SYMPOSIUM

Stress, Condition, and Ornamentation

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Parallel theories of condition dependency and responsiveness

In the latter half of the twentieth century, biologists interested in explaining the mechanisms for how vertebrates respond to stressful environmental circumstances created a conceptual framework based primarily on physiological measures. This field of stress responsiveness became the domain primarily of neuroendocrinologists, and researchers in this field focused on the physiological actions of the hypothalamus, pituitary gland, and adrenal glands (the HPA axis) (Herman and Cullinan 1997; Sapolsky et al. 2000; Romero 2004). Great advances were made in demonstrating how the HPA serves as a key mediator of the responsiveness of vertebrates to environmental perturbations by regulating physiology and behavior (e.g., Wingfield et al. 1997; Reeder and Kramer 2005; Breuner et al. 2008). Glucocorticoids, particularly cortisol and corticosterone, were identified as important signaling molecules that link external stressors to internal physiological responses—particularly immune and metabolic responses—in vertebrates (Wingfield et al. 1998; Buchanan 2000; Sapolsky et al. 2000). The mechanisms by which individuals cope with stress became a major area of study in physiological ecology.

In a parallel universe that sometimes co-existed within the same laboratory group studying responsiveness to stress, a theory of condition-dependent signaling emerged to explain why female animals use males’ ornamentation as a criterion in mate choice. This theory of sexual signaling began by invoking the costs of ornamentation as necessary to maintain honesty (Zahavi 1975; updated in Kotiaho [2001]). Initially, discussions of costs were focused on the maintenance of ornamentation, and display traits were viewed as potential handicaps to survival with direct negative effects on fitness (Maynard-Smith 1976, 1978; Zahavi 1977; Nur and Hasson 1984). As theory developed, explanations for honest signaling shifted to the costs of production and particularly to the challenges of allocating energy away from body maintenance to ornamentation (Kodric-Brown and Brown 1984; Rowe and Houle 1996; Morehouse 2014). More recently, it has been proposed that no fitness costs or tradeoffs of resources are required for honest signaling, so long as the production of ornaments is inexorably linked to system function through shared biochemical pathways (Hill 2011, 2014).

The union of the theory of stress responsiveness with concepts of condition-dependent signaling was inevitable because the connections between stress, condition, and ornamentation are inescapable. By definition, environmental stressors are expected to reduce the condition of individuals (Badyaev 2005; Charmandari et al. 2005; Careau et al. 2014). Moreover, ornaments are proposed to be sensitive signals of individual condition (Cotton et al. 2004; Hill 2011) and hence should reflect the degree to which an individual is impacted by stressors such as parasites or poor nutrition (Andersson 1994; Peters et al. 2014; Schmidt et al. 2014). Thus, for decades, ornamental traits have been viewed as signals of either the ability to avoid stressors (e.g., Hamilton and Zuk 1982; Balenger and Zuk 2014) or the ability to cope with stressors (Westneat and Birkhead 1998; Bortolotti et al. 2009), but discussions of honest signaling typically have not integrated known pathways and conceptual frameworks about mechanisms for responding to stress.
Synthesizing theories of stress and ornaments

The first widely discussed attempt to unite concepts of neuroendocrinal responses to stress- and condition-dependent signaling was the immunocompetence-handicap hypothesis (Folstad and Karter 1992). This hypothesis proposed that testosterone imposed a two-edged sword on males, stimulating the production of ornaments and also suppressing the immune system. It was proposed that ornamentation was an honest signal of quality because only males in good condition (i.e., males with large pools of resources) could withstand the immunosuppressive effects of the high testosterone needed to stimulate production of full ornamentation. This idea led to much discussion and follow-up research, but it was ultimately deemed inadequate as a general description of honest signaling (Roberts et al. 2004; Hill 2011).

Since the pioneering attempts by Folstad and Karter (1992) to consider connection between ornamentation and hormonal mediation of stress, there has been a growing awareness that the connections among environmental stressors, the HPA axis, and ornamentation are much more complex than simply testosterone-mediated redistribution of resources (Bortolotti et al. 2009; Mougeot et al. 2010). Even if a simple system of testosterone-mediated tradeoffs of resources between ornamentation and immune defense were in place for some vertebrates, models predict that the relationships between stress, ornamentation, and immunocompetence will be complex in such a system, with rather unpredictable outcomes (Getty 2002, 2006; Morehouse 2014). Studies over the past few decades, however, showed that testosterone is not the only, or, indeed, even the primary mediator of either the production of ornaments or the regulation of the immune system (Buchanan 2000, 2011; Owen-Ashley et al. 2004). There is a growing focus on corticosterone in studies of stress and ornamentation (Roberts et al. 2007; Husak and Moore 2008). The focus on corticosterone as a key mediator between the HPA axis and ornamentation is reflected in the symposium contributions that either assessed associations between environmental challenges, corticosterone, and ornamentation (Peters et al. 2014) or assessed the effects on ornamentation when corticosterone is manipulated (Schmidt et al. 2014). However, stress and levels of corticosterone are not always related (Careau et al. 2014).

