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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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].

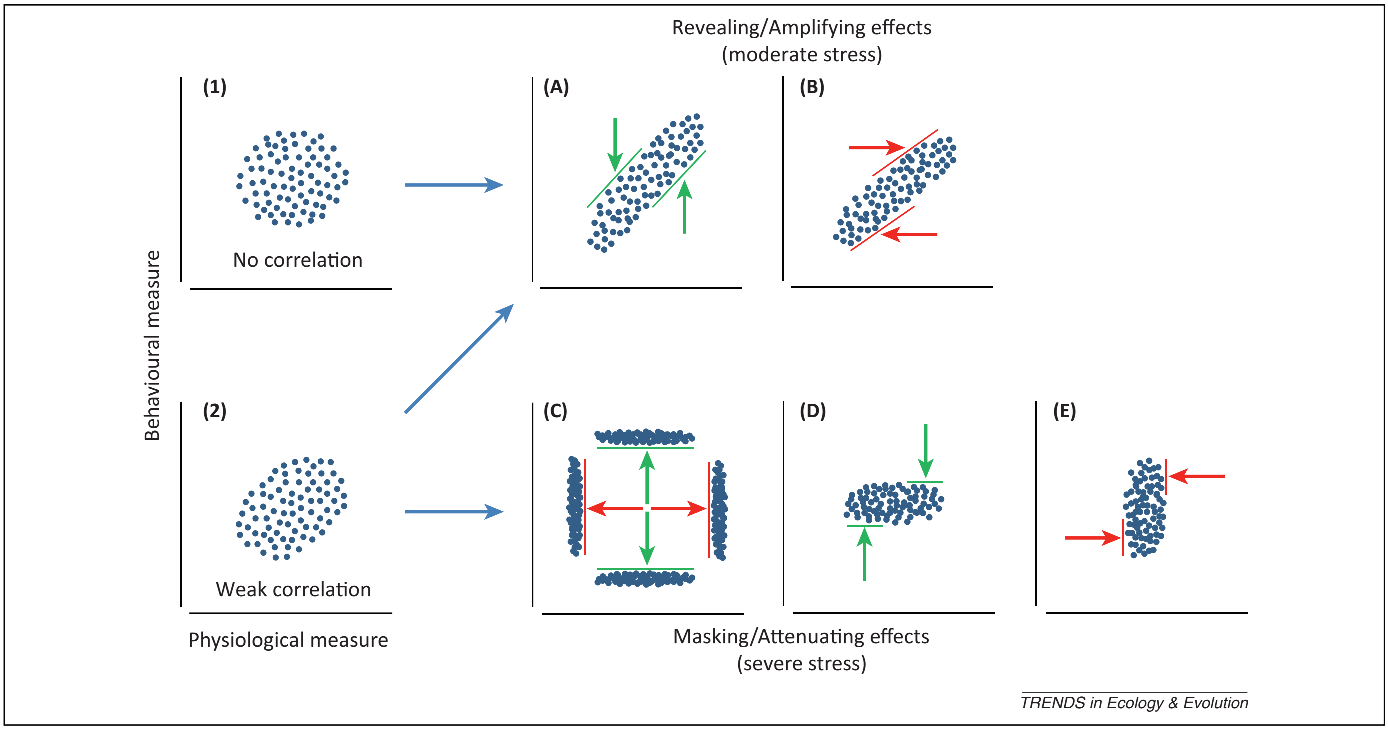

Figure 1. Schematic representations of the revealing/amplifying and masking/attenuating effects of stressors on the relationship between specific physiological and behavioural traits. In each panel, each data point represents one theoretical individual. The panels on the far left represent correlations between measured physiological and behavioural traits under relatively unstressed conditions, in which the correlation is nonexistent (panel 1) or weak (panel 2). The magnitude of the correlation can change once the animals are exposed to a stressor, either revealing or amplifying the relationship (top row) or masking or attenuating the relationship (bottom row). Milder stressors are predicted to be more likely to strengthen the observed associations between physiological and behavioural traits (top row), whereas more severe stressors can diminish or eliminate such relationships (bottom row). See Table 1 for examples of scenarios **(A) to (E)**. Stressors that affect the degree of behavioural and physiological variation among individuals are illustrated by green and red arrows, respectively. Multiple effects within a given panel in (A) to (E) need not occur simultaneously (i.e., red versus green arrows or arrows of the same colour working in opposing directions).

