RESEARCH ARTICLE

Sources of Variation in Fecal Cortisol Levels in Howler Monkeys in Belize

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High cortisol levels are known to cause low fecundity and increased mortality; thus, the prospect of using cortisol as a measure of population health is an exciting one. However, because so many factors can interact to influence cortisol release, it can be difficult to interpret what exactly is creating changes to cortisol levels. This study investigates variation in fecal cortisol levels in a population of black howlers (*Alouatta pigra*) from 350 fecal samples collected from 33 individuals in more than 4 years. A general linear mixed model revealed that cortisol varied significantly with fruit availability and contact with tourists. When fruit availability was low, cortisol increased, likely because when fruit availability is low monkeys eat less fruit, thus obtaining less sugar. This result may simply reflect cortisol's metabolic function of mobilizing glucose. It also indicates that these monkeys may be experiencing periods of food stress throughout the year, which was earlier thought to be minimal for a primarily folivorous species. Presence of tourists was the only other factor found to lead to high cortisol; with exposure to tourists increasing stress levels. These results highlight the importance of understanding how physiological factors can influence cortisol, making it easier to interpret results and determine the external social or ecological stressors that may increase cortisol. Am. J. Primatol. 72:600–606, 2010.

Key words: *Alouatta pigra*; howler monkeys; fecal cortisol; ecological stressors; diet; tourism; nutritional stress

INTRODUCTION

An important theme in animal behavior studies is to understand the physiological responses of individuals to environmental and social stressors. Specifically, with the development of noninvasive techniques to measure steroids in urine and feces [Strier & Ziegler, 2005], there has been a rise in studies reporting on the effect of these stressors on hormone levels in wild populations [Altmann & Altmann, 2003]. Cortisol, in particular, has received considerable attention in primate research because it is released to help the body handle and recover from stressful situations by helping to restore homeostasis. Regardless of the type of stressful stimuli, stress induces the flight or fight response, which serves to mobilize glucose for immediate use [Sapolsky, 1992]. Therefore, the metabolic goal of the stress-response is to free up energy to be used by the body until the stressful situation is over. Although this mechanism is beneficial in the short term, if it is activated too often or for too long it can have deleterious effects on the body, as energy is constantly being removed potentially leading to immunosuppression and decreased growth and reproductive rates [Abbott, 1987; Avitsur et al., 2001; Bercovitch & Ziegler, 2002; Saltzman et al., 1998; Sapolsky, 1992; Ziegler et al., 1995]. However, because the stress response is nonspecific and the body will react similarly to different types of stimuli, social, ecological, and physiological stressors will all have the same effect [Sapolsky, 1992].

Social stress has received the most attention in studies of wild primate populations. Of particular interest have been the roles of both dominance and mating on cortisol release. For example, it has been suggested that it is the stability of the hierarchy and not rank per se that is the real predictor of cortisol [Creel, 2001]. Competition for access to mates also creates social stress for male primates, particularly in seasonally breeding species where cortisol levels increase immediately before or during the mating

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season [Barrett et al., 2002; Fichtel et al., 2007; Lynch et al., 2002; Strier et al., 1999].

Although the majority of cortisol studies in primates have focused on social stressors, more recently, studies have investigated the effects of ecological factors, some of which include season, habitat fragmentation, fruit availability, and predation. In female yellow baboons (*Papio cynocephalus*), cortisol levels are higher during the dry season, primarily owing to hotter temperatures [Gesquiere et al., 2008]. Habitat fragmentation is associated with increased cortisol in black howlers (*Alouatta pigra*) [Martinez-Mota et al., 2007] and red colobus monkeys (*Piliocolobus tephrosceles*) [Chapman et al., 2007], and some primates show increased cortisol when food availability is low [chimpanzees (*Pan troglodytes*): Muller & Wrangham, 2004; baboons (*Papio anubis*): Sapolsky, 1986; ring-tailed lemurs (*Lemur catta*): Cavigelli, 1999], indicating a link between diet quality and cortisol. Additionally, chacma baboon females (*Papio hamadryas ursinus*) had higher fecal cortisol levels during months when predation was seen, which could be owing to stress associated with the predation events; however, cortisol levels were especially high for females who lost a close relative, suggesting that loss of a relative plays a major role in the elevated stress levels [Engh et al., 2006].

