Cortisol metabolites vary with environmental conditions, predation risk, and human shields in a wild primate, *Cercopithecus albogularis*

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A B S T R A C T

Environmental challenges are often associated with physiological changes in wildlife that allow animals to maintain homeostasis. Among these, scarcity in resources, and risks from predators, competitors, and humans can all result in psychological and physiological stress. Yet, for habituated species, it is not clear whether this relationship with humans still holds to a lesser degree or is outweighed by the benefits of human presence – such as serving as a buffer from competitors or predators. We investigated how human presence and environmental challenges such as resource availability, weather, predation, and competition may be associated with variation in fecal cortisol metabolite levels (FCMs) in a group of samango monkeys (*Cercopithecus albogularis*) in the Soutpansberg Mountains, South Africa. FCMs can often broadly track environmental challenges and perturbations. Initially, we employed an exploratory analysis comparing candidate models representing biological hypotheses and found that those incorporating information on human presence had less weight than models for food availability, thermoregulation, and water scarcity. When we examined a subset of the data that included information on intergroup competition and predator alarm calls, we found that FCMs were higher on the day following potential predator encounters but not competitive interactions. As observer numbers increased, responses to predators flattened, indicating that the presence of several humans might deter predators and/or affect samangos' perception of danger – yet we could not distinguish between these possibilities. Together, these results suggest that ecological perturbations track with FCMs in this study population and challenge long-held assumptions that human presence has negligible effects on habituated study animals.

1. Introduction

Physiological stress in wild vertebrates is often correlated with relative changes in glucocorticoids (GCs), a suite of steroid hormones whose production is triggered by the hypothalamic–pituitary–adrenal (HPA) axis and at normal levels are involved with energy regulation (Sapolsky et al., 2000, 1986). GCs can mobilize glucose stores during challenges to homeostasis and their study has become a major focus of the growing field of conservation physiology (Dantzer et al., 2014). Natural, seasonal variation in GCs with food availability, weather, competitive pressure, and predation are not necessarily deleterious or indicative of "stress" but are often an indication of health and an animal's ability to quickly adapt to new circumstances (Busch and Hayward, 2009; Dantzer et al., 2014). However, human-induced environmental change, including heightened human activity and habitat fragmentation can shift these responses to being maladaptive when animals are forced into more crowded habitats (Chapman et al., 2015, 2006; Stetz et al., 2013). Thus, if individual variation is well understood, relative shifts may indicate where conditions are especially challenging and serve as an early warning for managers (Dantzer et al., 2014). These methods may also allow us to investigate whether human presence may be comparable to other environmental challenges by

serving as an indicator of psychological.

Individuals and species vary in their sensitivities to human presence (Allan et al., 2020; Berger, 2007). Most wildlife tend to perceive humans as a threat (Smith et al., 2017; Suraci et al., 2019), but those that are tolerant of humans, through passive visitation to protected areas or purposeful habituation for research or tourism, may benefit by using humans as a buffer against predators or competitors. For example, prey may often learn to associate people and their infrastructure with safety due to a decreased presence of comparatively sensitive large carnivores (Berger, 2007), and these effects may cascade through ecosystems, indirectly affecting numerous other species (Suraci et al., 2019). This "human shield" effect has been detected in numerous species (Atickem et al., 2014; Moll et al., 2018; Nowak et al., 2014; Sarmento and Berger, 2017). In contrast, a recent study using flight and visual orientation distance experiments to measure tolerance to people in a habituated group of chacma baboons (*Papio ursinus*) found that certain individuals remained sensitive to human presence after years of study (Allan et al., 2020). These potentially conflicting effects of fear or attraction to humans are little-studied. Yet, a better understanding of how human presence, in the absence of overt habitat alteration, could still have distinct impacts on different species is crucial for protecting ecosystems in future. Here we take a new approach by using physiological indicators of stress to better understand the individual or group-level effects of seemingly benign researcher presence on a wild social primate by comparing these responses to other environmental challenges.

2. Present study

Samango monkeys (*Cercopithecus albogularis*), also known as Sykes' monkeys in parts of their range and considered conspecific with blue monkeys (*C. mitis*), have a wide distribution across eastern and southern Africa and are considered 'least concern' by the IUCN (Butynski and de Jong, 2019), but South African populations suffer from severe habitat fragmentation and are considered nationally endangered (Linden et al., 2016). Here we address the question of what environmental challenges might predict GC levels in a studied group of wild samangos (*C. a. schwarzi*) inhabiting the Soutpansberg Mountains in South Africa. We also ask to what extent might human presence poses an additional challenge or instead buffers encounters with predators or other groups, reducing the overall effects of these encounters.

Populations in the Soutpansberg deal with overnight temperatures much colder than those in lowland or coastal environments (Coleman and Hill, 2014a), but over the coming decades, the Soutpansberg is expected to become hotter and dryer (Kephe et al., 2016), potentially affecting native plant communities and the animals that rely on them. Evidence from other populations of this species that deal with less seasonal variation indicates that reduced food availability is a major predictor of heightened fecal GC metabolite levels (Foerster et al., 2012; Foerster and Monfort, 2010), and fecal cortisol metabolites (FCMs) more specifically (Thompson et al., 2020). Thus, we might expect similar relationships with this population.

In addition to dealing with seasonally fluctuating temperatures, rainfall, and food availability, this study population is also subject to aggressive encounters with other conspecific groups and to predation by eagles, leopards (*Panthera pardus*), and rock pythons (*Python sebae*) (Coleman and Hill, 2014a; LaBarge et al., 2020; Williams et al., 2018). For predation risk in particular, animals can reduce their risk of encounters pre-emptively through behavioral responses which will often impose nutritional constraints on prey, but if predator encounters are relatively unpredictable, then the overall costs of avoiding predators are likely to be stress-mediated (Creel, 2018). Previous studies on this population have found evidence that animals avoid locations where they are attacked by eagles (the most common primate predator at our field site) (Coleman and Hill, 2014b). If our study population can reduce risk and unpredictability to a sufficient degree by behavioral responses alone, then background predation risk may not generally induce

additional physiological stress. Yet, as acutely stressful events, reactive responses to predator encounters likely still result in short-term responses leading to elevated serum GC levels; however, as short-term events it is not certain whether any hormonal consequences of predation would be apparent in relative levels of excreted metabolites (Clinchy et al., 2004, 2013; Creel et al., 2009; Narayan et al., 2013).