Chemical contaminants could also amplify relationships between physiological and behavioural traits. There can be intraspecific variation in physiological resistance to some pollutants [22], creating the potential for divergence in linked behavioural tendencies during toxic exposures. Vulnerability to toxic effects can also differ among behavioural types; for instance, differences in ionoregulation, circulating cortisol, or MR that are linked to social status can make subordinate fish more prone to toxic effects of heavy metals [23]. Individuals with specific social ranks could therefore display disproportionately large changes in behaviour that exaggerate the observed links between physiological and behavioural traits (Figure 1A).

A general finding is that there is a link between physiological measures of stress responsiveness (e.g., through the hypothalamic–pituitary–adrenal [HPA] axis) and behavioural measures of personality in animals, with individuals that show stronger or more acute physiological responses to stress (e.g., higher peak levels of glucocorticoid stress hormones such as cortisol or corticosterone) tending to be less bold [24–26]. This link can, however, vary with environmental conditions; whereas boldness was negatively correlated with peak corticosterone levels within two populations of dark-eyed junco (*Junco hyemalis*) following a standardised handling procedure, birds from a more urban (and presumed stressful) environment showed greater boldness for a given circulating level of stress hormones than did those from a more rural environment [26].

Biotic stressors such as predation threat could also strengthen relationships between physiology and behaviour. When exposed to visual or olfactory cues from predators, for example, prey individuals tend to decrease activity or adopt other protective behaviours [27]. There is variation in this response within species [28,29], which might be linked to energetic demands and hormone profiles [14,15,27]. It is possible that shy individuals, with relatively low MR under more benign conditions, become even shyer when stressed by a predator (Figure 1A). Although not yet examined, the metabolic or endocrine response to predation threat might differ between bold and shy individuals, leading to divergence of physiological variables among individuals during predator–prey encounters (Figure 1B). The intense physical activity by both predators and prey during their interactions is predominantly anaerobic, but recovery is dependent on aerobic metabolism [30,31]. Thus, individuals with a higher MR or aerobic scope could recover faster [32], leading to quicker resumption of normal activities after an encounter.

Aggressive encounters and competition with conspecifics could also strengthen or reveal an association between behavioural and physiological traits. It is well documented that aggression associated with the establishment of dominance hierarchies can cause status-related variation in circulating levels of glucocorticoid stress hormones [1,4,33]. Interestingly, the magnitude and direction of this covariation can depend on the animal's social environment. In some bird species, threats to social hierarchies cause

Table 2. Example mechanisms by which several stressors could reveal/amplify a relationship between specific physiological and behavioural traits when mild or mask/attenuate such a relationship when severe[a]

