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Male Endocrine Response to Seasonally Varying Environmental and Social Factors in a Neotropical Primate, *Cebus capucinus*

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ABSTRACT

Objective: Circannual variation in reproduction is pervasive in birds and mammals. In primates, breeding seasonality is variable, with seasonal birth peaks occurring even in year-round breeders. Environmental seasonality is reportedly an important contributor to the observed variation in reproductive seasonality. Given that food availability is the primary factor constraining female reproduction, predictions concerning responsiveness to environmental seasonality focus on females, with studies of males focusing primarily on social factors. We examined the influence of both environmental and social factors on male fecal testosterone (fT) and glucocorticoids (fGC) in moderately seasonally breeding white-faced capuchin monkeys (*Cebus capucinus*) in Costa Rica.

Methods: Over 17 months, we collected 993 fecal samples from 14 males in three groups. We used LMM to simultaneously examine the relative effects of photoperiod, fruit biomass, rainfall, temperature, female reproductive status (i.e., number of periovulatory periods, POPs), and male age and dominance rank on monthly fT and fGC levels.

Results: Male age and rank had large effects on fT and fGC. Additionally, some hormone variation was explained by environmental factors: photoperiod in the previous month (i.e., lagged photoperiod) was the best environmental predictor of monthly fT levels, whereas fGC levels were best explained by lagged photoperiod, fruit biomass, and rainfall. POPs predicted monthly fT and fGC, but this effect was reduced when all variables were considered simultaneously, possibly because lagged photoperiod and POP were highly correlated.

Conclusions: Males may use photoperiod as a cue predicting circannual trends in the temporal distribution of fertile females, while also fine-tuning short-term hormone increases to the *actual* presence of ovulatory females, which may occur at any time during the year. Am J Phys Anthropol 000:000–000, 2016.

Circannual variation in the timing of reproductive events, such as ovulation and births, is pervasive in birds and mammals (Helm et al., 2013). Primate reproductive seasonality is highly variable, ranging from strictly seasonal to year-round breeders. Yet, even among species that mate and conceive throughout the

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year, seasonal birth peaks are often observed (non-human primates: Brockman and van Schaik, 2005; Janson and Verdolin, 2005; humans: Bronson, 1995; Wehr, 2001; Ellison et al., 2005). Given that initiating reproductive events at sub-optimal times can have drastic fitness consequences, environmental seasonal variation is reportedly an important contributor to reproductive seasonality in birds (Drent and Daan, 1980; Dawson, 2008) and mammals (Bronson, 2009), including human and non-human primates (Bronson, 1995; Wehr, 2001; Ellison et al., 2005; Janson and Verdolin, 2005). Seasonally varying environmental factors such as photoperiod (i.e., day length), food availability, rainfall, and temperature may serve as time-keeping cues and/or may impose constraints on the timing of reproduction.

Hormones appear to mediate physiological thresholds in reproductive decision-making (Stearns, 1989). Among males, androgens—a group of hormones including testosterone (T) and dihydrotestosterone—support basic reproductive functions, such as spermatogenesis, and the development of secondary sexual characteristics (Neill et al., 2006; Dixson, 2014). Additionally, androgen elevations beyond those necessary for basic reproductive functions appear to be associated with male mating effort (e.g., challenges for access to mates: Wingfield et al., 1990), but may also vary in response to stimuli from receptive females and seasonally varying environmental factors (Goymann et al., 2007). Glucocorticoids (GC)—including cortisol and corticosterone—are associated with the stress response; they direct energy toward mechanisms that regulate homeostasis while shifting energy away from areas not immediately relevant to survival (e.g., growth, reproduction). This response is adaptive in the short-term but long-term elevations may have an inhibitory effect on reproduction (Sapolsky et al., 2000).

Male reproductive physiology is expected to be driven in part by competition for access to females, which can be the most energetically demanding reproductive activity for males (Trivers, 1972). As such, variation in male hormones associated with reproductive effort (e.g., androgens) is expected to be driven in part by the temporal distribution of fertile females, which is influenced by whether females adopt an income-, capital-, or mixed breeding strategy (Brockman and van Schaik, 2005). Fur seals (e.g., *Arctocephalus gazella*) are often cited as a classic example of income breeders who make reproductive decisions based on their rate of energy intake (Stearns, 1989), because foraging trips by mothers during the lactation period support this stage of reproduction, whereas "true" seals (e.g., Grey seal, *Halichoerus grypus*) are capital breeders that rely on energy stores (Stearns, 1989) since females make no such foraging trips and thus rely solely on stored energy for lactation (Boyd, 2000). While few female primates employ a strict income or capital breeding strategy, the framework is still useful for understanding how the predictability of seasonal food peaks (i.e., timing of energy intake) influences the timing of female reproduction (Emery Thompson, 2013), which in turn influences male physiology. Brockman and van Schaik (2005) recognized that some primates resemble income breeders since females depend heavily on external cues such as photoperiod to initiate and time reproductive events with peaks in food availability (e.g., some strepsirrhines). In these species, male hormones should vary seasonally in response to changes in female reproductive state and/or to environmental cues that reliably predict female reproductive status (Brockman and van Schaik, 2005). Other female primates are better characterized as capital breeders who rely more on internal cues such as body condition for reproductive decision making (e.g., apes). In capital breeding species, the unpredictable and non-seasonal distribution of fertile females means that male hormones should entrain to the presence of fertile females at various times throughout the year and should thus follow a less seasonal pattern than predicted for males of income breeding species (Brockman and van Schaik, 2005). In reality, most female primates employ a mixed or "relaxed income" breeding strategy (*sensu* Brockman and van Schaik, 2005; or "Income-II": Janson and Verdolin, 2005), in which reproductive events are cued by both external environmental factors that predict upcoming food availability and by internal cues regarding existing energy stores (Brockman and van Schaik, 2005), such that conceptions can occur year-round but still have seasonal peaks. Therefore, in relaxed-income breeding species, males may experience a seasonal increase in hormones, in addition to short-term peaks in response to the presence of fertile females even if female ovulation occurs outside the conception season.

