 401 water-temperature datasets for T_b , and thus ignore behavioural thermoregulation and micro-scale
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31 402 environmental variation (Kearney *et al.* 2009; Sears *et al.* 2011; Potter *et al.* 2013). In the
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33 403 simplest cases, such as a soil ectotherm that does not thermoregulate, $p(T_b)$ will be very close –
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35 404 if not identical – to the distribution of operative temperatures, $p(T_e)$, measured in the soil.
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37 405 However, the assumption that $T_e = T_b$ is often extended into heterogeneous situations, to animals
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39 406 with significant capacity to regulate T_b , or to animals whose T_b is affected by morphology,
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41 407 thermal inertia, or surface coloration; in these situations, instantaneous $T_e \neq T_b$. Moreover,
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43 408 behavioral thermoregulation and physiology can decouple T_b from T_a in space and time (Fig. 7;
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45 409 Sunday *et al.* 2014). Interspecific interactions can also shift $p(T_b)$: grasshoppers exposed to
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47 410 avian predators move to lower (cooler) positions in the vegetation (Pitt 1999). Thus, properly
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49 411 quantifying $p(T_b)$ is essential for improving the accuracy and precision of conclusions about
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51 412 ectotherm responses to climate change.
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6 414 Many ectotherms can actively behaviorally thermoregulate to maintain a $p(T_b)$ with a mean and
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8 415 variance that are substantially different from $p(T_e)$. Behavioral thermoregulation can be highly
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10 416 active, such as in lizards that shuttle from shade to sun (Kearney *et al.* 2009), or more passive,
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12 417 such as the periwinkle *Echinolittorina peruviana*, which orients its narrower sides towards the
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14 418 sun on hot days (Muñoz *et al.* 2005). There are hard limits to plasticity of CT_{max} in at least some
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16 419 species (Stillman 2003), which means that behavioral thermoregulation will be essential for
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18 420 survival of tropical stenotherms with limited plasticity and small TSMs (Kearney *et al.* 2009;
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20 421 Sunday *et al.* 2014).
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27 423 In many animals, T_b can be measured directly in nature and thus generate accurate values for
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29 424 $p(T_b)$. Methods for estimating T_b of free-ranging animals in nature include telemetry (e.g.
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31 425 Mitchell *et al.* 1997; Briscoe *et al.* 2014) as well as instantaneous measurements of T_b in freshly-
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33 426 captured animals (e.g. 'grab and stab' in insects; Bartholomew & Heinrich 1973). Telemetry
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35 427 does not interfere with an organism's thermoregulation and movements, and allows
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37 428 measurements during both active and inactive periods, but can only be used on species large
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39 429 enough to surgically implant a sensor. However, small data loggers can also be attached or
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41 430 implanted, but must later be collected (Davidson *et al.* 2003).
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48 432 Alternatively, $p(T_b)$ can be estimated via physical models ('biomimetic sensors'), such as
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50 433 'robomussels' (Helmuth *et al.* 2002): such models can accurately mimic the physical properties –
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52 434 and thus equilibrium heat exchange – of specific organisms in a given microclimate (Bakken
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54 435 1992). Most such models are dry-skinned, so assume negligible evaporative heat loss (but see
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3 436 Köhler *et al.* 2011; Monaco *et al.* 2015), but do account for size, shape, and color in generating
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5 437 maps of T_b . Automatic recordings from biomimetic sensors can easily provide long-term (even
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7 438 multi-year) records (Helmuth *et al.* 2010); but (except for completely sessile organisms such as
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9 439 intertidal bivalves), they necessarily ignore behavioral thermoregulation. Other approaches
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11 440 deploy biomimetics in multiple potential habitats, and then estimate realized $p(T_b)$ using a series
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13 441 of behavioral rules, such as optimization of performance or avoidance of extremes (e.g. Monaco
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15 442 *et al.* 2015).

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22 444 An alternative (or adjunct) to using direct biomimics to estimate $p(T_b)$ is to develop biophysical
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24 445 (e.g. heat budget) models that predict T_b from environmental variables (e.g. wind speed, air
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26 446 temperature, and solar radiation) and the physical properties of the organism, and then use
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28 447 climate projections to develop an overall heat budget and thus estimate $p(T_b)$ (Kearney *et al.*
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30 448 2009). These relationships are not necessarily simple: the size, color, morphology, and
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32 449 orientation of organisms alters heat exchange with their environments (and thus T_b); the thermal
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34 450 properties of materials vary (e.g. shell has a lower specific heat capacity than wet tissues), as do
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36 451 the properties of surfaces presented to the environment. Similarly, body size can buffer rapid
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38 452 changes in temperature (larger animals have higher thermal inertia), but even large animals can
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40 453 modify heat exchange via thermal windows such as large bills, fins, or ears (e.g. Tattersall *et al.*
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42 454 2009). To account for all of this variety, biophysical models must be developed in a species-
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44 455 specific (and maybe even a life-stage-, morph-, or sex-specific) manner, making it difficult to
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46 456 extrapolate broadly in space, time, or across species.

