How to quantify thermal acclimation capacity?

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Main text

An experienced change in environmental temperature may cause phenotypic trait values to deviate from optimality. This may be due to acute phenotypic changes (i.e. passive phenotypic plasticity), and/or temperature-dependent optima. This in turn triggers an acclimation response that may last from days to months, whereby the organism attempts to regain optimality of phenotype. Their capacity to acclimate will influence their ability to cope with ongoing global changes in thermal regimes (Stillman 2003). To gain insights into the sources of variation in acclimation capacity Rohr et al. (2018) reanalyzed the data of Seebacher et al. (2015). However, we believe that their approach introduces two problems:

1) Data analyzed by Rohr et al. originate from studies that were primarily (322 out of 333 cases) conducted by measuring traits (mostly physiological/biochemical) in 2×2 factorial design experiments, with two acclimation temperatures and two measurement temperatures (Fig. 1a). Yet, they only use the data obtained when measuring the traits at the temperature that the individuals were acclimated to (‘post-acclimation response’), and define a high acclimation capacity as a flat post-acclimation response, independent of changes occurring during acclimation (Fig. 1a,b). This may introduce a bias, because it requires more pronounced changes in the quantity and quality of cellular biochemistry and structures to obtain a flat post-acclimation response for traits that show a steep acute response (Fig. 1a *vs*. 1b). Evidence of such a bias is revealed by a strong negative correlation between the index of acclimation capacity used by Rohr et al. and the estimated mean acute response measured in the same studies (i.e. high mean acute responses are associated with low acclimation capacity values, Fig 2, R = -0.55, df = 320, P < 0.001; cases selected as below). Therefore, variation in

acclimation capacity as calculated by Rohr et al. is largely driven by variation in the acute response.

2) The approach used by Rohr et al. follows the implicit assumption of Seebacher et al. (2015) that all acclimation responses cause a reduced thermal response in a trait post-acclimation compared to the acute response (Fig. 1a,b). We contend that any measure of acclimation capacity should acknowledge that acclimation may also result in organisms showing an *increased* trait response after acclimation is complete (Fig. 1c). This will occur if the optimal value of a trait increases with temperature, and animals need time to produce this altered phenotype. For example, when the zooplankter *Daphnia magna* is exposed to a high temperature they gradually (over ca. 5 days) increase their hemoglobin concentration to allow for oxygen supply to match demand (Seidl et al. 2005). This allows them to maintain fitness across temperatures by *increasing* the thermal response of a trait through acclimation. To evaluate the prevalence of this type of acclimation, we considered the data subset of Seebacher et al. analysed by Rohr et al. (333 cases), and compared post-acclimation (the slope of the ln-transformed trait against temperature for animals acclimated to the measurement temperature, $S_{post-acclim}$) and acute temperature responses (the mean acute slope $\overline{S_{acute}}$; defined in Fig. 1). For 286 of the 322 cases (11 excluded due to lack of data on mean acute responses), both types of slopes were ≥ 0 and the post-acclimation slope was steeper than the mean acute slope in 43% of these 286 cases (123 observations). Thus, rather than resulting in a reduced temperature response as assumed by Rohr et al., acclimation appears to increase the thermal response (as in Fig. 1c) in a substantial proportion of these data. The high frequency of this type of acclimation response is surprising. If such observations are primarily due to experimental error, this limits our ability to accurately

estimate the complex effects of various predictor variables on acclimation capacity based on these data.

Issues with how acclimation capacity is quantified can also be found in other studies. For example, Markle and Kozak (2018) define acclimation capacity as the magnitude of increase in standard metabolic rate (SMR) at a common measurement temperature when acclimated to a warmer temperature. This approach assumes that the optimal SMR increases with temperature. However, one might just as well argue that organisms that downregulate SMR when acclimated to high temperature counteract a potentially negative acute response to temperature, and hence have a high acclimation capacity.

We suggest that these issues can be dealt with by calculating acclimation capacity as the absolute value of the difference between the post-acclimation slope and the mean acute slope, i.e. $|S_{post-acclim} - \overline{S_{acute}}|$. By taking the absolute value of this difference, a large positive value (i.e. high acclimation capacity) is obtained independently of the type of acclimation response (an increase or decrease in slope). Furthermore, acclimation capacity is assessed relative to the magnitude of the acute response. We urge future comparative analyses to adopt our approach that better reflects the acclimation process *per se*.