Given that food quantity and quality are intricately related to body condition and are the primary factors constraining female reproductive success (Trivers, 1972; Wrangham, 1980), predictions concerning responsiveness to environmental seasonality tend to focus on females (Brockman and van Schaik, 2005; Janson and Verdolin, 2005; Emery Thompson, 2013; but see Ball and Ketterson, 2008). In contrast, predictions about variation in male reproduction tend to focus on social factors influencing access to fertile females, such as male dominance rank, challenges to dominance, and territoriality. Among primates, there is ample research indicating that androgen elevations are associated with male dominance and/or the presence of ovulatory females. Androgen increases can occur at a seasonal scale such as during mating seasons (Sapolsky, 1993; Lynch et al., 2002; Ostner et al. 2002, 2008a, 2011; Gould and Ziegler, 2007; Setchell et al., 2008; Higham et al., 2013; Girard-Buttoz et al., 2015), as well as on a finer scale in response to challenges from males, the presence of fertile females, or sexual behavior (Perret and Schilling, 1995; Strier et al., 1999; Muller and Wrangham, 2004a; Miller and Maner, 2010; Arlet et al., 2011; Schoof et al., 2014; Girard-Buttoz et al., 2015). Male GCs also frequently increase in these same circumstances (Sapolsky, 1993; Strier et al., 1999, 2003; Lynch et al., 2002; Muller and Wrangham, 2004b; Ostner et al., 2008a,b; Arlet et al., 2009; Setchell et al., 2010; Surbeck et al., 2012). While these studies suggest that male hormone fluctuations are responsive to changes in female fertility, less is known about how male hormones vary seasonally in relation to changing environmental factors such as photoperiod, food abundance, rainfall, and temperature in wild primates.

In the present study, we examine the endocrine responses of male white-faced capuchins (*Cebus capucinus*) to female reproductive status, photoperiod, and food abundance in relation to the income-capital breeding model, and also examine a possible effect of other seasonally varying environmental factors (i.e., rainfall, maximum temperature). The white-faced capuchins of the Santa Rosa Sector in the Área de Conservación Guanacaste, Costa Rica, are a useful model for examining seasonal variation in male hormones. Santa Rosa is a tropical dry forest located just outside the Equatorial belt (±10° of the Equator), and the park experiences a high degree of environmental seasonality. The field site receives an average of 1,800 mm of rainfall during the cooler wet season months of May through November, and almost no rainfall during the very hot dry season months of December through April, when daily maximum temperatures can reach greater than 42°C (Melin et al., 2014a). Fruit availability is also variable, with increased fruit abundance in the month prior to the onset of the wet season (Melin et al., 2014a). Although births and conceptions can occur throughout the year, white-faced capuchin females (*Cebus capucinus*) are characterized as relaxed income breeders that exhibit moderate breeding seasonality, with 44% of births occuring during a 3-month period that coincides with peak fruit abundance in May–July (Carnegie et al., 2011a). The majority of conceptions occur between November and February, a period that generally overlaps with the dry season (Carnegie et al., 2011a).

Given the relaxed-income breeding strategy and moderate breeding seasonality of capuchin females, males may exhibit intermediate responsiveness to both environmental and social cues. We have previously shown that social factors influence male fecal testosterone (fT) and glucocorticoid (fGC) metabolite levels: males have fine-scale (i.e., weekly) elevations of fT and fGC in the presence of periovulatory females, and alpha males have higher fT and fGC than subordinate males (Schoof et al., 2014). Furthermore, the strong positive correlation between fT and fGC suggests that increased male reproductive effort is associated with increased stress (Schoof et al., 2014). However, the influence of seasonally varying factors on capuchin male fT and fGC has not been examined simultaneously with social variables.

Female reproductive status

Several studies of wild primates, including those on white-faced capuchins, have shown that males have increased androgen and glucocorticoid levels in the presence of fertile females (see above). Therefore, we hypothesized that males will also be sensitive to *seasonal* patterns in female fertility (Brockman and van Schaik, 2005), and thus predict a positive relationship between both male fT and fGC, and the number of female periovulatory periods in a given month.

Photoperiod

In birds, photoperiod or day length is thought to be the primary proximate cue to the seasonal regulation of reproductive, molt, and/or migratory periods, while physiological (i.e., endocrine) sensitivity to short-term variability in food availability, rainfall, or temperature serves to fine-tune the timing of such events (reviewed in Dawson, 2008). In areas where fruit/flower peaks are seasonal and occur predictably (i.e., little interannual variation), photoperiod should be a good predictor of upcoming resource availability (Helm et al., 2013). Photoperiod may be a better predictive cue in temperate zones (latitudes >23.5 from the Equator) where there is more seasonal variation in the number of daylight hours, compared with lower latitudes where seasonal variation in photoperiod is limited. Nonetheless, there is evidence that some male hamsters and antbirds are sensitive to even small alterations in photoperiod, mimicking those occurring at latitudes ≤10° (Heideman and Bronson, 1993; Hau, 2001). Photoperiod may be especially important in long-lived species at latitudes where changes in daylight serve as reliable indicators of seasonal changes, thus allowing individuals to prepare for upcoming conditions (Bronson, 2009).

Males are expected to be sensitive to female reproductive status, but may also respond to cues that influence the timing of female reproduction (Ball and Ketterson, 2008). Therefore, males may be sensitive to photoperiod if it reliably cues changes in female reproductive status, and/or cues to seasonally variable factors that influence female fertility (Brockman and van Schaik, 2005). Changes in androgen levels and testes mass in relaxed-income breeding primate males often occur shortly before or concurrently with changes in female fertility, evidence that has been interpreted as an indication that males respond to the same environmental cues used by females to time reproductive events (Brockman and van Schaik, 2005). Among temperate birds, however, sex differences exist in the response to environmental cues: photoperiod plays a role in the activation of both male and female reproduction, but females also rely on additional cues (Ball and Ketterson, 2008). Similar sex differences have been reported for captive gray mouse lemurs (*Microcebus murinus*; Perret and Aujard, 2001). In rhesus macaques, photoperiod is sufficient to trigger testosterone increases (Chik et al., 1992), with additional fine-tuning by social and ecological cues (Higham et al., 2013).

