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RESEARCH ARTICLE

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# Group-level competition influences urinary steroid hormones among wild red–tailed monkeys, indicating energetic costs

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Various theories emphasize that intergroup competition should affect intragroup cooperation and social relationships, especially if the cost of *inter*group competition outweighs that of *intra*group competition. This cost of intergroup competition may be quantified by changes in physiological status, such as in the steroid hormones cortisol (C) and testosterone (T), which rise or are depressed during periods of energetic stress, respectively. Here we tested for changes in urinary C and T after intergroup encounters (IGEs) among wild red-tailed monkeys (*Cercopithecus ascanius*), a species that experiences frequent intergroup feeding competition, at the Ngogo station in Kibale National Park, Uganda. We assayed 108 urine samples, of which 36 were collected after IGEs, from 23 individuals in four social groups. Bayesian multilevel models controlling for various confounds revealed that IGEs increased C and decreased T relative to baseline, consistent with an energetic cost to IGEs. The C change was more apparent in samples collected early after IGEs, suggesting an anticipatory increase, whereas the T change was stronger in later samples, suggesting sustained energetic trade-offs. Hormone responses were not affected by the IGE outcome. This cost to intergroup competition, together with little evidence for intragroup competition in redtails and other guenons, establishes an interesting test case for theories emphasizing the effect of intergroup competition on intragroup cooperation.

**KEYWORDS**
behavioral endocrinology, between-group competition, cooperation, guenons, parochial altruism

## 1 | INTRODUCTION

All animals must compete over limited resources, and in social animals competition can take place both within and between social groups. The relative strengths of such intra- and intergroup competition are of considerable theoretical interest, and are at the heart of debates about the evolution of cooperation and levels of selection (McElreath & Boyd, 2007; Okasha, 2006; Wilson & Wilson, 2007). For instance, human cooperation is sometimes thought to have evolved in response to strong *inter*group competition, aided by decreased *intra*group competition because of reproductive leveling (Bowles, 2006; Choi & Bowles, 2007; Darwin, 1871; Sober & Wilson, 1998). A similar argument has been made for lions (Mosser & Packer, 2009), and ants (Nowak, Tarnita, & Wilson, 2010). Likewise among female primates, the extent and nature of intra- and intergroup competition, determined in large part by the distribution of food resources, is theorized to shape social organization and social relationships (Isbell, 1991; Isbell & Young, 2002; Sterck, Watts, & van Schaik, 1997; van Schaik, 1989; Wrangham, 1980). Monopolizable food sources may result in nepotistic dominance hierarchies and reproductive skew within groups, but if contested between groups they are also thought to increase intragroup cooperation and reduce the strength of hierarchies (Sterck et al., 1997). In support of this model, a recent comparative analysis found that intergroup contest competition was associated with intragroup bonding, as measured by grooming networks

  

(Majolo, de Bortoli Vizioli, & Lehmann, 2016). Thus, strong intergroup competition is thought to affect intragroup relationships.

As the consequences of a given behavior on relative lifetime fitness are notoriously difficult to measure, behavioral ecologists often use more immediate proxies such as time or energy (Davies, Krebs, & West, 2012; Nettle, Gibson, Lawson, & Sear, 2013; Winterhalder & Smith, 2000). Thus, a useful approach to quantifying the cost of competition, whether within groups or between, is to measure its associated physiological responses (Sobolewski, 2012; Sobolewski, Brown, & Mitani, 2012; Wittig, Crockford, Weltring, Deschner, & Zuberbühler, 2015; Wingfield, Hegner, Dufty, & Ball, 1990). In particular, glucocorticoids (C) and testosterone (T) both track energetic costs. C is secreted in response to physical or psychosocial stressors, and is responsible for increasing blood sugar levels, heart rate, and metabolic rate, at the expense of non-essential metabolic processes (Adkins-Regan, 2005; Anestis, 2010; McEwen & Wingfield, 2003; Sapolsky, 2000). Several studies have found C levels to be elevated in anticipation of (Hohmann, Mundry, & Deschner, 2009; Sobolewski, 2012; Wobber et al., 2010), or in response to competitive interactions (Sobolewski, 2012; Wittig et al., 2015) in nonhuman primates, as well as other species such as birds (Landys, Goymann, Schwabl, Trapschuh, & Slagsvold, 2010; van Duyse, Pinxten, Darras, Arckens, & Eens, 2004). Similarly, T shifts energy towards competitive aggression and associated tissues like muscles, often in male reproductive contexts, and away from parenting effort, and immune function (Crespi, 2016; Ketterson & Nolan, 1999; Muller, 2017; Trumble et al., 2016; Trumble, Jaeggi, & Gurven, 2015; van Anders, Goldey, & Kuo, 2011). As such, primate studies have documented increased T levels during male mating competition and territorial aggression (Sobolewski, Brown, & Mitani, 2013; Sobolewski et al., 2012; Surbeck, Deschner, Schubert, Weltring, & Hohmann, 2012). T also associates with competition in females, at least in humans (Jiménez, Aguilar, & Alvero-Cruz, 2012). Conversely, because of its costs, T is suppressed during periods of competing energetic demands, such as parental care (Gettler, McDade, Feranil, & Kuzawa, 2011; Wingfield et al., 1990), sickness (Simmons & Roney, 2009), food shortages (Trumble, Brindle, Kupsik, & O'Connor, 2010), or prolonged, intensive exercise (Longman et al., 2018; Nindl et al., 2007). Both C and T can be assayed from non-invasively collected urine samples in wild primates (Anestis, 2010; Behringer & Deschner, 2017; Higham, 2016; Whitten, Brockman, & Stavisky, 1998; Ziegler & Crockford, 2017). Thus, C and T can be useful indicators of energetic stress, and thereby track the costs of competition.

