Testing the beneficial acclimation hypothesis

Robbie S. Wilson and Craig E. Franklin

Recent developments in evolutionary physiology have seen many of the long-held assumptions within comparative physiology receive rigorous experimental analysis. Studies of the adaptive significance of physiological acclimation exemplify this new evolutionary approach. The beneficial acclimation hypothesis (BAH) was proposed to describe the assumption that all acclimation changes enhance the physiological performance or fitness of an individual organism. To the surprise of most physiologists, all empirical examinations of the BAH have rejected its generality. However, we suggest that these examinations are neither direct nor complete tests of the functional benefit of acclimation. We consider them to be elegant analyses of the adaptive significance of developmental plasticity, a type of phenotypic plasticity that is very different from the traditional concept of acclimation that is used by comparative physiologists.

To bring traditional comparative physiology into line with contemporary evolutionary biology, physiologists over the past decade or so have been using a more theoretical and hypothesis-driven approach to evolutionary questions in physiological research. Historically, many studies in comparative physiology proposed *post-hoc* adaptive stories to explain the functional significance of a physiological trait after elucidating its mechanistic basis. However, many critics of the adaptationist programme have highlighted that there are many alternatives to adaptive scenarios [1,2], including genetic drift, past selection, genetic correlations and historical attributes [3]. The strength and success of this new evolutionary approach to comparative physiology is reflected by the diversity of studies that are producing a deeper understanding of the evolution of physiological systems (e.g. Refs [4–6], reviewed in Ref. [7]).

The beneficial acclimation hypothesis

One of the best examples of this new approach to physiological research has been the experimental analysis of the adaptive significance of physiological ACCLIMATION [8–12] (see Glossary). Traditionally, acclimation has been defined as the adjustment of physiological traits in response to changes in a single environmental variable in the lab [13], whereas ACCLIMATIZATION refers to physiological responses to environmental variables in the field [13]. Physiologists often assumed that all acclimation changes to the phenotype enhanced the physiological performance or fitness of an individual organism in the environment

Robbie S. Wilson*
Dept of Biology,
University of Antwerp,
Universiteitsplein 1,
B-2610 Wilrijk, Belgium.
***e-mail:**
rwilson@uia.ua.ac.be

Craig E. Franklin
Physiological Ecology
Laboratory, Dept of
Zoology, The University
of Queensland, St Lucia,
QLD 4072, Australia.

in which those changes were induced. Adaptive arguments were often formulated after identifying the functional role of the phenotypic modification and usually involved logical arguments that showed how the phenotype enhanced reproductive success, growth or survival. This long-held assumption, now referred to as the beneficial acclimation hypothesis (BAH) [8], has recently received a significant amount of experimental interrogation.

The BAH has been tested predominantly by examining the acclimatory responses of ectotherms to temperature. The hypothesis predicts that animals acclimated to a particular temperature have enhanced performance or fitness at that temperature in comparison with animals acclimated to other temperatures. However, to the surprise of many comparative physiologists, all empirical examinations of the BAH so far have rejected its generality [8,10–12]. These studies have demonstrated that the phenotypic changes (PHENOTYPIC PLASTICITY) that occur in organisms during development in different thermal environments do not always lead to an increased fitness in that environment when compared with the fitness of organisms raised at other temperatures.

In the first test of the BAH, Leroi *et al.* [8] exposed genetically identical lines of the bacteria *Escherichia coli* to either 32°C or 41.5°C for 24 h (~6.7 cell generations d⁻¹ at 37°C) and then competed the two groups at both exposure temperatures (Fig. 1). The BAH was used to predict that the 32°C group would outcompete the 41.5°C group at 32°C, and vice versa at 41.5°C. However, bacteria grown up at 32°C outcompeted the 41.5°C-group at both temperatures, and so the BAH was rejected (Fig. 1). In a more extensive test of the BAH, Bennett and Lenski [9] raised *E. coli* at 22, 27, 32, 37 or 40°C and then competed the different acclimation groups against each other at each temperature. As in the previous study, many groups were outcompeted at their 'acclimation' temperature by bacteria raised at other temperatures (benefit for acclimation was found in only seven out of the 12 comparisons). Again, these results were used to reject the generality of the BAH.