To the best of our knowledge, this is the first study to incorporate information on threats from predators in this species and one of the few in primates (Arlet and Isbell, 2009; Engh et al., 2006). It is also relatively uncertain how human presence might affect individual GC levels and whether any changes might be apparent in cycles of weekly researcher presence/absence. Individuals within this study species could also show consistent and individualized responses to researchers due to inherent physiological and personality differences (Allan et al., 2020; Koolhaas et al., 2010). Thus, while this study group is considered 'habituated', some individuals may remain fearful and respond physiologically to the perceived threat of being observed from dawn-dusk. Alternatively, day-long observations might result in a 'human shield', reducing the number of daily encounters with potential predators, competitors, and/or subjects' perception of their own risk. Past experiments with this study group indicate that observer presence does alter their risk-sensitive behavior (Nowak et al., 2014), but whether any effect would be large enough or long-lasting enough to produce changes in GC values remains uncertain. If human presence reduces risk perception, then an overall relaxation in antipredator behavior could mean that when encounters do occur, they are unanticipated and paradoxically induce stress responses higher than those in unhabituated populations.

To explore these questions, we used a model comparison approach to address what climatic and resource variables might be most important for predicting samango GC levels. To do this, we compared models for the effects of 1) food availability, 2) water scarcity, 3) challenges to thermoregulation, and 4) observer presence/absence with a minimal model. A subset of data also included information on daily predator encounters/widespread alarm calls, intergroup encounters, and the number of observers that were with the study group. We used this subset to investigate the effects of potentially threatening stimuli on GC levels and whether the number of observers with a samango group might interact with either of these effects. We hypothesized that both risky encounters and human presence would be associated with variation in GC concentrations. Specifically, we predicted that the number of risky predator or intergroup encounters the previous day would be accompanied by a rise in measured GC levels. The number of researchers present with a group may also be associated with a rise in GCs if individuals were still sensitive to human presence. Alternatively, if observer presence resulted in a group experiencing fewer predator encounters and/or perceiving themselves to be safer due to the human shield effect, then observer numbers may modulate responses to unhabituated predators and competitors.

3. Methods

3.1. Study site and species

We conducted our study at the Lajuma Research Centre in the western Soutpansberg Mountains of Limpopo Province, South Africa (23° 02′S, 29° 26′E). Samango monkeys are medium-sized (adult females ~ 4.4 kg, adult males ~ 7.6 kg), arboreal guenons that live in single-adult male, multi-female groups typically with 10 to 65 individuals (Butynski and de Jong, 2019; Coleman and Hill, 2014a).

The study site encompasses an array of habitat types including tall moist Afromontane forest, deciduous woodland, acacia bush, and rocky grassland/cliffsides. This population has access to evergreen forest year-round but deals with seasonal fluctuations in food availability (Mostert et al., 2008; Parker et al., 2020). Natural predators of samangos at the site include crowned eagles (*Stephanoaetus coronatus*) and black eagles (*Aquila verreauxii*), the African leopard (*P. pardus*) (Williams et al.,

2018), caracal (*Caracal caracal*) (Nowak et al., 2014), and rock pythons (*P. sebae*).

We collected fecal samples from 13 known adult females within our "House" group (total N ~ 70–80) that have been studied via direct observation for >10 years. These known individuals had either been previously captured and tagged or had distinctive markings that allowed us to reliably identify them at various heights in this densely vegetated habitat. As most individuals were not identifiable in these groups, we had no information on relative rank differences which are a major source of variation in GCs in many social primates (Allwin et al., 2014), including in this species (Foerster and Monfort, 2010). We however include individual identity in all our analyses to account for some of these effects (see Analysis).

3.2. Ethical approval

We received research permission from the Limpopo Province Department of Economic Development and Tourism (Permit No. ZA/LP/81996). This research was also approved by the Institutional Animal Care and Use Committee of the University at Buffalo (IACUC No. ANT07037N) and the Durham University Animal Welfare Ethical Review Board. All project members and research assistants collecting direct behavioral data on these habituated groups received training and protocols to maintain human/animal safety through the Primate and Predator Project. Observers were trained to observe animals with binoculars from a distance, avoid direct eye contact and any other potentially disturbing behaviors to minimize observer bias and potential stress to animals.

3.3. Sample collection

We collected fecal samples opportunistically from the known adult females within a habituated group over 19 months from January 2018 to July 2019. The group was followed from dawn-dusk on four consecutive days a week by one to four field assistants. Samples collected on the first day of observation represent GC levels when no researchers were present, whereas those collected on days 2–4 represent GC levels when researchers were present. We collected samples on the mornings of follow days within the first 4 h of daylight to minimize variation due to circadian rhythms as fecal metabolite concentrations may decrease over the course of the day in this species (Foerster and Monfort, 2010). We attempted to sample evenly across individuals throughout the year by moving through a collection list. The mean number of samples we collected per individual was 14.76 (range 5–22; the individual with 5 samples left the group in 2018). Prior to sample collection we prepared 15 ml polypropylene sample tubes with 5 ml of 80 % ethanol. Each tube was weighed before being covered in parafilm so that the difference between the tube before and after collection could serve as the sample weight. In the field, we searched for known individuals based on ear tags or other identifying features and observed them at a distance with binoculars until they defecated. We homogenized the feces with a plastic or wooden utensil and collected ~0.5 g, carefully avoiding seeds or fibrous material which could artificially inflate sample weight (Allwin et al., 2014). Additionally, we avoided collecting samples contaminated with soil, water, or urine. Following collection, we recapped tubes and shook the samples by hand for 30 s to suspend the fecal matter. We reapplied parafilm and stored tubes upright to minimize evaporation or leakage until returning to camp.

3.4. Extraction protocol

We extracted samples in the field and stored them in a building with more even ambient temperature than the outside air. Our protocol followed Nugraha et al. (2017). After collection in the field, L.L. or an assistant transported the sample tubes to camp and obtained sample wet weights. Samples were extracted an average of 171 min (3 h) after collection. We then extracted hormone metabolites by shaking each tube for exactly 2 min. Following this we used a manual centrifuge to spin each sample tube for 2 min and then pipetted 1.5 ml of the supernatant into 2 ml polypropylene tubes. Experiments with other species have found that liquid extracts are stable at ambient temperatures for approximately 6 months (Nugraha et al., 2017). We transported samples to the U.S. for storage at −20 °C an average of every 5.7 months (June 2018, December 2018, and July 2019). We included time between sample collection and extraction and total storage time of extracts in each model.

Previous research on Sykes/blue monkeys found that glucocorticoids extracted from feces peak between 23 and 25 h post adrenocorticotropic hormone (ACTH) and biological challenge (Foerster and Monfort, 2010) and that cortisol is among these steroid metabolites that respond to variation in social/environmental challenges (Thompson et al., 2020). Thus, we assume that metabolite levels reflect broad relative changes in circulating GC from the previous day.

