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Do baseline glucocorticoids predict fitness?

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Baseline glucocorticoid (cort) levels are increasingly employed as physiological indices of the relative condition or health of individuals and populations. Often, high cort levels are assumed to indicate an individual or population in poor condition and with low relative fitness (the Cort–Fitness Hypothesis). We review empirical support for this assumption, and find that variation in levels of baseline cort is positively, negatively, or non-significantly related to estimates of fitness. These relationships between levels of baseline cort and fitness can vary within populations and can even shift within individuals at different times in their life history. Overall, baseline cort can predict the relative fitness of individuals and populations, but the relationship is not always consistent or present.

Field measures of glucocorticoids as a physiological index

Ever since the advent of the application of endocrine techniques in the field [1], researchers have sought to interpret the biological significance of variation in hormone levels in free-ranging animals. Glucocorticoids (see glossary), or stress hormones, are increasingly employed as physiological indices of the relative condition or health of individuals and populations [2,3]. More generally, glucocorticoid (cort) levels are interpreted as an index of stress, or allostatic load [4,5]. Cort is also often used as a tool for monitoring health and response to habitat disturbance in species and populations of conservation concern (e.g. [6,7]). Across these studies, higher levels of baseline cort are routinely assumed to indicate an individual or population in worse condition, and of reduced relative fitness, as compared to individuals or populations with lower levels of cort (e.g. [8–10]). Hereafter, we will refer to this as the Cort–Fitness Hypothesis [11].

Here we critically evaluate the theoretical foundations of the Cort–Fitness Hypothesis, its pervasiveness in the literature, and its support from empirical data. Tests of the Cort–Fitness Hypothesis are uncommon, but increasing in number, and these studies provide an important body of empirical data to evaluate the hypothesis (Table 1). We discuss potential explanations for the many instances where these empirical data are inconsistent with the Cort–Fitness Hypothesis.

Our review is focused on relationships between baseline cort levels and fitness. Breuner and colleagues [12] recently

reviewed the relationship between cort levels associated with the acute stress response and fitness. While the cort–fitness relationship expected for these two levels of hormone secretion is somewhat similar in theoretical underpinnings, the actions of cort at baseline and stress-induced levels are quite distinct [13].

Theoretical foundations and pervasiveness of the Cort–Fitness Hypothesis

Glucocorticoids are a highly conserved family of steroid hormones, secreted in all vertebrates as a result of the activation of the hypothalamic–pituitary–adrenal (or interrenal) axis and serving numerous functions essential to survival [14]. Broadly, cort can be considered a metabolic hormone, increasing in response to energetic needs associated with environmental challenges such as resource limitations or inclement climatic conditions. The positive response of baseline cort secretion to energetic demands forms the basic foundation of the Cort–Fitness Hypothesis.

Glossary

Acute stress: Unpredictable, short-term challenges that cause an individual to go into allostatic overload. Acute stress causes increases in cort levels beyond baseline levels, resulting in saturation of the low capacity, high affinity type I glucocorticoid receptors and binding of the high capacity, low affinity type II receptors [13].

Allostasis: maintenance of regulated internal conditions and energetic balance in the face of current and anticipated changes in energetic demands [5]

Allostatic load: cumulative current and anticipated energetic demands facing an individual [5]

Allostatic overload: negative energy balance, a condition facing individuals with an allostatic load that exceeds available resources [5]

Baseline: level of hormone secretion associated with normal physiological function. At baseline levels, cort is secreted to maintain allostasis in response to predictable energetic demands, resulting primarily in the binding of type I glucocorticoid receptors [13].

Chronic stress: Long-term allostatic overload. Cort levels remain above baseline (i.e., within range typically associated with acute stress, with type I receptors and type II receptors bound), and can have direct, negative effects on fitness [13,66,67].

Cort–Adaptation Hypothesis: a revision of the Cort–Fitness Hypothesis that includes reproductive effort as a challenge to allostasis (Box 1)

Cort–Fitness Hypothesis: hypothesis that baseline cort levels negatively covary with fitness

Fitness: an individual's contribution of genetic material to subsequent generations

Fitness metric: a quantitative estimate of fitness, often numbers of viable offspring produced or estimated survival

Glucocorticoid (cort): a class of steroid hormones found in all vertebrates, involved in many aspects of metabolism and energy balance, as well as response to environmental challenges [14]

HPA axis: the Hypothalamic–Pituitary–Adrenal (or interrenal) axis: the endocrine axis involved in regulation of secretion of cort. Signals originating in the hypothalamus trigger a cascade of events that includes secretion of cort from the adrenal cortical tissue [14].