The conception season in the Santa Rosa capuchin population coincides with the shortest days of the year. Therefore, we predict a negative relationship between both fT and fGC and photoperiod, since photoperiod may reliably predict seasonal increases in female fertility (i.e., number of ovulatory period is greatest in months with the fewest daylight hours).

Food availability

Among mammals, the influence of food on reproduction is likely weaker for males than for females given the sex-based differences in the energetic requirements associated with reproduction, with sperm production likely only under limited selection to be sensitive to food availability given the low metabolic cost of spermatogenesis (Bribriescas, 2001). In fact, evidence that androgen production is linked to food availability is limited and equivocal (in contrast to evidence that female hormones and reproductive function are linked to food availability; reviewed in Emery Thompson, 2013). For example, lean dry seasons were associated with low T and high GC in male savanna baboons, suggesting that nutritional stress may negatively influence T levels (Gesquiere et al., 2011). In contrast, low fruit availability was associated with higher androgen levels in wild chimpanzees and long-tailed macaques (Muller and Wrangham, 2005; Girard-Buttoz et al., 2015). Except during period of extreme nutritional stress, it would be adaptive for males to maintain elevated androgen levels even during periods of moderate fruit scarcity if these coincide with the presence of fertile females (Girard-Buttoz et al., 2015). The conception season in the Santa Rosa capuchin population is associated with a predictable seasonal decrease in fruit abundance (Carnegie et al. 2011a). Thus, if changes in female fertility are triggered by changes in food availability, we predict that male fT may have a negative relationship with food availability so long as males are not nutritionally stressed (i.e., high fGC).

Temperature and rainfall

Heat stress occurs when ambient temperatures increase body temperature beyond the thermal neutral zone, and may compromise reproductive function (Hansen, 2009). Evidence from mammals indicates that heat stress causes an initial but temporary decline in T concentrations despite continued elevated ambient temperatures (Hansen, 2009). In wild mangabeys and baboons living in seasonally variable environments, males had lower T when ambient temperatures were high (Arlet et al., 2011; Gesquiere et al., 2011), but GC levels were unaffected by temperature in baboons. There is some evidence from humans indicating that elevated temperatures in the summer may inhibit fertility in men at lower latitudes and may contribute to seasonal variation in human birth patterns (Wehr, 2001).

While temperature variation in the tropics may be limited, seasonal rainfall fluctuations are common (van Schaik and Phannes, 2005). Drinking water is an important behavioral mechanism for regulating body temperature in many primates (Hill, 2005), and extremely arid periods may affect male physiology. For example, during a severe drought, male olive baboons (*Papio anubis*) had significantly lower T levels than during non-drought years, but there was only a weak effect on GCs (Sapolsky, 1986). If extremely high temperatures during the dry season cause heat stress, we predict a positive relationship between maximum temperature and fGC, and a negative relationship with fT. Similarly, low or absent rainfall may cause dehydration stress such that we predict a negative relationship between rainfall and fGC, and a positive relationship with fT. Alternatively, the predictable nature of seasonal changes in temperature and rainfall may not be sufficient to cause heat and dehydration stress, and may instead be used by males as additional environmental cues to seasonal changes in female fertility, such that we might predict a positive relationship between fT and increasingly hot and dry weather as the conception season progresses, but only a weak or absent relationship with fGC.

METHODS

Study site and subjects

Between July 2008 and November 2009, we conducted fieldwork in the Santa Rosa Sector (henceforth Santa Rosa) of the Área de Conservación Guanacaste (ACG), Costa Rica (10°45′ to 11°00′ N and 85°30′ to 85°45′ W). The 108 km^2 park consists of primarily dry deciduous forest, with a mosaic of semi-evergreen and riparian forest fragments as well as areas that have been regenerating from pastureland since the early 1970s (Fedigan and Jack, 2012). The white-faced capuchins of Santa Rosa have been under near continuous observation since 1983 (Fedigan and Jack, 2012). Study subjects included all adult males (>10 years; $N = 8$, including 3 alpha males) and subadult males (>6–10 years; $N = 6$) residing in three long-term study groups (CP, GN, LV). All males were identifiable based on natural markings (e.g., scars, facial discolorations, missing digits). Research complied with protocols approved by the ACG, the Tulane University IACUC, the University of Calgary ACC, and adhered to the legal requirements of Costa Rica and the United States.

Male hormone data

Over the 17-month study period, we collected fresh samples ($N = 993$) from all 14 study males and kept them cool with ice packs until they could be frozen at the end of the field day. We conducted initial hormone extraction in the field using SPE cartridges (for detailed methods see Carnegie et al., 2011b and Schoof et al., 2014). Both fT and fGC were quantified using previously validated in-house EIAs at the Wisconsin National Primate Research Center (Carnegie et al., 2011b; Schoof et al., 2014; see Wheeler et al. 2013 for validation of non-invasive fecal analysis in the closely related *C. apella*). Prior to EIA, we separated fT from a portion of the sample using celite column chromatrography (Ginther et al., 2001).

Following Schoof et al. (2014), we replaced hormone metabolite values that fell below the standard curve of their respective assays with the minimum sensitivity of the assay (fT: 0.10 ng/g, $N = 18$; fGC: 1.58 ng/g, $N = 4$) and excluded one extreme fT outlier. For each male, we calculated a mean monthly fT and fGC value based on an average of 4.2 ± 0.9 samples per male, per month (median = 4), resulting in 237 individual monthly fT and fGC values across the 14 study males.

Predictor variables

Age and dominance rank. Males are subadults from the age of 6 to <10 years, and adults ≥10 years. Each of the three social groups contained one alpha male, easily identifiable on the basis of their robust appearance (Jack et al., 2014; Schoof et al., 2014). Following Schoof et al. (2014), we combined male age and dominance rank into a single predictor variable [age/rank] because alpha males are always adults, and subordinate subadult males (SADM) are almost invariably lower ranking than subordinate adult males (ADM). Previous research indicates that these age/rank categories are supported by physiological and behavioral differences (Jack et al., 2014). This variable was the only time-invariant predictor as there were no changes in male dominance in any of the three study groups, nor did any males mature into a new age category during the study period.

