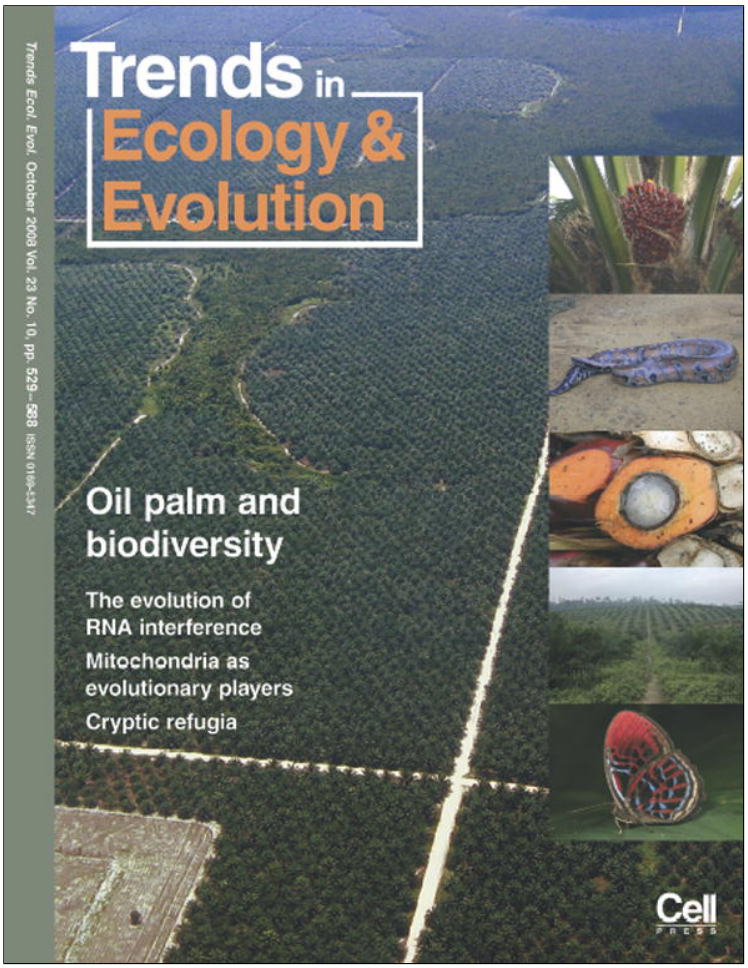

Research Focus

# Stress hormones and mate choice

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**A few recent studies have suggested that glucocorticoid stress hormones can play a role in sexual selection. In terms of mate choice, these studies have shown that individuals can exhibit preferences for mates with either low baseline or peak glucocorticoid levels. This appears to occur because stress hormones can be key mediators of many condition-dependent, sexually selected traits that serve as honest signals of mate quality. We suggest that our understanding of how sexual selection can influence the glucocorticoid stress response will be expanded by studying the interactions among glucocorticoid stress hormones, sex steroids and body condition.**

## Stress hormones as targets of selection

Vertebrates often respond to stressful situations by activating the hypothalamic-pituitary-adrenal axis, which triggers the release of glucocorticoid hormones (described in Box 1) [1]. Studies of hormonal aspects of stress in wild animals have primarily focused on ecology, behavior and conservation [1–4]. Few studies have investigated evolutionary aspects of the hormonal stress response, and those that have done so have primarily focused on the role of natural selection in molding the response rather than the role of sexual selection [5]. One thing that is becoming clear is that the hormonal stress response is extremely variable and complex. Variation in the stress response has been observed between the sexes, across seasons and according to reproductive status [2]. This variability in the stress response makes it an ideal candidate upon which sexual selection can act.

There have been some indications that sexual selection can act on the stress response. For example, the stress response is often downregulated during periods when stress could affect sexually selected traits. In birds, the stress response can be downregulated during molt, when feathers are being replaced [3]. This downregulation is hypothesized to be important for building strong feathers; however, it could also be important for building a feather that is attractive to potential mates. Furthermore, the stress response can be downregulated during breeding, when it could negatively impact courtship or competitive ability in males [4]. Previous studies have investigated stress and intrasexual competition, but have focused on species that establish dominance hierarchies [6]. A few recent papers, which we highlight below, have investigated the role of stress and glucocorticoid hormones in mate choice, thus placing the hormonal stress response in the context of intersexual selection. We propose that it might be a widespread phenomenon for glucocorticoid levels (both baseline and peak) to be under the influence of sexual selection either directly or indirectly. This occurs because the quality of sexually selected traits in a potential mate can be influenced by interrelationships between glucocorticoid hormones, sex steroids and body condition (Figure 1). The roles of sex steroids (such as testosterone) and body condition on sexually selected traits have been previously established but the exact role of glucocorticoids needs to be considered if we are to fully understand the mechanisms by which sexually selected traits serve as signals of mate quality.

