General and Comparative Endocrinology 215 (2015) 10–24

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Assessing adaptability and reactive scope: Introducing a new measure and illustrating its use through a case study of environmental stress in forest-living baboons

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ARTICLE INFO

Article history:
Received 21 February 2014
Revised 10 August 2014
Accepted 25 September 2014
Available online 18 October 2014

Keywords:
Allostasis
Biogeography
Ecological stressors
Nutritional constraints
Physiological adaptation
Primate endocrinology

ABSTRACT

In order to maintain regulatory processes, animals are expected to be adapted to the range of environmental stressors usually encountered in their environmental niche. The available capacity of their stress responses is termed their reactive scope, which is utilised to a greater or lesser extent to deal with different stressors. Typically, non-invasive hormone assessment is used to measure the physiological stress responses of wild animals, but, for methodological reasons, such measurements are not directly comparable across studies, limiting interpretation.

To overcome this constraint, we propose a new measure of the relative strength of stress responses, 'demonstrated reactive scope', and illustrate its use in a study of ecological correlates (climate, food availability) of faecal glucocorticoid (fGC) levels in two forest-living troops of baboons. Results suggest the wild-feeding troop experiences both thermoregulatory and nutritional stress, while the crop-raiding troop experiences only thermoregulatory stress. This difference, together with the crop-raiding troop's lower overall physiological stress levels and lower demonstrated fGC reactive scope, may reflect nutritional stress-buffering in this troop. The relatively high demonstrated fGC reactive scope levels of both troops compared with other baboons and primate species, may reflect their extreme habitat, on the edge of the geographic range for baboons.

Demonstrated reactive scope provides a means of gauging the relative strengths of stress responses of individuals, populations, or species under different conditions, enhancing the interpretive capacity of non-invasive studies of stress hormone levels in wild populations, e.g. in terms of animals' adaptive flexibility, the magnitude of their response to anthropogenic change, or the severity of impact of environmental conditions.

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1. Introduction

Understanding the physiological impact of different stressors on wild animals is pivotal to our comprehension of environmental adaptation (Wingfield 2005; Landys et al., 2006), and potentially also has an important role in the recognition and mitigation of impacts of anthropogenic change (Chapman et al., 2007; Wingfield, 2013). Animals experience stressors in two broad categories, ecological and social, and species are expected to be adapted to maintain regulatory processes in response to the particular types and severity of stressors usually encountered in their natural environment (Korte et al., 2005). Koolhaas et al. (2011) denoted the array of environmental conditions to which a species is adapted its 'regulatory range'; and Romero et al. (2009), building

Abbreviations: DRS, demonstrated reactive scope; DRScv, coefficient of variation of demonstrated reactive scope; fGC, faecal glucocorticoids; uGC, urinary glucocorticoids.

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http://dx.doi.org/10.1016/j.ygcen.2014.09.022
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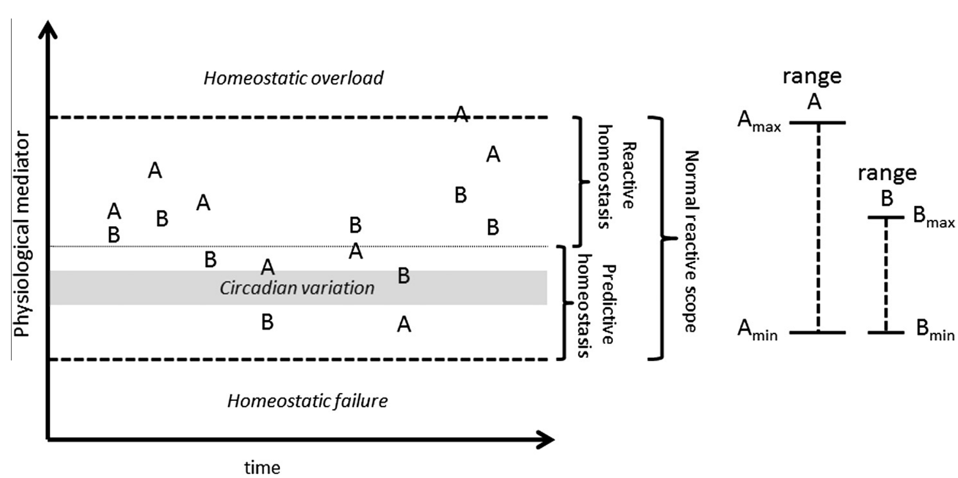
on the concept of allostasis, or maintaining stability through change (McEwen, 1998), termed a species' normal range of available stress response (physiological, behavioural or cognitive) its 'normal reactive scope'.