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Table 1. Studies reporting analyses of fitness correlates of baseline or fecal cort

Species	Fitness metric ^a	Method ^b	Findings ^c	Refs
Bluegill sunfish (<i>Lepomis macrochirus</i>)	R	C and E _E	-, +	[28]
Sockeye salmon (<i>Oncorhynchus nerka</i>)	R	C	-, +	[31]
Collared lizard (<i>Crotaphytus collaris</i>)	R	C	ns	[68]
Black-browed albatross (<i>Thalassarche melanophris</i>)	R	C	ns, -	[27]
Black-legged kittiwake (<i>Rissa tridactyla</i>)	R	C	ns, -	[69]
Black-legged kittiwake (<i>Rissa tridactyla</i>)	R	C	-	[53]
Black-legged kittiwake (<i>Rissa tridactyla</i>)	R	C	+	[70]
Black-legged kittiwake (<i>Rissa tridactyla</i>)	R	C	ns, -	[39]
Blue-footed booby (<i>Sula nebouxi</i>)	R	C	ns, -	[71]
Blue tit (<i>Parus caeruleus</i>)	R	C	ns, +	[72]
Common murre (<i>Uria aalge</i>)	R	C	ns, -	[51]
European starling (<i>Sturnus vulgaris</i>)	R	C	-, +	[59]
King penguin (<i>Aptenodytes patagonicus</i>)	R	C	ns, -	[73]
Pied flycatcher (<i>Ficedula hypoleuca</i>)	R	C	ns	[74]
Pied flycatcher (<i>Ficedula hypoleuca</i>)	R	C	+	[75]
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	R	C	+	[61]
Stonechat (<i>Saxicola torquata</i>)	R	C	ns, -	[76]
Tufted puffin (<i>Fratercula cirrhata</i>)	R	C	ns, -	[58]
White-crowned sparrow (<i>Zonotrichia leucophrys</i>)	R	C	ns, -	[29]
Yellow-eyed penguin (<i>Megadyptes antipodes</i>)	R	C	ns	[77]
Black-legged kittiwake (<i>Rissa tridactyla</i>)	R and S	C	ns, -	[78]
Tree swallow (<i>Tachycineta bicolor</i>)	R and S	C	ns, -	[11]
Marine iguana (<i>Amblyrhynchus cristatus</i>)	S	C	ns	[33]
Marine iguana (<i>Amblyrhynchus cristatus</i>)	S	C	-	[79]
Side-blotched lizard (<i>Uta stansburiana</i>)	S	C	+	[80]
Cliff swallow (<i>Petrochelidon pyrrhonota</i>)	S	C	nl, -	[81]
Eurasian treecreeper (<i>Certhia familiaris</i>)	S	C	-	[50]
European white stork (<i>Ciconia ciconia</i>)	S	C	ns	[82]
Common lizard (<i>Lacerta vivipara</i>)	R	E _C	ns, +	[83]
Barn owl (<i>Tyto alba</i>)	R	E _C	ns	[45]
Black-legged kittiwake (<i>Rissa tridactyla</i>)	R	E _C	-	[84]
Common eider (<i>Somateria mollissima</i>)	R	E _C	-	[44]
European starling (<i>Sturnus vulgaris</i>)	R	E _C	ns	[85]
White-crowned sparrow (<i>Zonotrichia leucophrys</i>)	R	E _C	ns	[46]
Side-blotched lizard (<i>Uta stansburiana</i>)	R and S	E _C	ns, -, +	[30]
Side-blotched lizard (<i>Uta stansburiana</i>)	R and S	E _C	ns	[86]
Barn swallow (<i>Hirundo rustica</i>)	S	E _C	-	[87]
Yellow-legged gull (<i>Larus michahellis</i>)	S	E _C	ns	[88]
European starling (<i>Sturnus vulgaris</i>)	R and S	E _{CE}	ns, -, +	[40]
Barn swallow (<i>Hirundo rustica</i>)	R	E _E	ns	[89]
Black-legged kittiwake (<i>Rissa tridactyla</i>)	R	E _E	+	[63]
European starling (<i>Sturnus vulgaris</i>)	R	E _E	+	[48]
Great tit (<i>Parus major</i>)	R	E _E	ns	[90]
House sparrow (<i>Passer domesticus</i>)	R	E _E	ns	[91]
Song sparrow (<i>Melospiza melodia</i>)	R	E _E	-	[47]
European wild rabbit (<i>Oryctolagus cuniculus</i>)	S	E _E	+	[32]
Greylag goose (<i>Anser anser</i>)	R	fC	+	[92]
Baboon (<i>Papio cynocephalus</i>)	R	fC	ns	[93]
Great gerbil (<i>Rhombomys opimus</i>)	S	fC	-	[94]
Great gerbil (<i>Rhombomys opimus</i>)	S	fC	ns, +	[95]
Ring-tailed lemur (<i>Lemur catta</i>)	S	fC	-	[96]
Black-tailed prairie dog (<i>Cynomys ludovicianus</i>)	R	fE _E	ns, -	[97]
Deer mouse and white-footed mouse (<i>Peromyscus sp</i>)	R and S	fE _E	-	[98]