Given that hormones are key signaling molecules and regulators, one of the frontiers for studies of stress, condition, and ornamentation is research aimed at understanding the targets of stress-responsive hormones (Hill 2011, 2014). Among the primary subcellular targets of stress hormones are mitochondria (Psarra et al. 2006) and the linking of HPA stress responsiveness to mitochondrial activity holds promise to clarify the associations between stress hormones and physiological responses such as changes in metabolism, up or down regulation of the immune system, and production of free radicals (Hill 2014). The prospect that the production of ornaments might be regulated by these same mitochondrial processes that are under the control of stress hormones (Hill and Johnson 2013; Johnson and Hill 2013) provides a glimpse into how stress, condition, and ornamentation are fundamentally connected at the cellular level and perhaps into the fundamental information content of condition-dependent signals (Johnson and Hill 2013).

As the many excellent papers in this symposium edition reveal, what is being signaled by ornamentation and how ornamentation connects to stressors and the condition of an animal are complex. Understanding such interactions requires detailed understanding of the mechanisms of trait production, the pathways involved in stress responsiveness, the targets of stress–response mechanisms, and the means whereby organisms mitigate stress and retain a homeostatic state. New breakthroughs in conceptual frameworks, experimental tools, and biochemical pathways, as described in the papers of this symposium, are leading to major advances in understanding of the true nature of how ornamentation connects to condition and stress, and the result will be a new understanding of the process of sexual selection.

Symposium papers

Three of the papers contributed to the symposium focus on the effect of environmental stress during development on performance by adult songbirds. Song is the focal ornament in two of these studies, and in all three studies, corticosterone is measured or manipulated to study its effects as a mediator of the stress response. Thus, each of these research programs draws connections between the action of the HPA and the production of ornaments. Across the subdiscipline, the model systems in research on developmental stress and song are laboratory-bred zebra finches (Taeniopygia guttata) and wild-caught sparrows in the genus Melospiza. Peters et al. (2014) focus on song in swamp and song sparrows (Melospiza georgiana and M. melodia), and in
particular on aspects of song that require learning. They argue that learned elements of the song serve as ornaments that indicate cognitive ability and hence should serve as excellent predictors of performance in other learning-related activities of birds. They survey studies that link learned song quality to conditions during early development that can affect development of the nervous system. In a related approach, Careau et al. (2014) consider the effects of food deprivation during early development on performance in adulthood zebra finches. They report that restriction of food during early development, which is known to affect singing performance (Nowicki et al. 1998, 2002), leads to females with higher levels of feeding, hematocrit, and basal metabolic rate than those of control females, suggesting stress-induced changes in pace-of-life for individual birds. Phenotypic plasticity lies at the heart of the connections between stress, condition, and ornamentation, and this paper provides an important overview of the mechanisms that could mediate such plasticity. Finally, in the third paper on stress and subsequent performance when adult, Schmidt et al. (2014) continue the theme of environmental stresses acting on song quality through the influence of the HPA axis on neurological development. Complementing the other two papers linking developmental stress and adults’ performance in this symposium, they look at the neural mechanisms, and specifically at the size of the region of the brain controlling song—HVC—that both is affected by stresses and affects song output. They show that the complexity of song reflects the size of the HVC and is correlated with several components of immune responsiveness. Complexity of the song, in contrast, is a reliable indicator of what an individual experiences during development. Together, these papers on HPA stress response, individual condition, performance, and song constitute among the most complete analyses for the connections between stress, condition, and ornamentation.