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55 458 *Can we predict future $p(T_b)$?*
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3 459 Global-scale predictions of responses to climate change require prediction of future $p(T_b)$. This
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6 460 is theoretically possible via biophysical models (Kearney *et al.* 2009), but changes in cloud-,
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8 461 plant-, and snow-cover could easily modify thermal environments, and thus $p(T_b)$, even without
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10 462 changes in climatic temperature. One approach to understanding how $p(T_b)$ may change is to
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12 463 observe how $p(T_b)$ changes in response to latitudinal or altitudinal gradients as an analogue to
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15 464 changes in time (space for time substitution) (Halbritter *et al.* 2013). However, such
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17 465 extrapolation is inherently problematic, because $p(T_b)$ may not change in time in the same way it
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19 466 does in space at present, and confounding factors, such as variation in cloud or vegetation cover
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21 467 or in radiation loads, are unaccounted for in a space-to-time substitution. In fact, empirical data
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23 468 show that geographic and altitudinal patterns do not always conform to simple gradients due to
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25 469 the over-riding importance of local environmental conditions. Thus, elevation and latitude can be
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27 470 misleading metrics of thermal stress in the future (Helmuth *et al.* 2002; Pearson *et al.* 2009), and
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29 471 they should be used as proxies only with appropriate caution.
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36 473 A simplistic (but common) approach is to use predicted changes in average air temperature (e.g.
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38 474 “+2 °C” for a given site) to predict future T_b and thus physiological responses and organismal
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40 475 vulnerabilities (Helmuth *et al.* 2014). However, such an approach ignores regional and temporal
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42 476 variation, the importance of extremes (weather events), or changes in variability regimes
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44 477 embedded within large-scale climate (Denny *et al.* 2009). In many cases, ecosystems are already
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46 478 experiencing local and short-term increases in temperature that exceed the projected changes in
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48 479 global averages over the next century. For example, sea surface temperatures in the Gulf of
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50 480 Maine are increasing faster than in the global ocean (Mills *et al.* 2013), and terrestrial
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52 481 temperatures are increasing significantly faster in the Arctic and Antarctic than in other biomes
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3 482 (Nielsen & Wall 2013). Thus, any TPC-based predictions of the responses of ectotherms to
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5 483 climate change are only as good as the assumptions underlying the ‘future climate’ data input
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8 484 into the model – an issue that has, in itself, received extensive discussion (see, e.g., Helmuth *et*
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10 485 *al.* 2014; Pacifici *et al.* 2015).

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15 487 Thus, although $p(T_b)$ has been explored, the temporal and spatial scale best used in ecological
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17 488 models remains subject to debate (Sears *et al.* 2011; Potter *et al.* 2013). Predicting $p(T_b)$ at a
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19 489 global scale will likely require a combination of actual measurements, biomimetic data and
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21 490 biophysical models that incorporate seasonal and ontogenetic variation with behavioral and
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23 491 microclimate modification (e.g. Levy *et al.* 2015). Crucially, these global-scale corrections of
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25 492 $p(T_b)$ will be needed to generate predictions by region or species. One way to generalise such
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27 493 predictions may be to develop models for particular combinations of animal and microclimate
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29 494 characteristics, and then conduct additional analyses to apply these models to appropriate
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31 495 location/species combinations.
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39 497 **Putting Humpty Dumpty back together again**

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41 498 In any science, a general theoretical approach to a problem can be destroyed by piling up
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43 499 multiple objections to its implicit and explicit assumptions, or by enumerating counter examples.
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46 500 With respect to TPCs and the modelling approach exemplified in eqn. 1, we could allow
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48 501 thousands of cuts – some are discussed above – to kill this idea. However, we currently do not
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50 502 see an obvious substitute for the TPC approach. Consequently, we suggest that the best way
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52 503 forward is to modify eqn. 1 to make it more robust, functional, and sensitive to real world issues.
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3 504 Thus, our goal now is to put the Humpty-Dumpty of TPCs (which we and others have now
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6 505 gently smashed) back together again.
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10 507 First, Table 1 demonstrates many challenges with measuring and interpreting $w(T_b)$, particularly
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12 508 in integrating across multiple levels of biological organization. These need to be resolved
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15 509 through laboratory investigations (e.g. using *Drosophila* or other models) to better understand
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17 510 the sources and consequences of inter-individual variation in TPCs, coupled with field-based
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20 511 studies to better understand TPCs in nature. A key goal will be to determine how best to
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22 512 incorporate and predict plastic and evolutionary capacities as well as within- and among-
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24 513 population variation in TPCs. Also, we need to better understand the relationship between
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27 514 instantaneous performance (the subject of most TPCs) and long-term fitness, for example via
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29 515 longitudinal studies in nature, or via molecular or physiological markers of performance
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32 516 characteristics of wild-caught animals. Such an approach will need to recognize that
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34 517 generalizations will not apply to all species and traits. In addition to existing "model systems"
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36 518 (for which we have considerable knowledge of their genetics, physiology, phylogeny and
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38 519 ecology), additional foci should include: ecologically important species that have a
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41 520 disproportionate impact in communities (such as keystone predators and habitat-forming
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43 521 species); invasive species and disease vectors; and species that provide important ecosystem
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46 522 services. Second, temperature is an effective master regulator, and is a good place to start, but we
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48 523 need to evaluate the impacts of multiple interacting stressors plus interactions with the
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50 524 microbiome, all of which modify predictions derived from TPCs. Third, we need to evaluate our
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53 525 estimates of contemporary $p(T_b)$, and consider how this affects our ability to predict future $p(T_b)$.
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55 526 For example, thermal microrefugia may prevent local extinctions (Potter *et al.* 2013), if those
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3 527 refugia persist under climate change (Lima *et al.* 2016). Likewise, we need a better
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5 528 understanding of how anthropogenic activities will affect key modifiers of microhabitat, such as
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8 529 shading, air and water flow or quality, and precipitation.
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12 531 Many opportunities exist for modifying our existing TPC models when making global-scale
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14 532 predictions (Table 1). Mechanistic models of species' distributions are already emerging that
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16 533 account for some of the assumptions we have identified (see Maino *et al.* 2016 for a recent
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18 534 summary). In terms of predicting $w(T_b)$ some cases (e.g. fluctuating temperatures, multiple
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20 535 stressors, biotic interactions) will require more empirical data to determine the extent to which
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22 536 TPCs are predictable and generalizable. In many cases, however, models can and should be
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24 537 adjusted to better account for assumptions we already know to be invalid, such as ontogenetic
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26 538 variation (Kingsolver *et al.* 2011; Levy *et al.* 2015). Earth System Models in the plant sciences,
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28 539 which predict photosynthetic responses to climate change on a global scale, demonstrate that
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30 540 large, complex, trait-based approaches are possible and can be (broadly) successful (Rogers
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32 541 2014). In the long term, we may realise that the current TPC model, which is based on
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34 542 instantaneous performance $p(T_b)$, is flawed, but we do not yet know whether its flaws are fatal
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36 543 and require us to move to a temperature-plus-time-series (and possibly -plus-energetics)
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38 544 approach to account for the complex temporal nature of thermal biology. However, for now, we
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40 545 believe that TPCs offer us at least an opportunity to explore climate change with broad strokes.
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50 547 Ultimately, the TPC-based approach is an heuristic starting point for evaluating the biological
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52 548 impacts of environment and environmental change. Understanding $w(T_b)$ is clearly important,
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54 549 but relating fitness to temperature will be difficult. Similarly, predicting $p(T_b)$ is essential, but
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3 550 currently flawed. Even so, the distribution of body temperatures is not the only physiological
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6 551 variable that matters. Moreover, $w(T_b)$ and $p(T_b)$ aren't independent: the T_b history can modify
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8 552 $w(T_b)$. This is biology. The way forward is thus either to embrace such complications into our
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10 553 theoretical models, or to find whether the biological signal of climate change is sufficiently
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12 554 strong to overpower these complications. Each of the assumptions explored here can be
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15 555 converted into testable hypotheses and then explored in empirical sensitivity analyses, which will
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17 556 provide insights into how much detail is needed and what can be ignored, reducing the
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20 557 uncertainty in the TPC-based approach to predicting the biological impacts of climate change.
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22 558 Simple models like TPCs may therefore have a future, provided we acknowledge the inherent
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24 559 assumptions.
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28 29 561 **Acknowledgements**