3.5. EIA protocol

We used a commercially produced enzyme immunoassay (EIA) (Arbor Assays, MI, USA) to measure total fecal cortisol metabolites (FCMs) from samango fecal extracts. This assay has been previously validated for use with non-human primates (Brand et al., 2016), including Old World monkeys (Chen et al., 2017) to successfully track changes in fecal cortisol. To validate this assay, we conducted a parallelism of slopes test and a spike and recovery test. Slopes of standards and diluted samples were similar ($r^2 = 0.98$) and mean recovery was 113 % (SD: 7.9, CV: 6.9). Our intra-assay coefficient of variation (CV) was 12.3 % and inter-assay CV was 10 %. Kits contained plates coated with goat anti-mouse IgG. Sensitivity of this assay was 27.6 pg/ml and the limit of detection was 45.4 pg/ml. We followed manufacturer instructions and created serial dilutions with cortisol standard (32,000 pg/ml) for each assay plate. Additionally, each sample was diluted to 1:20 with assay buffer to work within the range of this assay. We measured optical density using a SpectroMax plate reader at 450 nm wavelength. At the end of processing, we ended up with 192 useable samples (~14/individual).

3.6. Environmental data

3.6.1. Temperature and rainfall

Temperature and rainfall data were collected onsite with missing values filled in with missing temperature data from the ERA5 reanalysis near-surface temperature dataset provided by the Copernicus Climate Data Store (Hersbach et al., 2020). These satellite-derived data were strongly correlated with onsite measurements (maximum temperature $r = 0.97$, minimum temperature: $r = 0.83$) (Fig. 1). Twenty-four hour maximum and minimum temperatures were used as covariates. These values were not strongly correlated ($r = 0.15$), probably due to wide fluctuations in day and nighttime temperatures. Rainfall data was measured in mm and was collected via a standard 203 mm rain gauge.
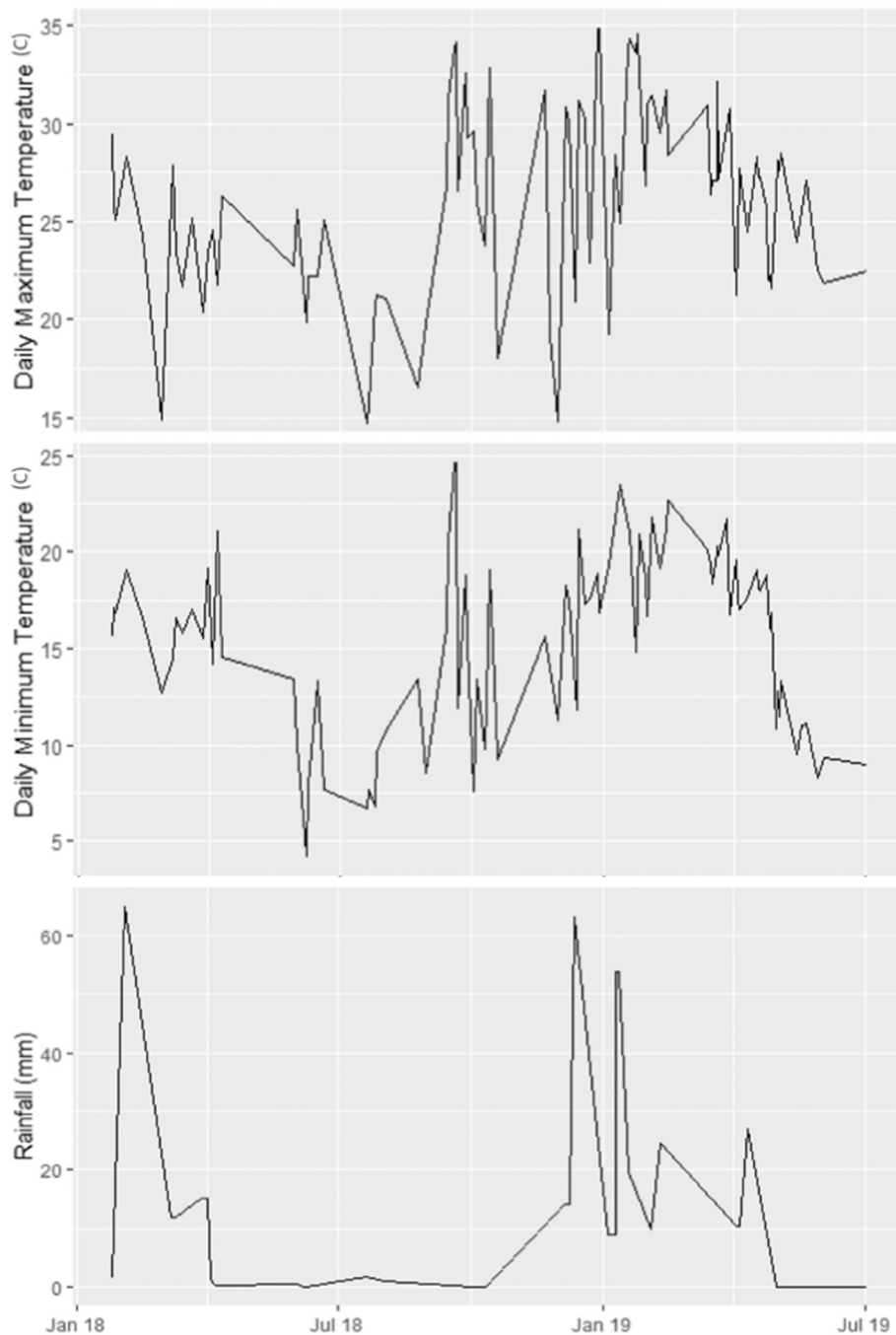
Fig. 1. Daily maximum and minimum temperature (C) and weekly total rainfall (mm) at Lajuma.

We later evaluated in analysis whether any covariates were correlated using variance inflation factors (VIF).

3.6.2. Food availability

To capture variation in food availability over the year, we collected data on fruit, leaf, and seed phenology patterns of 26 tree species known to be frequently used by samangos (Coleman and Hill, 2014b, 2014a). Every four weeks we estimated the total number of leaves, seed pods, and fruit on 520 individual trees spread across nine transects (20 individuals per food species). These 20 trees were of various ages and sizes (>10 cm DBH) so that they would be broadly representative of typical trees samangos might eat from. For each species, we calculated a monthly mean of total fruits, seeds, and leaves. This was then adjusted across the home range using data from randomly placed vegetation plots

($n = 405$ plots, 854 trees). To do this, we used an importance index based on Aristizabal et al. (2019) to measure the relative density, abundance and dominance of each of the 26 food tree species. We used a count of each individual species (N_{sp}) within the home range divided by the home range area (A_h) added to the quotient of N_{sp} and divided by the total number of trees sampled within the home range (N_t). We then divided mean basal area for each species (BA_{sp}) by the total basal area (BA_T) of all tree species and summed these values:

$$\text{Importance Index} = \left(N_{sp}/A_h\right) + \left(N_{sp}/N_t\right) + \sum_{i=1}^{n} \left(BA_{sp}/BA_T\right)$$