Gibert and co-workers [14] recently outlined another experimental test of the BAH. They raised *Drosophila melanogaster* from two different populations at 18, 25 or 29°C and then tested the walking speed of each developmental group at each temperature. The BAH was used to predict that flies would walk faster at their actual developmental temperature than would flies developed at other temperatures. However, in contrast with their predictions, flies reared at 25°C walked faster at all other temperatures than did those raised at 18 or 29°C, and the BAH was again rejected.

Acclimation or developmental plasticity?

We suggest that the empirical studies discussed here are neither direct nor complete tests of the functional

benefit of thermal acclimation, as defined from traditional physiological studies of acclimation. Rather, we suggest these studies are elegant analyses of the ADAPTIVE SIGNIFICANCE of DEVELOPMENTAL PLASTICITY. Acclimation responses studied by traditional comparative physiologists differ substantially to the developmental plasticity examined by Leroi *et al.* [8], Bennett and Lenski [9] and Gibert *et al.* [14]. Historically, comparative physiologists considered acclimation as a reversible response by an organism to changes (often seasonal) in a single environmental variable [13]. By contrast, developmental plasticity deals with the entire suite of phenotypic changes that occur as a result of differences in the developmental environment, not just the facultative physiological responses of an organism (acclimation).

Because of the highly sensitive nature of organisms during the early stages of development, small variations in the developmental environment can lead to a cascade of phenotypic changes [15–17]. Besides acclimation responses, developmental plasticity can arise from the direct biophysical effects of the environment, and can be detrimental, neutral or beneficial. Environmental factors that lead to these unavoidable, and often nonreversible phenotypic changes include temperature [18], oxygen tension [19–21], nutrition [22,23] and density of conspecifics [24]. For example, Matschak *et al.* [19] found that temperature-induced changes in muscle cellularity during embryonic development of the Atlantic salmon *Salma salar* were partly due to restricted oxygen availability at higher temperatures rather than to facultative responses to temperature. The egg capsule of embryonic salmon can act as an oxygen barrier, particularly at higher temperatures when there is an increased oxygen demand. Irreversible changes in the size and number of muscle fibres occur at high developmental temperature as a direct consequence of a constraint in oxygen availability. These high-temperature-induced developmental changes in muscle cellularity are clearly not facultative acclimation responses.

Obligatory developmental changes are particularly prevalent following exposure to stressful conditions, but their effects are often subtle. Hoffmann and Hewa-Kapuge [18] distinguished the relative contributions of different types of phenotypic change following exposure to high temperatures in the parasitic wasp *Trichogramma* nr. *brassicae*. Importantly, they found that some but not all phenotypic changes during development were the result of facultative acclimation responses. Hoffmann and Hewa-Kapuge [18] initially observed that adults of *T.* nr. *brassicae* exhibited an increased resistance to stressful temperatures following exposure to 33°C as pupae, but that these changes were accompanied by deleterious fitness effects. They suggested that these fitness decreases either reflected a general cost of increasing resistance to
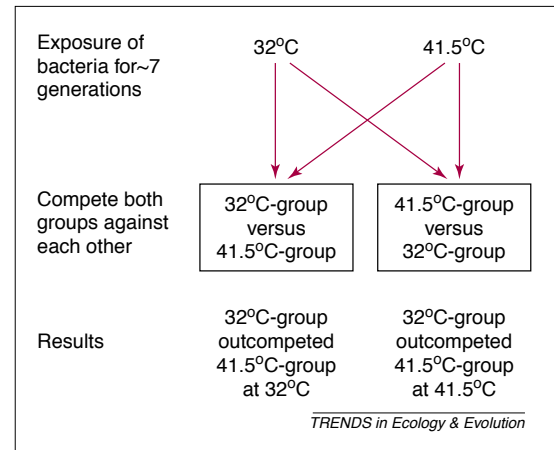

Fig. 1. Experimental investigation of the Beneficial Acclimation Hypothesis (BAH) by Leroi *et al.* [8]. The BAH was rejected in this case.

stressful temperatures (acclimation response) or were associated with direct phenotypic effects arising from damage or developmental constraints caused by the high temperatures.

