Plasticity of preferred body temperatures as means of coping with climate change?

Thermoregulatory behaviour represents an important component of ectotherm non-genetic adaptive capacity that mitigates the impact of ongoing climate change. The buffering role of behavioural thermoregulation has been attributed solely to the ability to maintain near optimal body temperature for sufficiently extended periods under altered thermal conditions. The widespread occurrence of plastic modification of target temperatures that an ectotherm aims to achieve (preferred body temperatures) has been largely overlooked. I argue that plasticity of target temperatures may significantly contribute to an ectotherm’s adaptive capacity. Its contribution to population persistence depends on both the effectiveness of acute thermoregulatory adjustments (reactivity) in buffering selection pressures in a changing thermal environment, and the total costs of thermoregulation (i.e. reactivity and plasticity) in a given environment. The direction and magnitude of plastic shifts in preferred body temperatures can be incorporated into mechanistic models, to improve predictions of the impact of global climate change on ectotherm populations.

Keywords: acclimation; climate change; ectotherms; thermoregulatory behaviour

1. INTRODUCTION

Many ectotherms effectively reduce variation in their body temperatures imposed by the thermal environment by using various behavioural adjustments. Recently, the role of behavioural thermoregulation in coping with climate change has been examined in several mechanistic models predicting the time budget, distribution and extinction probability of ectotherm populations under various global warming scenarios [1–4]. All these studies assumed that an ectotherm maintains its body temperature within a fixed range of ‘target’ body temperature (i.e. preferred body temperatures; $T_p$). Although acute adjustments (i.e. the reactive component of behaviour [5]) prevail in both ectotherms’ compensatory repertoires and thermoregulatory studies, thermoregulatory behaviour can be modified by a plastic physiological component, i.e. the seasonal or developmental plasticity (acclimation) of preferred body temperatures [6–9], whose role in coping with climate change has been largely neglected.

2. IMPORTANCE OF $T_p$ PLASTICITY UNDER CLIMATE CHANGE

The contribution of $T_p$ plasticity to an ectotherm’s non-genetic adaptive capacity (see [10]) seems obvious. According to climate warming scenarios, an increase in operative temperature may reduce activity time (e.g. [11]). The resulting restricted time budget may compromise fitness-related activities, such as foraging and mating, which will lead to population decline, and ultimately extinction. However, if the plastic response moves the $T_p$ range in the direction of local climatic trends, it broadens the time window for activity, and thereby partially or fully compensates for the climatic change. It follows that the compensatory potential of $T_p$ shift depends on the magnitude, direction and costs of plastic response.

3. WHY IS $T_p$ PLASTICITY IGNORED?

The reason why plasticity of preferred body temperatures has received limited attention from global change biologist remains unknown. Possibly several thermal biologist, working mostly on lizard models, may have failed to find flexible $T_p$, and thus the plastic response was often considered non-existent or unimportant. This prevalent view probably resulted for three reasons. Firstly, plasticity experiments were frequently carried out using an abrupt shift in constant temperature regimes, whereas most ectotherms are subject to a gradual change in the mean and magnitude of diel temperature fluctuations in the field [12]. It can be reasonably assumed that failure to detect the presence of $T_p$ plasticity represent an artefact of ecologically unrealistic experiments rather than biological reality. Indeed, diverse ectotherms decrease their preferred body temperatures after prolonged exposure to a given thermal regime [13–15], which is sometimes interpreted as a compensatory response to high and/or constant treatment temperatures [16,17]. Recent findings demonstrate that constant and fluctuating temperature regimes induced a seasonal shift in preferred body temperature (in the same direction), although responses to diel temperature fluctuations appear more pronounced than responses to constant temperature ([18]; figure 1a). Therefore, experiments realized under constant temperatures may underestimate the magnitude of $T_p$ plasticity.

Secondly, the magnitude of plastic shifts has been argued to be relatively small. Although numerous studies corroborate this [19,20], several facts should be considered before accepting this conclusion. Apart from the ‘constant temperature’ factor mentioned earlier, studies on $T_p$ plasticity have considered either a seasonal or developmental response. However, some species possess both a developmental and seasonal plastic capacity for $T_p$ (figure 1). If both developmental and seasonal influences contribute to $T_p$ plasticity additively, the overall plastic capacity of $T_p$ will be, in fact, higher than previously assumed.