Number of female periovulatory periods. To identify female periovulatory periods (POPs), we collected fresh fecal samples from all group females over the age of 5.5 years ($N = 28$) once every 3 days ($N = 2273$). Feces were processed in the field as described above for male samples. A subset of the female samples, which excluded pregnant females, were analyzed by EIA for progesterone ($N = 1{,}550$); samples from females who had fluctuating levels of progesterone were then further analyzed by radioimmunoassay for estradiol (N = 932) (Ziegler et al., 1987; Carnegie et al., 2011b). We defined the POP as the day of the rise in fecal progesterone level ±3 days (Strier et al., 2003; Schoof et al., 2014). We identified 26 POPs based on female hormone profiles. Twelve of these POPs resulted in conceptions, indicating a mean gestation length of 157.08 ± 10.26 days (median = 156 days; see also Carnegie et al., 2011b). We calculated the monthly total number of POPs in each study group. For the six POPs that overlapped 2 months, we included them in the month with the most POP days. Additionally, four females for whom we lacked reliable hormone data conceived during the study period (Schoof et al., 2014). We estimated the month in which these four conceptive POPs occurred by subtracting mean gestation length from the date of birth.

Photoperiod data. The daily duration of daylight hours for Santa Rosa (N 10°50′, W 85°37′) between 1 July 2008 and 31 November 2009 were obtained from the United States Naval Observatory website (http://aa.usno.navy.mil/data/docs/Dur_OneYear.php). We calculated mean monthly number of daylight hours, defined as "the total time that any portion of the Sun is above the horizon" (US Naval Observatory). Given the hypothesized predictive cueing of photoperiod, we also calculated a 1-month "lagged photoperiod" (i.e., the value of "lagged photoperiod" for October 2008 is the same as the value for "photoperiod" in September 2008).

Food availability. We estimated monthly biomass of ripe fruit based on monthly phenological records for 33 tree species (~10 individuals per species) that are consistently important sources of ripe fruit for capuchin monkeys in Santa Rosa. For each individual tree, we multiplied the proportion of the crown covered in fruit (measured in increments: 0, 0.01–0.25, 0.25–0.49, 0.50–0.74, 0.75–1.00) by the proportion of fruit that were ripe (also measured in 0.25 increments) to get a ripe fruit index (RFI) ranging from 0 to 1 each month. We multiplied the mean RFI of each species each month by the fruit production potential (FPP) of that species in Santa Rosa. FPP in grams fruit ($47^*DBH^{1.9}$; Peters et al., 1988) for each tree was converted to kg and summed for all individuals of the same species recorded in 100 m × 2 m botanical transects ($N = 151$), covering a total area of 3.02 ha. Following Melin et al. (2014b), only trees greater than the minimum DBH required for capuchin foraging (i.e., species-specific) were included (Supporting Information Table S1). The ripe fruit biomass was then summed across all 33 species for each month and divided by the sampling area in hectares (ha) to estimate total kg of fruit/ha produced.

Weather data. Daily rainfall records were obtained using a rain gauge located near the field house, without cover from buildings or canopy. For each month, we calculated the cumulative rainfall in millimeters. Daily temperature data were collected using a Kestrel weather instrument located in the shade. We calculated a monthly mean maximum temperature in degrees Celsius (17–31 days per month, median = 30 days).

Statistical analyses

We used log-transformed mean monthly fT and fGC values for each male, resulting in 14 measures per month over a period of 17 months ($N = 237$). We used linear mixed effects models (LMM) to predict each male's monthly fT and fGC level using the nlme package (Pinheiro et al., 2015) in R (R Core Team, 2015). To limit the potential effect of variation resulting from inter-individual and group differences in metabolic rate, hormone metabolism, and diet (Goymann, 2012), we: (1) used monthly average fT and fGC values from each male as our outcome variable, and (2) fit random intercept models with male identity nested within group identity as a random factor. We used an AR(1) covariance matrix to model dependencies between individual monthly hormone levels (Pinheiro and Bates, 2000).

To examine the effect of each individual predictor on fT and fGC, we ran a series of linear mixed models in which we included only one predictor at a time. We then applied an exhaustive model search strategy with all possible additive combinations of predictors (i.e., age/rank, monthly female POPs, photoperiod, lagged photoperiod, fruit biomass, cumulative rainfall, and maximum temperature) using the MuMIn package in R (Barton, 2015); note that the search procedure did not allow both photoperiod and lagged photoperiod to be included in the same model. We present the top five models returned by the model selection procedure and use the difference (Δ) in Bayesian Information Criterion (BIC) to compare between models ("best models" have $\Delta > 2$ BIC; Burnham and Anderson, 2002). We tested for collinearity within models using a conservative variance inflation factor (VIF) threshold of $\text{VIF} \leq 4.0$ (Chatterjee et al., 2000). We also conducted Pearson correlations between lagged photoperiod and the other time-varying predictors since it has been suggested that photoperiod is a reliable indicator of seasonal changes (Bronson, 2009).

RESULTS

Levels of fT peaked in December while fGC peaked in February; both hormones were at their lowest levels between July and September (Fig. 1; see Supporting Information Table S2 for monthly summary of outcome and predictor variables). In any given month, there were between 0 and 4 periovulatory periods (POP) per social group (Fig. 2; range: 0–7 across all three groups combined). Mean monthly number of daylight hours ranged from 11 h 30 min to 12 h 45 min (Fig. 2). Monthly cumulative rainfall ranged from 0 to 805.5 mm. Monthly fruit biomass ranged from 30.68 kg/ha in the leanest month to 373.02 kg/ha, but variation did not align with seasonality in rainfall (i.e., the dry season was not uniformly low in fruit availability; Fig. 2). Daily maximum temperatures ranged from 24.1°C to 36.4°C, and monthly mean maximum temperature was 25.7°C to 32.9°C (Fig. 2).

Effects of individual predictors on fT and fGC

Male age/rank was a significant predictor of fT and fGC: alpha males had significantly higher fT and fGC than subordinate adult and subadult males (Table 1). Male fT and fGC were higher when there was a greater number of female periovulatory periods (Table 1). Both photoperiod and lagged photoperiod had large negative effects on fT and fGC, though lagged photoperiod had a larger effect size and explained more of the hormone variation than photoperiod (i.e., lower BIC for lagged photoperiod, Table 1). Fruit biomass was negatively associated with fT and fGC, with lower hormone metabolites when fruit biomass was high, but this effect was weak for fT (Table 1). Cumulative monthly rainfall had no effect on fT, but was a strong negative predictor of fGC, with low rainfall months associated with high fGC levels (Table 1). Maximum temperature had no significant effect on monthly fT or fGC (Table 1).