To test this idea, the authors examined whether the increased resistance to high temperatures in *T.* nr. *brassicae* could occur without any of the observed decreases in fitness [18]. Pupae of *T.* nr. *brassicae* were exposed to 33°C for 2, 3 or 4 h d^{-1} for four days [18]. For each treatment group, there was an increase in adult resistance to higher temperatures. However, fitness decreased only in the groups exposed to 33°C for 3 or 4 h d^{-1}. Thus, decreases in fitness following exposure to high temperatures were clearly not caused by the increased resistance to stressful temperature (acclimation) but rather to either general damage to the phenotype or developmental constraints imposed by the high temperatures. Increased resistance to temperature without fitness costs has also been observed in the egg parasitoid *T. carverae* in both laboratory and field experiments [25].

Exposing organisms to stressful conditions confounds any analysis of the BAH (Box 1). Besides acclimation responses possibly aimed at minimizing the stress of the environment, pathological damage to the phenotype also occurs. In spite of these confounding effects, several analyses of the BAH have incorporated stressful conditions [8,9,26,27]. Metabolic costs and general phenotypic damage could overwhelm any positive acclimation responses in a stressful environment and the BAH might be incorrectly rejected. Rather than comparisons among organisms raised under stressful conditions for analyses of the BAH, Woods and Harrison [27] advocate examining the costs and benefits of specific acclimation responses.

Not all developmentally inevitable changes to the phenotype are caused by stressful conditions. In the specific case of temperature, it is doubtful that every physiological process that is affected by temperature

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Box 1. Experimental analysis of the BAH under stressful conditions

Woods and Harrison [a] addressed whether the acclimation of *Manduca sexta* caterpillars to water stress was beneficial.

• Treatments
Larvae were raised from the first instar on low- (69%) or high-water (80%) artificial diets. After reaching the fifth instar, growth rates for both groups were measured on the same or opposite diet for 36 h. Several determinants of larval water budget were also recorded.

• Results
Caterpillars raised on high-water diet grew faster than did those raised on low-water diet when tested on both diets. Thus, no benefit for previous exposure to low-water diet was observed. However, larvae responded to short-term hydric stress (low-water diet) by minimizing water excretion by increasing rectal water absorption, and to long-term hydric stress by significantly reducing faecal water excretion.

• Conclusions
The authors concluded that, under current usage, the beneficial acclimation hypothesis (BAH) had to be rejected in this case. However, we suggest that phenotypic damage owing to hydric stress confounds any analysis of the benefits of acclimation.

Do the lower growth rates of larvae raised on a low-water diet (when tested on both diets) reflect pathological phenotypic changes owing to stress OR a lack of beneficial acclimation? We suggest that the pathological effects of chronic stress might overwhelm any possible beneficial acclimation responses.

Reference
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can 'acclimate' to different temperatures. This will inevitably lead to phenotypic differences between organisms from different developmental temperatures that are simply due to the direct effects of temperature on these developmental pathways [17,19–21]. These phenotypic changes are certainly not those that were traditionally described as acclimation responses by comparative physiologists, but are undoubtedly included in the studies of Leroi *et al.* [8] and Bennett and Lenski [9]. Thus, previous analyses of the BAH using developmental plasticity are confounded by including several types of phenotypic plasticity. A more compelling experimental analysis of the benefit of acclimation would be based around the concept of acclimation that traditional comparative physiologists were criticized for assuming was always beneficial.

Exploring the BAH using competing hypotheses
In two additional studies exploring the BAH, both Huey and Berrigan [11] and Huey *et al.* [12] advocated a strong inference approach to examining questions relating to the thermal acclimation of ectotherms. Their approach involved testing among competing hypotheses that make different predictions as to how developmental temperature influences the thermal sensitivity of performance (Box 2).

