Opinion

# Environmental stressors alter relationships between physiology and behaviour

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**Although correlations have frequently been observed between specific physiological and behavioural traits across a range of animal taxa, the nature of these associations has been shown to vary. Here we argue that a major source of this inconsistency is the influence of environmental stressors, which seem capable of revealing, masking, or modulating covariation in physiological and behavioural traits. These effects appear to be mediated by changes in the observed variation of traits and differential sensitivity to stressors among phenotypes. Considering that wild animals routinely face a range of biotic and abiotic stressors, increased knowledge of these effects is imperative for understanding the causal mechanisms of a range of ecological phenomena and evolutionary responses to stressors associated with environmental change.**

## Physiology and behaviour: an unstable relationship

Both behavioural (e.g., boldness, aggression, activity level) and physiological (e.g., metabolic rate (MR), hormonal profiles) traits often show wide and consistent variation among individuals of the same species and this variation can have clear consequences for fitness and the evolution of life histories [1,2]. In conjunction, there are links between specific behavioural and physiological traits that underlie an enormous array of ecological phenomena, including but not limited to foraging, competitive interactions, mate choice, predator–prey interactions, and habitat selection [3,4]. A surge of research interest has highlighted this covariation between behavioural and physiological traits in a range of animal taxa [4–6], but the causal mechanisms of these associations are not well understood. Moreover, several studies have found that the nature of the correlations between aspects of an animal's physiology and its behaviour is variable and can depend on the prevailing ecological conditions (Table 1).

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*Keywords:* stress; metabolic rate; aerobic scope; environmental change; personality; intraspecific variation.

0169-5347/$ – see front matter.
 http://dx.doi.org/10.1016/j.tree.2013.05.005

We propose that the presence of an environmental stressor can alter the relationship between specific physiological and behavioural traits (Figure 1 and Table 2). Here we define a stressor as any intrinsic or extrinsic factor that challenges individuals and obliges them to adjust behaviour or physiology to cope, therefore either demanding higher performance or constraining the expression of traits. These include abiotic stressors such as low oxygen availability or temperature shifts, but also biotic stressors such as the presence of predators or increased competition with conspecifics. The effects of many such environmental factors on behaviour and physiology have previously been examined from the standpoint of environmental gradients and reaction norms [7–9], but in this review we focus on specific scenarios where these factors become stressors. Animals are continually faced with a range of stressors that act as agents of selection, so increased understanding of how relationships between physiology and behaviour are modified by stress is crucial to our understanding of physiological, behavioural, and evolutionary ecology. Further, although prior work has considered the effects of adverse environmental conditions on the stability of genetic correlations and life-history strategies [10–12], we still lack understanding of the proximate causes of these effects. Investigating the influence of stressors on relationships between behavioural and physiological traits could provide insights into this area.

Drawing on the limited work that has been done on this subject, we discuss mechanisms by which various stressors might affect the link between aspects of physiology and behaviour. We then describe ways in which these proximate underpinnings might ultimately help us understand the cause-and-effect relationship among physiological and behavioural traits and be relevant to a range of ecological phenomena and evolutionary processes, particularly in the face of environmental change. Given urgent concerns over the effects of environmental change on species abundances and distributions, understanding forces that modulate the relationship between physiology and behaviour in individual animals is critical for predicting how populations may

**Table 1. Studies examining relationships between behavioural and physiological traits with and without the presence of an environmental stressor[a]**