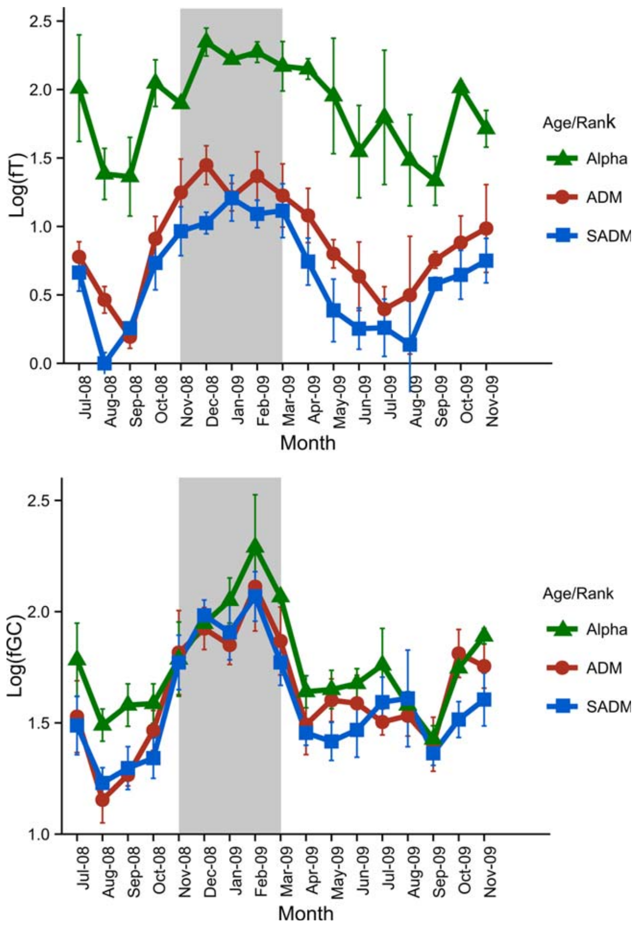

Fig. 1. Mean monthly log-transformed values of fecal (**a**) testosterone and (**b**) glucocorticoid metabolite levels (ng/g) for males grouped by their age/rank category for the study period from July 2008 to November 2009. Alpha = adult alpha male, ADM = adult subordinate male, SADM = subadult subordinate male. Light grey highlighting represents the conception season.

Exhaustive model selection

When we considered the effects of all the predictor variables on fT simultaneously, the exhaustive model selection procedure returned a single best model ($\Delta > 2$ BICs; Table 2a) that explained a high proportion of the fT variation (conditional $r^2 = 0.68$). The best model retained the time-invariant age/rank predictor and lagged photoperiod as the only environmental predictor. Examination of all top five fT models reveals that lagged photoperiod was the only time-varying predictor retained in all models, although the number of POPs, fruit biomass, rainfall, and maximum temperature each appear once in these top models, but their effect sizes are very small (Table 2a).

When we considered the effects of all the predictor variables on fGC simultaneously, the exhaustive model search indicated two closely matched models (Model 1 and 2 $\Delta < 2$ BICs from one another, but $\Delta > 2$ BICs from the next closest model; Table 2b) that explained almost half of the fGC variation (conditional $r^2 = 0.42$). In the two best models, fGC was predicted by lagged photoperiod, fruit biomass, and rainfall, and one of these two models also retained age/rank as a predictor of fGC. Examination of all top five fGC models reveals that lagged photoperiod was the environmental predictor with the largest effect size, followed by rainfall and fruit biomass (Table 2b). Although POPs and maximum temperature appear in some of these fGC models, their effect sizes are smaller than the other predictor variables (Table 2b).

Relationship between photoperiod and other time-varying predictors

There was a strong negative correlation between lagged photoperiod and the number of female POPs (Pearson's $r = -0.61$, $P < 0.001$), and a weak negative correlation with maximum temperature (Pearson's $r = -0.15$, $P = 0.02$). Lagged photoperiod was positively correlated with fruit biomass (Pearson's $r = 0.21$, $P < 0.01$) and cumulative rainfall (Pearson's $r = 0.33$, $P < 0.01$). Similar, but weaker, relationships were identified between photoperiod (i.e., non-lagged photoperiod) and the other time-varying predictors.

Exhaustive model selection excluding lagged photoperiod

Given that lagged photoperiod was strongly correlated to the number of female POPs, and that previous research indicates that males have increased fT and fGC levels in the presence of periovulatory females (Schoof et al., 2014), we conducted *post hoc* analyses by rerunning the model selection procedures excluding lagged photoperiod. This search procedure did not return a single best fT model (i.e., all within 2 BICs; Table 3a), and these models explained less of the fT variation (conditional $r^2 = 0.45$–0.52) than the best model that did include lagged photoperiod as a predictor (Table 2a). Overall, the fT models excluding lagged photoperiod were generally similar to those that included lagged photoperiod, except: (I) the number of POPs was a predictor of fT in three of the five top models, and (II) fruit biomass was also retained as a predictor of fT in three of the five top models (Table 3a).

The search procedure excluding lagged photoperiod yielded fGC models that were very similar to the models in which this predictor was included, except that the number of POPs replaced lagged photoperiod as a predictor variable in the two best fGC models (Tables 2b and 3b). However, these two best models explained less of the fGC variation (conditional $r^2 = 0.31$–0.34) than the best models that did include lagged photoperiod as a predictor.

