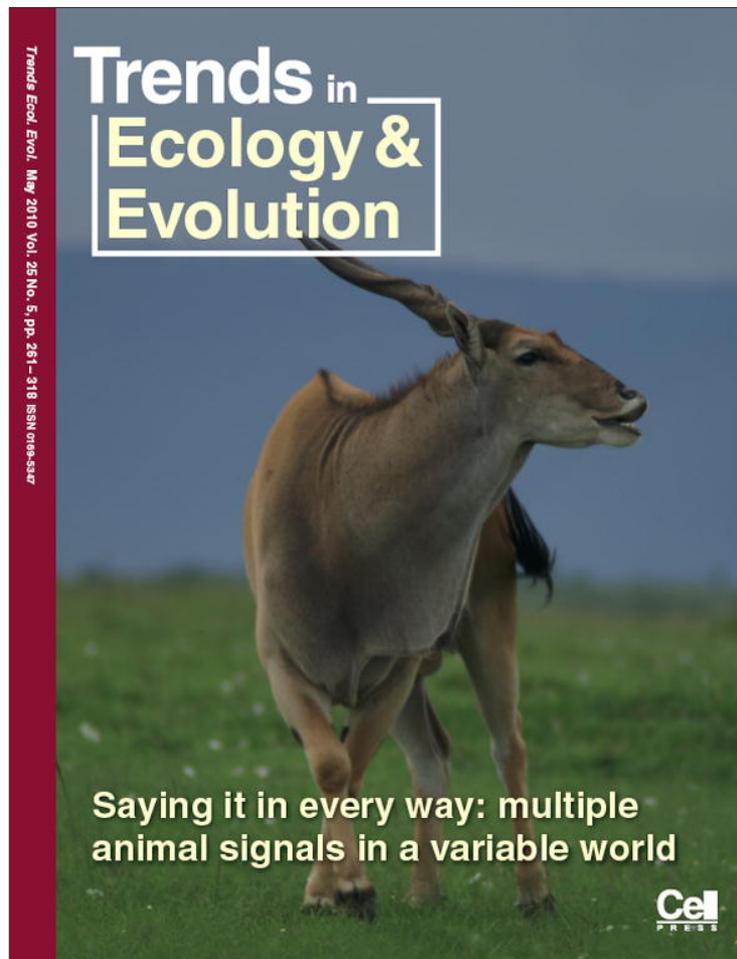


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# Why is there variation in baseline glucocorticoid levels?

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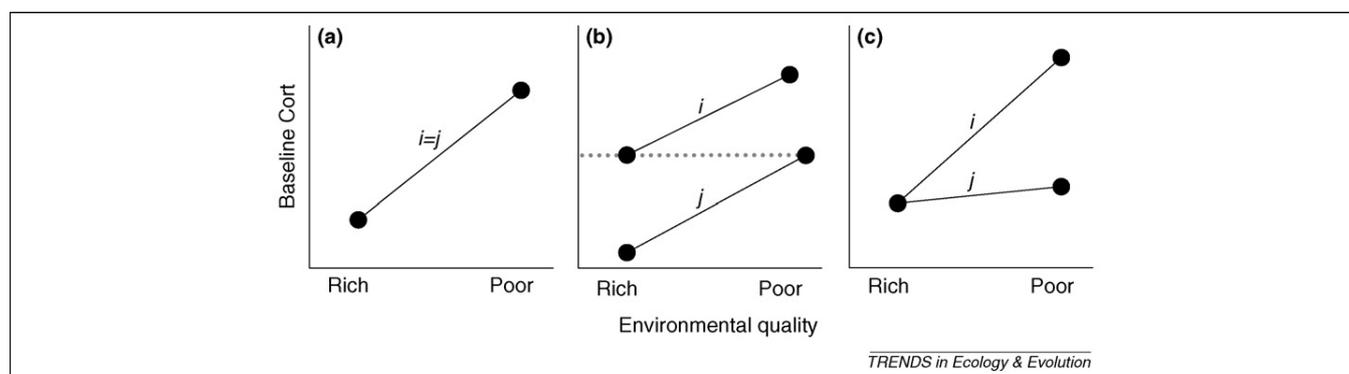
In a recent article in *TREE*, Bonier and colleagues [1] reviewed the support for the Cort-Fitness Hypothesis, which states that baseline glucocorticoid (cort) levels are elevated in individuals, or populations, that experience challenging conditions, therefore signalling low future fitness. The idea is that the optimal level of resources allocated towards self-maintenance (immediate survival) versus long-term survival and/or reproduction differs across environments, with selection favouring individuals investing in self-maintenance when the environment becomes 'challenging.' The hypothesis states that this re-allocation of resources can be achieved by altering baseline levels of cort. Their literature review did not support the hypothesis, as it revealed much variation in sign and shape of the relationship between cort and residual fitness within and across species, populations, and life-history stages [1]. We here propose that the inability to find unequivocal support for the Cort-Fitness Hypothesis is a side effect of Bonier *et al.*'s implicit assumption that individual variance components can be ignored when testing evolutionary hypotheses, a phenomenon recently coined the 'tyranny of the Golden Mean' [2].