Here we report responses in C and T to intergroup competition among wild red-tailed monkeys (*Cercopithecus ascanius*; hereafter "redtails") at the Ngogo research station in Kibale National Park, Uganda. Redtails at Ngogo live in one-male groups and in some seasons interact with neighboring groups up to eight times per week (Brown, 2011). Intergroup encounters (IGEs) occur when two groups happen to meet in the area where their home ranges overlap; ~40% of encounters become overtly aggressive (with chasing and sometimes grappling, hitting, and biting) when females and/or males defend high-value feeding sites (Brown, 2011, 2013). By contrast, intragroup competition in redtails at Ngogo appears weak, with very low rates of agonism, no consistent differences in energy balance among females and no intragroup mating competition for males (M. Brown, unpub. data). Similarly, the closely related blue monkeys (*Cercopithecus mitis*) do not show any rank effects on the probability of conception (Roberts & Cords, 2013) or survival (Thompson & Cords, 2018), nor does intragroup competition affect glucocorticoid levels (Foerster, Cords, & Monfort, 2011). However, more subtle rank-related benefits may include better access to fruit and correspondingly lower glucocorticoid levels, especially when nursing (Foerster et al., 2011). Thus, the cost of competition between redtail groups may outweigh that of competition within groups, making them an interesting test case for theories relating intergroup competition to intragroup relationships (Bowles, 2006; Sterck et al., 1997). Hence we measured the cost of intergroup competition in redtails by assaying urinary C and T levels at baseline and after IGEs.

## 2 | METHODS

### 2.1 | Behavioral observations and sample collection

M.B. and a team of field assistants observed six groups of redtails at the Ngogo research station in Kibale National Park, Uganda, from January 2012 through June 2015 in a study of individual motivations for aggressive participation during IGEs. The behavioral data and urine samples analyzed here represent a portion of the broader study for which urine samples were available for additional assays, and come from four groups, each followed for 1–2 multi-month periods lasting 5–7 months each between January 2012 and February 2014 (total = 40 group-months).

The Ngogo site consists primarily of old-growth rainforest with interspersed grasslands, regenerating forest, and gallery forest (Struhsaker, 1997). Redtails are small (males: 3.7 kg; females: 2.8 kg; Cords & Sarmiento, 2013), diurnal, arboreal monkeys that consume ripe and unripe fruit as well as insects (Brown, 2013). At this site, they live in social groups consisting of one adult male, 5–25 adult females, 1–9 subadults, and varying numbers of juveniles and infants. Females are philopatric whereas males disperse as subadults. Groups occupy home ranges of (mean ± SD) 0.42 ± 0.06 $km^2$ ($N$ = 6 groups), much of which is shared with neighboring groups; for example, the central group had exclusive access to only ~9% of its home range. Group density was relatively high at 5.6 groups/$km^2$, which facilitates frequent IGEs.