We then multiplied this importance index by species-specific monthly fruit, seed, and leaf availability counts and summed all values for each food item to obtain an adjusted food availability index
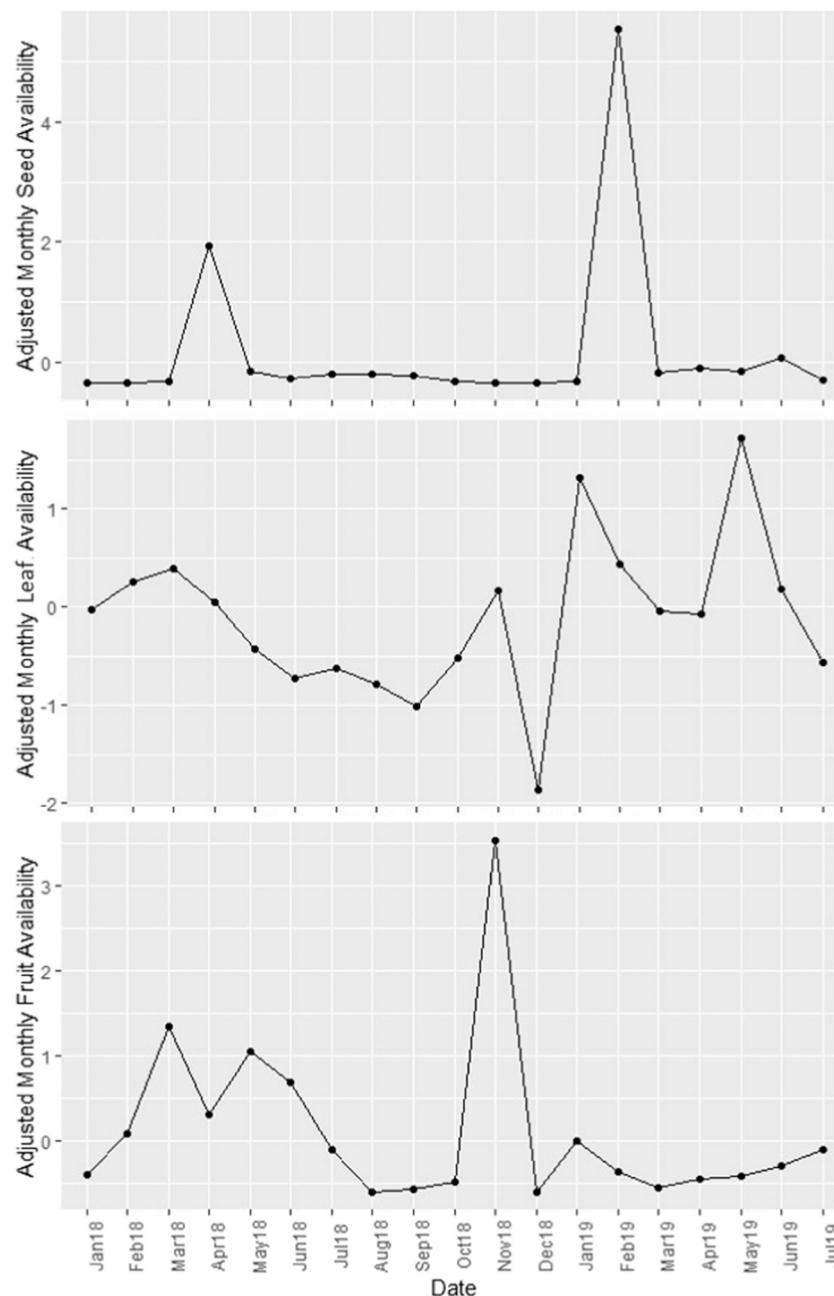
Fig. 2. Adjusted food availability indexes across the group's home range for each of the three main edible plant parts. Values are scaled for visual comparison where the mean is set to zero.

for each month (Fig. 2). Thus, these values reflect the relative density and abundance of each food item across the home range.

3.6.3. Predator and intergroup encounters

Cumulative alarm calls from the previous day that occurred >15 min apart were used as a proxy for perceived predation risk (72 samples collected following days with one or more group-wide alarms). We only counted alarms that elicited a response from most of the group and/or when a predator was spotted, because some juveniles alarm at non-threatening wildlife without eliciting a response from the rest of the group. For most alarms, the cause was unknown, but the most common predators encountered were crowned eagles and domestic dogs. In one instance, the group encountered and responded to a black mamba (*Dendroaspis polylepis*). During the study period, the group also encountered black eagles and African leopards, although we were not

able to collect samples from known individuals the following day. We could not tell predator type from alarm calls but note that threat calls during competitive interactions sounded distinctly different than alarm calls. We separately recorded the occurrence of encounters with other groups (25 samples collected following these events). Most of these encounters resulted in individuals from either group making threat charges and vocalizations, but more rarely they could involve chasing and physical contact. The typical duration of these encounters was two group scan periods (total range of ~15–40 min). None of the encounters that we witnessed resulted in any physical injuries and were typically short, although longer encounters lasting an hour or more are known to occur (LaBarge et al., 2020). Generally, these encounters occurred only once per day and therefore we used a binary variable for whether these.

3.7. Analysis

FCMs should appear in samples on a nearly 24 h lag in this species; therefore, challenges associated with daily temperatures, rainfall, and predator or intergroup encounters should reflect an animal's physiological state from the previous day (Foerster and Monfort, 2010; Lambert, 2002; Thompson et al., 2020). Thus, we set our daily covariates on a 24 h lag to discern which variables may be important. The exceptions to this were food availability, as our phenology measurements occurred every four weeks, and rainfall which we included as the previous weekly total (mm), as this would influence levels of available drinking water.

We initially compared four basic model types against a minimal model which included information on time of collection to offset changes due to an animal's circadian rhythm, time from collection to extraction, and total time the extract was stored before transport to a −20 °C freezer to account for any additional storage effects as fixed effects. These variables were included in every subsequent model. The first model included fruit, seed, and leaf availability as fixed effects. The second included the lowest and highest daily (24 h) temperature only. The third included an interaction between rainfall and season, as water is generally not scarce in the wet season. The fourth included a fixed effect for whether the group had been followed the previous day (binary yes or no). We expected unmeasured individual differences to predominate over most other potential factors, as traits such as age, body size, social relationships/rank and overall health should affect how resilient individuals are to environmental challenges (Foerster, 2009; Foerster and Monfort, 2010). Therefore, each model included individual identity as a random intercept, and we compared versions of each model with and without random slopes to allow for variation between individuals (e.g., where some individuals have strong responses to a stimuli and others do not). We therefore compared a total number of eight models representing four distinct biological hypotheses along with the ninth minimal model (model 0) (Table 1).