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31
32 562 This manuscript arose from the 'Gastropod thermal biology and climate change in the tropics'
33
34 563 workshop held in Brunei Darussalam in December 2014, sponsored through Universiti Brunei
35
36 564 Darussalam (the iCUBE initiative) and the Company of Biologists. KEM was supported by a
37
38 565 postdoctoral fellowship from the Natural Sciences and Engineering and Research Council of
39
40 566 Canada (NSERC); RBH was supported by NSF IOS 1038016 Stine Slotsbo by a grant from The
41
42 567 Danish Council for Independent Research (0602-01369B); CDGH and BJS were supported by
43
44 568 NSERC Discovery Grants; CSW by NSF IOS 1155325; BSH by NSF IOS 1557868; MAS was
45
46 569 supported by the University of Auckland; DLL was supported by the Universiti Malaysia
47
48 570 Sarawak postdoctoral scheme. Thanks to Jackie Lebenzon for the animal vignettes used in the
49
50 571 figures, and to Mike Angilletta, Mark Denny, and an anonymous referee for comments that
51
52 572 improved an earlier version of the manuscript.
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798 **Table 1.** A summary of assumptions often made in evaluations of the relationship among the environment, body temperature, and
 799 fitness, and on their consequent hypotheses and predictions. Many of these have already been shown to be false as general rules; see
 800 text for discussion.

Assumption	Hypothesis	Prediction(s)
<i>Relationship between trait and fitness</i>		
1 The trait x measured reflects fitness	Performance of trait x is directly correlated with W	Individuals with a greater value of x have greater lifetime reproductive output.
<i>Variation in developmental and evolutionary contexts</i>		
2 Thermal performance does not change with development and reproduction	The form of the TPC is static through an individual's lifetime if the environment is static	Measured $TPCs$ will not change during development/maturation in a predictable manner for a given species
3 Thermal performance does not vary across a species' geographic range	$w(T_b)$ is invariant within a species	No local adaptation of $TPCs$
4 $TPCs$ will not change with climate change in the short term	$w(T_b)$ does not evolve rapidly	No rapid evolution of $TPCs$
5 $TPCs$ can be extrapolated to higher taxonomic levels	$w(T_b)$ is phylogenetically constrained	Hierarchical taxonomic structuring of TPC properties
<i>Physiological variation</i>		
6 Prior thermal experience does not matter	$w(T_b)$ is invariant with respect to prior temperature exposure	1. $TPCs$ are independent of the order of temperature exposure 2. $TPCs$ do not change with repeated exposures
7 Extreme exposures do not matter	$w(T_b)$ does not change if temperature cycles cross physiological thresholds	1. $TPCs$ will not change after pre-exposure to temperatures above the T_{opt} or close to the CT_{max} and CT_{min} 2. $TPCs$ will not vary even with multiple exposures to a thermal cycle
8 Rate of temperature change does not matter	$w(T_b)$ is invariant with respect to rate of temperature change	$TPCs$ will not differ between rapid or slow temperature transitions
9 Duration of temperature exposure does	$w(T_b)$ estimates are robust to the	$TPCs$ will not differ when calculated from long or short

1	not matter	duration of thermal exposure	exposure to each temperature
2			
3	<i>Temperature as the primary driver of fitness</i>		
4	10	Variation in thermal performance due	The majority of inter-individual
5		to stochastic variation or biotic impacts	variation in $w(T_b)$ is heritable
6		(e.g. in parasitism, microbiota, and	1. Heritable variation in <i>TPCs</i> exceeds plasticity
7		nutrition) can be ignored	2. <i>TPCs</i> and $p(T_b)$ are not affected by inter- and intra-
8			specific interactions
9			
10	11	Temperature is the only environmental	$w(T_b)$ is invariant across gradients
11		parameter whose changes affect fitness	of additional abiotic factors
12			The <i>TPC</i> will not change with variation in non-thermal
13			environmental parameters.