All individuals in the study groups were habituated to the presence of human observers and were identifiable by the shape and size of the white nose spot; the characteristics of nipples on females; and scars, stiff fingers, and permanent bends in the tail. M.B. maintained a database of labeled photos and typed descriptions of each animal, which all observers accessed in the forest using Apple iPod Touch units. Each month, M.B. and assistants followed 2–3 redtail groups simultaneously for 11 ± 3 days; after 5–7 months of following a set of groups, they switched to another set. On each follow day, a team of 2–3 people sought out their study group shortly after dawn and followed it until dusk. All agonistic

interactions between group mates (spontaneous submission, approach-retreat, and contact aggression; *sensu* Cords, 2000) were recorded during individual focal follows (conducted as part of a related study on redtail personality) and ad libitum during group follows. We were unable to calculate ranks using standard methods because of the low rate of agonistic interactions (e.g., from focal follows on adult females: mean ± SD = 0.07 ± 0.10 interactions per hour, $N = 378$ 10-min follows) and the difficulty in identifying the fleeing or non-focal animal, thus we were unable to include rank as a covariate. On each follow day, the field team recorded each female's reproductive state as a combination of nursing state and carrying state. "Nursing" refers to frequent nipple contact (yes/no—where "yes" indicates multiple bouts per day), "carrying" refers to transporting the offspring between trees while traveling (yes/no). Here we compare females with young, nursing infants (nursing = yes, carrying = yes) with everyone else because their energetic requirements, and hence C levels, are expected to be highest. We were unable to infer reliably whether females were pregnant at the time of observation.

An IGE began when the observers estimated the nearest edges of two groups to be separated by <50 m regardless of whether there was aggression, and ended when the two groups regained a distance of >50 m. This threshold was based on the typical distance at which individuals appeared to be able to see the opposing group and began to react to its presence (staring, alarm-calling, and sometimes lunging toward, chasing or physically attacking members of the other group). We noted the timing and identity of individuals who chased or physically attacked the other group. An individual who participated aggressively in at least one IGE during a 5–7 month observation period was considered a "cooperator" during that period; the 42% of individuals who were never observed to participate aggressively during the period were considered "non-cooperators." We recorded the locations of the two groups for 90 min after the encounter to determine the outcome: a group that remained in the encounter location after the departure of other group was considered a winner, the departing group a loser; if both groups stayed nearby (but >50 m apart) or both groups departed, the outcome was considered a draw.

Whenever possible, M.B. and field assistants collected urine samples immediately after a monkey urinated, usually by pipetting the droplets from vegetation. Samples were put on ice and brought to the research camp at dusk where they were stored in a −12 °F solar-powered freezer until they could be transported to the Hominoid Reproductive Ecology Lab at the University of New Mexico (6–12 months). After assaying for creatinine and urinary C-peptide of insulin (which was the original focus of the broader study), any leftover samples were shipped to the Human Biodemography Lab at UCSB. As such, these samples had undergone 1–4 freeze/thaw cycles before being assayed for this study. While steroid hormones are generally stable across multiple freeze/thaw cycles (Comstock et al., 2001; Jiménez, De La Torre, Segura, & Ventura, 2006), we also controlled for the number of cycles in all our analyses. Furthermore, we provide all raw data in a Supplementary File such that our hormone concentrations can be compared to other studies.

We included 108 samples total (mean 4.7 per individual, range 1–12), of which 36 were collected during an IGE or up to 317 min after an IGE ended (mean 1.6 samples per individual, range 1–5); we refer to these 36 as post-IGE samples and the rest as baseline samples. The samples came from 23 of the 107 adult and sub-adult individuals in the study groups, of which all except one individual provided both baseline and post-IGE samples (see Supplementary Table). Unlike in similar studies on chimpanzees (Crockford et al., 2013; Wittig et al., 2015), it was not possible to sample all urination events occurring after a behavior of interest, given that the focus was on the whole social group, and given the difficulty of identifying and catching urine from small monkeys high in the canopy.

## 2.2 | Laboratory analyses

A.V.J. and B.C.T. ran both hormone assays simultaneously at the Human Biodemography Lab at UCSB, with each sample assayed in duplicate. We measured C with in-house enzyme immunoassay R4866 (Trumble et al., 2010), diluting specimens 1:100 in 0.1% bovine serum albumin (BSA) blocking buffer. Within and between plate CVs were 4.6% and 6.9% for the high control (1184.8 pg/ml), and 6.5% and 12.8% for the low control (239.2 pg/ml). We measured T with in-house enzyme immunoassay R156/7 (Trumble et al., 2010). We diluted specimens 1:100 in 0.1% BSA blocking buffer. Within and between plate CVs were 5.3% and 5.3% for the high control (1088.4 pg/ml), and 6.0% and 6.8% for the low control (202.6 pg/ml). In-house antibodies for C and T were supplied by C. Munroe (University of California, Davis).