We used models with Skew Normal distributions and log links run in the stan computational environment and accessed through the R package brms (Bürkner, 2017). For all models we used the default Student-t priors (df = 3, mean = 0, scaling factor = 10). n the case of the standard deviations of the random effects, these parameters are forced to be positive, so the default is a half Student-t prior. To compare candidate models, we used Pareto smoothed importance sampling leave-one-out cross-validation (PSIS-LOO) to calculate predictive densities for each model (Yao et al., 2017). We then used a method known as 'stacking' to combine and compare Bayesian posterior predictive distributions. This is done by first obtaining and maximizing predictive densities of the combination distribution (of candidate models) from PSIS-LOO and then assigning a weight ranging from 0 to 1 for each model. In this method, all models are combined by maximizing the LOO predictive density of their combined distribution. Stacking outperforms Akaike style weights obtained from other Bayesian model comparison procedures and is more suitable for comparing similar models with and without random slopes as stacking jointly optimizes their weights (Yao et al., 2017). Importance sampling gives reliable estimates when the Pareto diagnostic estimate

$(\widehat{k})$ is <0.7, and we only considered models at or better than this threshold.

Following this analysis, we then asked if the external events of intergroup encounters or predator encounters might be associated with changes in FCM levels using just the subset of data where we had information from the previous day ($n = 82$). To do this, we used a single model with the same distribution, and we set the previous days' cumulative incidence of predator alarms and the presence/absence of intergroup encounter events as fixed effects. Identity of each individual was set as random intercepts to account for individual-level responses to each stimulus. We used a count of the number of observers as an interaction in this model to explore whether increasing human presence might be related to higher FCMs due to sensitivity to observers or, alternatively, might dampen responses to predators or competitors due to a human-shield. This analysis was conducted using a single model and we used Bayesian 95 % credible intervals and probability of direction (PD). PD values indicate how much of a posterior distribution is entirely positive or negative and ranges from 50 to 100 %, with values >97.5 % indicating a true effect (Kruschke, 2014).

3.8. Data statement

Data for this article is available at Figshare at doi: https://doi.org/10.6084/m9.figshare.20282025.

4. Results

Incorporation of random slopes to better account for differing responses between individuals did not improve the predictive ability of any of our models. Model 2 had the highest weight, but weight was also shared with model 1 and 3 to a lesser extent, indicating that unique components of each were predictors of FCMs in this population while model 0 (human observer presence) had no weight (Table 2). In model 2, higher minimum temperature was associated with lower FCM levels (estimate: −0.09, estimated error: 0.04, 95 % CI: −0.16, −0.02), indicating support for the prediction that challenges to thermoregulation and cold stress would result in increased glucocorticoid production (Fig. 4). Examination of model 1 revealed that among the monthly food availability predictors, only seed availability was associated with FCM levels (estimate: −0.10 estimated error: 0.05, 95 % CI: −0.22, −0.02) though this relationship may be driven by relatively few observations in months with very high seed availability (Fig. 3). Finally, in model 3, higher total rainfall per week (mm) was associated with lower FCM values, but only in the dry season (estimate: −0.40, estimated error: 0.19, 95 % CI: −0.84, −0.08) (Fig. 5). Neither of our models incorporating information about whether the group was observed the previous day had any support. Additional examination of this predictor in model 4 revealed that its credible interval included zero suggesting that whether a researcher was present (or not) did not substantially affect levels of FCMs in samango monkeys compared to other ecological factors.

We used the subset of data ($n = 82$) when the group was followed the previous day to investigate whether the cumulative total of brief, but

Table 1

Each candidate model representing a biological hypothesis included the covariates of model 0 to account for circadian rhythms, season, and storage time which were two separate predictors for time between collection and extraction and months before transport. Continuous variables (food availability, temperature, and rainfall) were all scaled. Observer was a binary 0 or 1 for whether the group had been followed the previous day. Each model was run with individual identity as a random intercept. We also ran a duplicate of each candidate model (1–4) with relevant fixed effect variables set as random slopes for a total of nine models.

Hypothesis	Model	Fixed effects
–	0	Intercept + time of day + storage time
Food availability	1	Model 0 + Leaf availability + fruit availability + seed availability
Thermoregulation	2	Model 0 + maximum daily temperature + minimum daily temperature
Water availability	3	Model 0 + rainfall * season
Observer effects	4	Model 0 + observer

Table 2
ELDP is the expected log pointwise predictive density calculated by leave-one-out cross validation. ELPD_Diff is the difference in values, with respect to the model with the best predictive accuracy (model 2, Thermoregulation). SE is the standard error in the differences between models.

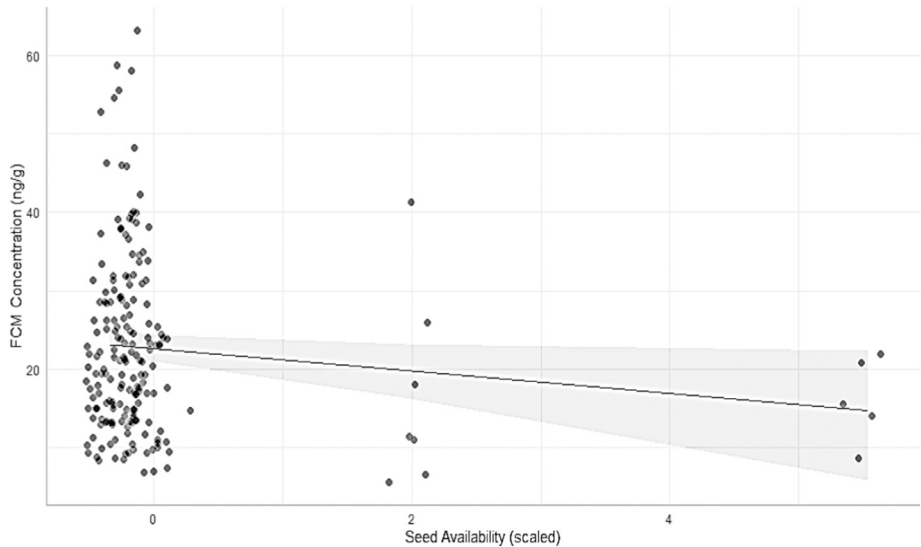| Model	ELPD_Diff		SE		Stacking weight	
	Population-level	Random slopes	Population-level	Random slopes	Population-level	Random slopes
0	−2.7	–	2.3	–	0.00	–
1	−0.9	−3.2	2.8	2.9	0.36	0.00
2	0.0	−1.5	0.0	0.6	0.55	0.00
3	−2.5	−2.3	2.3	2.4	0.02	0.09
4	−3.5	−3.5	2.4	2.4	0.00	0.00