For Review Only

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3 801 **Text Box 1: A Glossary of Thermal Biology Terms**
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5 802 CT_{\max} – critical thermal maximum, upper thermal limit of performance.
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8 803 CT_{\min} – critical thermal minimum, lower thermal limit of performance.
9

10 804 OCLTT – oxygen- and capacity-limited thermal tolerance; hypothesis that thermal
11
12 performance at high and low T_b is limited by oxygen availability.
13
14

15 806 T_a – ambient temperature, an imprecise term often used as a synonym for air temperature,
16
17 but can also reflect microhabitat temperature or the (measured) temperature of an animal's
18
19 immediate surroundings.
20
21 808

22 809 T_b – body temperature (usually core).
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24 810 T_{br} – breadth of thermal performance.
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27 811 T_e – operative temperature – equilibrium T_b of a specific organism in a specific
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29 microenvironment, assuming no metabolic heat increment or evaporative cooling.
30
31

32 813 T_{opt} – optimum body temperature, at which performance is maximal.
33

34 814 TPC – thermal performance curve; depicting performance as a function of T_b
35

36 815 T_p – preferred (selected) body temperature, often measured in a laboratory thermal gradient.
37

38
39 816 TSM – thermal safety margin; various definitions are in use, but TSM is generally inversely
40
41 proportional to the risk of an animal experiencing temperatures above CT_{\max} . Here we
42

43 818 define it as the difference between T_{opt} (or maximum T_b in the field) and CT_{\max} .
44

45
46 819 $p(T_b)$ – frequency distribution of body temperatures.
47

48 820 $p(T_e)$ – frequency distribution of operative temperatures.
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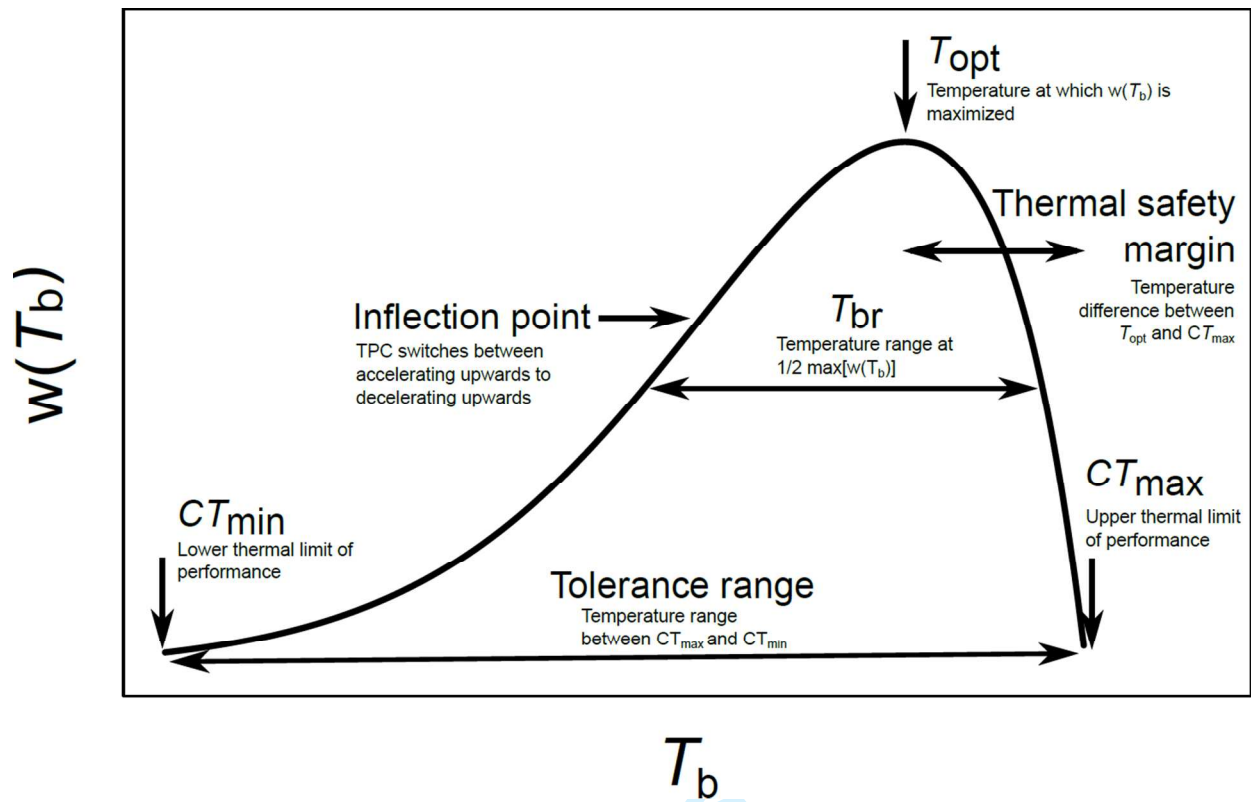
50 821 W – total fitness integrated over some time interval.
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52
53 822 w – fitness.
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55 823 $w(T_b)$ – relationship between fitness with body temperature.
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824 **Figure 1**