Hormone values were normalized using specific gravity (Miller et al., 2004) to avoid the confounding effect of muscle mass or activity on creatinine levels (Behringer, Deschner, Deimel, Stevens, & Hohmann, 2014); levels normalized with specific gravity were highly correlated with levels normalized with creatinine (T: Pearson's $r = 0.75$, $p < 2.2^{-16}$; C: $r = 0.93$, $p < 2.2^{-16}$). For both assays, all of an individuals' urine samples were run on the same assay plate.

## 2.3 | Defining peak excretion windows

Not all urine samples collected after an IGE capture the peak hormone reactivity associated with the IGE. Field researchers studying chimpanzees proposed that urine samples collected within 2–4 hr after an event should capture peak steroid excretion (Sobolewski et al., 2012; Wittig et al., 2016, 2015), mostly based on one C infusion study (Bahr, Palme, Möhle, Hodges, & Heistermann, 2000). The one macaque in the same study showed high levels almost immediately following infusion and lasting up to at least 6 hr, with a slight peak at 5.5 hr (Bahr et al., 2000). Given this earlier and less peaked steroid excretion as well as the often unclear boundaries of an IGE (primates might be aware of the presence of another group long before human observers are, and determining the end of an IGE can be similarly ambiguous) we slightly expanded these time windows relative to the ones used for chimpanzees. Thus, urine samples that were collected within 120 min after the *start* of an IGE and 300 min after the end of an IGE were classified as reflecting the peak steroid response (Figure 1); in

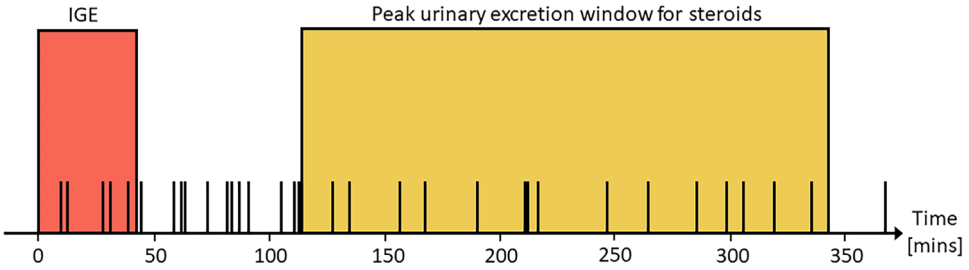


**FIGURE 1** Illustration of presumed peak urinary excretion windows for steroid hormones as adapted for redtailed monkeys (see section 2.3, 'Defining peak excretion windows'). Time starts at 0 min with the beginning of an intergroup encounter (IGE), here shown in red with the average duration of 44 minutes. The peak excretion window (yellow) begins at 120 min and ends 300 min after the end of the IGE. The peak excretion window is shown here in reference to the average IGE length, but was adjusted to each individual IGE. Vertical black lines indicate time points of sample collection. All lines shown are post-IGE samples, but only the ones in the yellow period are peak-excretion samples

other words, counting back from the time of urination, if an IGE was on-going between 2 and 5 hr prior, that sample was classified as capturing the peak levels. These presumed peak excretion windows contained 15 samples (out of 36 total post-IGE samples), which we refer to as *peak-excretion samples*. The remaining 21 post-IGE samples may reflect steroid levels before IGEs began (19 samples collected within 2 hr after the start of an IGE), as well as after the end of an IGE (two samples collected over 5 hr after the end of an IGE). This difference between peak-excretion samples and the remaining post-IGE samples can be seen in Figure 1, though note that the length of IGEs, and thus the width of the peak excretion window varies for each sample.

## 2.4 | Statistical analyses

For each hormone, a set of biologically relevant control variables was included. This included individual and group-level attributes, namely age, sex, cooperator (see section 2.1, *Behavioral observations*), whether a female was nursing an infant during the month in which the urine sample was collected, and group size. In addition, we controlled for time of day and the number of freeze/thaw cycles. The main test variable was whether the sample was post-IGE or baseline, with models based on all post-IGE samples (Model 1), or only on peak-excretion samples (Model 2). Peak-excretion samples were further divided by IGE outcome (win/draw/loss; Model 3) since outcome can affect steroid levels (Jiménez et al., 2012). Lastly, we allowed possible outcome effects on T to vary by sex using an interaction (Model 4). These models were also compared to a null model (Model 0) which did not differentiate between baseline and post-IGE samples. All hormone levels were log-transformed and centered on the mean of all baseline samples and all continuous variables were either centered or converted into *z*-scores. All models included random intercepts for individual and group ID as well as observation month to account for variance in hormone concentrations at these levels. We also considered random slopes to allow for individual- and group-level variation in the hormonal response to predictors, however random slope models were not favored by information criteria—indicating that individuals and groups responded in similar ways—and are not reported here; the main inferences would be the same.