Huey and Berrigan [11] and Huey *et al.* [12] then used the datasets of several previous studies, such as that by Zwaan *et al.* [28], to compare the hypotheses. Zwaan *et al.* [28] analysed the effect of developmental temperature on adult longevity in *D. melanogaster* and found that flies raised at intermediate temperatures survived longer as adults than did those flies raised at cool or high

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Box 2. Set of competing hypotheses

This set of competing hypotheses is as suggested by Huey and Berrigan [a], and Huey *et al.* [b].
Beneficial Acclimation Hypothesis (BAH): organisms acclimated to a particular environment have enhanced performance or fitness in that environment relative to organisms acclimated to other environments [c].
Optimal developmental Temperature Hypothesis (OTH): organisms raised at intermediate temperatures have higher relative fitness across all temperatures than do organisms raised at high or low temperatures. The OTH was suggested as an alternative to the BAH by Zamudio *et al.* [d], Huey and Berrigan [a] and Huey *et al.* [b].
Cooler is Better Hypothesis (CBH): organisms raised at cool temperatures have higher relative fitness across all temperatures than do organisms raised at intermediate or high temperatures. The CBH is based on the assumption that the larger size of cool-developed organisms is

sufficiently advantageous to outweigh any benefits of acclimation [b].
Warmer is Better Hypothesis (WBH): organisms raised at high temperatures have higher relative fitness across all temperatures than do those raised at intermediate or cool temperatures. The WBH is the reciprocal of the CBH of Huey *et al.* [b].

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b Huey, R.B. *et al.* (1999) Testing the adaptive significance of acclimation: a strong inference approach. *Am. Zool.* 39, 323–336
c Leroi, A.M. *et al.* (1994) Temperature acclimation and competitive fitness: an experimental test of the beneficial acclimation assumption. *Proc. Natl. Acad. Sci. U. S. A.* 91, 1917–1921
d Zamudio, K.R. *et al.* (1995) Bigger isn't always better: body size, temperature and male territorial success in *Drosophila melanogaster*. *Anim. Behav.* 49, 671–677

Glossary

Acclimation: any facultative modification in a physiological trait in response to changes in an environmental variable in the lab. Changes can be in response to the developmental environment or long-term environmental shifts during the later stages of the life history of an organism (more traditionally studied). Responses can be beneficial, neutral or negative.
Acclimatization: facultative modifications in a physiological trait in response to changes in one or more environmental variables in the field.
Adaptive significance: (in context of plasticity) fitness advantages and disadvantages associated with the expression of phenotypic plasticity across a range of environments. Fitness consequences can be positive, negative or neutral.
Developmental plasticity: phenotypic changes induced by variation in the developmental environment. Changes can include facultative responses by the organism (e.g. acclimation) or unavoidable biophysical consequences of the environment (obligatory and/or pathological).
Phenotypic plasticity: environmentally induced variation in morphology, physiology and/or behaviour of an organism.

temperatures, regardless of the temperature at which the adult flies were kept. These data were used by Huey and Berrigan [11] and Huey *et al.* [12] to again reject the generality of the BAH in favour of the optimal developmental temperature hypothesis (OTH).

However, as with the previous analyses of the BAH, we suggest this experimental design is also confounded by several different types of plasticity underlying the phenotypic changes, not just acclimation responses. We consider that, in this context, the OTH, cooler is better hypothesis (CBH) and warmer is better hypothesis (WBH) all deal specifically with the adaptive consequences of the developmental environment, regardless of the source of phenotypic changes. However, the BAH refers only to the facultative physiological responses of the organisms and is thus only one specific type of phenotypic plasticity. We suggest that the OTH, CBH and WBH are not mutually exclusive to the BAH. For example, it is possible that the developmental constraints imposed on the phenotype by some temperatures are so great that the overall performance is dominated not by the acclimation responses (if they occur), but by these phenotypic inevitabilities. In other words, there might be an optimal temperature for development that is determined solely by the unavoidable changes to the phenotype that occur in the different thermal environments. This, of course, says nothing about the relative merit of the 'acclimation' changes in each environment.