Central American black howler monkeys (*A. pigra*) live in either unimale or multimale social groups that contain between 2–12 individuals. The howler monkeys we have studied at Monkey River, in Belize, live in egalitarian social groups and are not documented to have linear dominance hierarchies, although recent studies from Palenque National Park, Mexico, have documented the presence of a central male that monopolizes access to fertile females in multimale groups [Van Belle et al., 2009a]. Both sexes are thought to disperse from the group at sexual maturity, and as a result the amount of time spent in social interactions is low [Behie & Pavelka, 2005; Van Belle & Estrada, 2008].

Owing to their primarily folivorous diet, *A. pigra* are expected to experience primarily indirect scramble competition for food [Sterck, 1997]; however, the expected relationship between group size and day journey length was not found in an earlier study of *A. pigra* at Monkey River [Knopff & Pavelka, 2006], and several studies of folivores have failed to detect evidence of feeding competition [Chapman & Chapman, 2000; Isbell, 1991; Teichroeb & Sicotte, 2009]. However, it has recently been suggested that some species of folivores do show signs of scramble competition when food availability is controlled [Snaith & Chapman, 2008], indicating that the effects of scramble competition on folivores may be more subtle than earlier believed.

Here, using a large set of samples collected from multiple social groups across a 4-year period, we explored variation in cortisol levels in the Monkey River black howler population in relation to a range of factors, including group size, presence of tourists, maximum monthly temperature, and fruit availability.

METHODS

Study Site and Population

The Monkey River study site is an 86 ha site in Southern Belize that is part of a 96 km^2 area of lowland, semi-evergreen, broadleaf riparian forest in a subtropical moist life zone [16°21′N, 88°29′W] (Fig. 1). This land is privately owned, but permission to conduct research has been given by the landowners and the Monkey River Tour Guide Association. This area was hit by a hurricane in 2001, the effects of which have been described elsewhere [Behie & Pavelka, 2005; Pavelka & Behie, 2005; Pavelka & Chapman, 2006; Pavelka et al., 2007]. The study population consists of six howler groups, from which behavioral and ecological data have been collected since 1999 (Fig. 1).

Ecological Data Collection

To calculate food availability, we first determined spatial availability by sampling forty-eight 20 m × 20 m vegetation plots each May from 2001–2008. Within each plot, all trees with a diameter at breast height (DBH) > 20 cm were counted, measured, and identified to species level. To determine temporal food availability, bimonthly phenology surveys were conducted on 200 trees that are used as feeding trees, by the study groups. These trees are from the top 12 species in the diet of the monkeys. During each survey, we measured the percentage of the crown that was covered with different plant parts (new, mature, and old leaves, unripe and ripe fruit, flower buds, and flowers). A food availability index was then calculated by taking the average monthly plant part coverage scores and multiplying them by the relative density of the tree species. These were then summed across species for each plant part.

Maximum and minimum monthly temperatures as well as rainfall data were obtained from the Savannah Weather Station in Belize, located 17 km from the study site.

Collection of Fecal Samples and Hormone Analysis

We collected 350 fecal samples over a 4-year period (May–July 2004, January–July 2005, and February 2006–May 2007—totaling 21 months). One sample was collected each month from the 16 recognizable adults living in the 6 groups that ranged within the 86 ha study site. To increase monthly sample size, samples were also collected from four monkey groups outside the designated study area for which individuals could all be identified, including