## Stress, glucocorticoids and mate choice

Empirical studies show that females often choose males of high body condition [7]. Because body condition is often negatively related to baseline plasma glucocorticoid levels (Box 1), females should choose males with low baseline glucocorticoid levels if they are interested in choosing high-quality mates. These males with low baseline glucocorticoid levels could potentially provide direct benefits to females by being better at providing food to females or offspring. If the hormonal stress response is heritable [8], it is possible that high-quality males might also provide indirect benefits by producing higher-quality offspring with concordantly low glucocorticoid levels. However, for females to choose males with low glucocorticoid levels, there must be a mechanism of assessment. Glucocorticoids are released into the general circulation and receptors are near ubiquitous in tissues throughout the body, meaning that the quality of many traits assessable by potential mates could be susceptible to variation in glucocorticoid levels.

Previous studies demonstrated that stress and glucocorticoids can negatively affect the quality of male bird song [9–11], a classic example of a sexually selected trait used in mate choice. In zebra finches, *Taeniopygia guttata*, both dietary stress and experimentally elevated levels of glucocorticoids during development have negative effects on song quality [10] by affecting the high vocal center in the brain [9]. The relationship between glucocorticoids and song appears to continue into adulthood as males with lower glucocorticoid levels produce longer and more frequent song [11]. In anuran amphibians, stress affects the quality of male vocalizations that females use in mate choice [12,13]. Female Great Plains toads, *Bufo cognatus*, prefer the calls of males with low baseline glucocorticoid levels, apparently because their calls are of longer duration. This appears to be related to glucocorticoid levels rather than testosterone levels, even though testosterone is traditionally implicated when the hormonal mediation of sexually selected traits is investigated [13]. Non-calling satellite males, which try to sneak copulations with

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**Box 1. Stress, reproduction and condition**

The hypothalamic-pituitary-adrenal axis of vertebrates is often activated in response to a real or perceived threat and culminates with the release of glucocorticoids (corticosterone and cortisol are two of the most prominent) into the general circulation. These hormones redirect the physiology and behavior of the animal toward survival, and their actions include mobilizing energy stores as well as suppressing processes and behaviors that are unnecessary for immediate survival. The actions of glucocorticoid hormones can be modulated by altering production or clearance of either circulating hormone titers, plasma binding proteins or receptors [16]. Typically, investigators measure baseline (or initial) as well as peak (e.g. 60 min after capture and handling) glucocorticoid levels. This technique gives a basic understanding of background stress levels, as well as reactivity of the stress response system. Modulation of plasma binding protein levels and receptor expression can influence the effects of the hormones, both throughout the body and within individual cells, respectively.

One of the first described actions of glucocorticoid stress hormones was suppression of reproductive activity [4]. However, further study has determined that the relationship is not so simple. Because glucocorticoid hormones mobilize energy stores, they can actually facilitate energetically expensive reproductive behavior [2,3]. Thus, the relationship between levels of stress and sex steroids (e.g. testosterone in males) might be positive when an animal is not under direct threat (baseline levels) and only become negative during a challenging or stressful event that results in peak glucocorticoid levels [17]. In addition, plasma binding proteins in some species can bind both glucocorticoids and sex steroids, thus having a strong influence on the dynamic changes among these hormones and potentially affecting how they influence sexually selected traits [18,19].

Stress hormone levels can be closely associated with body condition, and decreased food availability and poor body condition have been linked with elevated stress hormone levels in a variety of animals [2]. The negative relationship between stress and body condition is not surprising, given the role of glucocorticoid hormones in energy mobilization. However, the cause and effect of this relationship remains unclear. Glucocorticoids can simply be produced in response to low energy availability, or they can mediate fat metabolism and muscle catabolism which can negatively affect body condition. Disentangling the relationships between glucocorticoid stress hormones, sex steroids (such as testosterone) and body condition is important, as they can each affect sexually selected traits and the relationships among them can be quite strong but causality is often unclear.

females attracted to calling males, are also perceptive of call differences and preferentially associate with males having low glucocorticoid levels [13]. These studies in birds and amphibians suggest the possibility of a general relationship across species between stress hormones and sexually selected targets of vocal communication.

Two recent studies have demonstrated that visual cues can also be used to choose mates with lower glucocorticoid levels. Specifically, sustained elevated glucocorticoid levels can negatively affect plumage ornaments used by birds in mate choice. Roberts *et al.* [14] found that female zebra finches chose males from a breeding line selected for their lower peak glucocorticoid stress response. Female preference was strongly predicted by male glucocorticoid line and color characteristics of the cheek region and beak, the quality of which were presumably influenced by stress hormones. Curiously, despite these results, there were no detectable differences in coloration between males from the two breeding lines. These findings raise the important question of what traits the females used in their assessment of males. The authors suggest that differences in behavior or morphology between the two breeding lines might explain the preference. This issue, as well as the relationship between baseline and peak glucocorticoid levels, needs to be clarified in future studies in this system. Nonetheless, the significant preferences exhibited by females for low peak glucocorticoid males is striking and sets the stage for future studies to determine exactly what sexually selected traits are influenced by peak glucocorticoid levels and how they are affected.