^aFitness metric employed: R, estimate of reproductive success; S, estimate of survival.

^bMethod employed: fecal cort measures denoted by f prefix; C, correlational; E_C, experimental manipulation of cort levels; E_E, experimental manipulation of environmental challenges, including reproductive effort; E_{CE}, experimental manipulation of both cort levels and environmental challenges.

^cFindings: ns, non-significant; nl, nonlinear; +, linear positive relationship; -, linear negative relationship. These findings refer only to relationships between baseline cort and fitness metrics, although some studies report findings of other analyses. Some studies report more than one result depending variously on sex, morph, breeding stage, and fitness metric included in analyses.

High levels of baseline cort might be associated with low relative fitness for several reasons. First, an individual encountering environmental challenges is predicted to increase cort secretion, leading to elevated levels of baseline cort. Elevated cort levels are thought to trigger a reallocation of resources away from normal activities of reproduction and survival to cope with the environmental challenge, thus reducing fitness (Figure 1). Second, variation in baseline cort levels has a heritable component in

several species (e.g. [15–17]) and is tightly associated with a suite of other phenotypic traits [18,19]. Thus, levels of baseline cort could provide an honest signal of individual quality, secreted at higher levels by lower quality individuals who might perceive their environment as challenging [20]. Third, the direct fitness effects of chronic increases of cort to levels typically associated with acute stress are often invoked to explain the predicted negative relationship between cort and fitness [21,22]. These three perspect-

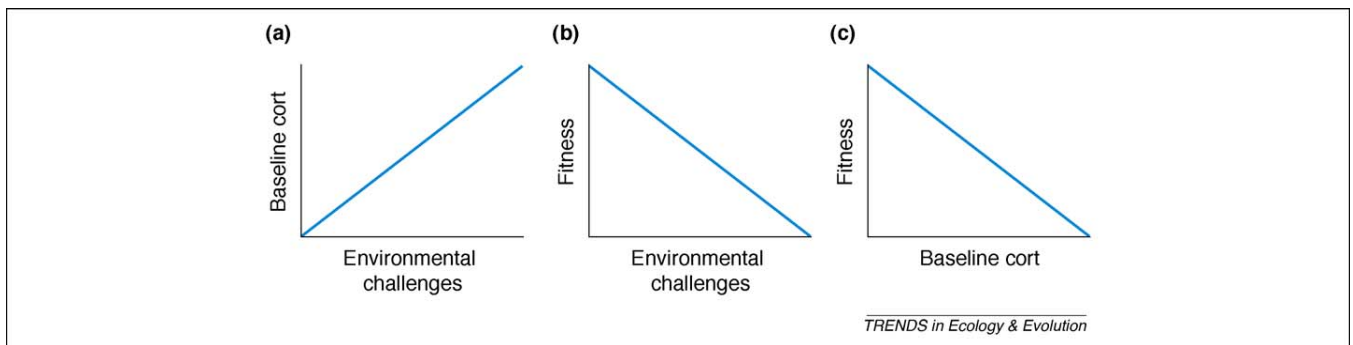


Figure 1. The theoretical foundation of the Cort–Fitness Hypothesis. (a) Baseline cort levels are predicted to increase with environmental challenges (*tenet 1*). (b) Increasing environmental challenges are associated with decreasing fitness because resources must be reallocated towards coping with these challenges at the expense of reproduction or self-maintenance (*tenet 2*). (c) In combination, these two tenets lead to the central prediction of the Cort–Fitness Hypothesis: a negative relationship between baseline cort and fitness.

ives are not mutually exclusive, and all predict a positive relationship between cort and environmental challenges, and a negative relationship between cort and fitness.