Fig. 3. Greater seed availability was associated with lower FCM concentrations in this samango group.
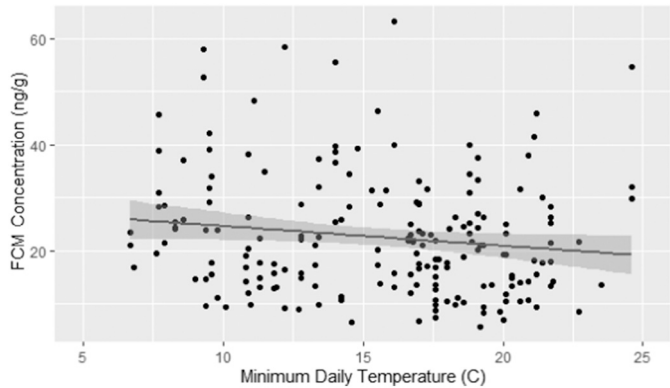

Fig. 4. FCM levels tended to be higher in this population of wild samangos when the minimum daily temperature was low.

potentially dangerous intergroup and predator encounters would affect FCM levels 24 h after. We also used this dataset to investigate whether the number of observers, rather than simple presence/absence of humans might be important (Table 3). Here we found that with only a single observer, the number of recorded group-wide antipredator alarms was associated with higher FCM levels. This relationship changed as the number of observers increased and with 3 or more observers, the apparent trend with alarms flattened (Fig. 6). The PD for this interaction term was 98.93 %, indicating strong support for the existence of this effect and its highest density interval (HDI) did not contain 0 [−0.11, −0.02]. In contrast, we found no support for an association between intergroup encounters and FCMs or an interaction between observers and these encounters (Table 3).
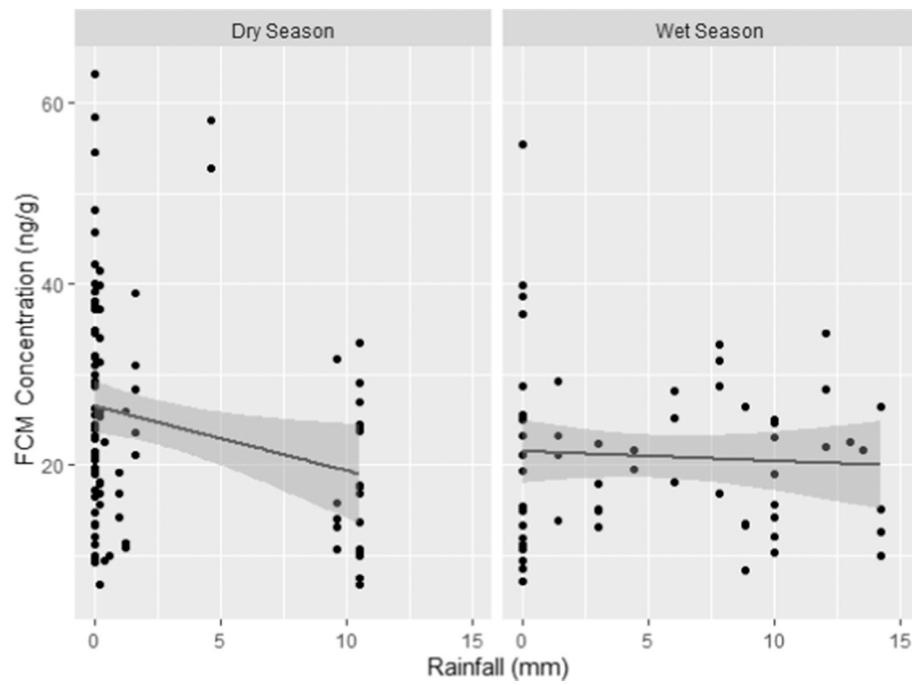
Fig. 5. Relationship between weekly total rainfall (mm) and FCMs in the dry and wet seasons.
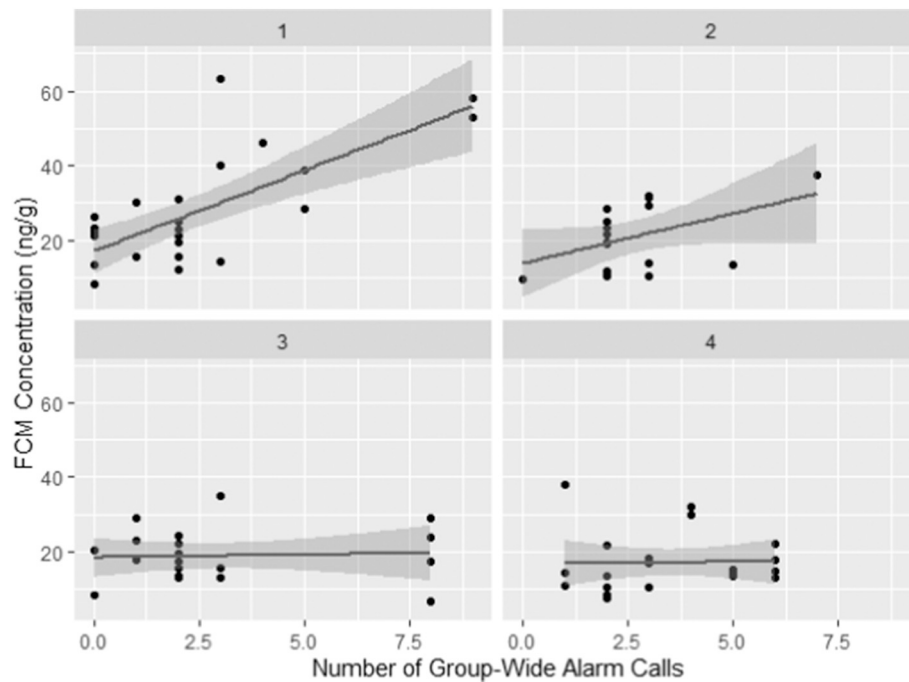

Fig. 6. FCM concentrations and the daily count of predator encounters/widespread alarms when different numbers of observers were with the group 24 h prior to sample collection. Four or more observers were grouped together.

Table 3

Population-level estimates from the joint posterior distribution, estimated error, and lower and upper 95 % credible intervals for each parameter. PD is the probability of direction and Rhat is the scale reduction factor on split chains, indicating convergence at 1.00. L-HDI and U-HDI are the lower and upper 89 % highest density intervals of the posterior distribution. 'Collection Time' is how long after sunrise a sample was collected. 'Storage Time' was the number of months until extracts were transported to a −20 °C freezer before assay. 'Time to Extraction' was the amount of time between collection in the field and extraction at the field station. 'Observers' is the number of observers with the group 24 h prior to collection of a sample. 'Alarm' is the cumulative number of predator encounters or widespread alarm calls that could be reasonably attributed to a predator recorded the previous day. 'Intergroup' encounters is a binary variable for whether an extra-group encounter events occurred the previous day.

