Review

Do baseline glucocorticoids predict fitness?

Frances Bonier[1,2], Paul R. Martin[1], Ignacio T. Moore[2] and John C. Wingfield[3]

[1] Queen's University, Biology Department, Kingston, Ontario, K7L 3N6, Canada
[2] Virginia Tech, Department of Biological Sciences, Blacksburg, VA 24061, USA
[3] University of California, Davis, Department of Neurobiology, Physiology, and Behavior, Davis, CA 95616, USA

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].

Corresponding author: Bonier, F. (bonierf@queensu.ca).

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

[a] Fitness metric employed: R, estimate of reproductive success; S, estimate of survival.

[b] Method 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.

[c] Findings: 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-

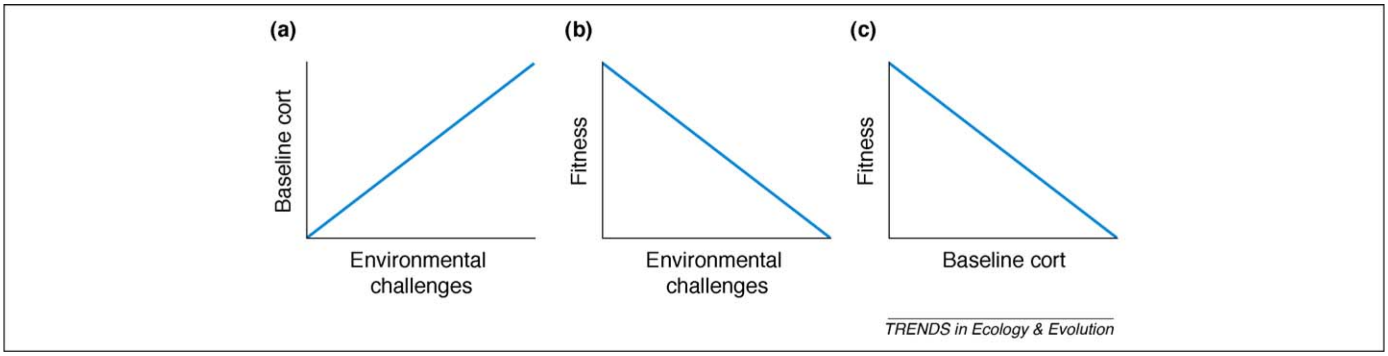

Figure 1. The theoretical foundation of the Cort–Fitness Hypothesis. **(a)** Baseline cort levels are predicted to increase with environmental challenges (*tenet 1*). **(b)** Increasing environmental challenges are associated with decreasing fitness because resources must be reallocated towards coping 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.

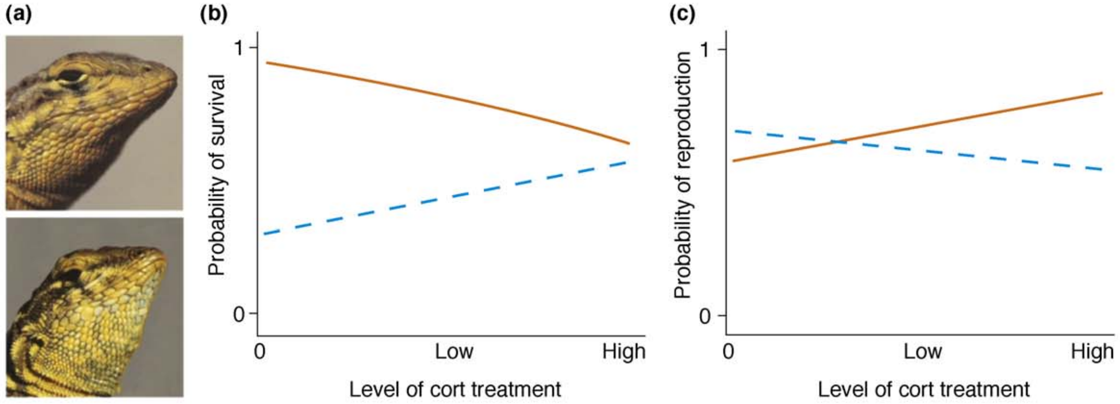

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Figure 2. Variation in the cort–fitness relationship within a species. **(a)** Experimentally increased cort had opposite effects in female side-blotched lizards (*Uta stansburiana*), of two morphs with distinct reproductive strategies (orange, r-strategist 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 experimental 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 I, [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].