Finally, $T_p$ plasticity is often considered to be less important for coping with climate change than acute thermoregulatory adjustment. To evaluate the relative contribution of both thermoregulatory $T_p$ components to population persistence, I used the recently published model by Chevin et al. [21] (see also the electronic supplementary material). In the case of
thermoregulatory behaviour, the persistence of ectotherm populations in the presence of climate change depends on a strategy that minimizes deviation of the thermal reaction norm for $T_p$ from the environmental sensitivity to selection of this trait, i.e. change in its optimum value with environmental temperature (figure 2). Since sensitivity to selection is largely determined by reactive component of thermoregulatory behaviour, the less effective thermoregulation is compensated by the higher extent of plastic capacity of $T_p$ and vice versa. However, this strategy critically depends on the total cost of employing both components. If costs are high, an optimal strategy relaxes the compensatory potential of both components.

Figure 1. (a) Seasonal and (b) developmental thermal acclimation of preferred body temperatures in the alpine newt, Ichthyosaura alpestris. (a) Body temperatures were measured sequentially after overwintering at 5°C and after six weeks exposure to 15°C or 10°C–20°C (Hadamová & Gvoždík [18]; ©2011 The University of Chicago Press). (b) Body temperatures of 3-day-old larvae that were subjected to disparate fluctuating thermal regimes during embryogenesis (R. Smolinský & L. Gvoždík 2010, unpublished data).

Figure 2. The influence of the absolute difference between the reactive component of thermoregulatory behaviour ($R$) and plasticity of preferred body temperatures ($P$) on the maximum rate of sustainable climatic change (i.e. shift in environmental temperature when population growth $> 0$) under various total (i.e. reactive and plastic) costs of thermoregulation ($c_t$). If $c_t$ is relatively low, a population sustains a higher rate of environmental change as $|R - P|$ approaches zero. Under high $c_t$, the best strategy is to relax both components at the expense of lowered capacity of thermoregulation for coping with climate change. The parameter $R$ is the slope of function showing how the local adaptive optimum in preferred body temperatures ($T_p$) changes with mean operative temperature in a given habitat. $R$ is determined by the effectiveness of acute thermoregulatory adjustments. $P$ is the slope of the thermal reaction norm for the mean preferred body temperature ($T_p$). Total costs of thermoregulation involve both costs of maintaining body temperatures within the $T_p$ range and costs of plastic modifications (seasonal or developmental plasticity) of $T_p$. Modified after Chevin et al. [21]. See the electronic supplementary material for details.
As a result, plasticity of $T_p$ should be advantageous in habitats where reactivity of thermoregulatory behaviour does not fully buffer variation in the thermal environment and the total costs of thermoregulation are relatively low.

4. FUTURE PROSPECTS

The arguments mentioned earlier suggest that plasticity of $T_p$ may be widespread and potentially an important part of ectotherms adaptive response to climate change. However, to fully understand the role of $T_p$ plasticity in this context, more information is needed. To improve the current state of knowledge, I highlight three areas for further research. (i) Reactivity of thermoregulatory behaviour and plasticity of $T_p$—although components of behavioural thermoregulation have been frequently examined individually, studies that consider both reactive and plastic components are lacking. Concerning the plastic component, attention should be dedicated not only to seasonal responses but also to plasticity induced during development. The developmental plasticity of $T_p$ seems particularly important in tropical species that are, in general, subjected to lower seasonal variation in operative temperatures than temperate taxa [12]. (ii) Costs of thermoregulation—clearly, costs of thermoregulation are more complex than previously thought. The costs of a reactive component, such as energy and time spent thermoregulation or predation risk have been examined several times [23–25]. In contrast, the various costs of $T_p$ plasticity may be much more diverse (see [26–28]) and are virtually unknown. (iii) Mechanistic models—it seems likely that ignoring $T_p$ plasticity overestimates the influence of global warming on the dynamics and persistence of ectotherm populations. Indeed, recent analyses demonstrated that mechanistic models based on fixed $T_p$ range predicted more pronounced range shifts in response to climate change than correlation models [29]. Further elaboration of mechanistic models by incorporating both $T_p$ plasticity and total costs of behavioural thermoregulation should yield more reliable predictions about the impacts of ongoing climate change.

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