Many authors suggest that cort mediates a trade-off in self-maintenance versus reproduction (for review, see [22]), with increasing cort levels favoring the reallocation of resources to self-maintenance at the expense of reproduction. We focus instead on what we view as the two central tenets of the Cort–Fitness Hypothesis: (1) baseline cort increases with environmental challenges, and (2) fitness declines with increasing environmental challenges. When combined, these tenets predict a negative relationship between baseline cort and fitness (Figure 1).

In response to environmental challenges, increased levels of cort and subsequent reallocation of resources might increase the survival of an individual. In this sense, the cort response could increase fitness of an individual relative to others with a less effective cort response who are experiencing exactly the same challenges. However, when comparing across individuals or populations with varying environmental challenges (within the same life history stage, sex, age class), cort will be negatively related to fitness simply because variation in levels of baseline cort provides a proxy for variation in environmental challenges that directly influences fitness. Thus the potentially adaptive nature of the cort response to environmental challenges does not necessarily predict a positive relationship between cort and survival (or fitness) when comparing among individuals and populations.

To quantify the pervasiveness of the Cort–Fitness Hypothesis in the literature, we conducted a keyword search of two of the top endocrine journals, *Hormones and Behavior* and *General and Comparative Endocrinology*. We identified 72 articles published between January 2004 and December 2008 reporting the results of studies involving measurement and/or manipulation of cort levels in free-ranging animals. Of these, 39 (54%) based hypotheses or interpretations of findings at least in part on the Cort–Fitness Hypothesis. This estimate of the pervasiveness of the Cort–Fitness Hypothesis is probably conservative. Beyond endocrinology journals, cort measures are widely used by ecologists and conservation biologists because cort is assumed to provide an index of population and individual health and condition [2,3], an assumption that is based on the Cort–Fitness Hypothesis. Thus, across all of the

literature, the Cort–Fitness Hypothesis appears to broadly influence the direction and interpretation of research.

Empirical support for the Cort–Fitness Hypothesis

In a subsequent, thorough review of all of the literature, we found 53 studies that examined the relationship between components of fitness and baseline cort (46 studies) or fecal cort (7 studies) (Table 1). We identified these studies using exhaustive searches of combinations of several relevant keywords (adrenocortical, corticosteroid, cortisol, corticosterone, or glucocorticoid, and fitness, fecundity, reproductive success, or survival) in the Web of Science and Google Scholar databases. We excluded studies that did not report either baseline or fecal levels of cort. Fecal cort measures incorporate variation in hormone levels over a broad period of hormone secretion, metabolism, and excretion, and thus might be quite distinct from baseline levels [23]; therefore, we include these studies primarily for comparison with the results of studies involving baseline levels. We excluded studies involving species with social systems leading to reproductive suppression which directly limits fitness of some members of the group (e.g. social subordinates; see [24,25] for review). We included studies involving direct manipulation of hormone levels. We are cautious in interpreting these studies, because of potential problems with hormone manipulations that include initial spikes in circulating hormone levels beyond the range of baseline, and the potential stimulation of negative feedback mechanisms in response to high levels of supplementary hormone [26]. We excluded studies that used indirect measures of reproductive success or survival, such as offspring provisioning rate, mass of eggs or offspring, and measures of body condition or immune response. We focused instead on studies with direct estimates of reproductive success (e.g. number of viable eggs or offspring) or survival.

Our review encompasses a broad sample of studies representative of the available data on cort–fitness relationships. However, we might have missed some studies where the authors did not highlight fitness measures. An encouraging trend in the literature is the increasing number of field endocrine studies that include fitness metrics in their analyses, from just five papers published between 1987 and 2000 to 48 studies between 2000 and 2009. Overall, 37 of the 53 studies were conducted in birds,

along with two in fish, seven in reptiles, and seven in mammals.

Twenty-three of the 46 studies involving baseline measures (50%) and four of the seven studies involving fecal cort measures (57%) reported the predicted negative relationship between cort and fitness, consistent with the Cort–Fitness Hypothesis. Twenty-eight of the baseline studies (61%) and three of the fecal cort studies (43%) reported a non-significant relationship between baseline cort levels and fitness, while 14 baseline cort studies (30%) and two fecal cort studies (29%) found a positive relationship. The sum of the findings of these studies exceeds 100% because several studies found more than one relationship between levels of baseline cort and fitness. In these studies, the relationship between cort and fitness varied depending on the fitness metric used [e.g. cort negatively correlated with current reproductive success but not with cumulative reproductive success, 27], the timing of sampling [e.g. cort negatively correlated with reproductive success during early stages of breeding, but positively correlated with reproductive success during later stages of breeding, 28], the sex of the individual [e.g. cort negatively correlated with reproductive success in males but not females, 29], and the reproductive strategy of the individual [e.g. experimental increases in cort had opposite effects on two morphs of side-blotched lizard, *Uta stansburiana*, that differed in their life history strategies, 30].

