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Hormonal correlates of energetic condition in mantled howler monkeys

Pedro Américo D. Dias [a,*], Alejandro Coyohua-Fuentes [a], Domingo Canales-Espinosa [a], Roberto Chavira-Ramírez [b], Ariadna Rangel-Negrín [a]

[a] Primate Behavioral Ecology Lab, Instituto de Neuroetología, Universidad Veracruzana, Xalapa, Veracruz, Mexico
[b] Instituto de Ciencias Médicas y Nutrición Salvador Zubirán, México D.F., Mexico

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ABSTRACT

Hormones have a key role in energy allocation, so their study allows understanding individual metabolic strategies. Because different hormones convey different information on the responses of individuals to energetic demands, a simultaneous analysis of variation in multiple hormones may offer a more reliable picture of metabolic strategies than single hormone assessments. In this study we focused on determining which factors were related to variation in fecal glucocorticoid and thyroid hormone metabolites in wild mantled howler monkeys (*Alouatta palliata*). Over 12 months, we determined fecal glucocorticoid and thyroid hormone metabolite levels of 11 adults belonging to two groups, and examined the relationship between hormone metabolites and a variety of behavioral, physiological, and ecological factors (e.g., food intake, sex/reproductive state, activity, participation in agonistic interactions). We found that glucocorticoids were elevated in gestating and lactating females compared to males and cycling females, and were also higher when individuals were more active and participated in agonistic interactions. Thyroid hormone levels were also related to sex/reproductive state and activity, but were additionally positively related to fruit intake and negatively related to young leaf intake. Our study demonstrates that the non-invasive measurement of glucocorticoid and thyroid hormones of howler monkeys allows assessing different underlying physiological processes. By combining different biomarkers, which has seldom been done with wildlife, we could also parse the influence of psychological vs. metabolic challenges for individual energetic condition, which may be instrumental for deciding which factors should be accounted for when studying different hormone-behavior interactions.

1. Introduction

Energetic condition affects fitness through its effects on physiology and behavior. Individuals allocate energy to different functions (e.g., growth, reproduction) depending on their energetic condition, and hormones have a key role in energy allocation, as they act as mediators or as products of such allocation (Emery Thompson, 2016). Their study allows therefore understanding the underlying mechanisms and functional consequences of variation in energetic condition.

Recent advances in hormonal measurement in excretions, have made possible the non-invasive assessment of the energetic condition of free-ranging animals (Hodges and Heistermann, 2011; Beehner and Whitten, 2004; Palme, 2005). In this context, glucocorticoids and thyroid hormones are particularly useful as non-invasive biomarkers of energetic condition: on the one hand, both are involved in metabolic processes, including gluconeogenesis and cellular metabolism (Sapolsky et al., 2000; Kim, 2008); on the other hand, after metabolization these hormones are excreted in the urine and feces, reflecting the biosynthesis occurring over several hours (urine) or days (feces) (Norman and Litwack, 1997). Therefore, the concentrations of excreted glucocorticoid and thyroid hormone metabolites represent an integrative measure of the energetic condition of individuals. Accordingly, fecal metabolite concentrations of both hormones, for example, increase during periods of high energetic demands (molting) in Hawaiian monk seals (*Monachus schauinslandi*; Gobush et al., 2014). However, whereas glucocorticoid secretion occurs in response to environmental (e.g., food availability: Lewanzik et al., 2012; Bourbonnais et al., 2013), physical (e.g., climate: de Bruijn and Romero, 2011; Houser et al., 2011), intrinsic (e.g., reproductive status: Bacci et al., 2014; Viblac et al., 2016), and psychological (e.g., social stress: Corlatti et al., 2014; Stocker et al., 2016) challenges, thyroid hormones seem to be unaffected by psychological stress (Ayres et al., 2012; Gobush et al., 2014; but see Walpita et al., 2007). Additionally, when individuals face nutritional constraints, basal metabolic rate decreases and as a consequence thyroid hormone secretion is downregulated as part of an energy-saving

* Corresponding author.
E-mail address: pdias@uv.mx (P.A.D. Dias).

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strategy (Eales, 1988; Hulbert and Else, 2004; Cristóbal-Azkarate et al., 2016), whereas glucocorticoid levels increase to promote the mobilization of stored energy reserves (Sapolsky et al., 2000). Therefore, the combined measurement of these hormones allows discriminating between 1) psychological and energetic influences on the energetic condition of individuals, and 2) different hormonal coping strategies aimed at maintaining energetic balance (Emery Thompson, 2016). This has been, however, only rarely performed with wildlife (e.g., Ayres et al., 2012; Gobush et al., 2014; Vynne et al., 2014), and to the best of our knowledge, no such information exists for wild primates.

Howler monkeys (*Alouatta* spp.) are frugivore-folivore, arboreal, Neotropical primates with a wide geographic distribution (Mexico to Argentina). The concentrations of fecal glucocorticoid metabolites (for simplicity, glucocorticoid levels hereafter) of howler monkeys have been reported to vary as a function of the exchanging of agonistic interactions, the interaction between female reproductive state and participation in agonistic interactions (i.e., pregnant and lactating females involved in agonistic interactions show higher glucocorticoid levels than males and cycling females: Gómez-Espinosa et al., 2014), male rank (Van Belle et al., 2009), the presence of extragroup males (Cristóbal-Azkarate et al., 2007), time spent traveling (Martínez-Mota et al., 2007; Dunn et al., 2013), protein intake (Martínez-Mota et al., 2016), fruit availability (Behie et al., 2010; Martínez-Mota et al., 2016), habitat size (Martínez-Mota et al., 2007; Rangel-Negrín et al., 2014; but see Rimbach et al., 2013), habitat quality (Aguilar-Melo et al., 2013), anthropogenic disturbance (presence of tourists: Behie et al., 2010; undefined anthropogenic disturbances: Gómez-Espinosa et al., 2014; Rangel-Negrín et al., 2014; but see Rimbach et al., 2013), and climatic seasonality (Gómez-Espinosa et al., 2014; Rangel-Negrín et al., 2014). These factors represent environmental, physical, intrinsic, and psychological challenges to the maintenance of energetic condition, and their impact on glucocorticoid levels has been widely described in primates (Abbott et al., 2003; Beehner and McCann, 2008; Rangel-Negrín et al., 2009; Anestis, 2010; Foerster et al., 2012; Chapman et al., 2015; Schoof et al., 2016).