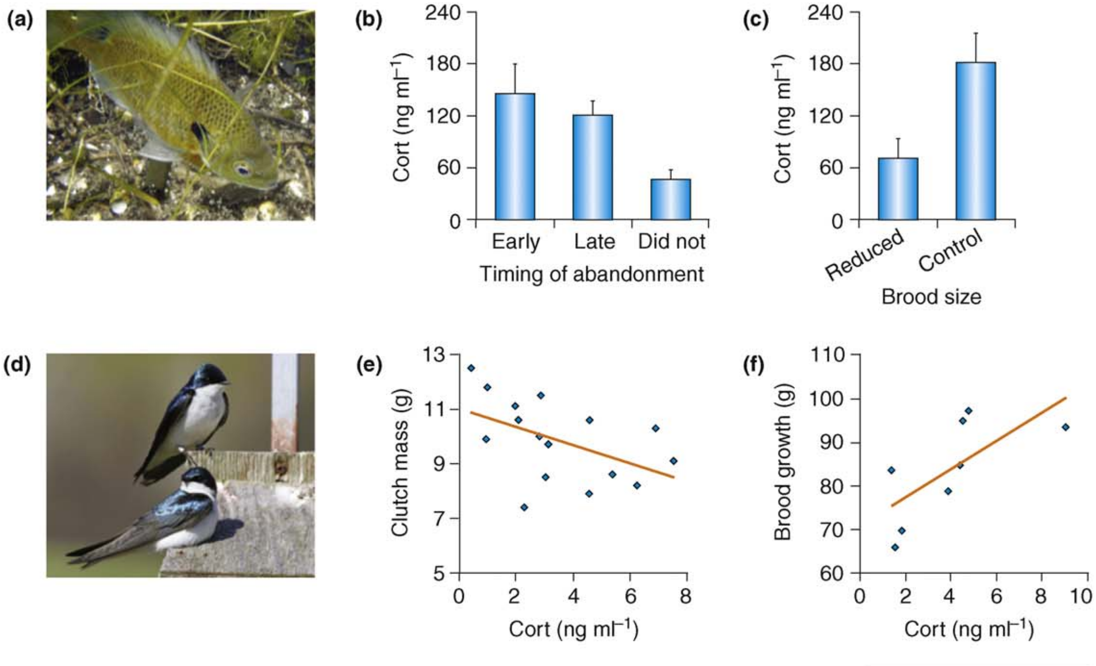

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Figure I. Empirical support for the Cort–Adaptation Hypothesis. Baseline cort levels measured early in breeding were negatively correlated with reproductive success in male bluegill sunfish [28] (*Lepomis macrochirus*), **(a)**. Males with higher baseline 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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References