We found no differences between correlational and experimental studies in their likelihood of detecting a significant relationship between levels of cort and fitness. For studies that report a significant relationship between cort and fitness, we found no differences between correlational studies and experimental studies in their likelihood of a positive or negative pattern between cort and fitness. We also found no differences in the relationship between cort and fitness that coincided with the sex of focal individuals or with estimates of survival versus reproductive success.

Overall, empirical evidence does not overwhelmingly support predictions of the Cort–Fitness Hypothesis. The 50% of studies that report a negative relationship between

baseline levels of cort and fitness is probably an overestimate if non-significant findings are under-reported. Below we discuss possible reasons why the Cort–Fitness Hypothesis might fail.

When should the Cort–Fitness Hypothesis fail?

Given that empirical data do not consistently support the predictions of the Cort–Fitness Hypothesis, we review below several plausible explanations for instances where the Cort–Fitness Hypothesis is not supported. We draw broadly from the literature to assess potential causes of the breakdown of the Cort–Fitness Hypothesis found in our review above.

Underlying assumptions I: repeatability of cort measures

Lifetime reproductive success for an individual is not variable, but cort levels are dynamic. Thus, levels of cort must vary in their relationship with fitness within an individual. Most studies sample cort at only one time point for each individual, and this point sample might provide an inaccurate measure of an individual's overall condition and fitness. If variation among individuals in levels of cort or fitness is relatively small, then within-individual variation might obscure among-individual patterns, particularly if other environmental factors (e.g. sex, life history stage, time of day) are not controlled.

Underlying assumptions II: repeatability of cort–fitness relationships

Many studies assume that the relationship between cort and fitness is static. This assumption is probably flawed because most animals live in changing environments, and cort–fitness relationships might vary with environmental conditions. In addition to environmental effects, recent studies have demonstrated that the cort–fitness relationship can vary both within a group of individuals sampled at different times [11], and among individuals of different sex [29] and reproductive strategy [30] (Figure 2). Even the direction of the cort–fitness relationship can vary from positive to negative among and within individuals (e.g.

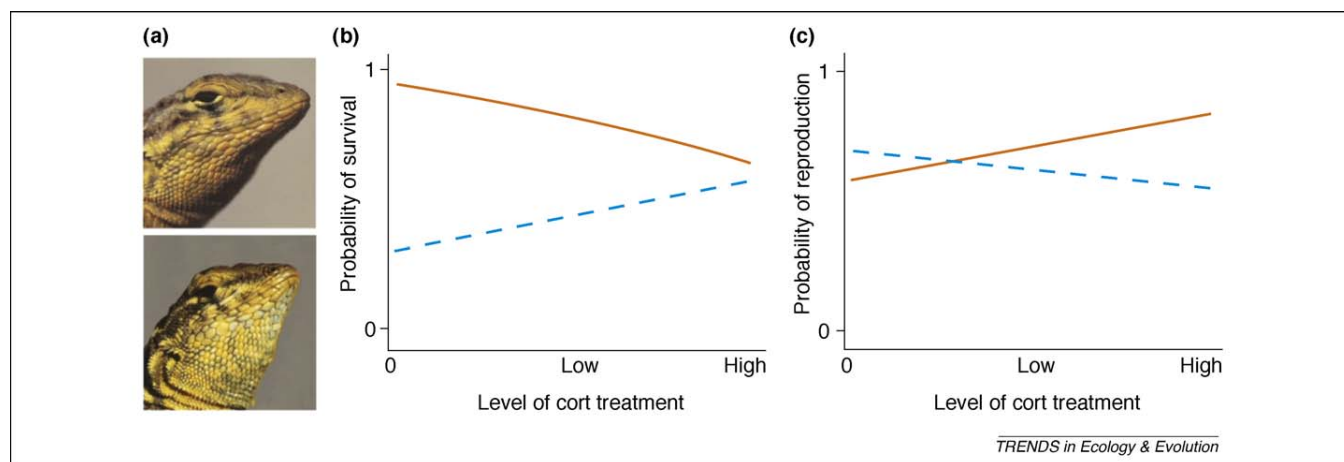


Figure 2. Variation in the cort–fitness relationship within a species. (a) Experimentally increased cort had opposite effects in female side-blotched lizards (*Uta stansburiana*), of two morphs with distinct reproductive strategies (orange, r-strategist and yellow, K-strategist females). High cort increased the probability of short-term survival (b) but decreased the probability of reproduction (c) in yellow females (dashed blue line), and increased reproduction but reduced survival in orange females (solid orange line). (a) reproduced with permission from Barry Sinervo. (b) and (c) reproduced from [30] with permission.