	Estimate	Est. Error	l - CI	U - CI	Rhat	PD	l - HDI	U - HDI
Intercept	2.62	0.22	2.18	3.04	1	100 %	2.26	2.96
Collection time	−0.19	0.11	−0.39	0.02	1	95.87 %	−0.35	−0.02
Storage time	−0.05	0.02	−0.10	−0.00	1	98.13 %	−0.09	−0.01
Time to extraction	0.26	0.11	0.04	0.47	1	98.80 %	0.08	0.44
Observers	0.06	0.06	−0.06	0.18	1	80.57 %	−0.05	0.16
Alarm	0.22	0.06	0.10	0.33	1	99.97 %	0.13	0.31
Intergroup encounters	−0.09	0.23	−0.51	0.35	1	66.07 %	−0.45	0.28
Observers * alarm	−0.06	0.03	−0.12	−0.01	1	99.37 %	−0.11	−0.02
Observers * intergroup	−0.02	0.11	−0.23	0.18	1	59.27 %	−0.18	0.15

5. Discussion

The act of fleeing from an attacking predator is an acute stressor that should not necessarily be apparent in measurements of FCMs, given that such measurements may instead reflect daily variation in overall perceived risk (Clinchy et al., 2013; Voellmy et al., 2014). As expected, when one or two alarm calls occurred throughout the day in our study groups, we found no accompanying rise in FCM concentrations. But as the number of alarms or predator encounters increased, so did measured FCMs. Despite a lack of effect from human presence in our initial analysis, we subsequently found evidence of an important interaction between observer numbers and the daily total of predator encounters/ widespread alarm calls when we examined a smaller dataset for which we had information from the previous day. With only one observer present, we found a positive trend between the number of predator events and FCMs measured the next day. In contrast, responses to potential predator encounters were apparently dampened when three or more observers were present. Whether this effect was due to subjects perceiving themselves to be safer while in the presence of observers or because the cause of widespread alarm calls was less serious on days when more observers were present is uncertain. In contrast, we found no evidence for an effect from intergroup encounters or that observer effects might alter responses to these events. These events were short in duration and, in contrast to predator encounters, did not often occur more than once in the day before sample collection. Thus, these events may represent an acute stressor that was difficult to detect in fecal metabolites. These results add to a growing body of literature suggesting that human presence can affect otherwise 'habituated' animals in important ways (Allan et al., 2020; Nowak et al., 2014; Shutt et al., 2014).

We found evidence that certain ecological challenges predicted FCM levels in a group of wild samango monkeys in the western Soutpansberg Mountains of South Africa. Lower seed availability, lower minimum daily temperatures, and extended absences of rainfall in the dry season were all predictors of higher FCM levels. These three effects suggest that water scarcity and thermoregulation have important physiological effects on this mountain-dwelling population, resulting in changes to glucocorticoid secretion. Including information on human presence did not improve the predictive accuracy compared to models incorporating information on resource availability or climate. We also found no apparent association with fruit or leaf availability, despite the former being preferred food (Coleman and Hill, 2014a). We would note that in our initial analysis, stacking did not favor models incorporating random slopes, but this was possibly due to the challenges of fitting with a relatively small sample size, making the predictions of those models less precise than non-slope models. For this reason, we do not rule out the possibility of individual-level effects, which should be the focus of future

work, especially if varying levels of observer tolerances can be assessed in identifiable individuals (e.g. Allan et al., 2020). Thus, future studies with larger sample sizes may be better suited to addressing how individualized these responses are.

5.1. Climate and resource availability

Samango monkeys on the Soutpansberg Mountains experience greater seasonal shifts than other populations of Sykes/blue monkey living throughout coastal southern and eastern Africa or low-elevation equatorial forests. Despite our study site being within the tropics (north of 23.5°S), dry season minimum temperatures can dip near freezing on occasions (Fig. 1), posing a challenge for thermoregulation. Surprisingly, we found little evidence for varying slopes indicating strong individualized responses (Table 2), despite evidence that body size can modulate the effects of cold stress (Beehner and McCann, 2008; Foerster et al., 2012). This lack of distinctly individual responses may be because we only sampled adult females who tend to be similarly sized and/or because females, subadults, and juveniles huddle together in their sleep trees (personal obs.), which makes it possible that individuals vary somewhat randomly in their ability to secure a sleep partner across different days (e.g. McFarland et al., 2015). It is also possible that juveniles or adult males might respond differently to this stressor, although previous studies with similarly sized primates have not found substantial differences based on sex alone (Henzi et al., 2017). However, larger studies with a greater number of known individuals across a longer period might better address this question. Future research using arboreal camera traps or GPS collars with temperature probes might also be better able to address individualized questions (Lewis Baida et al., 2021).

An absence of rainfall in the dry season (but not in the wet season) was associated with higher FCMs, indicating that water scarcity might be a challenge for these animals. This western Soutpansberg population has had to contend with increasing drought over the past several decades (Kephe et al., 2016), suggesting that this effect may increase if climate change causes this pattern to continue. This result was somewhat surprising given that this Soutpansberg population has year-round access to natural springs near the cliffs overhanging their typical sleep sites. Yet, during the dry season, fruits may contain less water and the animals may have to spend more time drinking from the ground where it is potentially more dangerous (Emerson et al., 2011; Nowak et al., 2014) or travel further to reach water sources.

We hypothesized that fruit availability would be important for measured concentrations of samango FCMs as fruits are a major energy source for all populations across eastern and southern Africa (Coleman and Hill, 2014b). Nevertheless, we only found evidence that increased seed availability was a strong predictor of decreased FCM levels. One

reason for this may be that the seeds of paperbark acacia tree (*Vachellia sieberiana*) all become edible around the same time of year (Fig. 2), allowing this group to consume excess calories in a relatively short window of time. This relationship was driven by a relatively smaller number of observations during the peak seed months (Fig. 2). One reason for a lack of strong association for fruit availability and FCMs in this population may be that fruit was relatively available throughout the year (compared with stronger dips and spikes in leaf and seeds) (Fig. 2), thus this population did not go through any major periods of scarcity during the study. Yet, while we lack shorter term data on food availability due to our monthly phenology sampling, it is possible that a weekly or biweekly measure would have been more strongly associated with FCM variation. However, other studies examining food availability on primate hormones have found that monthly or seasonal variation in food availability is better associated with FCMs than daily information on feeding or food availability, likely because these long-term measures are more important for body condition than short-term feeding behavior (Berghänel et al., 2016). We additionally note that while dietary fiber can have a major impact on measured GC metabolite concentrations (Allwin et al., 2014), we attempted to sample only from the fecal matrix to avoid this issue.