1 Wingfield, J.C. and Farner, D.S. (1976) Avian endocrinology – field investigations and methods. *Condor* 78, 570–573
2 Walker, B.G. *et al.* (2005) Field endocrinology and conservation biology. *Integr. Comp. Biol.* 45, 12–18
3 Wikelski, M. and Cooke, S.J. (2006) Conservation physiology. *Trends Ecol. Evol.* 21, 38–46
4 Korte, S.M. *et al.* (2005) The Darwinian concept of stress: benefits of allostasis and costs of allostatic load and the trade-offs in health and disease. *Neurosci. Biobehav Rev.* 29, 3–38
5 McEwen, B.S. and Wingfield, J.C. (2003) The concept of allostasis in biology and biomedicine. *Horm. Behav.* 43, 2–15
6 Creel, S. *et al.* (2002) Snowmobile activity and glucocorticoid stress responses in wolves and elk. *Conserv. Biol.* 16, 809–814
7 Wasser, S.K. *et al.* (1997) Noninvasive physiological measures of disturbance in the northern spotted owl. *Conserv. Biol.* 11, 1019–1022
8 Arlettaz, R. *et al.* (2007) Spreading free-riding snow sports represent a novel serious threat for wildlife. *Proc. R. Soc. B Biol. Sci.* 274, 1219–1224
9 Sands, J. and Creel, S. (2004) Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. *Anim. Behav.* 67, 387–396
10 Thiel, D. *et al.* (2008) Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: a new methodological approach. *J. Appl. Ecol.* 45, 845–853
11 Bonier, F. *et al.* (2009) The relationship between fitness and baseline glucocorticoids in a passerine bird. *Gen. Comp. Endocrinol* 163, 208–213
12 Breuner, C.W. *et al.* (2008) In search of relationships between the acute adrenocortical response and fitness. *Gen. Comp. Endocrinol.* 157, 288–295
13 Romero, L.M. (2004) Physiological stress in ecology: lessons from biomedical research. *Trends Ecol. Evol.* 19, 249–255
14 Sapolsky, R.M. *et al.* (2000) How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr. Rev.* 21, 55–89
15 Evans, M.R. *et al.* (2006) Heritability of corticosterone response and changes in life history traits during selection in the zebra finch. *J. Evol. Biol.* 19, 343–352
16 Federenko, I.S. *et al.* (2004) The heritability of hypothalamus pituitary adrenal axis responses to psychosocial stress is context dependent. *J. Clin. Endocrinol. Metab.* 89, 6244–6250
17 Satterlee, D.G. and Johnson, W.A. (1988) Selection of Japanese quail for contrasting blood corticosterone response to immobilization. *Poult. Sci.* 67, 25–32
18 Koolhaas, J.M. *et al.* (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav Rev.* 23, 925–935
19 Overli, O. *et al.* (2007) Evolutionary background for stress-coping styles: relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. *Neurosci. Biobehav. Rev.* 31, 396–412
20 Husak, J.F. and Moore, I.T. (2008) Stress hormones and mate choice. *Trends Ecol. Evol.* 23, 532–534
21 Tilbrook, A.J. *et al.* (2000) Effects of stress on reproduction in non-rodent mammals: the role of glucocorticoids and sex differences. *Rev. Reprod.* 5, 105–113
22 Wingfield, J.C. and Sapolsky, R.M. (2003) Reproduction and resistance to stress: when and how. *J. Neuroendocrinol.* 15, 711–724
23 Millspaugh, J.J. and Washburn, B.E. (2004) Use of fecal glucocorticold metabolite measures in conservation biology research: Considerations for application and interpretation. *Gen. Comp. Endocrinol.* 138, 189–199
24 Creel, S. (2001) Social dominance and stress hormones. *Trends Ecol. Evol.* 16, 491–497

25 Goymann, W. and Wingfield, J.C. (2004) Allostatic load, social status and stress hormones: the costs of social status matter. *Anim. Behav.* 67, 591–602

26 Fusani, L. (2008) Endocrinology in field studies: problems and solutions for the experimental design. *Gen. Comp. Endocrinol.* 157, 249–253

27 Angelier, F. *et al.* (2007) Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behav. Ecol. Sociobiol.* 61, 611–621

28 Magee, S.E. *et al.* (2006) Plasma levels of androgens and cortisol in relation to breeding behavior in parental male bluegill sunfish, *Lepomis macrochirus*. *Horm. Behav.* 49, 598–609

29 Bonier, F. *et al.* (2007) Sex-specific consequences of life in the city. *Behav. Ecol.* 18, 121–129

30 Lancaster, L.T. *et al.* (2008) Corticosterone manipulation reveals differences in hierarchical organization of multidimensional reproductive trade-offs in r-strategist and K-strategist females. *J. Evol. Biol.* 21, 556–565

31 Cooke, S.J. *et al.* (2006) Mechanistic basis of individual mortality in Pacific salmon during spawning migrations. *Ecology* 87, 1575–1586

32 Cabezas, S. *et al.* (2007) Physiological stress levels predict survival probabilities in wild rabbits. *Horm. Behav.* 51, 313–320