| Species | Behavioural measure | Physiological measure | Stressor | Statistical results | Effect of stressor | Refs |
|---|---|---|---|---|---|---|
| *Salmo salar* | Activity | Standard metabolic rate | Absence of cover | Significant interaction with treatment | Masking | [56] |
| *Salmo salar* | Territory acquisition | Routine metabolic rate | Unpredictable food and absence of structure | Significant interaction with treatment | Revealing | [72] |
| *Salmo salar* | Territory acquisition | Standard metabolic rate | High conspecific density | Significant interaction with treatment | Revealing | [57] |
| *Dicentrarchus labrax* | Risk-taking | Routine metabolic rate | Food deprivation | Increased strength of correlation; significant interaction with treatment | Revealing | [14] |
| *Dicentrarchus labrax* | Risk-taking | Routine metabolic rate | Hypoxia | Increased strength of correlation; significant interaction with treatment | Revealing | [19] |
| *Liza aurata* | Position in school | Aerobic scope | Water velocity | Increased strength of correlation; significant interaction with treatment | Revealing | [17] |
| *Peromyscus maniculatus sonoriensis* | Activity | Resting, daily maximal metabolic rate | Temperature | Decreased strength of correlation | Masking | [43] |
| *Microtus oeconomus* | Proactivity | Resting metabolic rate | Seasonal change | Significant interaction with season | Masking | [37] |

[a]A stressor is said to have a revealing effect when it causes a relationship between specific behavioural and physiological traits to emerge or strengthen when it was otherwise nonexistent or subtle. A stressor is said to have a masking effect when it hides or attenuates a relationship between specific behavioural and physiological traits. See the main text and Table 2 for mechanisms that could cause such effects.

respond. Indeed, the effect of adverse environmental conditions on whole-animal physiology and behaviour is the interface at which the evolutionary trajectories of populations could be determined in response to environmental change.

## Mechanisms of modulation

### *Stress as a revealing or amplifying factor*

When exposed to a stressor, animals alter the priority of specific behaviours and physiological functions. For example, fasted individuals can become more active as they attempt to find food, those exposed to higher predation risk become more likely to hide, and individual endotherms exposed to cold generally increase metabolic heat production. Importantly, the extent of such reprioritisation appears to vary among individuals with different behavioural or physiological characteristics (e.g., bold versus shy, high versus low MR). Although individuals of the same species can show repeatable variation in a range of physiological and behavioural traits [1,4,5], differential sensitivity to a stressor among individuals can further increase the observed intraspecific phenotypic variation of such traits. In association with this, higher demands on performance can accentuate the importance of specific traits, making differences among individuals more obvious and causing links between behaviour and physiology to emerge where they were otherwise subtle or invisible (Figure 1A,B). This can be viewed from the perspective of reaction norms: if individuals have differing norms of reaction to an environmental stressor (i.e., different sensitivities) that also vary between traits (i.e., behavioural and physiological), the extent of the correlation between traits will depend on the environment in which it is measured (Box 1).

To illustrate this, consider the effects of stressors that challenge energy balance, such as food deprivation or an acute temperature change, where an individual's MR might influence how rapidly it enters a state of physiological disequilibrium. In the case of food deprivation, some individuals lose mass more rapidly than others when short of food and those that lose mass fastest tend to be those with the highest resting MR [13,14]. Fasted animals generally show increased boldness and foraging activity, suggesting that mass loss itself increases feeding motivation [15]. The result is an exacerbation of the effects of MR on behaviour – under conditions with adequate food there may be little evidence of a correlation between MR and risk-taking during foraging, but with food shortage a positive relationship between an individual's MR and its boldness during foraging becomes more evident [14] (the general mechanism is illustrated in Figure 1A). Similarly, the link between social status and levels of stress hormones (both baseline and maximal) might appear only in years of low food availability [16].

Several other abiotic stressors can also strengthen relationships between physiology and behaviour. In aquatic animals, for example, exposure to environmental hypoxia appears to most affect individuals with the highest MR or lowest capacity to increase their metabolism [17,18] (i.e., aerobic scope). This can cause them to prioritise securing oxygen supply at the expense of safety, revealing an influence of MR on boldness and activity that was invisible in normoxia [19] (Figure 1A). Individuals also differ in their behavioural response to thermal stress, with an acute temperature shift causing some to become bolder and others to become more shy [20]. It is plausible that these behavioural responses of individuals to temperature change depend on individual metabolic demand or aerobic scope. In deer mice (*Peromyscus maniculatus*), for example, the extent of the decrease in activity at cold temperatures varies among individuals and is likely to depend on metabolic capacity for heat production [21].