Physiological appraisal of the impact of stressors on wild mammals has been greatly enhanced by the development of non-invasive methods of hormone level assessment from excreta (Whitten et al., 1998). However, the inability to calibrate the relative strengths of detected stress responses hampers the interpretation of results in terms of animals' comparative responsiveness, robusticity and resilience (Wingfield, 2013). This is due to the lack of direct comparability of measures from different assays, of different hormone metabolites excreted by different species, in different matrices (urine or faeces), and differential faecal composition dependent on diet. Here, we propose quantifying a new measure, 'demonstrated reactive scope' (DRS), to overcome these constraints. This can be used to assess the relative stress experienced by different individuals, populations or species in response to the same or different stressors. We explore the analytical and interpretive value of this measure through a case study investigating variation in glucocorticoid levels in two troops of forest-living baboons (*Papio anubis*), in Gashaka Gumti National Park, Nigeria, in relation to climatic factors and food availability. Using the new measure, we assess the relative stress levels experienced by this population compared to other baboons and other primates, and consider the results both in relation to the location of the study troops, at the geographic and environmental edge of baboon distribution, and to the effects of anthropogenic impact.

Common vertebrate physiological stress responses function similarly across a broad range of stressors, both physical and psychological (Sapolsky, 1992). Activation of the hypothalamic–pituitary–adrenal (HPA) axis is a major component of the vertebrate stress response battery that results in the release of glucocorticoids, which have a wide variety of effects. These include the direct mobilisation of energy, behavioural adjustments, and preparative processes which prime physiological systems for predictable events and changes such as circadian cycles of rest and activity, different life history stages including growth and reproduction, and seasonal climatic variation (Sapolsky et al., 2000; Romero, 2002; Wingfield, 2005); the corresponding glucocorticoid response levels are denoted the predictive homeostatic range in the Reactive Scope Model (Romero et al., 2009; Fig. 1). Greater glucocorticoid responses to more random, though still normal stressors for an animal's environment, such as injury, disease and predation avoidance (Wingfield, 2005), fall within the reactive homeostatic range of the Reactive Scope Model. Together, the predictive homeostatic range and the reactive homeostatic range comprise normal reactive scope (Romero et al., 2009; Fig. 1). The basic effects of the release of glucocorticoids are protective, and variation in glucocorticoid levels within normal reactive scope acts to achieve allostasis, or physiological stability, in the face of environmental challenges (McEwen and Wingfield, 2003; Landys et al., 2006). Such variation is adaptive. Conceptual models for the stress response, such as the Reactive Scope Model, envisage that there is a cumulative cost in terms of wear and tear, or allostatic load, to maintaining stability in response to such challenges, but that this is within an animal's adaptive capability (McEwen and Wingfield, 2003; Romero et al., 2009). Potentially, a species' habitat or geographic distribution may be restricted by its physiological limitations (Busch et al., 2011), such as the range of its normal reactive scope, which delimits its capacity to respond effectively and efficiently to varying environmental stressors, such as food availability or climate.

Extreme or unpredictable stressors may stimulate a stress response beyond the normal reactive scope of a species,



$$DRS_X = (X_{max} - X_{min}) / X_{min}) \times 100$$

$$DRScv_X = (\text{standard deviation}_X / \text{mean}_X) \times 100$$

$$DRS_A > DRS_B$$
$$DRScv_A > DRScv_B$$

Fig. 1. Figure depicting the Reactive Scope Model (after Romero et al., 2009), for a non-seasonally reproducing organism, and two sets of data, A and B, which could be from two individuals, troops, species etc., on levels of a physiological stress mediator. The figure depicts the basic circadian range of physiological mediator levels; increases or decreases beyond this range, within the predictive homeostatic range, which occur in response to predictable changes and occurrences; and further increases within the range of reactive homeostasis, in response to more unpredictable events. All of this variation is incorporated within the normal reactive scope, within which the organism experiences wear and tear, but not pathological effects of stress. If physiological mediator responses rise above the range of normal reactive scope to levels of homeostatic overload, this may result in pathological effects. For the examples shown, Set A experiences a greater range of physiological mediator levels than Set B. Although the means of measurement for the two sets of data may be different, and hence the measures not directly comparable, values for demonstrated reactive scope (DRS) are higher for Set A than for Set B, reflecting Set A's full use of the normal reactive scope, whereas physiological mediator levels for Set B fall well within its bounds. The higher DRS and DRScv for Set A than Set B reflect the greater overall stress, and hence the greater wear and tear, experienced by the former Set.

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