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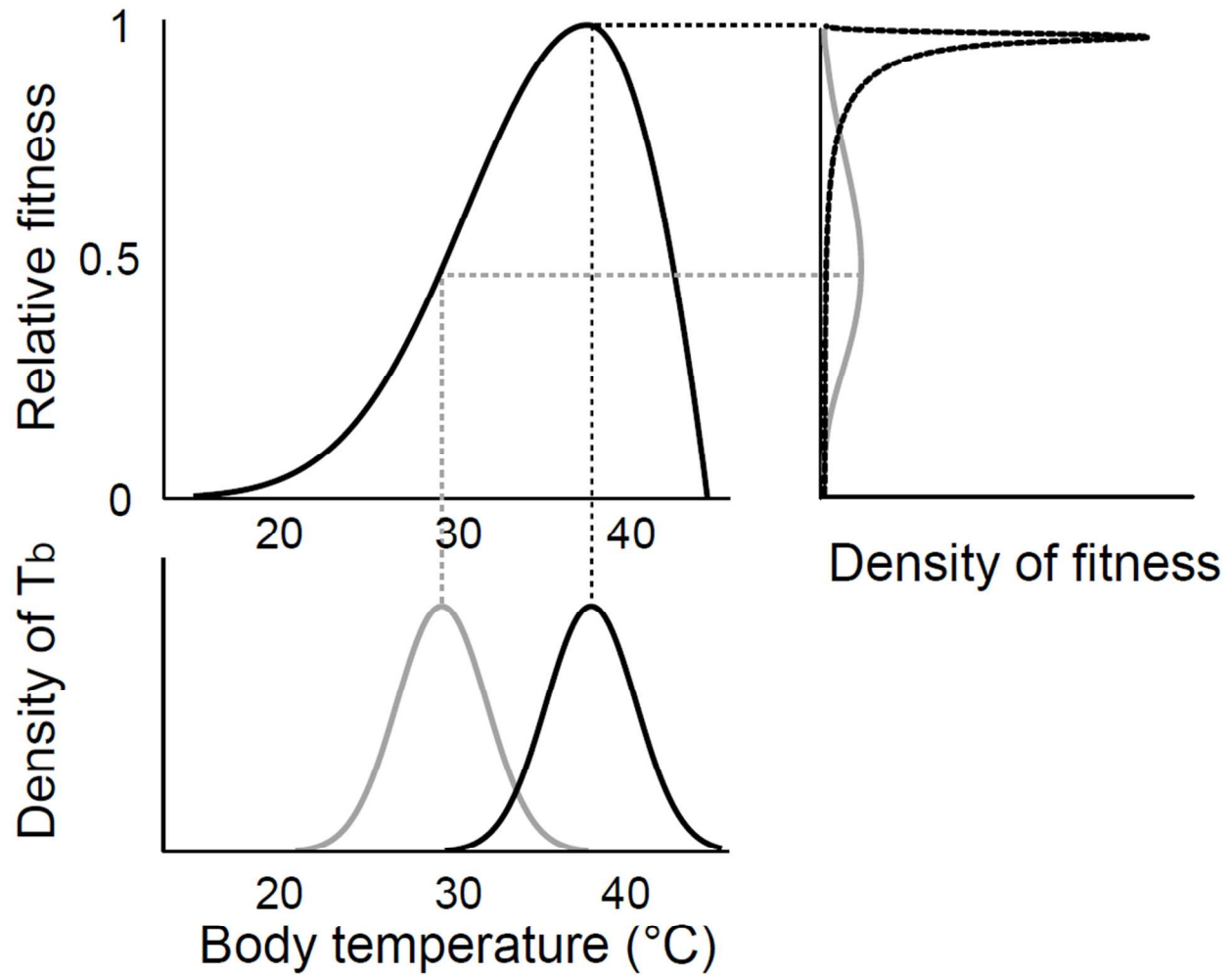
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828 **Figure 1.** A typical thermal performance curve relating body temperature, T_b to fitness $w(T_b)$,
 829 with critical features highlighted (based on Huey & Stevenson 1979). CT_{min} and CT_{max} : Critical
 830 thermal minimum and maximum, respectively; T_{opt} : thermal optimum; T_{br} : Thermal breadth.
 831 This curve is based on the digestion equation from Stevenson et al. (1985).

832 **Figure 2**

833



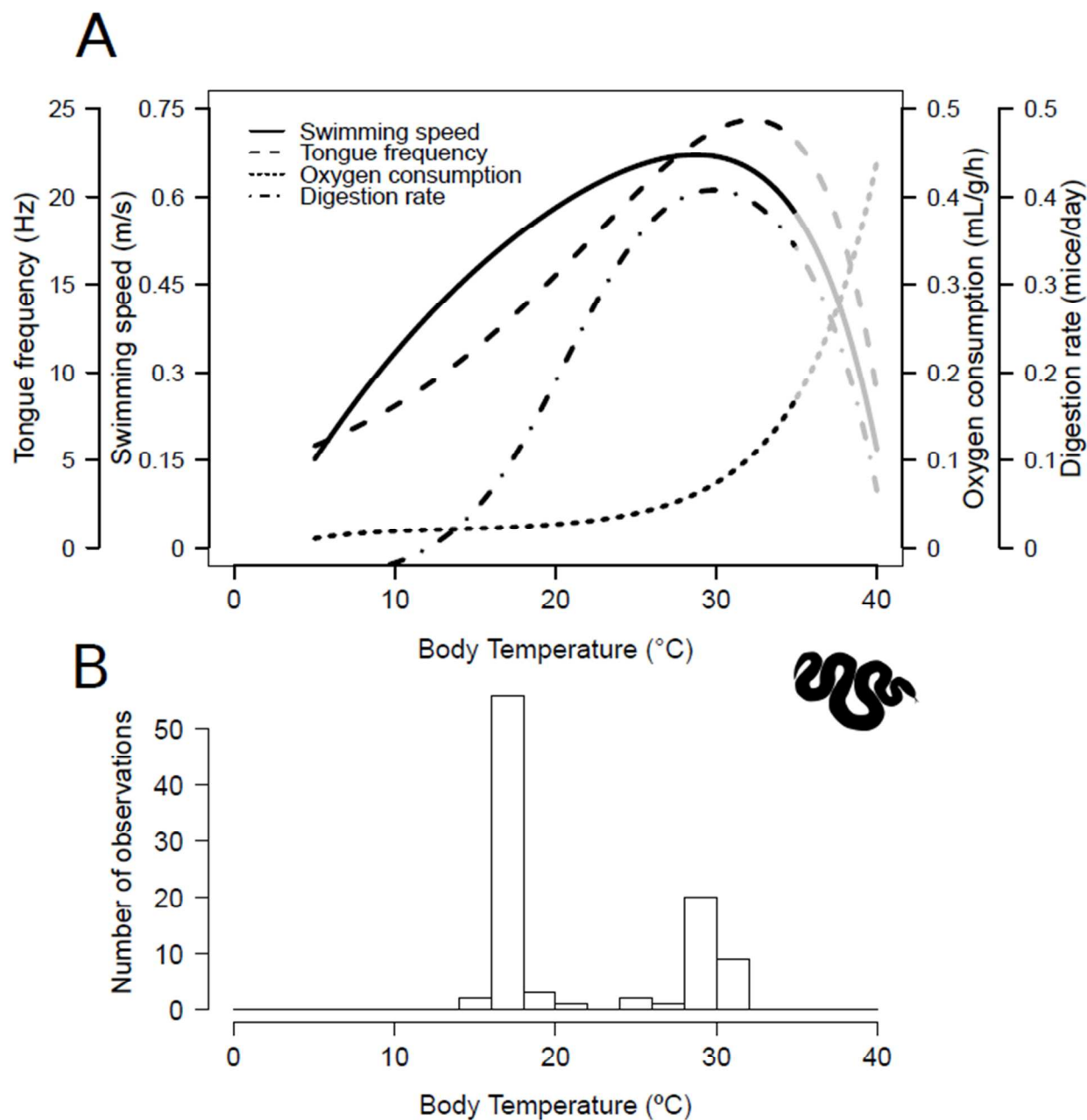
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836 **Figure 2.** a) An hypothetical *TPC* showing relative fitness (0 to 1) as a function of body
 837 temperature (see also Fig. 1). b) Two representative distributions of body temperatures (grey =
 838 low T_b , black = high T_b). c) Density of relative fitness for the two T_b distributions in b),
 839 calculated from Eqn. 1. The average fitness is much higher for the ectotherm with the higher T_b
 840 distribution. Based on Vasseur et al. (2014).