A large number of behavioral or contextual variables—such as the intensity or outcome of the IGE, individual behavior during the IGE, or intragroup affiliation after the IGE—could potentially explain variation in the hormonal responses to IGEs. We conducted exploratory analyses to determine which contextual variables explained variation in within-individual hormone reactivity; however, because of the small sample size these analyses were not deemed reliable and are not reported here.

All analyses used Bayesian multilevel models implemented in the *MCMCglmm* package (Hadfield, 2010) in R 3.2.3. (R Development Core Team, 2015) with log hormone levels modeled as stemming from Gaussian distributions. We used the standard inverse gamma priors (Hadfield, 2016) with shape parameters of 0.001 for the residual variance and 0.1 for random intercepts. For the fixed effects we used weakly informative priors (normal distribution with mean = 0, standard deviation = 10), which put more prior probability on or close to 0 and thus help with model convergence and are slightly more conservative than flat priors (McElreath, 2016). Markov chains were run for 100,000 iterations with a burn-in of 20,000 and were thinned to 8,000 samples per model. The effective sample sizes for all parameters were routinely around 8,000, indicating low autocorrelation, with no parameter having <4,000 effective samples. Model convergence was further confirmed visually by inspecting trace plots as well as formally by calculating Gelman and Rubin's convergence diagnostic using the *coda* package (Plummer et al., 2015); the diagnostic equaled one in all cases, indicating no convergence issues.

Bayesian models produce a posterior probability distribution for each estimated parameter, and these distributions can be summarized in various ways (McElreath, 2016). Here we report the mean and 95% Highest Posterior Density Interval (HPDI) of the distribution for each parameter. We also report the proportion of samples that fall on the same side of 0 as the mean, which can be read as the posterior probability (PP) that a given predictor was indeed associated with the outcome. Lastly, we also plot the entire posterior probability distribution for the main parameter of interest, that is, the change in hormone levels from baseline to post-IGE. To compare the fit of different models, we report the Deviance Information Criterion (DIC, which makes fewer assumptions than the AIC, and is more appropriate for Bayesian multilevel models); a lower DIC indicates that the model

makes more generalizable predictions (McElreath, 2016). DIC weights were calculated with the MuMIn package (Barton, 2015) and can be read as the probability that a given model out of a set makes the most generalizable predictions. Model comparison thus quantifies the level of support for different scientific hypotheses, formalized as different statistical models (Burnham, Anderson, & Huyvaert, 2011), and provides an additional mode of inference.

### 2.5 | Ethics statement

Permissions to conduct this study were granted by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology and the Uganda Office of the President. Data collection protocols were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of New Mexico (11-100661-MCC), and deemed exempt by the IACUC at the University of California, Santa Barbara. M.B. conducted all research activities in compliance with Ugandan national laws and the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

## 3 | RESULTS

Post-IGE samples had substantially lower levels of T and higher levels of C compared to baseline (Table 1, Figures 2, and 3), and models including the baseline/post-IGE predictor received more DIC support than null models without that distinction (Model 1 vs. Model 0, Table 2). However, when we used only peak-excretion samples, C levels were no longer different from baseline (mean slope [b] = 0.13; 95% Highest Posterior Density Interval [HPDI] = −0.42, 0.66; Proportion of samples on same side of 0 as mean [Posterior Probability, PP] = 0.69), while the effect of IGEs on T levels more than doubled and its probability increased (b = −0.41; HPDI = −0.70, −0.14; PP = 1.00; Figure 3). The peak-excretion model also received more DIC support for T but not C (Model 2 vs. Model 1, Table 2).

The observed hormone changes were not caused by winner or loser effects, as models dividing peak-excretion samples by outcome received less DIC support (Model 3, Table 2), T levels decreased regardless of outcome (*wins*: $b = -0.32$; 95% HPDI = −0.80, 0.17; PP = 0.91; *draws*: – = −0.36; 95% HPDI = −0.76, 0.01; PP = 0.97; *losses*: $b = -0.75$; 95% HPDI = −1.41, −0.10; PP = 0.99), and C changes did not differ from baseline regardless of outcome (*wins*: $b = 0.53$; 95% HPDI = −0.42, 1.45; PP = 0.87; *draws*: $b = -0.09$; 95% HPDI = −0.61, 0.80; PP = 0.61; *losses*: $b = -0.53$; 95% HPDI = −1.80, 0.72; PP = 0.80). An interaction between outcome and sex for T was also not supported by the model comparison (Model 4, Table 2).