Stressor	Revealing/amplifying effect	Masking/attenuating effect
Food deprivation	Mass loss during food deprivation linked to energy demand, causing divergence in behavioural tendencies (A)	Starvation results in reduction in activity and MR among all individuals, reducing overall phenotypic variation (C)
Thermal stress	Differential changes in behaviour as a function of metabolic response to temperature change (A,B); individuals with the smallest aerobic scope most affected (A)	Behaviour strongly suppressed for all individuals at extreme temperatures or following rapid temperature changes; altered MR and aerobic capacity (C)
Hypoxia	Differential susceptibility due to variation in oxygen demand and aerobic capacity, coupled with changes in behaviour (A)	Behaviour strongly suppressed during severe hypoxia or anoxia (D); reductions in MR and aerobic scope (C,E)
Dehydration	High MR or stress-responsive phenotypes increase activity or boldness to obtain water (A)	Behaviour restricted during extreme dehydration (C); individuals with small aerobic scope or high MR might be more susceptible, leading to reduction in behavioural variation (D); most active individuals become dehydrated faster (D,E)
Hypercapnia	Differential susceptibility among behavioural or physiological phenotypes, causing further divergence in traits (A,B)	Disruption of maintenance functions and MR among all individuals (C); reduced sensory capabilities and disruption of normal behaviour (C)
Pollution/contaminants	Mode of toxicity related to physiological or behavioural traits, such that some phenotypes are more susceptible and more likely to alter behaviour (A) or physiology (B)	Disruption of behaviour to the extent that normal links with physiological variation are lost (C); decreased variation in physiological and behavioural traits (C,D,E)
Predation threat	Shy individuals become shyer (A); post-attack recovery from exercise can lead to variable resumption of normal behaviour (A); divergence in MR or endocrine profiles (B)	All individuals show strong reduction in activity (C); increased stress response or rise in MR among shy individuals could decrease variation in MR (E)
Social stress/competition	Increased motivation to compete for resources linked to energetic demand or hormonal profile (A); shy or subordinate individuals become more suppressed in groups (A); increased hormonal expression in dominant individuals during threats to territory or social hierarchy (B)	Presence of highly dominant individual or hierarchy reduces variation in behaviour and supersedes importance of physiological traits among all subordinates (C)
Lack of shelter/habitat	Shy or low-MR phenotypes might show a further reduction in activity and exploration (A)	All individuals show disruption in behaviour or decrease in activity (C); shy individuals show relatively large stress-related increase in activity, MR, or circulating stress hormones (D,E)
Disease/parasites	Increased metabolic load can increase rates of foraging, especially among specific phenotypes (e.g., bold individuals) (A); shy or less active individuals might be more susceptible to parasitic infection, causing further reduction in activity (A)	Reductions in behaviour, changes in physiological parameters; all behavioural and physiological phenotypes equally susceptible and responsive to infections (C,D,E)
Light/noise pollution	Increase in perceived level of threat causes specific phenotypes (e.g., shy or low-MR individuals) to become even more shy (A)	Increased perception of threat leads to extreme reduction in activity among all individuals (C)

[a]Each description is followed by a letter representing the corresponding general mechanism illustrated in Figure 1.

elevations in hormones such as testosterone in dominant individuals (Figure 1B), but differences in hormone profiles between dominant and subordinate individuals often disappear once the hierarchy is re-established [34]. Moreover, in some social breeders, the link between dominance status and chronic levels of stress hormones depends on the current social environment; dominant helper individuals in the cooperatively breeding cichlid *Neolamprologus pulcher* have higher cortisol levels than subordinates only when the breeding pair is present, suggesting that dominant helpers work harder to suppress subordinates (and so are more stressed) when a reproductive event is more likely [35]. Similarly, MR can correlate relatively weakly with various behaviours in isolated animals, but when animals are competing for resources in groups this relationship might strengthen, because those with the highest MR and feeding motivation are driven to become more aggressive to secure resources (Figure 1A). Increased competition for resources and mating opportunities during reproductive periods could also enhance differences in behaviour among individuals related to differences in physiology, resulting in associations that were not observable during non-breeding [36,37].

There are other scenarios where the need to perform an activity could generate differences in behaviour among individuals, as a function of their relative aerobic scopes and locomotor capacities. These include long-distance migrations [38] or simply changes in environmental conditions that necessitate increased activity and energy expenditure [39,40]. For individuals in fish schools, for example, individual aerobic scope has no influence on spatial positioning when groups are swimming at low speeds, but fish with a greater aerobic scope tend to occupy the front portion of schools when swimming against faster currents [17] (Figure 1A). Occupying the front of a school could allow individuals to obtain more food, but could also expose them to increased risk of predation [41], suggesting that a link between aerobic scope and boldness will be apparent in only some environments but will then have fitness consequences.