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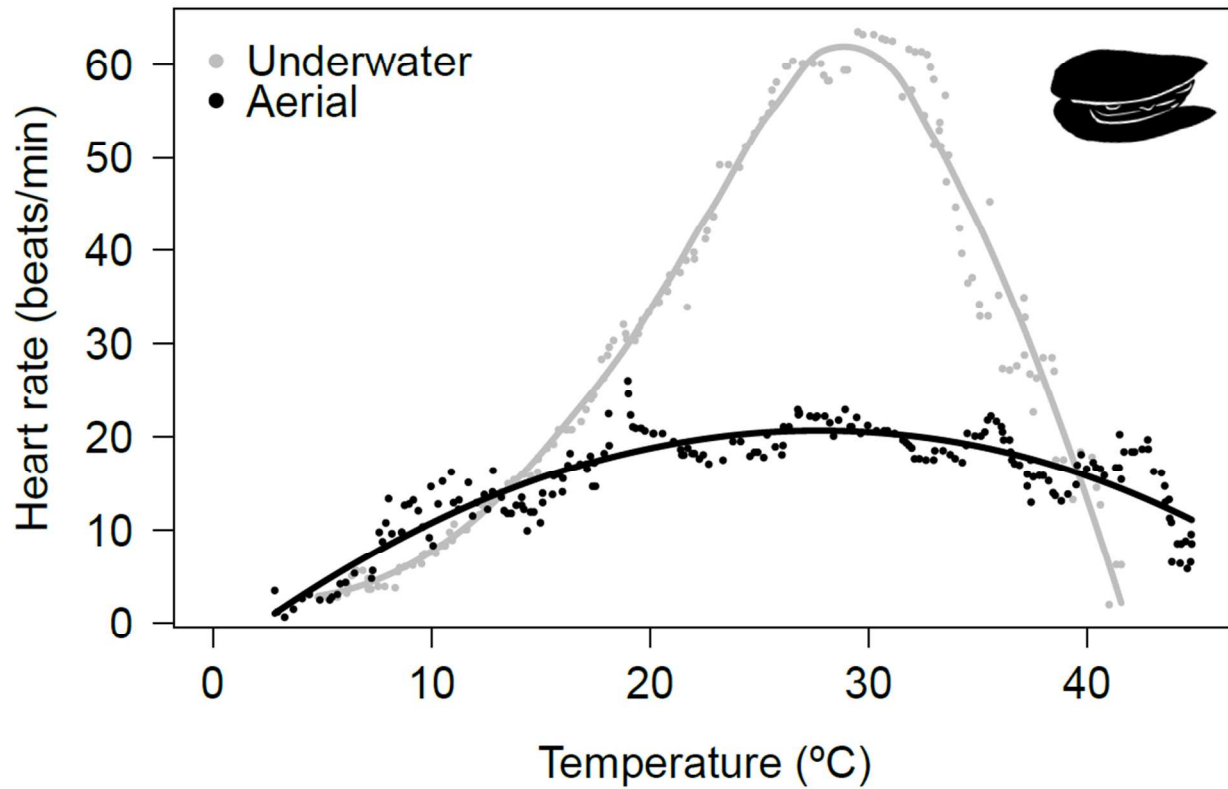
842

843 **Figure 3**

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845
846 **Figure 3.** A) Variation in thermal performance curves for four different traits measured in the
847 western garter snake *Thamnophis elegans*. Grey lines indicate parts of the curve that were
848 extrapolated beyond the range of empirical data. B) The distribution of *T. elegans* field body
849 temperatures as measured by radiotelemetry at 15 min intervals over the course of 24 h. Note the
850 significant difference between the distribution of body temperatures and the TPC. Data from
851 Stevenson *et al.* (1985).