It is also noteworthy that groups vary much more in their hormone levels than individuals, with the group-level random intercept explaining five to ten times more variance than the individual-level one (Table 1).

## 4 | DISCUSSION

We reported data on hormonal responses to IGEs in redtail monkeys to measure the cost of intergroup competition. As expected, C and T

**TABLE 1** Results of Model 1 predicting urinary hormone levels

| | Cortisol | Testosterone |
|---|---|---|
| Intercept[a] | −0.07 (−1.11, 0.90), 0.55 | −0.13 (−1.02, 0.76), 0.62 |
| Sample = Post-IGE | 0.3 (−0.07, 0.65), 0.95 | −0.15 (−0.34, 0.05), 0.94 |
| Age = Subadult | −0.63 (−1.43, 0.23), 0.93 | −0.51 (−0.99, −0.03), 0.98 |
| Sex = Male | 0.25 (−0.47, 1.05), 0.75 | 0.25 (−0.20, 0.70), 0.87 |
| Cooperator = yes | −0.05 (−0.79, 0.66), 0.55 | 0.12 (−0.31, 0.54), 0.72 |
| Nursing = Yes | 1.41 (0.11, 2.64), 0.99 | −0.34 (−1.04, 0.36), 0.84 |
| Group Size[b] | 0.26 (-0.51, 1.15), 0.76 | 0.34 (−0.32, 1.19), 0.87 |
| Time of Day[b] | −0.17 (−0.35, 0.02), 0.96 | −0.03 (−0.13, 0.08), 0.71 |
| Number of Thaws[b] | 0.07 (−0.14, 0.30), 0.74 | −0.11 (−0.24, 0.01), 0.96 |
| Individual variance | 0.15 (0.02, 0.36) | 0.07 (0.02, 0.14) |
| Group variance | 0.79 (0.01, 2.49) | 0.76 (0.01, 2.64) |
| Month variance | 0.20 (0.02, 0.49) | 0.10 (0.02, 0.23) |
| Residual variance | 0.68 (0.48, 0.90) | 0.20 (0.14, 0.26) |

For each parameter, we report the mean of the posterior probability distribution and 95% Highest Posterior Density Interval (in parentheses), as well as the proportion of samples on the same side of 0 as the mean, that is, the posterior probability that a predictor was associated with the outcome. Figure 3 displays the full posterior distribution for the post-IGE parameter, either counting all post-IGE samples (as done here) or only peak-excretion samples (Model 2, see Table 2).

[a]Reference levels are age = adult, sex = female, sample = baseline; hormone levels are on the log scale and centered on the baseline mean.

[b]Group size and time of day were standardized such that 0 represents the sample mean (group size: 14.1 individuals, time of day: 1:30pm), and units are standard deviations (group size: 7.1, time of day: 91 min); number of thaws was centered on the sample mean (1.75 thaws prior to this study).

**TABLE 2** Model comparison based on Deviance Information Criteria (DIC)

| | Cortisol | | | Testosterone | | |
|---|---|---|---|---|---|---|
| **Baseline vs. post-IGE predictor:** | **DIC** | **ΔDIC[a]** | **Weight[b]** | **DIC** | **ΔDIC[a]** | **Weight[b]** |
| 0: Absent | 290.0 | 2.53 | 0.18 | 155.2 | 7.62 | 0.02 |
| 1: All post-IGE samples | **287.5** | **0** | **0.64** | 155.2 | 7.64 | 0.02 |
| 2: Peak-excretion samples | 291.0 | 3.51 | 0.11 | **147.5** | **0** | **0.67** |
| 3: Peak outcome = win/draw/loss | 292.1 | 4.59 | 0.07 | 149.9 | 2.33 | 0.21 |
| 4: 3 with outcome*Sex interaction | | | | 151.4 | 3.85 | 0.10 |

The candidate models vary only in the baseline vs. post-IGE predictor. Model 0 does not differentiate between baseline and post-IGE samples, model 1 contrasts all post-IGE samples with baseline, model 2 only peak-excretion samples (see Figure 1), model 3 further differentiates peak-excretion samples based on IGE outcome (win/draw/loss), and model 4 (only for T) adds an interaction between outcome and sex to model 3. The best supported model for each hormone is bolded.