Box 1. Studying the altering effects of stressors

Alternative study designs for examining covariation in behaviour and physiology across a range of conditions are shown in Table I, ranging from the most informative multivariate reaction norm design to much simpler protocols. Ideally, physiological and behavioural traits should be measured simultaneously within the same individual under a given set of conditions whenever possible. This is becoming more feasible with advances in biotelemetry that can allow logging of behavioural and physiological parameters in animals in the field or large arenas [38,73,74]. A promising approach for studying links between behaviour and MR is to measure behaviours directly in a respirometry chamber with and without a stressor. Respirometers are usually compact and restrict activity, but even a small increase in volume can be beneficial for observing differences in behaviour among individuals and how this affects metabolic demand in relation to factors such as temperature, oxygen availability, predator, or social cues [75] or contrasting habitat structures [76]. However, it can be difficult to measure the true response to a stressor if measurement requires restraint or confinement, because this alone might affect the animal's behaviour and physiological state.

In studies observing the same animal under multiple conditions, at least two measurements should be performed for each trait to allow separation of intra- from interindividual variation (see [77] for a detailed discussion). Such a dataset also facilitates an examination of how multiple traits (i.e., physiological and behavioural) respond simultaneously to environmental variation or the presence of a stressor using multivariate reaction norm approaches [77]. Unfortunately, multiple measurements are not always feasible due to logistical constraints or habituation during repeated behavioural trials or physiological acclimation to stressors.

In a broad methodological context, the effects of stressors could obscure results in studies of behavioural or physiological ecology, because even a mild stressor or variation in environmental conditions among treatments or studies could cause unexpected differences in the strength of covariation in physiological and behavioural traits. A significant problem is determining what constitutes a 'stressor' when performing experimental manipulations. In studies examining physiology and behaviour under 'benign' resting conditions, the nature of the laboratory housing or the experimental protocols could in themselves constitute a form of stressor that strengthens or weakens links between the physiological and behavioural traits being measured. Furthermore, in studies investigating the altering effects of stressors, it might be the case that the 'unstressed' initial condition could itself have exerted some degree of stress on the animals being tested. Factors such as these should be considered when drawing comparisons among correlations obtained under different laboratory conditions and between different studies.

Table I. Potential study designs for examining the effects of an environmental stressor on the relationship between specific physiological and behavioural traits[a]

	Type 1		Type 2		Type 3		Type 4		Type 5	
Condition	Physiology	Behaviour	Physiology	Behaviour	Physiology	Behaviour	Physiology	Behaviour	Physiology	Behaviour
Unstressed	✔	✔	✔	✔	✔	✔	–	✔	✔	–
Stressed	✔	✔	–	✔	✔	–	✔	–	–	✔

[a]A checkmark indicates a design in which data are collected for a particular category (i.e., physiology or behaviour) under a given condition (i.e., stressed or unstressed). All designs assume that the same individuals are measured under both unstressed and stressed conditions. Type 1 is where both behaviour and physiology are measured both with and without stress. This is the most informative because it will reveal how both traits and their covariation respond to the presence of a stressor, so allowing evaluation of multivariate reaction norms (see [77]). Type 2 measures behaviour with and without the stressor, but physiology only under benign conditions – a less informative design, but suitable for studying, for instance, the effects of baseline energy requirements on behavioural responsiveness to stress. Type 3 is the converse design, which can be suitable for the study of coping styles, where intrinsic behavioural characteristics (e.g., boldness or aggressiveness) can be related to physiological responses to stress. Types 4 and 5 are where behaviour or physiology are assessed separately and under only one condition; this is sometimes the only option for field studies in which measurements are first made under controlled conditions and then the animals are released into the wild for behavioural observation or physiological evaluation.