852 **Figure 4**

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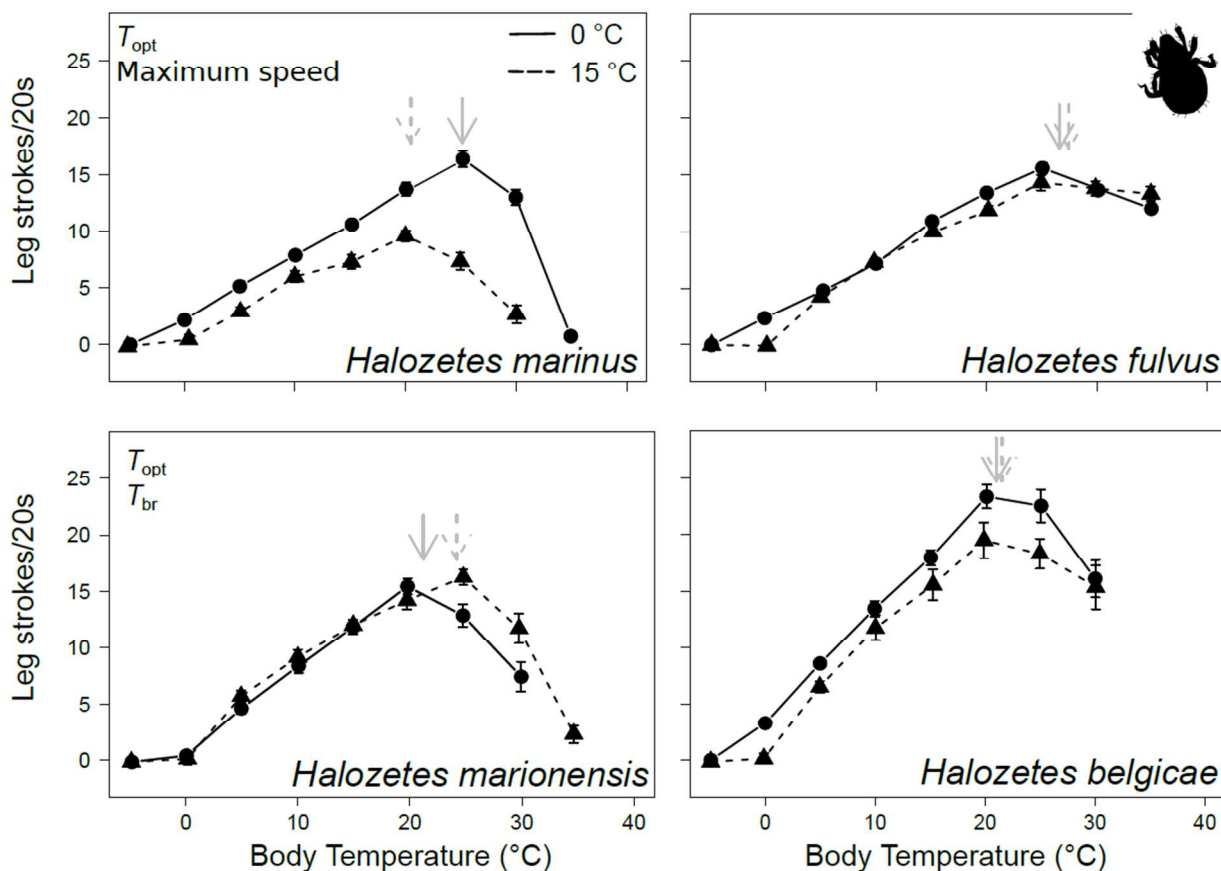
855

856 **Figure 4.** Sensitivity of thermal performance of heart rate to immediate conditions in the brown
857 mussel *Perna perna*. Black lines and points are for emersed mussels, grey lines and points for
858 immersed. Data from Tagliarolo and McQuaid (2015). Lines of best fit are plotted using a
859 locally-weighted polynomial regression implemented by the loess function in R.

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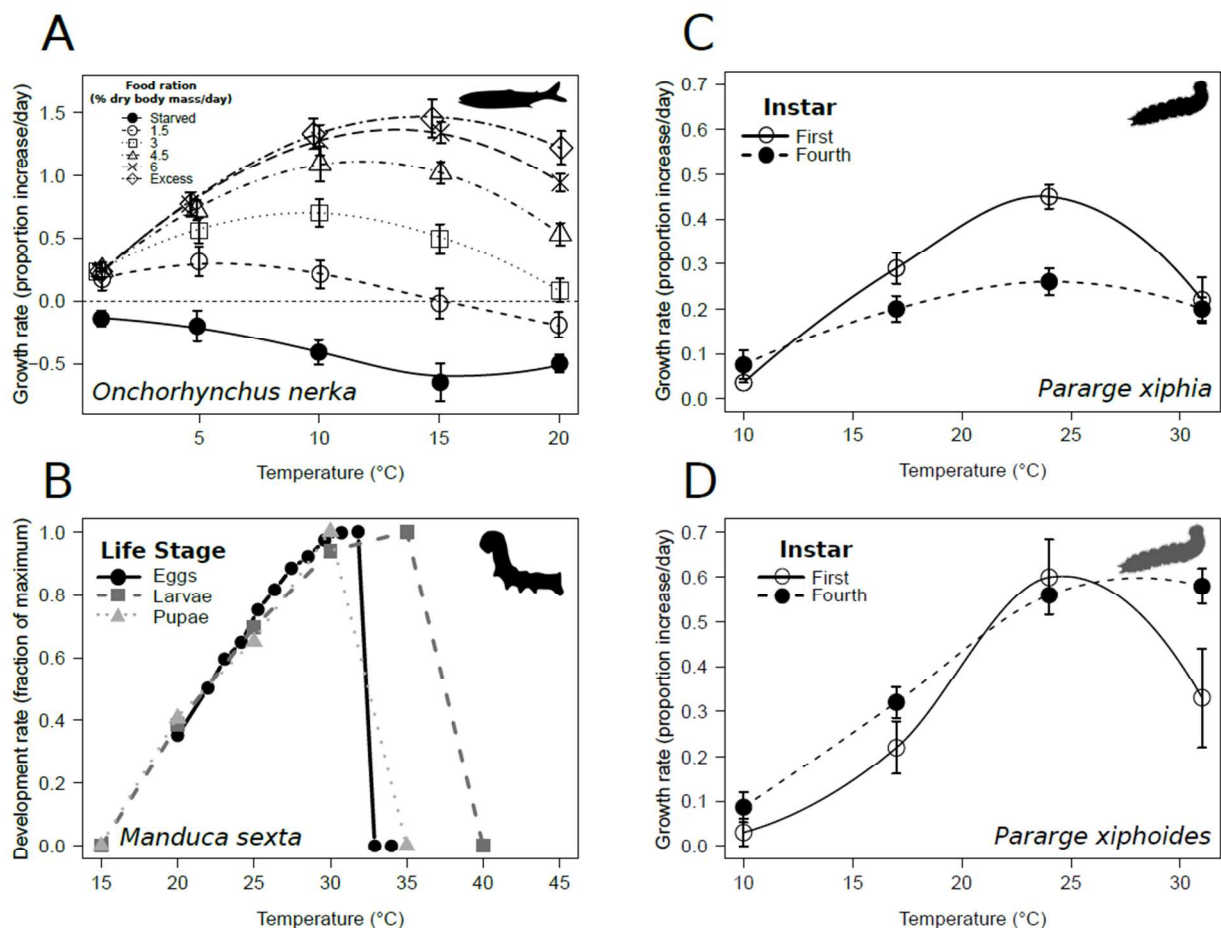
861