[a]DIC, Difference in DIC relative to the best model.

[b]Weight = the probability that this model makes the best predictions out of the candidate model set.

were associated with IGEs in this study (Figures 2, and 3). However, only C was elevated while T was decreased after IGEs. Furthermore, the increase in C was apparent only in samples collected during or soon after an IGE, but not in samples collected later, during the presumed peak excretion window, while the opposite was true for T. This could indicate anticipatory increases in C, similar to anticipatory increases in C before intragroup (Hohmann et al., 2009; Wobber et al., 2010) and intergroup competition (Sobolewski, 2012) reported in other primates. Our data unfortunately do not allow us to test whether redtails were simply more energetically stressed on IGE days prior to encountering the neighboring group, or whether they somehow were aware of the imminent IGEs (which may occur anywhere in the home range). Alternatively, C may simply be excreted sooner in redtails than in macaques, on which the peak excretion window was based (Bahr et al., 2000), and the observed C increase reflects a response to IGEs rather than an anticipation. C increases in association with intergroup competition have been observed in various species ranging from birds (Landys et al., 2010; van Duyse et al., 2004) to chimpanzees (Sobolewski, 2012), though several studies have found no or negative associations between C and territoriality (DeNardo & Sinervo, 1994; Meddle et al., 2002; Selva et al., 2011). Thus, whether anticipatory or not, C increases indicate an energetic cost to IGEs.

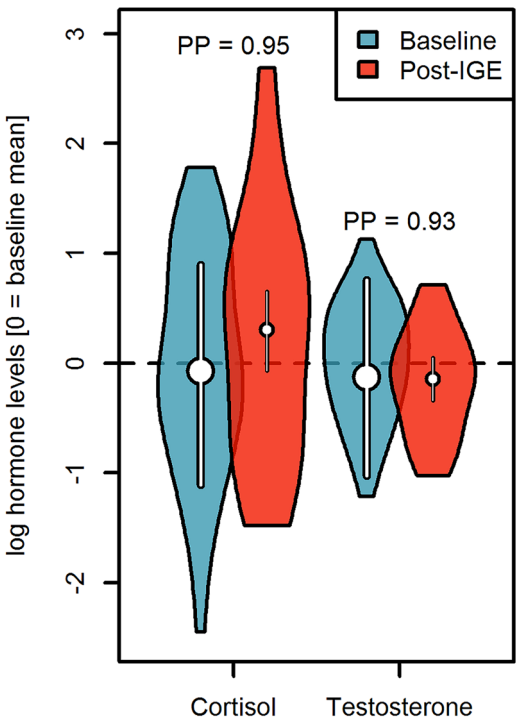


**FIGURE 2** Urinary hormone levels at baseline (blue) and post inter-group encounters (IGE, red). Violin plots show the density distribution of the observed data, points and lines show predicted means with 95% Highest Posterior Density Intervals (see Table 1) and are proportional in thickness to the number of samples in each category. The numbers above each pair indicate the posterior probability (PP) that post-IGE levels were different from baseline when using all post-IGE samples (see Table 1, Figure 3). Horizontal dashed line behind boxplots indicates mean baseline hormone levels

T responses did not exhibit a winner or loser effect (as seen e.g., in some human competition; Jiménez et al., 2012), as any outcome of IGEs resulted in lower T levels. Thus T did not seem to be mediating aggressive behavior during IGEs. Though T may be reduced during coalitional aggression in humans (Flinn, Ponzi, & Muehlenbein, 2012), and is not involved in territorial defense in some birds (Landys et al., 2010; Soma, 2006; van Duyse et al., 2004), this contrasts with increases in T before and after chimpanzee intergroup competition (Sobolewski et al., 2012). Rather than mediating or being mediated by territorial aggression, it is more likely that the decrease in T represents an energetic tradeoff, similar to declines in T in response to prolonged exercise, illness, or reduced energy intake (Longman et al., 2018; Nindl et al., 2007; Simmons & Roney, 2009; Trumble et al., 2010). More speculatively, depressed T could also aid with intragroup bonding following IGEs, as has been proposed for low T levels found during chimpanzee meat sharing (Sobolewski et al., 2012). Several species