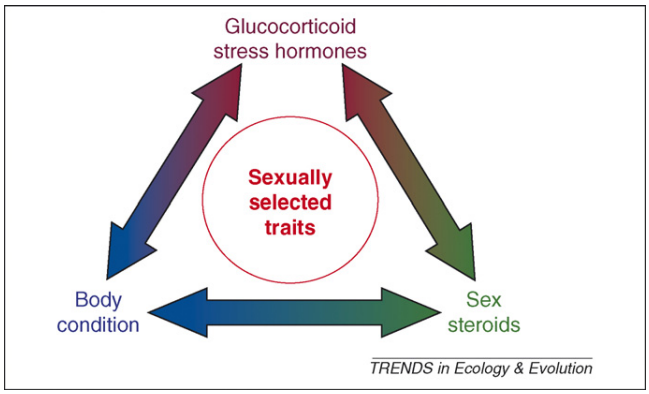


**Figure 1.** It is becoming apparent that the interrelationships between glucocorticoid stress hormones, sex steroids (such as testosterone) and body condition can determine the quality of sexually selected traits. It is often unclear where the causation exists in the correlations between these three factors. As individuals are often choosing a mate based on a sexually selected trait, the interactions of these factors need to be investigated to understand the mechanisms underlying mate choice.

Another bird study has demonstrated the link between glucocorticoid stress hormones and a sexually selected plumage trait, this time melanin based [15]. In barn owls, *Tyto alba*, melanic plumage appears to be a sexually selected trait important in mate choice for both males and females. Due to the interrelated nature (feedback loops and direct inhibition of gene transcription) of melanin and glucocorticoid production, Roulin *et al.* [15] hypothesized that increased glucocorticoid levels during a stress response should decrease melanogenesis in plumage. In an experiment, they showed that placing glucocorticoid implants in nestling owls, and thus elevating baseline levels compared to control owls, resulted in a reduction in the deposition of melanin in the developing feathers of both males and females. Thus, glucocorticoid hormones seem to serve as the mechanism whereby stress negatively affects an ornament that is used in mate choice. However, the authors found that unmanipulated baseline levels of glucocorticoids were not correlated to melanin-based coloration. As with the results of Roberts *et al.* [14], the work of Roulin *et al.* [15] suggests that the intensity of sexually selected plumage traits might reliably indicate some aspect of an individual's glucocorticoid stress response.

## Directions for future study

Glucocorticoid hormones are typically thought to enhance the probability of survival in the face of a threat, but it is becoming apparent that they can also be associated with sexual selection. In terms of mate choice, it appears that glucocorticoid stress hormones could be mediating some of

the condition-dependent traits used to assess mates. It is evident that two-way interactions exist between glucocorticoid stress hormones, sex steroids (such as testosterone) and body condition, and that these can influence the quality of sexually selected traits (Figure 1). However, causation is often unclear in these correlations. In the cases described above, it appears that sexual selection is probably not acting directly on stress hormone levels but instead indirectly through the traits that stress hormones influence. Thus, we suggest that future studies should investigate exactly what traits are being selected by mates and how glucocorticoids, sex steroids and body condition interact with those traits to influence mate choice. Understanding the interrelationships between glucocorticoids, sex steroids and body condition will help elucidate what factors are directly and indirectly influencing the sexually selected traits used in mate choice.

Due to the complex nature of glucocorticoid actions and the stress response, a second line of future investigations should seek to explain what aspects of the glucocorticoid stress response (i.e. baseline or peak levels, plasma binding proteins, receptor densities, recovery time) are responsible for individual differences in sexually selected traits. As plasma binding proteins can bind both sex steroids and glucocorticoids in some species (Box 1), they could strongly influence sexually selected traits and must be taken into account when measuring hormone levels. It is also possible that sexual selection could act differentially on baseline and peak glucocorticoid levels, or on other aspects of the stress response (see Box 1). For example, if baseline levels represent the background level of stress an animal perceives in its environment, then it is reasonable to hypothesize that individuals should prefer mates with low baseline levels. However, it is more difficult to predict whether individuals should choose mates with peak glucocorticoid levels that are low or high. On one hand, individuals might prefer mates with peak levels that are high because they are better prepared to cope with challenges in their environment. On the other hand, individuals might prefer mates with peak levels that are low, as in the studies described above, because those individuals can avoid the negative consequences which can be associated with elevated levels of glucocorticoids. Thus, further investigation on the relative roles and interrelationships of both baseline and peak levels of glucocorticoids on sexually selected traits is necessary to understand the role of sexual selection on the hormonal stress response.

In summary, it is becoming clear that glucocorticoid stress hormones can be associated with mate choice. This novel role for glucocorticoids firmly places the hormone in the realm of sexual selection. Glucocorticoids might be acting directly on sexually selected traits or indirectly through interactions with sex steroids and body condition. Untangling the interrelationships between stress hormones, sex steroids and body condition will further our understanding of the mechanisms mediating the expression of sexually selected traits and how these influence mate choice.

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