Hormones and Behavior 58 (2010) 685–697

Contents lists available at ScienceDirect

Hormones and Behavior

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

Fecal glucocorticoids as indicators of metabolic stress in female Sykes' monkeys (*Cercopithecus mitis albogularis*)

Steffen Foerster [a,b,*], Steven L. Monfort [c]

[a] *Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York, USA*
[b] *Institute of Primate Research, National Museums of Kenya, Nairobi, Kenya*
[c] *Smithsonian Conservation Biology Institute, Front Royal, Virginia, USA*

ARTICLE INFO

Article history:
Received 9 December 2009
Revised 2 June 2010
Accepted 2 June 2010
Available online 9 June 2010

Keywords:
Cercopithecus mitis
Glucocorticoids
Metabolic stress
Proximate causes
Social behavior
Feeding ecology
Temporal variation
Individual differences
Rank effects

ABSTRACT

Because of their mediating role in the stress response and potential effects on fitness, glucocorticoid (GC) hormones are increasingly used to assess the physiological costs of environmental and behavioral variation among wild vertebrates. Identifying the proximate causes of GC variation, however, is complicated by simultaneous exposure to multiple potentially stressful stimuli. Here, we use data from a partially provisioned social group of Sykes' monkeys to evaluate the effects of potential psychological and metabolic stressors on temporal and individual variation in fecal GC (fGC) excretion among 11 adult females. Despite high rates of agonism over provisioned foods fGCs declined during periods of high provisioning frequency when fruit availability was dominated by neem (*Azadirachta indica*), an item requiring great feeding effort. Provisioned foods did not prevent fGC increases when availability of the most preferred main fruit item, tamarind (*Tamarindus indica*), declined drastically. Although rank-related differences in access to provisioned foods and rates of agonism did not lead to an overall effect of rank on fGCs, low-ranking females excreted more fGCs than high-ranking females during a period of high provisioning intensity and low fruit availability. The emergence of this rank effect was associated with elevated feeding effort in all females, a greater access to provisioned items by high-ranking females, and a higher proportion of time spent moving in low-ranking females. Our findings suggest that metabolic stressors were the primary determinants of both temporal and individual variation in fGCs, indicating potential fitness benefits for high-ranking females when food availability is limited.

Introduction

In vertebrates, glucocorticoids (GCs) play an essential role in mediating adaptive physiological responses to acute stressors by increasing the availability of glucose (Felig and Frohman, 2001) and stimulating aspects of the immune system (Dhabhar, 1998). When chronically elevated, however, GCs can exert a range of negative effects on bodily processes that include a variety of disease syndromes (Selye, 1936), loss of reproductive functioning (Tilbrook et al., 2000), and suppression of the immune system (McEwen, 2000; Segerstrom and Miller, 2004). Because of these potentially harmful effects, characterizing GC variation may be a useful approach for evaluating the fitness consequences of behavioral strategies among wild animals, particularly in long-lived species for which actual fitness measures are difficult to obtain.

Studies on wild social vertebrates have focused primarily on the physiological costs of social interactions and dominance rank (Abbott et al., 2003; Creel, 2001; Goymann and Wingfield, 2004), building on the early work by Sapolsky who showed that GC variation in wild male baboons was determined not only by rank but also by social context and individual behavioral strategies (Sapolsky, 1993, 1994; Sapolsky and Ray, 1989). Facilitated by the development of non-invasive methods for quantifying GC metabolites in excreta (Wasser et al., 2000; Whitten et al., 1998), numerous studies have since assessed GC variation in relation to psychological stressors like aggression, social instability, coping behaviors, threat of infanticide, mother–infant conflict, and anti-predator behaviors (Beehner et al., 2005; Crockford et al., 2008; Ostner et al., 2008a,b; Wittig et al., 2008).

Variation in the magnitude and duration of GC production can also be determined by metabolic stressors, including injury, strenuous exercise and temperature extremes (Huber et al., 2003; Kanaley and Hartman, 2002; Rasooli et al., 2010; Selye, 1936), or by nutritional stress resulting from energy imbalances (Champoux et al., 1993; Kitaysky et al., 1999; Muller and Wrangham, 2004; Pride, 2005a). As metabolic stress can reduce energy allocation for reproduction (Bonier et al., 2009), evaluating GC variation in relation to potential

---

* Corresponding author. Department of Ecology, Evolution and Environmental Biology, Columbia University, 1200 Amsterdam Ave, 10th Floor Schermerhorn Extension, New York, NY 10027, USA.
E-mail address: sf2041@columbia.edu (S. Foerster).

0018-506X/$ – see front matter © 2010 Elsevier Inc. All rights reserved.
doi:10.1016/j.yhbeh.2010.06.002

metabolic stressors can give valuable insights into the fitness implications of environmental and social conditions, particularly in females whose reproductive performance is limited by nutritional status (Bronson, 1985; Emlen and Oring, 1977). A number of recent studies on non-human primates attempted to relate GCs to proxies of food availability such as rainfall, temperature and day length (Beehner and McCann, 2008; Crockford et al., 2008; Foley et al., 2001; Gesquiere et al., 2008; Girard-Buttoz et al., 2009; Weingrill et al., 2004) or to broad behavioral indicators of feeding effort such as the total time spent feeding or moving (Crockford et al., 2008; Gesquiere et al., 2008; Weingrill et al., 2004). Results of these studies generally suggested seasonal GC variation related to environmental stressors. The exact causes of this variation and its relation to nutritional status, however, are not always easy to deduce, because factors such as dietary flexibility and variation in food quality and food intake within and between seasons can play an important role in determining individual energy balances (Barton and Whiten, 1994; Schülke et al., 2006). Accordingly, the strongest support for temporal and individual variation in nutritional stress comes from studies that directly assessed the influence of food availability or fruit intake rates on GC variation in urine and feces (Behie et al., 2010; Muller and Wrangham, 2004; Pride, 2005a).