Two symposium papers consider traits that function primarily in intersexual agonistic interactions rather than in females’ choice of a mate. Tibbetts (2014) provides an overview of, and a new theoretical focus for, the theory that maintenance of honesty in traits signaling the potential for holding resources (i.e., armaments) occurs through social mediation. She reviews how armaments influence social behavior and how social behavior influences aspects of physiology, such as hormone titers. She proposes that honest signaling benefits both signallers and receivers because of the cost imposed both by social mediation and by the effects of social mediation on physiology. Johns et al. (2014) provide an alternative (although not mutually exclusive) perspective on the maintenance of honesty in signals of the potential for holding resources. They focus on traits that typically function as armaments, including particularly the horns of beetles. They present data supporting a mechanistic link between the production of morphological traits such as horns and the sensitivity of the insulin receptor that controls the production of morphological traits functioning in sexual displays. These papers on armaments hint at fundamentally different relationships between the sexual signals and the mechanisms for traits that arise through intrasexual as opposed to intersexual selection.

Two papers consider the relationships between stress, condition, and ornamentation for pigment-based coloration. Giraudet and McGraw (2014) use a gradient in urbanization as a source of variable environmental stress on a population of house finches (Haemorhous mexicanus). Urbanization imposes a range of stressors on wild animals such as house finches. Giraudet and McGraw (2014) show a strong effect of urbanization both on vitamin A levels, which can be sensitive indicators of stress (Hill and Johnson 2012), and on production of red ketolated carotenoids that create ornamental red coloration. The paper by Giraudet and McGraw (2014) has implications both for the mechanisms linking stress, condition, and ornamentation as well as for conservation biology by showing subtle physiological effects of urbanization. D’Alba et al. (2014) consider the condition dependency melanin-based coloration, a trait that has been the object of many studies related to sexual signaling and for which evidence for condition-dependent expression is ambiguous (Hill and Brawner 1998; McGraw and Hill 2000; Griffith et al. 2006; Hill 2006). They compared the structural anatomy and coloration of feathers first from black-capped chickadees (Poecile atricapillus) with, and without, a developmental disorder that affects the synthesis of keratin, and second, from zebra finches either fed ad libitum or subjected to deprivation of food. The chickadees with developmental disorders and the finches on reduced food both grew feathers that were grayer (brighter) than the deep black of fully ornamented feathers but the effects were not from differences in melanin deposition. Rather, in both cases, difference in brightness resulted from differences in the microstructure of the feathers. Their insights can help explain the confusing patterns presented by studies of melanin coloration. Together these papers on pigmentation of feathers highlight why the coloration of plumage remains a model for understanding the inter-relationships of stress, condition, and ornamentation.
Finally, the symposium ends with three papers that consider the theory of honest signaling. Balenger and Zuk (2014) reconsider the Hamilton–Zuk hypothesis, which is among the most important foundational ideas in the field of condition-dependent signaling (Hamilton and Zuk 1982). The Hamilton–Zuk hypothesis is often now presented as a general hypothesis that ornaments signal a resistance to parasites, but the original paper was a specific model for the maintenance of heritable variation for resistance to disease in the face of strong selection. In refocusing on the original paper, Balenger and Zuk (2014) emphasize the central role of the co-adaptive cycles between hosts’ resistance and parasites’ virulence, which is the central idea of the Hamilton–Zuk hypothesis but which has not been adequately tested. Balenger and Zuk (2014) point out that new molecular tools may make a definitive test of this aspect of the Hamilton–Zuk hypothesis possible.

Morehouse (2014) provides an in-depth assessment of how tradeoffs of resources might mediate ornament-expression. He focuses specifically on the relationship between acquisition versus allocation of resources. The results of experimental studies looking at the effect of nutritional resources on the production of ornaments have generated ambiguous results, and Morehouse (2014) underscores the complex interactions between allocation of resources to ornaments versus allocation for body maintenance within the framework of the particular life history of the organism under study.

Finally, Hill (2014) closes the symposium issue by reviewing evidence that cellular respiration is the central cellular pathway that links stress, condition, and ornamentation. A growing literature suggests that a primary target of thyroid and steroid hormones is regulation of the bioenergetic activities of mitochondria. Mitochondria, in turn, control a host of parameters associated with individual condition, including lipogenesis, oxidative state, and innate immune response. Hill (2014) proposes that ornamental traits are also tightly linked to mitochondrial function such that the primary function of condition-dependent ornaments is signaling efficiency of cellular respiration.

**Integrating levels and approaches**

The principal message from the symposium “Stress, Condition, Ornamentation” is that significant contributions and insights into the function and evolution of ornaments, as well as of armaments, come from studies at a range of scales from biochemical pathways to social interactions and from gene frequencies to plastic developmental responses. The challenge for organismal biologists in the twenty-first century is to integrate the biomedical, neuroendocrinological, behavioral, and evolutionary literatures into a coherent framework for understanding ornaments and armaments.

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**References**