33 Romero, L.M. and Wikelski, M. (2001) Corticosterone levels predict survival probabilities of galapagos marine iguanas during El Niño events. *Proc. Natl. Acad. Sci. U. S. A.* 98, 7366–7370

34 Romero, L.M. and Wikelski, M. (2002) Severe effects of low-level oil contamination on wildlife predicted by the corticosterone-stress response: preliminary data and a research agenda. *Spill Sci. Technol. Bull.* 7, 309–313

35 Breuner, C.W. *et al.* (2006) Plasma-binding globulins and acute stress response. *Horm. Metab. Res.* 38, 260–268

36 Liu, D. *et al.* (1997) Maternal care, hippocampal glucocorticoid receptors, and hypothalamic-pituitary-adrenal responses to stress. *Science* 277, 1659–1662

37 Seckl, J.R. and Meaney, M.J. (2004) Glucocorticoid programming. *Ann. N. Y. Acad. Sci.* 1032, 63–84

38 Endler, J.A. (1986) *Natural Selection in the Wild.* Princeton University Press

39 Lanctot, R.B. *et al.* (2003) Are corticosterone levels a good indicator of food availability and reproductive performance in a kittiwake colony? *Horm. Behav.* 43, 489–502

40 Love, O.P. and Williams, T.D. (2008) The adaptive value of stress-induced phenotypes: effects of maternally derived corticosterone on sex-biased investment, cost of reproduction, and maternal fitness. *Am. Nat.* 172, E135–E149

41 Kingsolver, J.G. and Pfennig, D.W. (2007) Patterns and power of phenotypic selection in nature. *Bioscience* 57, 561–572

42 Hayward, L.S. and Wingfield, J.C. (2004) Maternal corticosterone is transferred to avian yolk and may alter offspring growth and adult phenotype. *Gen. Comp. Endocrinol.* 135, 365–371

43 Kitaysky, A.S. *et al.* (2006) A mechanistic link between chick diet and decline in seabirds? *Proc. R. Soc. B Biol. Sci.* 273, 445–450

44 Criscuolo, F. *et al.* (2005) Corticosterone alone does not trigger a short term behavioural shift in incubating female common eiders *Somateria mollissima*, but does modify long term reproductive success. *J. Avian Biol.* 36, 306–312

45 Almasi, B. *et al.* (2008) Parental investment and its sensitivity to corticosterone is linked to melanin-based coloration in barn owls. *Horm. Behav.* 54, 217–223

46 Bonier, F. *et al.* (2007) Maternal corticosteroids influence primary offspring sex ratio in a free-ranging passerine bird. *Behav. Ecol.* 18, 1045–1050

47 Clinchy, M. *et al.* (2004) Balancing food and predator pressure induces chronic stress in songbirds. *Proc. R. Soc. B Biol. Sci.* 271, 2473–2479

48 Cyr, N.E. and Romero, L.M. (2007) Chronic stress in free-living European starlings reduces corticosterone concentrations and reproductive success. *Gen. Comp. Endocrinol.* 151, 82–89

49 Cash, W.B. and Holberton, R.L. (2005) Endocrine and behavioral response to a decline in habitat quality: Effects of pond drying on the slider turtle, *Trachemys scripta*. *J. Exp. Zool. A Comp. Exp. Biol.* 303, 872–879

50 Suorsa, P. *et al.* (2003) Forest management is associated with physiological stress in an old-growth forest passerine. *Proc. R. Soc. B Biol. Sci.* 270, 963–969

51 Kitaysky, A.S. *et al.* (2007) Stress hormones link food availability and population processes in seabirds. *Mar. Ecol. Prog. Ser.* 352, 245–258

52 Kitaysky, A.S. *et al.* (1999) Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Funct. Ecol.* 13, 577–584

53 Buck, C.L. *et al.* (2007) Interannual variability of black-legged kittiwake productivity is reflected in baseline plasma corticosterone. *Gen. Comp. Endocrinol.* 150, 430–436

54 Homan, R.N. *et al.* (2003) Impacts of varying habitat quality on the physiological stress of spotted salamanders (*Ambystoma maculatum*). *Anim. Conserv.* 6, 11–18