To understand the proximate causes of GC variation among wild social groups of social vertebrates, potential metabolic stressors and their relation to GC variation should be considered simultaneously with psychological stressors. Doing so, however, is made difficult by the fact that metabolic and psychological stressors may be confounded; metabolic stress related to food and feeding effort is potentially influenced by psychological stressors such as agonistic competition, which may in turn co-vary with food availability, quality, and distribution (Koenig, 2002; Pruetz and Isbell, 2000). In general, then, GCs are expected to vary with both foraging and social strategies that modulate the exposure and response to potential psychological and metabolic stressors. To the extent that an individual's use of these foraging and social strategies is related to its rank, rank effects on GC production may emerge, the magnitude and direction of which will be determined by the relative benefits and costs of a particular strategy. For example, some (e.g., high-ranking) individuals may be subject to less metabolic stress than others (e.g., subordinates) if they maintain priority access to high quality food resources (Barton and Whiten, 1993; Janson, 1985), but that benefit may come at the price of increased aggression in defense of those resources that may lead to metabolic and/or psychosocial stress (Cavigelli et al., 2003; Creel, 2001; Kruk et al., 2004; Muller and Wrangham, 2004). Less competitive (e.g., low-ranking) individuals, on the other hand, may or may not have the opportunity to avoid either type of stressor through alternative foraging strategies and appropriate coping responses. Therefore, individual (e.g., rank-related) differences in GC levels are likely to depend greatly on the options available to females for maintaining a sufficient food intake while minimizing exposure to psychological stressors or maximizing social coping responses.

Here, our aim is to expand on previous field studies of non-human primates and evaluate the effects of potential daily life metabolic and psychological stressors on physiological stress responses of adult female Sykes' monkeys. We refer to “potential stressor” as any event or experience that may activate the hypothalamic–pituitary–adrenal (HPA) axis, and to “stress” as the period of disturbed physiological or psychological balance during which GCs are produced as part of the organism's effort to regain homeostasis and assure long-term survival (McEwen and Wingfield, 2003; Sapolsky et al., 2000). While agonism is a common potential psychological stressor, stress responses to agonism depend on the frequency of its occurrence, its predictability (Levine, 2000) and the availability and use of coping strategies (Abbott et al., 2003; Koolhaas et al., 1999). Similarly, variation in food availability as well as indicators of food consumption and feeding effort can present potential metabolic stressors, but actual levels of nutritional stress will ultimately depend on the balance between energy intake and expenditure.

Based on our current understanding of the determinants of GC variation in social primates and other vertebrates (Abbott et al., 2003; Goymann and Wingfield, 2004), we do not expect agonistic interactions in a natural feeding context to lead to prolonged GC elevations among female Sykes' monkeys. First, female *C. mitis* are known to form stable dominance relationships (Cords, 2000) and should therefore encounter little unpredictability in social interactions that would trigger prolonged physiological stress responses (Levine, 2000). Second, females compete most over food (Cords, 2000; Pazol and Cords, 2005), which may mean that the metabolic benefits of successful competition would outweigh the potential costs of stress responses to agonistic interactions, particularly when high quality food is of limited supply. Third, females establish close affiliative bonds with relatives and friends (Cords, 2002) that may provide sufficient coping opportunities to deal with acutely stressful social interactions. Lastly, their dietary flexibility (Chapman et al., 2002) and a dense forest environment may facilitate the spatial avoidance of individuals and reduce exposure to social stressors (Janson, 1990). If these predictions are accurate, we expect most GC variation to be associated either with confounding factors such as reproductive status (Mastorakos and Ilias, 2003), or with variation in metabolic stress as a result of differential food intake or, more generally, energy balances.

Our study group did not rely on natural food sources alone, but was partially and seasonally provisioned by tourists, primarily with small quantities of bananas (see Methods). We expected this food supplementation to reduce exposure to metabolic stress, all else being equal, but also hypothesized that the extent of this effect would depend on the seasonal fluctuation of provisioning intensity and how this variation related to the availability of natural food items. In addition, food supplementation likely increased exposure to potential psychological stressors because of increased agonistic competition (Berman and Lil, 2002; Boccia et al., 1988; Southwick et al., 1976). A recent study on our focal group (Kadane, 2009), for example, showed that rates of agonism per hour of feeding on provisioned items exceeded rates outside of provisioning sessions by more than 400%, and that the increase was greatest for more intense forms of agonism (threats, chases, lunges, and contact aggression). It is possible that such elevated levels of contest competition overwhelmed evolved coping responses to agonistic conflict (but see Ram et al., 2003), which could lead to prolonged psychological stress.

Thus, elevated rates of agonism as a result of food supplementation combined with seasonal fluctuations in the type and distribution of food available to our study group suggested that females might be exposed to both psychological and metabolic stressors. By identifying the actual effects of these different stimuli on temporal and individual GC variation we hope to gain insights into the most challenging aspects of environmental and social conditions for the females of this social group and improve our understanding of the proximate mechanisms behind GC variation in wild social groups of non-human primates.

Methods

Study site and subjects

Data for this study come from one social group of Sykes' monkeys at the Gede Ruins National Monument, Coast Province, Kenya. Apart from excavated ruins of an ancient city (Reynolds and Bobo, 2001), the habitat includes three main forest types: 1) neem forest, dominated by the invasive *Azadirachta indica* (neem tree), 2) old growth coastal forest, dominated by *Combretum schumannii*, *Gyrocarpus americanus*, *Tamarindus indica* (tamarind), and *Adansonia digitata* (baobab), and 3) mixed woodland, comprising diverse species