[28,30,31]). These studies clearly illustrate that the relationship between baseline cort levels and fitness can vary, and thus represent a major challenge to the Cort–Fitness Hypothesis.

Underlying assumptions III: biological significance

If baseline cort levels and the relationship between cort and fitness are not repeatable within individuals, then researchers must conduct validations of cort–fitness relationships across life history stages to ascertain the biological significance of variation in cort levels. To date, there have been very few such validations (but see [11]). Only three of the cort–fitness studies we reviewed assessed relationships between baseline cort and survival in non-breeding individuals [32–34]. Further, other factors such as variation in receptor density and binding globulin concentration influence the biological activity and effects of cort [35–37], but are often not accounted for or considered in interpretations.

Appropriateness of fitness metrics

The relationship between baseline cort levels and fitness might vary because of the estimates of fitness used. Researchers are rarely able to measure lifetime reproductive success or other long-term estimates of fitness, especially in multiparous species. Instead, we commonly measure fitness components that are assumed to directly correlate with lifetime reproductive success [38]. In some cases, measures of fitness components might not reflect variation in lifetime reproductive success, causing patterns inconsistent with the Cort–Fitness Hypothesis. In our review of the literature, we found several instances where the cort–fitness relationship varied within populations, depending on the fitness metric employed (e.g. [27,39,40]).

Nonlinear relationships

Measuring fitness correlates of trait variants can be difficult for a variety of reasons [38,41]. The negative relationship between cort and fitness predicted by the Cort–Fitness Hypothesis focuses only on fitness correlates of higher levels of cort secretion. However, an individual with a cort level of zero will have zero fitness because some minimal level of cort is required for survival [14]. Thus the relationship between cort and fitness might be non-linear across the full range of variation in cort levels, with stabilizing selection favoring some optimal cort level. Few studies explicitly test for non-linear relationships between cort and fitness.

Genetic and developmental effects

Among-individual variation in genetic background (e.g. [15]), maternal effects (e.g. [42]), and the environment experienced during development (e.g. [43]) can result in lasting differences in sensitivity and activity of the cort response, and might influence the relationship between cort and fitness. For example, we find two patterns of cort secretion associated with two distinct, heritable coping styles (proactive and reactive) in several species, suggesting selective maintenance of variation in cort secretion patterns within populations [18,19]. Lancaster and colleagues documented opposite effects of experimen-

tal manipulation of cort levels on survival and reproduction in female side-blotched lizards of differing, genetically determined reproductive strategies (Figure 2, [30]). Other genetic or developmental variation among individuals might similarly influence cort–fitness relationships, but have been poorly studied.

Experimental limitations

Designing the appropriate experimental tests to elucidate cort–fitness relationships is challenging. In many experimental studies, supplemental cort is employed with the prediction that cort-supplemented individuals should show reduced fitness, often in the form of reduced reproductive success (e.g. [44,45]). However, if the relationship between cort and fitness is not causal, but instead reflects a response to environmental challenges that directly reduce fitness, then in the absence of environmental challenges, experimentally increasing cort levels might have no effect, or unexpected effects, on fitness. Furthermore, hormone manipulations might cause variation in cort levels outside those typically found in baseline variation. In nature, very small differences in cort levels (i.e. within the range of baseline) can influence many biological traits (e.g. offspring sex ratios, [46]) and vary with fitness components (Table 1). However, experimental manipulations of cort, particularly those employing silastic tube implants, often cause transient increases in cort well beyond the range of baseline. These spikes in supplemental cort might induce negative feedbacks that paradoxically cause net decreases in circulating hormone levels (for review, see [26]), making interpretations of results difficult. Recently developed alternative means of supplementing hormone levels might provide more modest changes in circulating cort more relevant to natural variation in baseline cort [26].

Experimental approaches to elucidating cort–fitness relationships extend beyond the modification of hormone levels. Other aspects of the cort–fitness relationship can also be modified, including resource availability and other environmental challenges, and reproductive investment through augmentation or reduction of brood sizes (e.g. [28,40,47,48]). Such manipulations have provided important advances in our understanding of cort–fitness relationships.