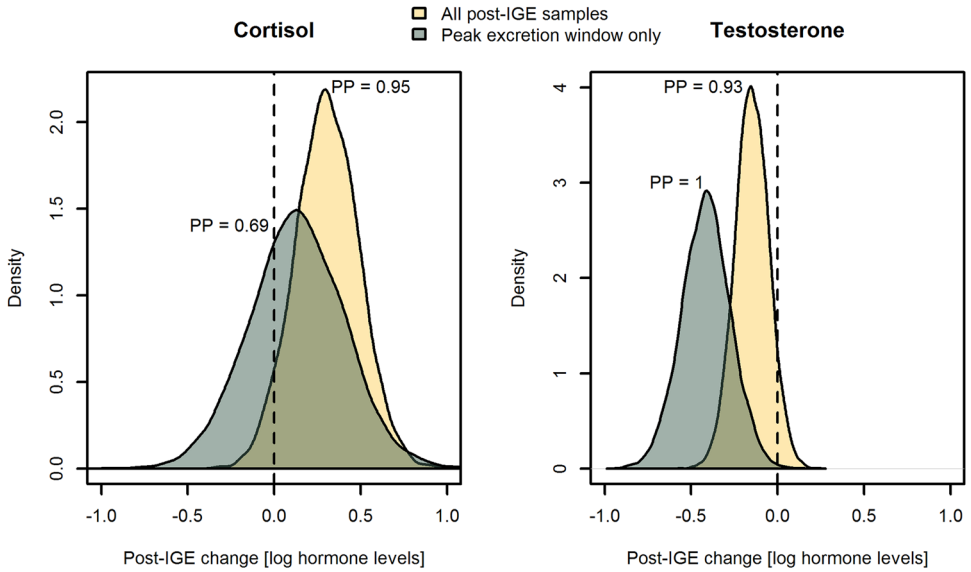


**FIGURE 3** Posterior probability distribution for the difference between baseline and post-IGE hormone levels, with post-IGE including all post-IGE samples (yellow), or only peak-excretion samples (green, see Figure 1). PP is the proportion of the posterior distribution that falls on the same side of 0 (indicated by dashed vertical lines) as the mean, that is, the posterior probability that there was a difference in hormone levels between baseline and post-IGE samples

exhibit increased intragroup affiliation following IGEs (Arseneau-Robar et al., 2016; Radford, 2008; Radford, Majolo, & Aureli, 2016) including other guenons (Cords, 2000; Chism & Rogers, 2003; Rowell, Wilson, & Cords, 1991) and redtails often engage in grooming frenzies (after 19/25 IGEs reported here). It is unclear whether depressed T would be required for intragroup affiliation though; while many studies indicate that high T can impede cooperative behavior in humans (Bos, Terburg, & van Honk, 2010; Crespi, 2016; Eisenegger, Haushofer, & Fehr, 2011; Zak et al., 2009), others find that T can also support cooperative behavior, especially with group members (Reimers & Diekhof, 2015), and/or in conjunction with other hormones like oxytocin (Jaeggi, Trumble, Kaplan, & Gurven, 2015). In sum, IGEs in redtails were associated with decreases in T, indicating energetic trade-offs.

Several control variables provided biological validations of our assays, as subadults had substantially lower baseline T levels than adults, and C decreased with time of day and was higher in females with young, nursing infants (see also Foerster et al., 2011), though our measure of nursing (or indeed, reproductive status) was crude. Further, while our analyses were based on a relatively small number of post-IGE samples ($n = 36$), Bayesian models are very well suited to deal with small sample sizes (McElreath, 2016), and we provide multiple modes of inference (model comparison, various ways of examining the posterior probability distribution for a baseline–post-IGE difference) that all converge on the same major findings.

In conclusion, intergroup competition among red-tailed monkeys was associated with changes in C and T, highlighting energetic costs to intergroup competition, consistent with behavioral observations of feeding competition at the group level (Brown, 2013). Together with little evidence for intragroup competition or benefits to high rank in redtails and closely related species (Roberts & Cords, 2013; Thompson & Cords, 2018), this establishes an interesting test case for the evolution of intragroup cooperation through intergroup competition (Bowles, 2006; Mosser & Packer, 2009; Sterck et al., 1997). In this context, it is intriguing that variance in C and T was much higher between groups than between individuals (Table 1), and the same is true for energetic status, as measured by urinary c-peptide (M. Brown and M. Emery Thompson, in prep.). Future studies are needed to quantify variation in other fitness outcomes at the group- versus individual levels, test for associations between success in group-level competition and reproductive success, describe the extent of behavioral coordination during IGEs in different groups, and measure responses in other hormones associated with group-level competition and within-group cooperation such as oxytocin (De Dreu, 2012; Samuni et al., 2017) or vasopressin (Donaldson & Young, 2008; Rilling et al., 2012).

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## SUPPORTING INFORMATION

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