55 Rich, E.L. and Romero, L.M. (2005) Exposure to chronic stress downregulates corticosterone responses to acute stressors. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 288, R1628–R1636

56 Hakkarainen, H. *et al.* (2008) Survival of male tengmalm's owls increases with cover of old forest in their territory. *Oecologia* 155, 479–486

57 Breininger, D.R. *et al.* (2006) Landcover characterizations and Florida scrub-jay (*Aphelocoma coerulescens*) population dynamics. *Biol. Conserv.* 128, 169–181

58 Williams, C.T. *et al.* (2008) Corticosterone levels of tufted puffins vary with breeding stage, body condition index, and reproductive performance. *Gen. Comp. Endocrinol.* 158, 29–35

59 Love, O.P. *et al.* (2004) Mediation of a corticosterone-induced reproductive conflict. *Horm. Behav.* 46, 59–65

60 Moore, I.T. and Jessop, T.S. (2003) Stress, reproduction, and adrenocortical modulation in amphibians and reptiles. *Horm. Behav.* 43, 39–47

61 Beletsky, L.D. *et al.* (1989) Relationships of steroid-hormones and polygyny to territorial status, breeding experience, and reproductive success in male red-winged blackbirds. *Auk* 106, 107–117

62 Bortolotti, G.R. *et al.* (2008) Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. *Funct. Ecol.* 22, 494–500

63 Golet, G.H. *et al.* (2004) Determinants of reproductive costs in the long-lived black-legged kittiwake: a multiyear experiment. *Ecol. Monogr.* 74, 353–372

64 Ilmonen, P. *et al.* (2003) Stress, immunocompetence and leukocyte profiles of pied flycatchers in relation to brood size manipulation. *Oecologia* 136, 148–154

65 Bókony, V. *et al.* (2009) Stress response and the value of reproduction: are birds prudent parents? *Am. Nat.* 173, 589–598

66 Sapolsky, R.M. (1985) Stress-induced suppression of testicular function in the wild baboon: role of glucocorticoids. *Endocrinology* 116, 2273–2278

67 Moore, I.T. *et al.* (2005) Physiological evidence for reproductive suppression in the introduced population of brown tree snakes (*Boiga irregularis*) on guam. *Biol. Conserv.* 121, 91–98

68 Husak, J.F. *et al.* (2006) Faster lizards sire more offspring: Sexual selection on whole-animal performance. *Evolution Int. J. Org. Evolution* 60, 2122–2130

69 Angelier, F. *et al.* (2007) Corticosterone levels in relation to change of mate in black-legged kittiwakes. *Condor* 109, 668–674

70 Chastel, O. *et al.* (2005) Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird. *Horm. Behav.* 47, 459–466

71 Wingfield, J.C. *et al.* (1999) The effects of an "El Niño" Southern oscillation event on reproduction in male and female blue-footed boobies, *Sula nebouxii*. *Gen. Comp. Endocrinol.* 114, 163–172

72 Müller, C. *et al.* (2007) Circulating corticosterone levels in breeding blue tits *Parus caeruleus* differ between island and mainland populations and between habitats. *Gen. Comp. Endocrinol.* 154, 128–136

73 Groscolas, R. *et al.* (2008) Spontaneous egg or chick abandonment in energy-depleted king penguins: a role for corticosterone and prolactin. *Horm. Behav.* 53, 51–60

74 Eeva, T. *et al.* (2005) Pollution related effects on immune function and stress in a free-living population of pied flycatcher *Ficedula hypoleuca*. *J. Avian Biol.* 36, 405–412

75 Silverin, B. (1998) Territorial behaviour and hormones of pied flycatchers in optimal and suboptimal habitats. *Anim. Behav.* 56, 811–818

76 Scheuerlein, A. *et al.* (2001) Predators as stressors? Physiological and reproductive consequences of predation risk in tropical stonechats