DISCUSSION

White-faced capuchins are characterized as relaxed income breeders, a strategy in which females time reproductive events using cues from seasonal variation in resource availability as well as internal body condition, resulting in a pattern of moderate breeding seasonality with a conception peak from November to February (Carnegie et al., 2011a). We predicted that male hormones would be sensitive to seasonal variation in female fertility, as well as to seasonally variable factors that may serve as cues to changes in female fertility. Our results indicate that lagged photoperiod was the best seasonally variable predictor of fT, and male age/rank consistently had a large effect on fT. In contrast, fGC levels were consistently predicted

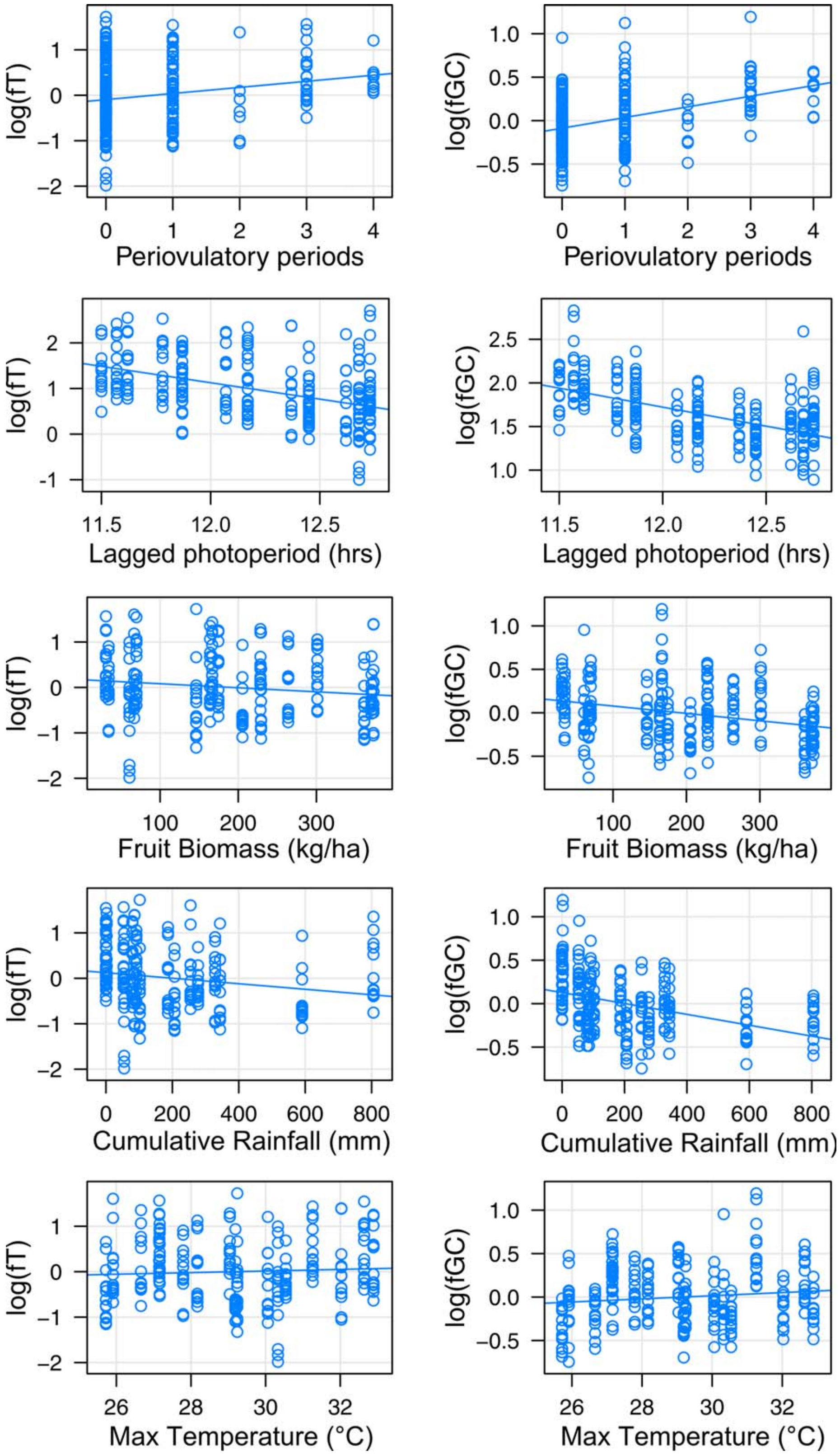

Fig. 2. Male monthly average log-transformed fT and fGC metabolite levels (ng/g) plotted against monthly time-varying predictors. A simple linear model (y ~ x) is presented to aid in identifying trends.

by lagged photoperiod, fruit biomass, and cumulative rainfall, and to a lesser extent by female fertility and temperature.

Consistent with predictions for relaxed income breeders and with previous research (Brockman and van Schaik, 2005; Schoof et al., 2014), female reproductive

TABLE 1. Models quantifying the independent effects of age/rank, number of periovulatory periods, photoperiod, 1-month lagged photoperiod, fruit biomass, cumulative rainfall, and maximum temperatures on fT and fGC

	Fecal testosterone		Fecal glucocorticoids	
Predictor	β (sd)	BIC	β (sd)	BIC
Age/rank: adult vs. alpha	−1.40 (0.19)*	526.63	−0.41 (0.24)	672.14
Age/rank: subadult vs. alpha	−1.74 (0.19)*	526.63	−0.55 (0.23)*	672.14
No. periovulatory periods	0.13 (0.05)*	546.18	0.33 (0.07)*	652.92
Photoperiod	−0.32 (0.05)*	519.33	−0.39 (0.07)*	645.49
Lagged photoperiod	−0.43 (0.04)*	481.29	−0.54 (0.06)*	615.9
Fruit biomass	−0.09 (0.04)*	545.58	−0.20 (0.05)*	658.35
Cumulative rainfall	0.09 (0.05)	547.71	−0.32 (0.06)*	649.76
Maximum temperature	−0.01 (0.06)	550.62	0.06 (0.08)	671.75

Standardized coefficients (β) are presented for each predictor variable, along with their standard deviations (sd). *estimated coefficient P-value <0.05.