A critical analysis of the central tenets of the Cort–Fitness Hypothesis

The methodological considerations described above can explain many of the instances where the Cort–Fitness Hypothesis appears to fail. In the absence of such methodological problems, failure of the Cort–Fitness Hypothesis should be traceable to a breakdown in one of the two central tenets (Figure 1). We consider empirical support for each of these tenets below.

Tenet 1: baseline cort increases with increasing environmental challenges

A large body of literature reports correlations between cort and measures of environmental challenges. In many cases, evidence supports the first tenet of the Cort–Fitness Hypothesis; baseline cort levels generally parallel increasing

or decreasing environmental challenges (e.g. [49,50]). In seabirds, the relationship between cort levels and variation in food availability appears to be so strong that some authors have suggested using measures of baseline cort as proxies for food availability [51–53]. Non-significant relationships between cort and environmental challenges are also quite commonly reported (e.g. [29,54]), although these patterns might be caused, in part, by differences between a researcher's and an animal's perceptions of environmental challenges rather than a lack of a relationship between cort and environmental challenges. Additionally, among-individual variation in the context and perception of an environmental challenge undoubtedly influences hormonal reactions [13]. While cort levels usually increase with increased environmental challenges

across individuals, two experimental studies have found the exact opposite pattern - a decrease in cort levels with increased environmental challenges. This unexpected result was initially found in a captive study by Rich and Romero [55], but repeated in a field study by Cyr and Romero that experimentally induced environmental challenges (disturbance at nest boxes) in free-ranging European starlings (*Sturnus vulgaris*) [48]. In the field study, experimentally increased environmental challenges resulted in both reduced reproductive success and baseline cort levels [48]. Overall, the majority of the available data supports a positive relationship between cort levels and environmental challenges (the first tenet of the Cort-Fitness Hypothesis), while these two experimental studies suggest that the relationship might be more complex.

Box 1. The cort-adaptation hypothesis

Several studies have described positive relationships between reproductive success and baseline cort (e.g. Figure 1, [59,61,62]) that contradict the central expectation of the Cort-Fitness Hypothesis. One potential explanation for these observations comes from a modification of the definition of environmental challenges, rather than a rejection of the Cort-Fitness Hypothesis. The Cort-Adaptation Hypothesis expands the definition of environmental challenges to encompass all challenges to allostasis experienced by an organism, including those associated with reproduction [11]. When organisms are confronted with reproductive challenges, we predict a positive cort-fitness relationship if increased cort promotes the reallocation of resources to reproduction, increasing lifetime reproductive

success. Individuals in good condition that can invest the most resources in reproduction might also be expected to have the highest allostatic load and levels of cort, leading to a positive relationship between baseline cort and reproductive success across individuals. We might expect the nature of these relationships, and the validity of the Cort-Adaptation Hypothesis, to depend on the magnitude of reproductive investment or effort provided, and thus to vary among species and individuals with different reproductive strategies. Consistent with this idea, a recent meta-analysis of cort levels in 64 bird species revealed that baseline cort measured during periods of parental care was higher in species with a high value of the current brood relative to expected lifetime reproductive output [65].