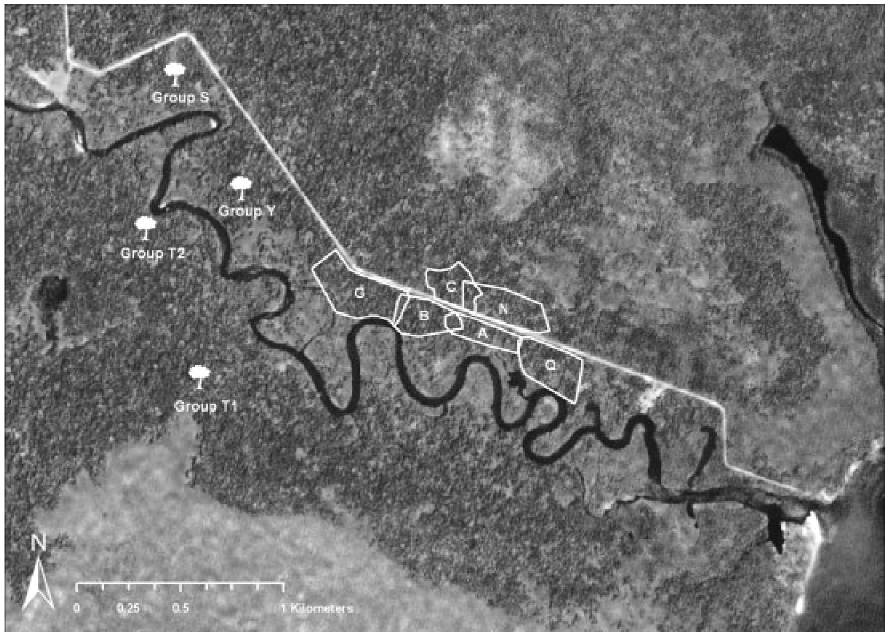

Fig. 1. Map of Monkey River Study Site. Home ranges of the six study groups are outlined and the location of the other four groups from which fecal samples were collected is identified. Groups T1 and T2 represent the groups visited by tourists on a regular basis.

TABLE I. Composition of Groups From Which Fecal Samples were Collected Along With the Number of Samples Collected From Each Group

	Number of individuals				
Group	Adult females	Adult males	Juveniles	Infants	♯ samples collected
Study group A	1	1	1	0	36
Study group B	2	2	1	0	62
Study group C	2	1	1	0	37
Study group G	3	1	1	2	26
Study group N	2	1	1	0	55
Study group Q	1	2	2	0	68
Group Y	2	1	1	0	13
Group S	2	2	2	0	20
Tourist group 1	2	1	0	1	27
Tourist group 2	2	2	1	1	16
♯ samples collected	196	154	0	0	350

Study groups are located within the long-term Monkey River Site, Belize. Group Y and S were recognizable groups outside the study site and tourist groups 1 and 2 were located across the river where local tour guides take tourists.

two groups on the south side of the river that are regularly visited by tourists. Study groups are well habituated to the quiet presence of one or two researchers and otherwise have little if any human contact (Fig. 1 and Table I).

Whenever possible, samples were collected from the first defecation of the morning, to attempt to control for diurnal variation in cortisol secretion [McCallister et al., 2004; Sousa & Ziegler, 1998]. To control for the effect of pregnancy and ovulation on cortisol [Bales et al., 2005, 2006], samples were only collected from adult females who were lactating. When each sample was collected, we recorded age, sex, group, location, and information on the current weather at the site (i.e. sunny, partly cloudy, cloudy, or rainy). Animals were determined to be adults by their size as well as by the development of a full beard on adult males. Sex was determined by external genitalia.

Immediately following defecation, samples were collected and placed in a plastic scintillation tube, then placed on ice. Later, the same day, steroids were extracted from the fecal samples following the protocol of Ziegler et al. [1995]: 0.1 g of fecal matter was mixed with 2.5 ml distilled water and 2.5 ml of 95% ethanol in a centrifuge tube. Samples were then vortexed for 10 min and centrifuged for 10 min at 2,000 g. Two milliliter of supernatant was removed from each centrifuge tube with a 5 ml syringe and passed through a Prevail SPE C18 cartridge (Alltech Associates, Inc., USA) to capture the cortisol. Cartridges were then stored out of sunlight until they were transported to the United States for analysis. Samples from 2004 and 2005 were sent to the Wisconsin National Primate Center for analysis, and samples from 2006 and 2007 were taken to the behavioral endocrinology lab at the University of Nebraska at Omaha for analysis. Both labs used the same extraction techniques and assay reagents were obtained from the same source (Coralie Munro, UC Davis, CA). Duplicate samples run at each lab produced virtually identical results and there was no statistical difference between mean cortisol values from samples analysed at each lab (lab 1 N: 149; Mean: 13.35 ng/g; lab 2 N: 201; Mean: 13.41 ng/g; Mann–Whitney U; $Z = -0.952$; $P = 0.356$).

In both labs, cartridges were rinsed with 1 ml of 5% methanol and reconstituted in 2 ml of 100% methanol before being completely evaporated on a hot plate and once again reconstituted in 1 ml of 100% ethanol. Samples were then re-evaporated and 1 ml of phosphate buffered saline solution was added before taking 50 µl to the plate in duplicate. Samples underwent enzyme immunoassay, earlier characterized by Smith and French [1997] and Van Belle et al. [2009b].

No captive animals from this species were available to conduct an ACTH challenge. However, Martinez-Mota et al. [2008] found increases in both fecal and serum cortisol in howler monkeys after anaesthesia, which acts as a stressor. Additionally, Van Belle et al. [2009b] used high pressure liquid chromatography on fecal extractions to determine the characteristics of the glucocorticoids being measured in the enzyme immunoassay and found the assay could reliably detect cortisol. Van Belle et al. [2009a, b] also demonstrated parallelism of serially diluted fecal extracts and the cortisol standard displacement curve, and reported an assay accuracy of 115+2.5%. In our study, we also demonstrated parallelism of extracted fecal samples with the standard curve. Repeated assay of a pooled sample of fecal extracts in duplicate on each plate yielded an intra-assay coefficient of variation of 6.7% and an inter-assay coefficient of variation of 14.9%.