TABLE 2. The top five (a) fT and (b) fGC models from the exhaustive model selection procedure with all predictors included

	fT models				
(a)	β (1)	β (2)	β (3)	β (4)	β (5)
Intercept	1.2500	1.2490	1.2500	1.2460	1.2490
Age/rank: adult vs. alpha	−1.4000	−1.4000	−1.4000	−1.4000	−1.4000
Age/rank: subadult vs. alpha	−1.7500	−1.7500	−1.7500	−1.7400	−1.7500
No. periovulatory periods				−0.0352	
Photoperiod					
Lagged photoperiod	−0.4281	−0.4165	−0.4131	−0.4491	−0.4299
Fruit biomass		−0.0536			
Cumulative rainfall			−0.0489		
Maximum temperature					−0.0130
BIC	462.4	465.8	466.4	467.4	467.8
Δ	0	3.41	3.95	4.93	5.35
	fGC models				
(b)	β (1)	β (2)	β (3)	β (4)	β (5)
Intercept	0.3726	0.0005	0.3831	0.3723	0.0006
Age/rank: adult vs. alpha	−0.4000		−0.4100	−0.4000	
Age/rank: subadult vs. alpha	−0.5400		−0.5500	−0.5400	
No. periovulatory periods			0.0957		0.0751
Photoperiod					
Lagged photoperiod	−0.4235	−0.4238	−0.3691	−0.4258	−0.3811
Fruit biomass	−0.1801	−0.1805	−0.1887	−0.1769	−0.1871
Cumulative rainfall	−0.2502	−0.2497	−0.2345	−0.2655	−0.2374
Maximum temperature				−0.0422	
BIC	595.1	596	598.4	600	600.2
Δ	0	0.92	3.27	4.88	5.09

Blank cells indicate the predictor was not retained in by the model selection procedure. Standardized coefficients (β) are provided to facilitate comparisons of each predictor's relative effect on fT and fGC. To facilitate model comparisons, we have also provided each model's BIC and difference in BIC (Δ) relative to the best model (i.e., Model 1 with the lowest BIC).

status is an important factor influencing fT and fGC in capuchin monkeys when examined in isolation (Table 1). However, the effect of the number of female POPs all but disappeared from the top fT and fGC models when environmental variables were included in the exhaustive model searches (Table 2). Much of the fT and fGC variation attributed to the number of POPs in the single-predictor models seems to have been absorbed by variation in lagged photoperiod. We also found that lagged photoperiod was strongly correlated to the number of female POPs in a given month. This is consistent with the hypothesis that for relaxed income breeders, where the timing of female reproductive events occurs somewhat predictably with seasonal changes, males will exhibit an endocrine response to environmental factors (e.g., photoperiod); this may be especially true if males and females are using the same cues to time reproductive events (Brockman and van Schaik, 2005). When we repeated the exhaustive model search without lagged photoperiod, we found that the best fGC models and most of the top fT models included some combination of the other time-varying predictors—including female POPs (Table 3). However, these models had higher BICs and explained less of the fT and fGC variation than models that included lagged photoperiod as a predictor.

Our results suggest that lagged photoperiod may predict *long-term* trends in the timing of female ovulation. A *post hoc* analysis provides support for this hypothesis, with 30 years of birth data ($N = 172$ reliable birthdates) from the Santa Rosa capuchin population indicating a strong negative correlation between lagged photoperiod and conception month (Pearson $r = -0.64$, $P = 0.026$). In

TABLE 3. The top five (a) fT and (b) fGC models from the exhaustive model selection procedure that excluded photoperiod and lagged photoperiod, but included age/rank, number of female POPs, fruit biomass, cumulative rainfall, and maximum temperature

	fT models				
(a)	1	2	3	4	5
Intercept	1.2660	1.2700	1.2500	1.2420	1.2650
Age/rank: adult vs. alpha	−1.4200	−1.4200	−1.4000	−1.4000	−1.4200
Age/rank: subadult vs. alpha	−1.7700	−1.7600	−1.7400	−1.7400	−1.7700
No. periovulatory periods	0.1617	0.1455			0.1441
Fruit biomass	−0.1035			−0.0866	−0.1108
Cumulative rainfall					−0.0922
Maximum temperature					
BIC	525.3	526.5	526.6	527	527.1
Δ	0	1.26	1.38	1.71	1.85

	fGC models				
(b)	1	2	3	4	5
Intercept	0.4065	0.0008	0.4063	0.0004	−0.0036
Age/rank: adult vs. alpha	−0.4300		−0.4300		
Age/rank: subadult vs. alpha	−0.5900		−0.5900		
No. periovulatory periods	0.2864	0.2680	0.2876	0.2696	
Fruit biomass	−0.2489	−0.2458	−0.2472	−0.2443	−0.2347
Cumulative rainfall	−0.2783	−0.2805	−0.2877	−0.2893	−0.3427
Maximum temperature			−0.0283	−0.0284	
BIC	622.1	624.1	627.3	629.3	635.1
Δ	0	2	5.24	7.26	13.02

Blank cells indicate the predictor was not retained in by the model selection procedure. Standardized coefficients (β) are provided to facilitate comparisons of each predictor's relative effect on fT and fGC. To facilitate model comparisons, we have also provided each model's BIC and difference in BIC (Δ) relative to the best model (i.e., Model 1 with the lowest BIC).

any given year, the number of POPs in a month may vary, but historically, more females ovulate and conceive between November and February (Carnegie et al. 2011a). Therefore, increases in male fT and fGC may be in response to changes in photoperiod, which are likely easier to predict than female reproductive state, and this timing may be under selection since the predictive value of photoperiod is strong in both the short- and long-term. In other words, changes in photoperiod may trigger increases in male fT and fGC levels just prior to the conception season, in anticipation of increasing numbers of fertile females. Seasonally elevated fT and fGC levels may be subject to further fine-tuning based on the actual presence of ovulatory females (Goymann et al., 2007), which is consistent with our previous research indicating that males are sensitive to the weekly presence or absence of fertile females (Schoof et al., 2014).