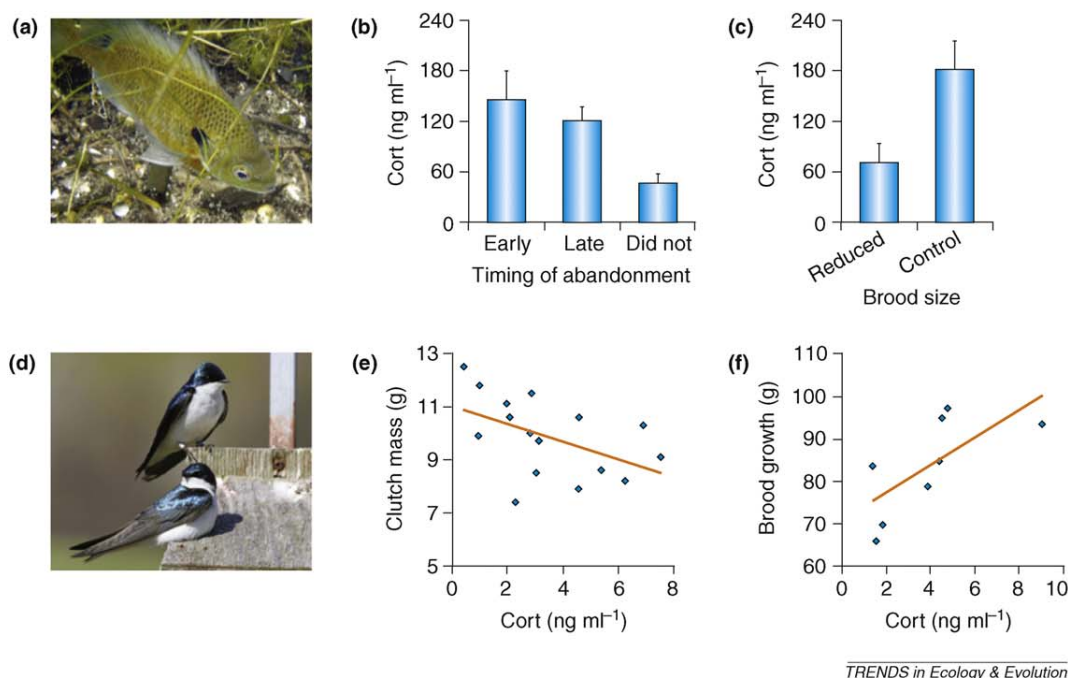


Figure 1. Empirical support for the Cort-Adaptation Hypothesis. Baseline cort levels measured early in breeding were negatively correlated with reproductive success in male bluegill sunfish [28] (*Lepomis macrochirus*), (a). Males with higher baseline cort were more likely to abandon their nests, while males that abandoned earliest had the highest cort levels (b). Later in the breeding effort, cort positively correlated with reproductive investment; an experimental reduction in brood size resulted in reduced baseline cort levels relative to fish with larger, unmanipulated broods (c). In breeding female tree swallows (*Tachycineta bicolor*) (d), we find a similar change in patterns, with a negative relationship between baseline cort and reproductive investment (clutch mass) early in the breeding season (e), and a positive relationship between baseline cort and another metric of reproductive investment (total growth of all nestlings in a brood over 8 days) later in the breeding season (f). (a) reproduced with permission from Bryan D. Neff, (b) and (c) adapted with permission from data provided in [28], (d) reproduced with permission from P-G Bentz, and (e) and (f) adapted with permission from [11].

Tenet 2: fitness should decline with increasing environmental challenges

More explicitly, this second tenet of the Cort–Fitness Hypothesis holds that environmental challenges associated with increasing cort should also be associated with decreasing fitness, because resources must be allocated away from normal activities of reproduction and survival to cope with these challenges. Several studies provide support for this tenet (e.g. [7,56,57]). Returning to one of the best-studied groups, seabirds, we find that the environmental challenge of reduced food availability is almost uniformly associated with both increasing baseline cort levels and decreased reproductive success [51,53,58].

One important exception to the second tenet of the Cort–Fitness Hypothesis concerns the energetic challenges associated with reproductive effort. Allocation of resources to gametes and parental investment in rearing offspring present energetic demands or challenges that can themselves elicit increased baseline cort [59] and at the same time increase fitness. Thus the demands of reproduction might be perceived as an environmental challenge by many organisms [60], resulting in increased secretion of cort, reallocation of resources to reproduction, and a positive relationship between baseline cort and fitness. These patterns are consistent with several studies reporting positive correlations between cort and fitness components [59,61,62], and experimental studies that have demonstrated higher or lower circulating cort levels in response to experimentally increased or decreased reproductive effort, respectively (e.g. through brood size manipulations, [28,63,64]). The Cort–Adaptation Hypothesis is a modification of the Cort–Fitness Hypothesis; it encompasses the expectation of a positive cort–fitness relationship when environmental challenges are influenced by reproductive effort (Box 1) [11].

Conclusions: do baseline glucocorticoids predict fitness?

Overall, we do not find overwhelming support for the Cort–Fitness Hypothesis. The majority of published analyses report significant relationships between cort and fitness (39 of 53, or 74%), but the nature of this relationship varies. The challenge confronting those who seek to interpret field-measured baseline cort levels is to determine how cort predicts fitness. The diversity of findings (negative, positive, non-significant) should serve as a caution to biologists, particularly those who would use cort levels as proxies for relative fitness without first directly validating the cort–fitness relationship. The Cort–Adaptation Hypothesis, which expands the definition of environmental challenges to encompass challenges associated with reproduction, provides a clearer picture of cort–fitness relationships in nature, but cannot explain all of the observed patterns. At least some of the reported patterns might result from methodological limitations that obscure cort–fitness relationships in natural populations. We recommend a combination of observational, experimental, and integrative studies along with meta-analyses to elucidate the nature of, and variation in, cort–fitness relationships in future work.

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