In contrast with the numerous studies on glucocorticoid variation, the concentrations of fecal thyroid hormone metabolites (for simplicity, thyroid hormone levels hereafter) of howler monkeys have been quantified only once. In captive female mantled howler monkeys (*A. palliata*), thyroid hormone levels declined with time post-capture in response to a sharp decrease in feeding (Wasser et al., 2010). This result converges with a positive correlation between thyroid hormone levels and food availability reported in the single study that has measured thyroid hormone levels in a wild primate (Barbary macaques, *Macaca sylvanus*: Cristóbal-Azkarate et al., 2016). Therefore, as in the case of glucocorticoids, thyroid hormone measurements allow assessing the responses of howler monkeys to factors that have the potential to affect their energetic condition.

Habitat size, activity levels, and human presence do not have the same effect on glucocorticoid levels of howler monkeys across studies (e.g., Aguilar-Melo et al., 2013 vs. Behie et al., 2010; Rimbach et al., 2013 vs. Rangel-Negrín et al., 2014). The combined measurement of glucocorticoid and thyroid hormone levels could assist in solving such inconsistencies by parsing different sources of metabolic demands as well as different hormonal coping strategies to deal with such demands (Emery Thompson, 2016). Thus, the aim of the present study was to examine variation in glucocorticoid and thyroid hormone levels in mantled howler monkeys as a function of energy acquisition and energy expenditure in order to better understand which factors affect individual energetic condition. We predicted that glucocorticoid levels should be negatively related to energy acquisition and positively related to energy expenditure, whereas thyroid hormone levels should be positively related to energy acquisition and expenditure. Furthermore, we predicted that energy expenditure factors associated with psychological demands (aggressive behavior) should affect variation in glucocorticoid but not in thyroid hormone levels.

2. Methods

2.1. Ethical note

This study was non-invasive and followed the "Guidelines for the treatment of animals in behavioural research and teaching" (Guidelines for the Use of Animals, 2012). Research protocols were approved by the Secretaria de Medio Ambiente y Recursos Naturales (permits SGPA/DGVS/10637/11 and SGPA/DGVS/04999/14) and adhered to the legal requirements of the Mexican law (NOM-059-SEMARNAT-2010).

2.2. Study site and subjects

Our study was conducted from January to December 2014 at La Flor de Catemaco (Veracruz, Mexico; 18°26′39″ N, 95°02′57″ W), which is part of the Los Tuxtlas Biosphere Reserve. La Flor de Catemaco is a 250-ha ranch dedicated to the sustainable production of ornamental plants, in which ca. 100 ha of the original evergreen forest are preserved.

The mantled howler monkey population living at La Flor de Catemaco has been studied since 2004 (Shedden-González and Rodríguez-Luna, 2010). There are currently 23 individuals in the population divided into three groups, two of which have been followed daily since 2012. Subjects were fully habituated to the presence of researchers (i.e., ignored our presence: Williamson and Feistner, 2011). We identified individuals easily through anatomical and physiognomic characteristics, including body size and proportions, scars, broken fingers, and genital morphology and pigmentation. Several individuals were marked with ankle bracelets. Adult females were classified in one of three reproductive states: lactating (i.e., females with an associated infant of 0 to 20 months: Balcells and Veà, 2009); gestating (i.e., females in the period encompassing the day before parturition to 186 days back from that date, which corresponds to the duration of pregnancy in this species: Glander, 1980); or cycling (neither lactating nor gestating). We based this classification on observations of births and nipple contact during the study, and on observations of newborns during daily visits to the study groups.

2.3. Assessment of ambient temperature

Weekly minimum and maximum ambient temperatures were determined from daily recordings performed at 1-h intervals with a handheld thermometer (Kestrel 3500 Weather Meter; Nielsen-Kellerman Company, PA, USA). During the study we accumulated a total of 1320 temperature recordings.

2.4. Behavioral sampling

We conducted 1 h continuous focal follows (from sunrise to sunset), during which we recorded the time budgets of 11 adult individuals living in the two main study groups (group 1: 2 adult females and 2 adult males; group 2: 3 adult females and 4 adult males). We categorized behavioral observations into the following: resting (sleep or static without interaction), feeding (inspection of food, bringing food to mouth, chewing and swallowing, moving while feeding within a food patch), traveling (movement to a new area or tree), and other behavior (remaining activities not categorized as resting, feeding or traveling) (Dunn et al., 2009). During feeding we recorded the food item consumed (fruit, flower, mature leaf, young leaf or other item). We also recorded all occurrences of agonistic interactions (Dias and Rangel-Negrín, 2015a). Finally, we numbered and geolocated with GPS each tree used by the howler monkeys.

We organized behavioral recordings in sampling sessions. A sampling session was defined as the period required for all adults to be sampled for their behavior and for collecting at least two fecal samples per individual (see next section). Sampling sessions lasted between one