In contrast to our predictions, food, rainfall, and temperature were not important predictors of male fT when these were examined simultaneously with lagged photoperiod, although there was a significant negative effect of fruit when this predictor was examined independently. A few primate studies have suggested that seasonal changes in androgen levels are associated with environmental factors that vary with hot/dry and cool/wet seasons, or with periods of fruit scarcity (e.g., Muller and Wrangham, 2005; Gesquiere et al., 2011; Girard-Buttoz et al., 2015). Unfortunately, these studies did not examine changes in photoperiod, making it possible that a portion of the androgen variation thought to be associated with changes in fruit, rainfall, or temperature may actually be better explained by the variation in photoperiod. Similarly, the vast majority of primate studies examining seasonal changes in male androgen levels in response to social variables, such as female fertility and male aggression, do not consider photoperiod. When we re-ran our models excluding lagged photoperiod as a predictor, we found that the number of periovulatory periods became a predictor of fGC and fT, and fruit biomass was also returned as a predictor of fT (Table 3 vs. Table 2). As noted by Goymann et al. (2007), it is worth considering what portion of the observed seasonal increase in hormones is associated with responsiveness to receptive/fertile females, male–male competition, and also non-social environmental cues such as photoperiod. In order to tease apart the effects of photoperiod and other seasonally varying factors on fT, it is necessary to conduct multiyear studies since interannual changes in photoperiod are negligible, while changes in fruit/flower flushing, rainfall, and temperature are more variable, especially in areas affected by El Niño/La Niña events (Campos et al., 2015), and seasonal variation in the availability of receptive female may also vary annually in response to these environmental factors.

Variation in fGC was more sensitive than fT to fluctuations in the number of female POPs, fruit biomass, and cumulative rainfall. Similar to the results obtained for fT, the number of POPs was a negative predictor of fGC in the single-predictor model (Table 1). Furthermore, the exhaustive model search indicated that the number of female POPs was not a predictor of fGC in the two best models (Table 2b). However, when lagged photoperiod was omitted from the exhaustive model search, the number of female POPs completely replaced lagged photoperiod as a predictor in most of the top models (Table 3b). This result suggests that when it comes to fGC, the variation accounted for by lagged photoperiod and female POPs have much greater overlap (compared with fT). Perhaps the seasonal increase in fGC is in response to the actual presence of ovulatory females, rather than historical trends in seasonal female fertility as predicted by lagged photoperiod.

Biomass of ripe fruits consumed by capuchins was highly variable throughout the year, and overall fruit abundance did not track precipitation, which is consistent with other reports from this site (Carnegie et al. 2011a, b; Melin et al., 2014a). When considering all predictors simultaneously, the exhaustive model search indicated a negative effect of low fruit biomass and rainfall on fGC. Consistent with our predictions, male fGC levels were higher in months when fruit biomass was low, suggesting that even brief periods of fruit scarcity may pose a nutritional challenge for white-faced capuchins. The moderate influence of fruit biomass on male fGC levels may be mitigated in omnivorous capuchins by their reliance on other non-fruit food resources, such as small vertebrates, eggs, and insects. While quantification of non-fruit food sources was not available during our study, other studies have indicated that extractive foraging of invertebrates is concentrated during months of low fruit abundance and caterpillars are consumed seasonally with the onset of the rains, although other invertebrates are also present in Santa Rosa and consumed year-round by capuchins (Melin et al., 2014a; Mosdossy et al., 2015). Also consistent with our predictions, male fGC levels were higher in months with little or no rainfall. However, at least some of the fruits consumed by capuchins in the dry season have a high water content (Melin, 2011), which may diminish the potentially stressful effects of low/no rainfall, such that the capuchins experience only limited fGC elevations. These results support our predictions that low fruit availability and rainfall may be associated with slight nutritional and dehydration stress; however, fGC levels are not sufficiently high or sustained for long enough periods of time to impair androgen production.

In contrast to our predictions, temperature was not a good predictor of either fT or fGC. Animals mitigate the effects of fluctuations in environmental variables through both behavioral and physiological mechanisms, such that stress may occur only under extreme and prolonged adverse conditions. While the daytime temperature at Santa Rosa can exceed 36°C in the dry season, which is beyond the estimated thermal neutral zone of capuchins (25°C–35°C, Campos and Fedigan, 2009), these extremes may be sufficiently short-lived that they do not cause thermal stress or impairment of androgen production, since monthly maximum temperatures did not exceed 33°C. Additionally, capuchins may use behavioral mechanisms (e.g., panting, increased resting and decreased travel during hot periods) that may limit any negative effects of high temperatures (Campos and Fedigan, 2009).

In the current study, we propose that seasonal increases in male hormones are triggered by changes in photoperiod since this variable is a strong predictor of female ovulation. At this time, we cannot discount the possibility that some of the seasonal hormone response is associated with challenges from extragroup males. In a previous study, we observed that elevated androgen and glucocorticoid levels in the late dry season were associated with higher rates of intergroup encounters (Schoof and Jack, 2013), a variable we were unable to assess in the present study. We must also consider the possibility that some of the seasonal variation in fecal hormone metabolites do not necessarily reflect circulating levels. Using methodological and statistical means, we have attempted to limit the potential effect of variation in inter-individual and group differences in metabolic rate and diet. However, seasonal changes in diet and temperature can impact hormone metabolism and excretion rates, and may potentially distort hormone values obtained from fecal samples, a limitation of non-invasive fecal sampling that must be considered in interpretations of seasonal as well as intra- and inter-individual differences (reviewed in Goymann, 2012).

The current study demonstrates that males exhibit variation in fecal hormone levels in response to male age and dominance rank, as well as to seasonally varying environmental and social factors. We found that more of the variation in fGC levels could be explained by a range of environmental factors (photoperiod, fruit biomass, rainfall) compared with testosterone, which was predicted primarily by lagged photoperiod. Interestingly, in isolation, the number of female periovulatory periods was a predictor of seasonal male hormone levels, but this effect weakened and effectively disappeared once environmental variables were included. The strong negative correlation between female periovulatory events and lagged photoperiod suggests that males may use the number of daylight hours as a predictor of historical trends in the seasonal distribution of female fertility. Our analyses suggest an association between these variables, but future work should test this association more directly to identify mechanisms linking photoperiod, female reproductive events, and male hormones (e.g., evaluation of sensory sensitivity to light changes). Taken together with previous results that show male hormone response to female ovulation on a shorter (i.e., weekly) time scale, our results suggest that males have seasonal increases in hormone levels—possibly in anticipation of increased presence of ovulatory females—while also fine-tuning short-term hormone increases to the actual presence of ovulatory females. Comparative studies of different white-faced capuchin populations with similar historical patterns of female conceptions but different patterns of environmental seasonal variation could further elucidate the relative roles of social and environmental influences on male endocrinology.

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