Stress as a masking or attenuating factor

There could also be situations where a stressor has such a restrictive effect on behaviour or physiology that it greatly reduces variation, so masking or attenuating any relationship that is apparent under non-stressed conditions (Figure 1C,D,E). Many of the same environmental stressors that act as amplifying factors could weaken or eliminate links between given physiological and behavioural measures if these stressors increase in severity or duration. Severe hypoxia, prolonged periods of food deprivation, or exposure to extreme temperatures or toxicants can all cause a range of adverse physiological effects, including altered metabolic function and diminished scope for aerobic and neuromuscular performance. In these circumstances, individuals that otherwise possess a physiological capacity for activity, boldness, or aggression might be prevented from expressing these traits. Although several studies have demonstrated a positive correlation between dominance rank and MR in various bird species, this relationship disappears in dark-eyed junco groups formed during cold winter conditions, probably due to the energy-saving reduction in aggression and androgen levels that occurs when food availability is low and thermoregulatory demands are high [42] (Figure 1C). Similarly, deer mice show a positive correlation between daily energy expenditure and activity at 25°C, but this link disappears when animals are tested at much colder temperatures [43] (Figure 1C). Exposure to high levels of toxicants can induce a range of restrictive effects including reduced responsiveness to predators [44], reduced social interactions [45,46], foraging behaviour [47,48], and reproductive activity [49].

Masking or attenuation of the covariation between physiological and behavioural traits could also occur when certain phenotypes are more sensitive to the stressor in question. Unlike revealing or amplifying mechanisms, however, which can also act via differential sensitivity among phenotypes, masking or attenuating effects arise through a decrease in pre-existing variation (Figure 1D,E). Dehydration, for example, is an especially prevalent threat for many arthropods, amphibians, and reptiles [50–52]. Certain phenotypes might be more prone to dehydration – for instance, individuals that are more active or that have higher MR will tend to have relatively higher rates of evaporative water loss. This could reduce observed behavioural differences between bold, high-MR and shy, low-MR phenotypes (Figure 1D,E). In support of this notion, intraspecific variation in social interaction and aggression in the lizard *Anolis aeneus* decreases with increasing water deprivation [50].

There can also be complex interactions among habitat characteristics that diminish correlations between physiological and behavioural traits. For instance, in various taxa, high-ranking individuals prevent subordinates from foraging at times or locations that are safer or of higher quality [53–55]. This interaction between social stress and predator pressure could oblige subordinate individuals, which in a range of species tend to have lower MR [1,4], to display increased risk-taking or boldness – traits that are often positively correlated with MR (Figure 1D). Links between MR and indicators of performance in juvenile Atlantic salmon (*Salmo salar*) that exist when the environment contains refuges or where food is spatially predictable (both of which allow resource defence) disappear in more stressful open habitats or those with spatially unpredictable food supplies [56,57]. Predatory threats can also induce strong hormonal or metabolic responses that could temporarily reduce physiological variation [58,59] (Figure 1C). Anthropogenic noise from industrial or urban areas could have a similar effect by increasing the perceived level of threat and decreasing activity rates [60].

Ecological and evolutionary implications

A major unknown we must address before we truly understand the role of intraspecific variation in affecting broad-scale ecological phenomena is the causal direction of the relationship between physiology and behaviour. On the one hand, physiological traits appear capable of either promoting or constraining certain types of behaviour. High energetic demand or hormonal cues, for instance, might drive individuals to obtain resources or territory, and hormonal signalling can also steer developmental trajectories and so shape the morphological capacity for behaviour [61]. On the other hand, intrinsic behavioural tendencies could drive changes in physiological state if bolder or more aggressive individuals develop energetically costly organs and cellular structures to support a more active lifestyle. There is also evidence that the outcome of certain behaviours – territorial competition, for example – can influence hormonal profiles and whole-animal physiology. Exploring changes in the correlations between physiological and behavioural traits in response to an environmental stressor could reveal the direction of causality of such relationships in specific contexts. The mechanisms described in this review suggest that there is no single causal mechanism linking physiology and behaviour. Instead, it is probable that different mechanisms act in different situations and over different temporal scales, with cause-and-effect relationships between particular physiological and behavioural traits dynamically shifting in response to varying environmental conditions. In particular, the presence of a stressor can cause a temporary change in the intensity or direction of the causal association, thus highlighting mechanisms that may be difficult to detect or study under more benign conditions.

