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Review Article

The next step for stress research in primates: To identify relationships between glucocorticoid secretion and fitness

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ABSTRACT

Glucocorticoids are hormones that mediate the energetic demands that accompany environmental challenges. It is therefore not surprising that these metabolic hormones have come to dominate endocrine research on the health and fitness of wild populations. Yet, several problems have been identified in the vertebrate research that also apply to the non-human primate research. First, glucocorticoids should not be used as a proxy for fitness (unless a link has previously been established between glucocorticoids and fitness for a particular population). Second, stress research in behavioral ecology has been overly focused on "chronic stress" despite little evidence that chronic stress hampers fitness in wild animals. Third, research effort has been disproportionately focused on the causes of glucocorticoid variation rather than the fitness consequences. With these problems in mind, we have three objectives for this review. We describe the conceptual framework behind the "stress concept", emphasizing that high glucocorticoids do not necessarily indicate a stress response, and that a stress response does not necessarily indicate an animal is in poor health. Then, we conduct a comprehensive review of all studies on "stress" in wild primates, including any study that examined environmental factors, the stress response, and/or fitness (or proxies for fitness). Remarkably, not a single primate study establishes a connection between all three. Finally, we provide several recommendations for future research in the field of primate behavioral endocrinology, primarily the need to move beyond identifying the factors that cause glucocorticoid secretion to additionally focus on the relationship between glucocorticoids and fitness. We believe that this is an important next step for research on stress physiology in primates.

Contents

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Stress in addition to being itself, is also the cause of itself, and the result of itself.

[(Roberts, 1950; a physician paraphrasing an address given by Hans Selye - , as quoted by Rosch 2010).]

1. Introduction

For nearly 40 years, researchers have sought to understand the causes and consequences of hormone fluctuations in wild animals (Wingfield, 1976). As a window into the energetic demands that accompany environmental challenges (Sapolsky et al., 2000), it is not surprising that glucocorticoids have come to dominate the majority of this research effort. However, it has been argued that this research effort has been disproportionately focused on the *causes* of glucocorticoid variation in wild vertebrate populations, rather than the fitness *consequences* (Bonier et al., 2009; Breuner et al., 2008; Dantzer et al., 2014). In this review, we argue that research on glucocorticoids in wild non-human primates suffers from a similar problem. Thus, we first outline some of the problems that unintentionally may have steered some of this research away from investigations into the adaptive nature of the "stress response". Second, to summarize the current state of glucocorticoid research in wild primate populations, we list all studies that have examined some aspect of stress physiology in wild primates. Our goal was to include any study that examined the relationship between environmental factors, the stress response, and performance/fitness variables. Remarkably, none of the primate research at the time of this review (Jan 2016) followed the connection between all three. Research efforts in the broader animal literature are increasingly being geared towards this end (e.g., Rivers et al., 2012; Marasco et al., 2015), and we suggest that primate research is ripe for this type of inquiry as well.

Centuries ago, the field of physics established the term "stress" as an external force that produces a proportional amount of "strain" (or deformation) on an object (Hooke's law). Importantly, the term "stress" describes the external cause, and the term "strain" describes the internal result. Today, in the mechanical engineering literature, there is little confusion about what constitutes stress versus strain, and we have many sound architectural structures as proof. By contrast, the adoption of the term "stress" for use in the physiological literature, has been more problematic (Levine, 2005). In 1936, Dr. Hans Selye introduced the term to physiology after he discovered that a noxious stimulus (e.g., injections) delivered repeatedly to laboratory rats produced peptic ulcers (Selye, 1936). He regrettably used the term "stress" interchangeably to describe both the cause (injections) and the effect (ulcers). (Selye later bemoaned that he would have rather gone down in history as the father of the "strain concept", Rosch, 2010). As exemplified in the opening quote to this review, early confusion surrounding the stress concept was due to the linguistic problem of using the same word to describe both the cause and effect (Romero et al., 2009) – and even more recent publications claim to "measure stress" without initially specifying whether this means they intend to measure the external stressor or the internal response (e.g., Moberg, 2000). One solution to this problem has been to use the term "stressor" to indicate the cause of stress (external or internal) and the term "stress response" to indicate the internal physiological response. However, by these definitions, the physiological reaction is deemed a "stress response" if it is triggered in response to a "stressor" – in what clearly becomes circular reasoning. To get around this, many researchers have successfully adopted an independent definition for a stressor – that is, any unpredictable and/or uncontrollable stimulus (Levine and Ursin, 1991), and this remains the most widely-used definition.

Yet, a deeper conceptual confusion remains. Perhaps because Hans Selye first discovered and reported the detrimental side of stress (i.e., chronic stress), the adaptive side to the stress response has never received the attention it deserves (i.e., the fitness-enhancing effects, with "fitness" defined as any proxy or direct measure of breeding success among individual animals in natural populations (Clutton-Brock, 1988)). To be clear, most studies on "stress" *do* explain the dual nature of the stress response. Nearly three quarters of the studies reviewed here include in their introductions a paragraph or two on the idea that although the initial physiological response to challenging stimuli is considered to be adaptive (typically with no empirical citations), a prolonged activation can cause severe reductions in health and longevity, with extensive empirical citations from the biomedical literature (e.g., Brotman et al., 2007; Juster et al., 2010; Lupien et al., 2009; Sapolsky, 2004a). The emphasis and focus is therefore on the latter, leaving a reader with the impression that this is a physiological response gone-wrong. The biomedical research has understandably focused on the negative health consequences that result from psychological stressors that impact the lives of humans. However, this "biomedical bias" has spilled over to non-biomedical literature and has unnecessarily influenced the direction and interpretation of research across many evolutionary and ecological disciplines (Boonstra, 2013).

With the exception of extreme situations, such as degraded habitats or captive environments, organisms in natural populations do not appear to experience net decreases in fitness from stress effects (Boonstra, 2013; Dantzer et al., 2014). Selection would not maintain a physiological response that routinely harmed an organism's fitness. This misunderstanding – mainly, that the stress response is harmful – could be alleviated if we had more evidence for the adaptive side of the stress response in natural populations (Fig. 1). As others have noted previously, research that seeks to link a stress response to an adaptive outcome has been scarce across behavioral ecology, more generally (Bonier et al., 2009; Breuner et al., 2008; Dantzer et al., 2014) and nearly entirely absent in primate behavioral ecology, specifically.

In this review, we start out with an attempt to clarify the conceptual framework behind the "stress concept", focusing on how this neuroendocrine response might mitigate the effects of a challenging environment. We focus on one particular physiological mediator, glucocorticoid secretion, because this class of hormones is the primary measure that is available from wild primate populations.

2. The stress concept – a conceptual framework

2.1. HPA activation

To understand the stress concept in an evolutionary conceptual framework, it is first necessary to outline the physiological mechanisms (see the following reviews for more comprehensive details: Charmandari et al., 2005; Johnstone et al., 2012; Romero and Wingfield, 2016; Sapolsky et al., 2000). First, sensory information from an unpredictable, uncontrollable, and/or aversive stimulus ("stressor")

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