Bonier *et al.* assume that animals react to environmental change by altering their phenotype, and that this response is adaptive. Selection would have favoured a particular relationship between cort and environmental quality. Such a relationship can be viewed as a line (Figure 1a) characterised by a certain elevation and slope, often called a 'reaction norm' [3]. If all individuals had the same reaction norm, the Cort-Fitness Hypothesis could be tested using a cross-sectional approach, where residual fitness is compared across individuals showing low versus high levels of cort [1], the approach taken in the review.

Baseline cort does, however, vary consistently across individuals, with certain individuals showing high and others showing low levels of cort under any type of condition (Figure 1b). The slope of the relationship between cort and environmental quality (i.e. plasticity) can also differ between individuals (Figure 1c) and both types of individual variation can be heritable (see [4,5]).

The presence of individual variation in average level (I), and plasticity (I × E), in baseline cort has consequences for how the Cort-Fitness Hypothesis should be tested. When I or I × E are present, high cort levels do not necessarily signal 'challenging' conditions. Imagine a situation (Figure 1b) in which two types of individuals exist, both showing adaptive increases in cort when the environment becomes challenging, but one type always has higher levels of cort. Both types could have exactly the same phenotype (dotted line in Figure 1b), because one experiences the environment as challenging whereas the other does not. A valid test of the hypothesis would therefore require the measurement of individual reaction norms (see [5]), expecting a negative association between cort level and residual fitness within individuals.

How should we then interpret the seemingly 'inconsistent' Cort-Fitness relationship? We suggest that it is caused by heterogeneous selection acting on the between-individual component of cort. Recent studies on natural populations show that temporal and spatial variation exists in selection acting on behaviours (e.g. [6]) that are genetically correlated with baseline cort [7]. Individual variation in cort might thus represent fundamental differences in how individuals cope with environmental challenges [7], implying that there might not be a single optimal response [8,9]. We encourage endocrinologists to try to disentangle



**Figure 1.** Hypothetical relationships between baseline levels of cort and environmental quality. Each line represents a type of individual present within the population. Two types of individuals (*i* and *j*) are present in population (b) and (c), a single type in population (a). For details see text.

within- versus between- individual variation in cort levels and to evaluate this variation within an evolutionary framework.

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#### Letters Response

## Clarifying the Cort-Fitness Hypothesis: a response to Dingemanse *et al.*

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Dingemanse *et al.* [1] suggest that the Cort-Fitness Hypothesis rests upon the idea that 'the optimal level of resources allocated towards self-maintenance (immediate survival) versus long-term survival and/or reproduction differs across environments, with selection favoring individuals investing in self-maintenance when the environment becomes "challenging"'. This interpretation is incorrect. Instead, the Cort-Fitness Hypothesis rests upon the idea that difficult or challenging conditions lead to low fitness (i.e. low future survival and/or low future reproductive success), and that glucocorticoid (cort) levels can be used as a proxy for the degree of environmental challenge facing individuals and populations [2]. Indeed, this proposed connection between high cort, difficult environmental conditions and low fitness is the main reason why conservation biologists use cort as a proxy for the health of individuals and populations.

The Cort-Fitness Hypothesis is not an evolutionary hypothesis and is not aimed at measuring selection. Instead, the Cort-Fitness Hypothesis is a simple pattern hypothesis whereby cort can be used as a proxy for environmental challenges facing individuals or populations. Ultimately, the proposed correlations between levels of cort, environmental challenges and fitness, if they exist, could result from one or more evolutionary selective pressures acting on cort secretion. However, the Cort-Fitness Hypothesis is not a hypothesis to explain why cort levels vary with fitness or the environment; it is simply addressing the common usage of cort as a proxy for the health of individuals and populations in the scientific literature.

We do not make the assumption that individual variation can be ignored when examining the Cort-Fitness Hypothesis. Among-individual variation in cort secretion, varying reaction norms and/or coping strategies might obscure relationships between levels of cort and fitness, and we discuss all of these possibilities in our original paper (e.g. 'Genetic and developmental effects' in [2], p. 638). The inconsistent relationships between cort and fitness (including positive, negative and no relationships) do not result solely from individual variation in the cort response across environments because some studies have found individuals with the highest fitness exhibiting both low and high cort levels relative to low fitness individuals, depending on the stage of breeding [e.g. 3,4].

Overall, our conclusion remains unchanged: levels of cort cannot be used as a proxy for environmental challenges or fitness without first understanding the relationship between cort, the environment and fitness in the organism of interest. We agree wholeheartedly that evaluating sources of within and among individual variation within an evolutionary framework can provide important advances in our understanding of these cort-fitness relationships, and we are presently taking this approach in our own work [e.g. 4–6].

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