A greater understanding of the relationship between physiology and behaviour is critical for predicting how populations will respond to aspects of environmental change [62]. Of major concern is whether populations will be able to adapt to changes in factors such as temperature, oxygenation, and food availability and, if so, which phenotypes will be selected [63]. Stressful conditions that amplify behavioural or physiological differences among individuals will also increase the phenotypic variation on which natural selection can act. In food-limiting situations, for example, individuals with higher MR lose the most mass, which can lead to them becoming the boldest in the population and so suffering an increased risk of predation as a direct consequence of their physiology. As a side-effect of this process, there could be correlated selection for certain personality types or behavioural syndromes, precipitated by the way in which demand for energy or oxygen causes animals to behave in response to acute stressors [5,64,65].

The effects of stressors on the proximate mechanisms discussed here have interesting parallels with the effects of adverse environmental conditions on genetic correlations among life-history traits. Life-history evolution can be affected by the destabilisation of genetic correlations and several studies have suggested instances where the genes important for fitness or the expression of life-history traits vary with the stressfulness of the environment [10,11]. Some of the mechanisms described here could underpin these context-dependent genetic correlations involving life-history traits [10]. For instance, in situations where a high-MR, high-activity lifestyle allows an increased growth rate but also makes individuals more sensitive to certain stressors, there could be a trade-off between growth potential and stress resistance, leading to a shift in the favoured developmental rate and life-history strategy when faced with environmental stressors [66]. The genetic capacity for plasticity might also be selected for in some circumstances, especially considering that climate change is predicted to result in greater heterogeneity in environmental conditions and resource availability [63,67]. This environmental inconsistency could itself be considered a form of stress (e.g., repeated or rapid changes in temperature), possibly resulting in a shift from environmental specialists to generalists, with selection favouring those animals most capable of adjusting their physiology or behaviour to cope with rapidly changing conditions.

For some species, certain developmental periods associated with specific life histories could constitute a significant intrinsic stressor that constrains behaviour, physiological function, or links between the two. Although there is some evidence that individual variation in behaviour can persist through major life cycle events such as metamorphosis [68,69], information on long-term consistency is currently very limited [70] and more longitudinal studies are needed to understand how links among physiological and behavioural traits covary within individuals over their lifetime. However, major events such as migration or metamorphosis often include a dramatic temporary increase in energetic demand accompanied by behavioural changes in preparation for a shift in ecological niche [38,71]. Both could alter the relationship between physiological and behavioural traits, as well as increase sensitivity to external stressors that vary among individuals.

Concluding remarks

Moderate stressors appear to reveal or amplify links between specific measures of physiology and behaviour, whereas severe stressors might mask or attenuate any pre-existing relationships. The strength of correlations between particular physiological and behavioural traits may thus be context dependent and vary in relation to environmental conditions. The exact mechanisms responsible for these effects differ among stressors, but in general could operate via differential sensitivity to the stressors among phenotypes (i.e., differing reaction norms) and by altering variation in the physiological or behavioural traits being examined. Increased knowledge of these mechanisms could provide insights into the causal link between physiology and behaviour in a wide variety of ecological contexts and also better understanding of the possible evolutionary implications of stressors caused by environmental change. To date, only a few studies have directly examined the effect of environmental stressors on the covariation of behavioural and physiological traits (Table 1), but the evidence that stressors can have modulating effects hopefully will encourage more researchers to explore this topic.

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