(*Saxicola torquata axillaris*). *Proc. R. Soc. B Biol. Sci.* 268, 1575–1582

77 Ellenberg, U. *et al.* (2007) Elevated hormonal stress response and reduced reproductive output in yellow-eyed penguins exposed to unregulated tourism. *Gen. Comp. Endocrinol.* 152, 54–63

78 Brewer, J.H. *et al.* (2008) Interannual variation in the adrenal responsiveness of black-legged kittiwake chicks (*Rissa tridactyla*). *Gen. Comp. Endocrinol.* 156, 361–368

79 Wikelski, M. *et al.* (2002) Marine iguanas die from trace oil pollution. *Nature* 417, 607–608

80 Comendant, T. *et al.* (2003) Social competition, corticosterone and survival in female lizard morphs. *J. Evol. Biol.* 16, 948–955

81 Brown, C.R. *et al.* (2005) Effects of endogenous steroid hormone levels on annual survival in cliff swallows. *Ecology* 86, 1034–1046

82 Blas, J. *et al.* (2007) Stress response during development predicts fitness in a wild, long lived vertebrate. *Proc. Natl. Acad. Sci. U. S. A.* 104, 8880–8884

83 Meylan, S. and Clobert, J. (2005) Is corticosterone-mediated phenotype development adaptive? Maternal corticosterone treatment enhances survival in male lizards. *Horm. Behav.* 48, 44–52

84 Angelier, F. *et al.* (2009) How does corticosterone affect parental behaviour and reproductive success? A study of prolactin in black-legged kittiwakes. *Funct. Ecol.* 23, 784–793

85 Love, O.P. *et al.* (2005) Stress hormones: a link between maternal condition and sex-biased reproductive investment. *Am. Nat.* 166, 751–766

86 Svensson, E.I. *et al.* (2002) Mechanistic and experimental analysis of condition and reproduction in a polymorphic lizard. *J. Evol. Biol.* 15, 1034–1047

87 Saino, N. *et al.* (2005) Stressed mothers lay eggs with high corticosterone levels which produce low-quality offspring. *J. Exp. Zoolog. A Comp. Exp. Biol.* 303A, 998–1006

88 Rubolini, D. *et al.* (2005) Effects of elevated egg corticosterone levels on behavior, growth, and immunity of yellow-legged gull (*Larus michahellis*) chicks. *Horm. Behav.* 47, 592–605

89 Saino, N. *et al.* (2002) Immune response of male barn swallows in relation to parental effort, corticosterone plasma levels, and sexual ornamentation. *Behav. Ecol.* 13, 169–174

90 Eeva, T. *et al.* (2003) Pollution-induced nutritional stress in birds: an experimental study of direct and indirect effects. *Ecol. Appl.* 13, 1242–1249

91 Hegner, R.E. and Wingfield, J.C. (1987) Effects of brood size manipulations on parental investment, breeding success, and reproductive endocrinology of house sparrows. *Auk* 104, 470–480

92 Kotrschal, K. *et al.* (1998) The relationship between social stress and dominance is seasonal in greylag geese. *Anim. Behav.* 55, 171–176

93 Altmann, J. *et al.* (2004) Life-history correlates of steroid concentrations in wild peripartum baboons. *Am. J. Primatol.* 64, 95–106

94 Rogovin, K. *et al.* (2003) Social correlates of stress in adult males of the great gerbil, *Rhombomys opimus*, in years of high and low population densities. *Horm. Behav.* 43, 132–139

95 Rogovin, K.A. *et al.* (2008) Long-term dynamics of fecal corticosterone in male great gerbils (*Rhombomys opimus* licht.) effects of environment and social demography. *Physiol. Biochem. Zool.* 81, 612–626

96 Pride, R.E. (2005) High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). *Biol. Lett.* 1, 60–63

97 Pauli, J.N. and Buskirk, S.W. (2007) Risk-disturbance overrides density dependence in a hunted colonial rodent, the black-tailed prairie dog *Cynomys ludovicianus*. *J. Appl. Ecol.* 44, 1219–1230

98 Pedersen, A.B. and Greives, T.J. (2008) The interaction of parasites and resources cause crashes in a wild mouse population. *J. Anim. Ecol.* 77, 370–377