5.2. Effects of humans, predators, and competitors

Studies investigating the effects of predator encounters and overall predation risk in vertebrate animals have so far found mixed evidence for stress-induced responses (Clinchy et al., 2004; Creel et al., 2009; Narayan et al., 2013; Sheriff et al., 2009). If predation risk is highly predictable in space and time, animals can adjust their movement and activity patterns to avoid most threats requiring reactive responses, resulting in fewer encounters but nutritional costs. In contrast, if individuals are unable to engage in proactive responses, then one consequence is overall heightened GC levels from dealing with the unpredictability of encounters (Creel, 2018). Previous studies have shown that monkeys tend to give alarm calls in areas concentrated around eagle nests (Shultz and Noë, 2002) and samangos in particular are also known to avoid those locations (Coleman and Hill, 2014b). However, as we observed up to nine group-wide alarm calls on some days, these animals clearly are not able to avoid all encounters. Whether these encounters simply lead to shorter-term responses or whether this population also suffers from chronically heightened GC levels compared with groups living under less predation risk is uncertain but should be explored with future studies. As eagles are the main predator of samangos at this site and can range widely above the canopy, it is possible that encounters may be relatively unpredictable. How responses might vary compared with groups who face predation from potentially more predictable predators (e.g. terrestrial felids).

These results also complement the findings of Voellmy et al. (2014), who found that levels of meerkat vigilance, rather than acute responses to alarm call playbacks, predicted higher FCMs. Thus, prolonged risk perception, rather than acute stressors may be more apparent in excreted metabolites. In another study of primate responses to predation risk, Arlet and Isbell (2009) found that male grey-cheeked mangabeys (*Lophocebus albigena*) that engaged in active defense against crowned eagles had elevated FCMs in the days following attacks, but non-defending males did not. Thus, particularly stressful experiences may result in these prolonged periods of heightened risk perception as well.

This reasoning may also help explain why we found an important interaction between alarms/predator encounters and the number of observers that were with a group. In our initial analysis, we found no evidence that models incorporating information on researcher presence had good predictive accuracy compared to ecological factors, and our subsequent analysis indicated that observer effects only appeared when three or more researchers were present. This is similar to results from Crofoot et al. (2010) who found that the presence of an observer did not affect ranging activity of wild white-faced capuchin monkeys (*Cebus*

capucinus). If multiple observers are more likely to inadvertently deter unhabituated predators, then the stimulus that triggers widespread alarm calling in these situations may tend to be less serious. For example, some of these alarms may have been triggered by predators walking on the periphery of the group that soon changed direction, rather than by actively hunting samangos. Alternatively, the presence of humans may cause the predators to leave an area, with the alarm calls given on sighting the departing predator. Previous studies with this group indicate that animals perceive less risk from terrestrial predators when near humans (Nowak et al., 2014), and studies on terrestrial predators like leopards (Van Cleave et al., 2018) indicate that these animals tend to avoid people. Unfortunately, we could not identify differences in responses between predator types, although some evidence indicates that this study population tends to respond more intensely to leopards and eagles than snakes (LaBarge et al., 2021). Additionally, with such a large study group, individuals are less likely to be near a single observer for long periods of the day. As observer numbers increase the human shield, the effect may also be perceived more consistently across all group members. Unfortunately, our study group inhabited a very dense environment and group spread could be >100 m, restricting our ability to record the cause of many alarm calls. Thus, we do not know for certain whether this result was due to a reduction in the riskiness of encounters or due to a reduction in risk perception (or both).

It may be that having only one researcher present with a study group could minimize overall effects on risk perception in samango monkeys and should be a recommendation wherever possible. Yet, while eagles may be less affected by a single observer, this likely does not hold for terrestrial predators who could very likely be displaced by a single hiker as most unhabituated animals, including apex carnivores, tend to perceive humans to be a risk (Suraci et al., 2019). Our study group's home range also overlapped substantially with the core area of our field site. If these monkeys perceive themselves to be safer around people, then we cannot rule out that they may stay closer to camps even when unobserved, reducing their predation risk on such off-days. Future studies would benefit from VHF or GPS collar data on the locations of study animals when unobserved. Such data could be linked with collar data from local predators to determine the type and length of encounters more precisely to have a better understanding of minimum predator exposure rates (Isbell et al., 2018).

We initially predicted that the presence of intergroup encounters during the day would also predict higher FCM levels. Encounters between samango groups tend to last between 20 and 40 min (one-two group scan periods for this study) and often involve threatening vocalizations, gestures, and chasing (LaBarge et al., 2020). In rare instances, encounters have led to serious injuries and death (personal obs) though none occurred during the study period. While other studies have found associations between fecal or urinary cortisol and intergroup competition (Cheng et al., 2021; Gabriel et al., 2018), we did not find a similar relationship here. This is potentially because other groups represent less serious threats to individual survival at our field site than other potential stressors, and any concomitant rise in FCMs associated with them may be too weak or ephemeral to detect with our methods. Additionally, none of these encounters led to injuries to be included within our analysis, but it is likely that these encounters would cause stress to both harmed individuals and associates (Wolf et al., 2018). Although we were typically unable to tell whether a group won or lost following these interactions as both groups would often move away, the focal samango group was much larger than most surrounding groups, and it is possible that individuals in the smaller group may have more intense or longer-lasting stress responses to these encounters. While predator encounters also tend to be brief, these events are often repeated throughout the day as unsuccessful eagles will often attack again later (see Fig. 6). It is therefore also likely that these short-lived events may not occur frequently enough to be apparent in fecal metabolite levels found 24 h afterwards. It is also possible that researchers may still affect the

frequency or intensity of these events by blocking or scaring away unhabituated groups; other methods such as monitoring multiple groups fitted with GPS or radio collars and associated physiological sensors, may be a more effective way of addressing this question.

6. Conclusions

Our study provides evidence that FCM concentrations of Soutpansberg samango monkeys track certain changes in their environment, but that increasing human presence may dampen the effects of interactions with predators. To our knowledge, this is the first evidence that a human shield may affect prey animals physiologically. Future studies should expand beyond a single group and incorporate remote sensing methods to determine predation pressure differences more precisely. While it was not possible here to link relative changes in FCMs to individual health or reproductive activity, future studies should build on this research to assess over longer periods of time how environmentally mediated variation in hormones affects animals of varying age-sex classes and whether within-individual trends correlate with reproductive success. If water scarcity tracks with FCMs, it is possible that climate change and further habitat fragmentation (which may disrupt local water tables) in the Soutpansberg will exacerbate existing physiological challenges for this population.

While a lack of overt increase in FCMs associated with human observation should be reassuring, this observation may not hold for other species (e.g., Shutt et al., 2014) or groups that have not been studied continuously for years. FCMs themselves may also be a weaker indicator of tolerance to humans than some behavioral measures (e.g., Allan et al., 2020). Indications that our presence as researchers may be affecting samangos' perception and/or actual risk of predation highlight a critical issue that needs to be addressed in future studies. We recommend incorporating elements that minimize direct observation whenever possible, using the growing variety of technologies and approaches to avoid interference with community interactions (Handcock et al., 2009; Pettorelli et al., 2014; Suraci et al., 2017).

Data availability

link to data is 10.6084/m9.figshare.20282025

Acknowledgements

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