References

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Figures

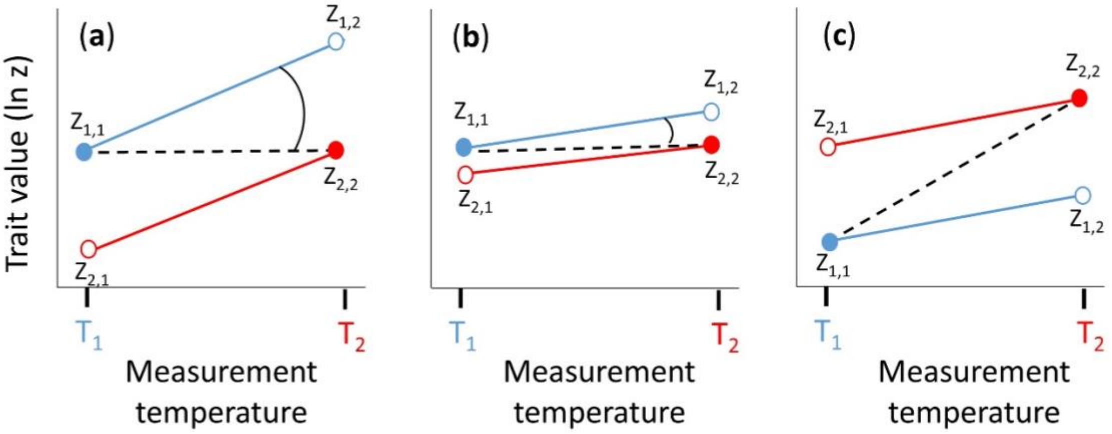

Fig. 1. Trait expression as a function of acclimation and measurement temperature. Blue and red solid dots ($Z_{1,1}$ and $Z_{2,2}$) represent trait values for individuals acclimated to and measured at low (T_1) and high temperature (T_2), respectively. Open circles represent trait values for animals when measured at a temperature different from their acclimation temperature ($Z_{2,1}$ and $Z_{1,2}$). The slope of the dashed line is the thermal response of the trait following complete acclimation ($S_{post-acclim}$), and the mean slope of the red and blue solid lines gives the mean acute response ($\overline{S_{acute}}$). Panels show (a) a high acclimation capacity (large difference in slopes between solid and dashed lines), and (b) a low acclimation capacity. In contrast, panels (a) and (b) would yield an identical high acclimation capacity according to index used by Rohr et al. (2018) ($-log_{10}(\left|1-\left(\frac{e^{Z_{2,2}}}{e^{Z_{1,1}}}\right)^{\frac{10}{(T_2-T_1)}}\right|+0.001)$). Panel (c) shows an increase in the thermal response of a trait through acclimation.

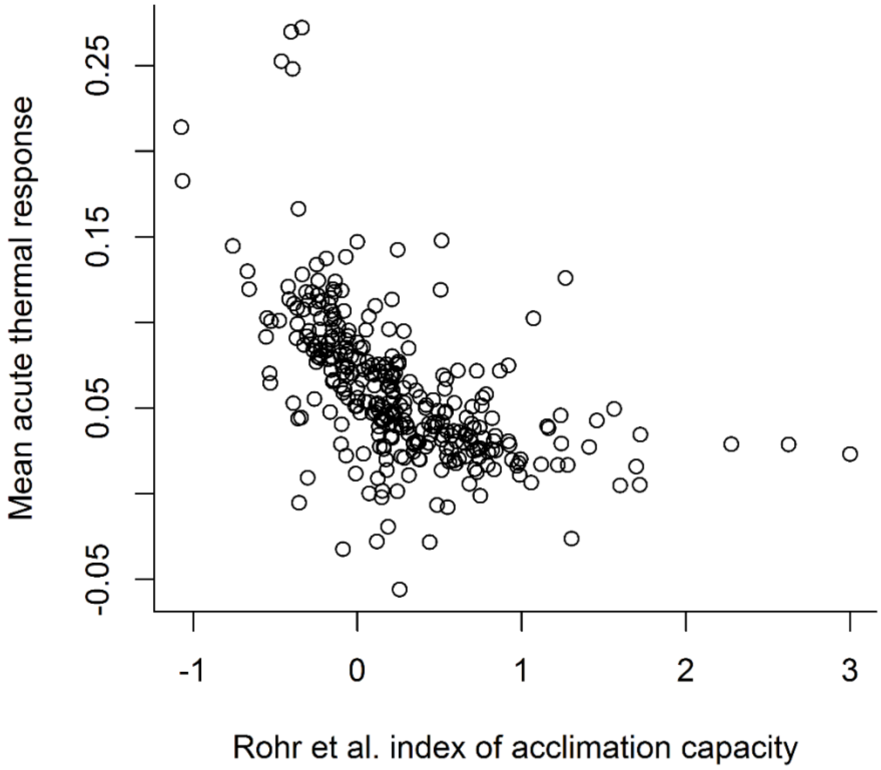

Fig. 2. Correlation between the index of acclimation capacity used by Rohr et al. (2018) and the mean acute thermal response.