862 **Figure 5**



863
 864 **Figure 5.** Variation in form and phenotypic plasticity of thermal performance curves of
 865 locomotor activity for four congeneric species of sub-Antarctic oribatid mites after acclimation at
 866 warm (15 °C, triangles, dashed lines and arrows) and cool (0 °C, circles, solid lines and arrows)
 867 temperatures for 7 d. Arrows indicate T_{opt} . Parameters that differ significantly between
 868 acclimation treatments are listed in the top left of each plot. Data from Deere and Chown
 869 (2006).

870

871 **Figure 6**

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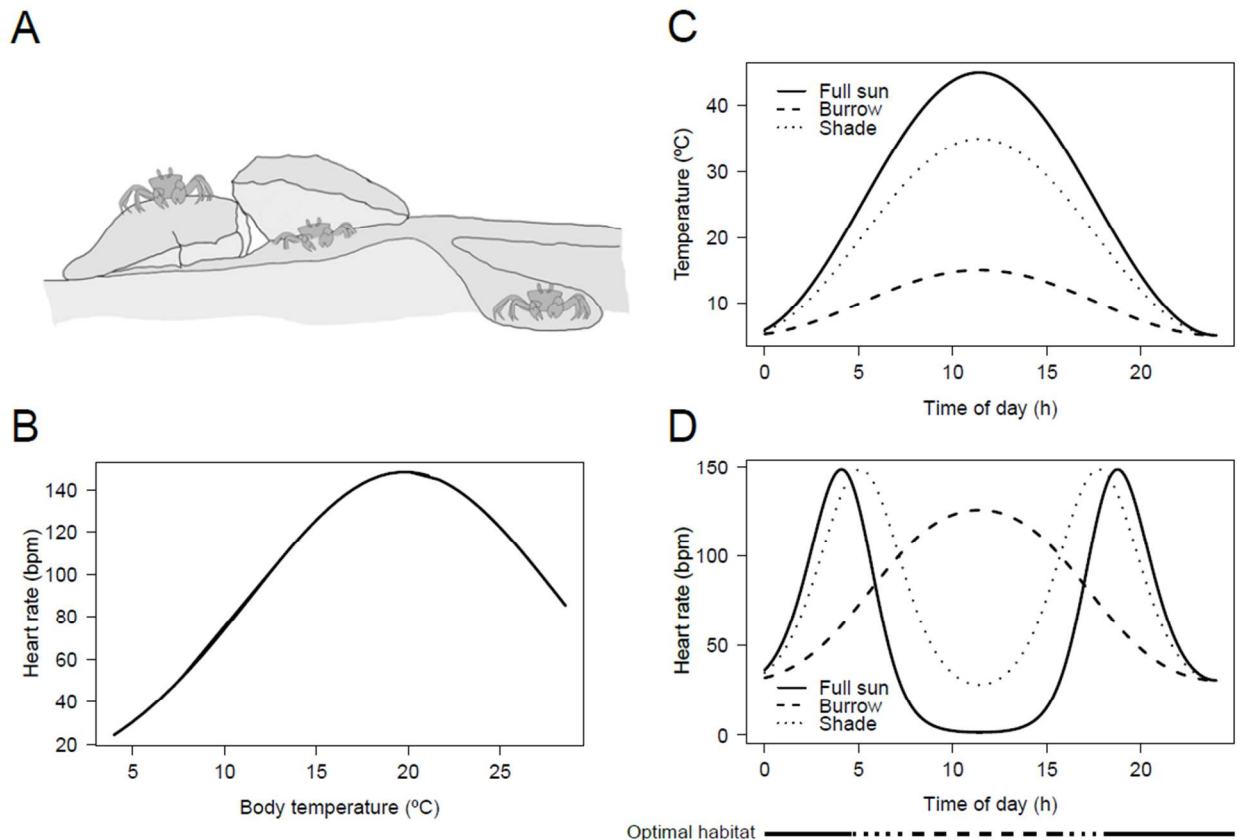
873

874 **Figure 6.** Both nutritional state and ontogenetic stage can affect TPCs. (A) Varying food ration
 875 substantially changes the TPC position and magnitude of T_{opt} or growth rate in juvenile sockeye
 876 salmon (*Oncorhynchus nerka*). Data from Brett et al. (1969). (B) TPC shape is determined by
 877 developmental stage (eggs, larvae, or pupae) in the sphinx moth *Manduca sexta*. Data from
 878 Kingsolver et al. (2011). (C, D) Species \times development interaction in TPCs for growth rate of
 879 nymphalid caterpillars in the genus *Pararge*. The among-species shift likely reflects behavioral
 880 differences: *P. xiphia* becoming increasingly nocturnal and *P. xiphoides* increasingly diurnal
 881 over the course of development. Data from Berger et al. (2011).

882

883 **Figure 7**

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887 **Figure 7.** Behavioral thermoregulation can decouple environmental temperature and body
 888 temperature. In this example, crabs may choose between full sun, shade, and burrow habitats
 889 (A). The TPC of heart rate in the porcelain crab *Petrolisthes violaceus* (B) is based on data from
 890 Gaitán-Espitia et al. (2014). Environmental temperature varies across habitats through the day
 891 (C), data from Schneider and Helmuth (2007), and so heart rate in *P. violaceus* (modelled from
 892 B and C) will depend on which habitat it is occupying at which time of day (D), with the optimal
 893 habitat (where heart rate is maximized) varying through the course of the day.

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