Permission to conduct this research was granted by the Government of Belize Forestry Department, and all research was approved by the Life and Environmental Sciences Animal Care Committee at the University of Calgary, and complies with the American Journal of Primatology's standards for the ethical treatment of nonhuman primates.

Data Analysis

Fecal cortisol levels were normalized through log transformation, although untransformed fecal cortisol values were used in the figures. To determine the causes of variation in fecal cortisol, we used a general linear mixed model (GLMM). This allowed us to examine the effect of numerous predictor variables and to enter individual identity and group as random factors in the model, as we had repeated samples from the same individuals and individuals in the same group. Our method of estimation was maximum likelihood with a diagonal covariance structure. The categorical variables used as predictors were sex, group size, and presence of tourists, and continuous variables were maximum monthly temperature and fruit availability. None of these variables were correlated with each other (all tests $P > 0.05$). Maximum monthly temperature obtained from the Savannah weather station was used in our data analysis; rainfall, however, was not included because it was significantly correlated to both fruit availability and maximum monthly temperature. We also did not include altitude or predation risk as ecological factors because the entire study site is located at sea level, and we have no evidence of predation on howlers at this site over the 10 years of study. Statistical significance for the model was set at$P < 0.05$ and analyses were conducted using SPSS 16.

RESULTS

Overall cortisol values for *A. pigra* at Monkey River, Belize ($N = 350$), ranged from 0.39 ng/g to 67.89 ng/g, with a mean of 12.93 ng/g, $\pm$ 9.74 ng/g. Neither sex ($F_{1,7.98} = 0.009$, $P = 0.928$), group size (GLMM: $F_{1,290.61} = 3.01$, $P = 0.84$), nor maximum monthly temperature (GLMM: $F_{1,282.98} = 5.01$, $P = 0.095$) influenced cortisol levels, but fruit availability ($F_{1,288.93} = 10.502$, $P = 0.001$) and the presence of tourists ($F_{7,8.85} = 3.92$; $P = 0.031$) did have a significant effect. Fruit availability was found to negatively influence cortisol release, with cortisol being higher during times of year when fruit availability is low (Fig. 2).

Both monkey groups, located on the South of Monkey River, which are regularly visited by tourists, had significantly higher cortisol values than any of the study groups or groups outside the study site, which are not visited by tourists. None of the non-tourist groups differed from each other in cortisol levels (Fig. 3).

DISCUSSION

The goals of this study were to explore sources of variation in a population of Central American black howlers in Southern Belize. We found that both fruit availability and the presence of tourists influenced cortisol levels.

First, cortisol levels were negatively related to fruit availability. Central American black howlers

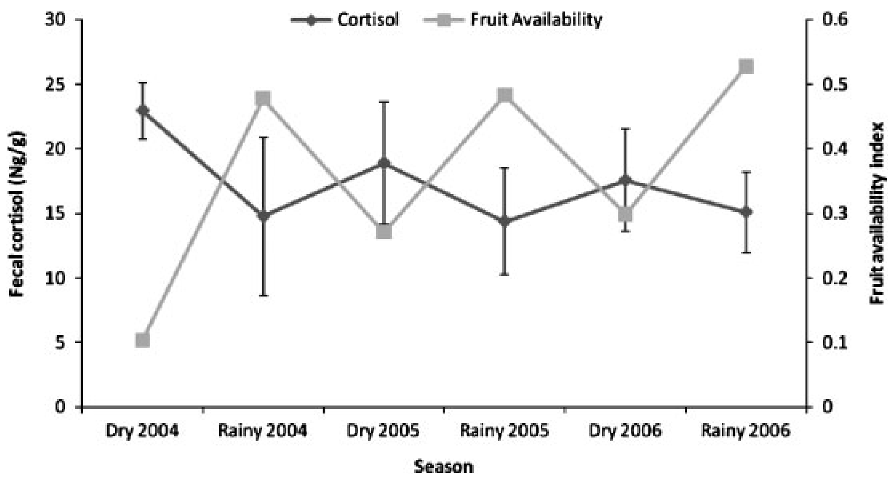

Fig. 2. Average seasonal fecal cortisol values (± standard errors) for all black howlers from which fecal samples were collected in relation to the availability of fruit. Fruit availability index was calculated based on the relative density and the production of fruit by each tree species.