Conclusions and future directions

Previous empirical tests of the BAH have elegantly demonstrated the evolutionary significance of thermally induced developmental plasticity [8,9], especially with the advent of a rigorous experimental design testing several competing hypotheses [11,12]. Importantly, these studies of the BAH have forcefully made the point that acclimation changes cannot just be assumed to be beneficial, but this is a hypothesis that must be rigorously tested. However, we believe that a detailed empirical examination of the adaptive significance of more traditional measures of physiological acclimation is now required to test the BAH. We challenge comparative physiologists to develop new inventive experimental designs to explore the benefits and costs of the more traditional acclimation responses. However, this will not be easy and using anything less that a close correlate of fitness to test the hypothesis, such as survival, reproductive success or competitive ability, would be less than desirable. Previous empirical tests of the BAH have certainly set a benchmark for examining the adaptive significance of phenotypic plasticity, regardless of the source of phenotypic variation.

One entertaining possibility for future tests of the BAH would be to examine the thermal acclimation of reproductive performance, especially in a system where females discriminate between displaying males. For example, in a species where females are choosy about their mates, females could be given the opportunity to discriminate between cool- and warm-acclimated males at various temperatures. The ability to attract and procure a female might depend on characters such as swimming performance, aerobic capabilities and general activity, all of which have been shown to acclimate to temperature in a variety of taxa [13]. In this specific case, the BAH would predict that, at high temperatures, females would find the warm-acclimated males more attractive than they would the cool-acclimated males and vice versa at cool temperatures. Even more compelling would be the inclusion of males that had been raised at different temperatures, so the relative merits of developmental plasticity could be compared with the more reversible-type acclimation responses. We suggest that future tests of the BAH should investigate traditional types of acclimation using the protocols developed for analysing developmental plasticity.

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Putting predators back into behavioral predator–prey interactions

Steven L. Lima

In the study of behavioral predator–prey interactions, predators have been treated as abstract sources of risk to which prey respond, rather than participants in a larger behavioral interaction. When predators are put back into the picture by allowing them to respond strategically to prey behavior, expectations about prey behavior can change. Something as simple as allowing predators to move in response to prey movements might not only (radically) alter standard expectations of prey behavior, but might also reveal new classes of behavioral phenomena that occur at large spatial scales. Similar revelations undoubtedly await many well-studied aspects of the behavioral interaction between predator and prey. Most examples studied to date, both theoretical and empirical, require attention from this 'predatory' perspective. Putting predators back into the picture will be challenging, but doing so might change the way in which biologists think about predator–prey interactions in general.

Steven L. Lima
Dept of Life Sciences,
Indiana State University,
Terre Haute, IN 47809,
USA.
e-mail:
S-Lima@indstate.edu

Over the past 20 years, the study of behavioral interactions between predator and prey has shed much light on prey behavior, and it is now clear that almost any aspect of prey decision-making (from foraging behavior to mate choice) can be influenced by the risk of predation [1–3]. A growing literature also suggests that nonlethal interactions between predator and prey (those driven by prey avoidance of predation) might be an important component of predator–prey interactions

in general [4–8]. Work on behavioral predator–prey interactions therefore provides an important bridge between the studies of behavior and ecology.

In spite of these many advances, our understanding of behavioral predator–prey interactions is limited by a simple oversight: we virtually forgot about the behavior of predators! Historically, we have been so focused on prey behavior that we (myself included) became comfortable with treating predators as unresponsive 'black boxes' rather than participants in a behavioral interaction. This oversight has not only led to an incomplete view of behavioral interactions between predators and prey, but has also obscured an entire class of such interactions that occurs at large spatial scales. My goal is to explore some of the insights gained from putting predators back into behavioral predator–prey interactions.

How were predators removed from the interaction?

The removal of predators from the behavioral predator–prey interaction is apparent in the ubiquitous 'fixed-risk' assumptions of constant attack rates over time and patch-specific risks of predation (e.g. Ref. [9]); such assumptions imply that predators are not influenced by prey behavior. As few would argue for the strict validity of this assumption, why were predators relegated to the status of unresponsive entities? In many ways, the fixed-risk approach (i.e. the assumption of unresponsive predators) was a sensible starting point. Characterizing predation risk as an environmental constant seemed reasonable given that predators can strike opportunistically and could be anywhere at a given time. Mathematical convenience might have also played a role: models of antipredator decision-making are much simpler under an assumption of fixed risk than they are when both predator and prey are allowed to respond to one another. Furthermore,