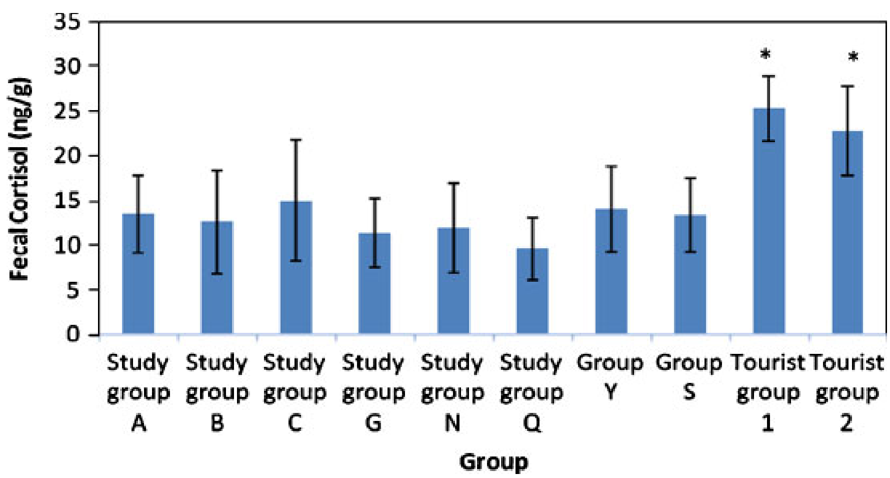

Fig. 3. Average fecal cortisol levels (± standard errors) for each group of howlers from which samples were collected in the Monkey River Watershed. All study groups have been observed and monitored since 2002. Groups Y, S are located near the study groups, but are not studied on a regular basis. Both groups are regularly visited by tourists.

are known to prefer fruit whenever it is available, and fruit consumption is directly correlated to fruit availability [Behie & Pavelka, in preparation; Silver et al., 1998]. Therefore, when fruit availability is low, the monkeys ingest less fruit and eat a diet containing primarily leaves that are low in sugar. This negative relationship between cortisol and fruit availability likely reflects the role cortisol plays in energy metabolism: when a low quality diet is ingested, cortisol increase occurs overnight, as a means to increase glucose mobilization that can be used during the day for energy [Muller & Wrangham, 2004]. Therefore, during the dry season when a diet low in energy is consumed, increases in cortisol may simply reflect this physiological response and not be indicative of any external stressor acting to elicit the flight or fight response.

This result also suggests that although black howlers are primarily folivorous and past studies have typically not found the expected evidence for scramble feeding competition [Chapman & Chapman, 2000; Isbell, 1991; Knopff & Pavelka, 2006; Struhsaker & Leland, 1987], they are indeed experiencing some degree of food stress at certain times of the year. This supports the recent suggestion that evidence of feeding competition in folivores may be more subtle than earlier studies have been able to detect [Snaith & Chapman, 2008]. Although our results did not show a relationship between group size and cortisol, the largest of the study groups had only seven individuals and the effects of scramble competition may not appear until groups get larger [Knopff & Pavelka, 2006]. Despite the lack of a group size effect, this population is showing signs of nutritional stress when fruit is less available, which suggests that these monkeys may be limited by food availability and more reliant on fruit than earlier believed (see Milton [1979, 1981]).

Unpredictability in the availability of fruit may be the proximate factor acting as a stressor at Monkey River. After the Hurricane in 2001, fruit availability changed markedly and it took 3 years to return to pre-hurricane levels. The highest cortisol levels were found in the dry season in 2004, before fruit consumption returned to pre-hurricane levels.

Our second key result was that cortisol levels were higher in the groups with more experience with tourists. Predictability is also believed to play a role in this result. Monkeys living in the area of the forest that is regularly exposed to groups of tourists also had significantly higher cortisol than did the study groups, which experience limited human contact. Tourist and guide behavior is much more intrusive than that of researchers, as tourists make more noise and guides bang on trees in an attempt to get the monkeys to howl. Howling is an energetically costly behavior and may require extra energy to be expended, leading to extra cortisol release. Additionally, just the fact that tourist visits are unpredictable could be increasing cortisol [Sapolsky, 1992].

The results from this study indicate that stress levels increase with exposure to tourists and fruit availability decreases, which emphasizes the importance of the physiological role of cortisol. It also suggests that this primarily folivorous species may be more affected by food availability than earlier believed.

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