

*Male Response to Female Ovulation
in White-Faced Capuchins (Cebus
capucinus): Variation in Fecal
Testosterone, Dihydrotestosterone, and
Glucocorticoids*

**Valérie A. M. Schoof, Katharine M. Jack
& Toni E. Ziegler**

International Journal of Primatology
The Official Journal of the International
Primatological Society

ISSN 0164-0291

Int J Primatol
DOI 10.1007/s10764-013-9742-4



Your article is protected by copyright and all rights are held exclusively by Springer Science +Business Media New York. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Male Response to Female Ovulation in White-Faced Capuchins (*Cebus capucinus*): Variation in Fecal Testosterone, Dihydrotestosterone, and Glucocorticoids

Valérie A. M. Schoof · Katharine M. Jack · Toni E. Ziegler

Received: 26 February 2013 / Accepted: 25 July 2013
© Springer Science+Business Media New York 2013

Abstract Reproductive success is linked to dominance in male primates, reflecting the benefits of male competition. However, not all males compete successfully, suggesting that the costs of obtaining and maintaining high dominance status are significant. Here we examine the fecal metabolites of testosterone (fT) and dihydrotestosterone (fDHT) as bioactive androgens reflecting male reproductive effort, as well as fecal glucocorticoid (fGC) excretion as an index of stress in male white-faced capuchins (*Cebus capucinus*). We investigated the influence of female fertility (perioviulatory vs. nonovulatory) on the hormonal responses of alpha and subordinate males. Over a 17-mo field season, we collected and analyzed weekly fecal samples ($N = 992$) from all 14 adult (> 10 yr) and subadult (≥ 6 –10 yr) males residing in three study groups in the Santa Rosa Sector of the Área de Conservación Guanacaste, Costa Rica. Fecal samples ($N > 2250$) were also collected from group females ($N = 28$) to identify the fertile period using progesterone and estradiol assays. Alpha males had significantly higher fT, fDHT, and fGC levels than subordinate males independent of female reproductive state; further, adult subordinates had significantly higher fT, but not fDHT or fGC, than subadult subordinates. Male fT, fDHT, and fGC levels were significantly higher in the presence of fertile females, regardless of male dominance status and age. These findings indicate that the higher reproductive effort of alpha males comes with some costs (increased fGCs), and the presence of perioviulatory females is associated with specific endocrine responses reflecting male reproductive effort and stress in white-faced capuchins.

V. A. M. Schoof (✉) · K. M. Jack
Department of Anthropology, Tulane University, New Orleans, Louisiana 70118, USA
e-mail: vschoof@gmail.com

K. M. Jack
e-mail: kjack@tulane.edu

T. E. Ziegler
National Primate Research Center, University of Wisconsin-Madison, Madison, Wisconsin 53715, USA
e-mail: ziegler@primate.wisc.edu

Keywords Androgens · Allostatic load · Dominance · Fertile females · Reproductive strategies

Introduction

Research on male reproduction has emphasized the benefits of male competition, namely the link between high dominance status and reproductive success (Di Fiore 2003; Majolo *et al.* 2012). Not all males achieve high status, however, suggesting that dominance may be associated with substantial costs. Male reproductive effort, which reflects the time and energy devoted to physiological and behavioral processes associated with reproduction (Hirschfield and Tinkle 1975), varies according to male life-history stage and social environment (Sapolsky 1993).

Androgens, including testosterone (T) and its metabolite dihydrotestosterone (DHT), maintain reproductive physiology, influence sexual motivation, and lead to the development of secondary sexual characteristics (Dixson 2012). Wingfield and colleagues (1990) also proposed that T elevations, beyond those required for basic reproduction, mediate aggression in a reproductive context, i.e., access to fertile females, challenges to dominance status. Thus, androgen production is often associated with male reproductive effort. Furthermore, male dominance status and androgens are positively associated in several species of wild group-living primates (*Leontopithecus rosalia*: Bales *et al.* 2006; *Propithecus verreauxi*: Kraus *et al.* 1999; *Pan troglodytes*: Muller and Wrangham 2004a; *Papio hamadryas ursinus*, Beehner *et al.* 2006; *Lemur catta*: Gould and Ziegler 2007; *Mandillus sphinx*: Setchell *et al.* 2008; *Papio cynocephalus*: Gesquiere *et al.* 2011; *Lophocebus albigena*: Arlet *et al.* 2011), though not in others (*Brachyteles hypoxanthus*: Strier *et al.* 1999; *Sapajus apella*: Lynch *et al.* 2002; *Eulemur fulvus fulvus*: Ostner *et al.* 2002, 2008a; *Macaca fascicularis*: Girard-Buttoz *et al.* 2009; *Macaca assamensis*: Ostner *et al.* 2011).

In both seasonal and nonseasonal breeders, the presence of fertile females is often associated with an upsurge in male reproductive competition and pronounced increases in androgens (Bales *et al.* 2006; Girard-Buttoz *et al.* 2009; Ostner *et al.* 2011), T (Arlet *et al.* 2011; Gould and Ziegler 2007; Lynch *et al.* 2002; Muller and Wrangham 2004a; Ostner *et al.* 2002; Setchell *et al.* 2008; *Macaca fuscata*: Rostal *et al.* 1986; *Propithecus verreauxi*: Brockman *et al.* 1998; *Homo sapiens*: Miller and Maner 2010), and/or DHT (Rostal *et al.* 1986). However, androgen levels may increase disproportionately in dominant males compared to subordinate males as a result of differences in reproductive effort (Arlet *et al.* 2011; Kraus *et al.* 1999) or may occur only in those males actively engaged in aggressive mating competition (Gould and Ziegler 2007). Therefore, it appears that male reproductive effort, as measured by androgen levels, increases in the presence of fertile females. In spite of the benefits provided by androgen, they may also carry costs, such as chronic glucocorticoid elevation, immunosuppression, and compromised survivability (Braude *et al.* 1999; Sapolsky 1993; Wingfield *et al.* 2001). Thus, the variability in androgen production is influenced by such factors as dominance style, group stability, female reproductive state, and/or life history stage, and likely reflects selection on males to facultatively increase androgen levels during periods when the potential benefits outweigh the costs (Hirschenhauser and Olivera 2006; Sapolsky 1993).

Several studies of male primates have examined T specifically, or androgens in general, but only a few have looked explicitly at patterns of the T metabolite DHT (*Macaca fascicularis*: Meusy-Dessolle and Dang 1985; *Macaca fuscata*: Rostal *et al.* 1986; *Pongo pygmaeus*: Maggioncalda *et al.* 1999; *Saguinus oedipus*: Ginther *et al.* 2002). T is reduced to DHT by 5- α -reductase in target tissues before being metabolized by the liver and excreted in the urine and feces (Stocco and McPhaul 2006). DHT is a potent androgen whose relative abundance determines changes at puberty (Plant and Witchel 2006; Weiner *et al.* 1996), the development of secondary sexual characteristics (Griffin and Wilson 1998; Maggioncalda *et al.* 1999), facilitates behavior required for successful copulation (Ginther *et al.* 2002; Wallen 2005), and may be associated with dominance, though this is less well known.

Allostatic load reflects the cumulative energetic costs incurred to maintain homeostasis during daily activities (McEwen and Wingfield 2003). Changes in glucocorticoids (GCs), such as cortisol and corticosterone, are most frequently associated with the body's response to stressors, i.e., increase in allostatic load or "stress". Acute or short-term GC increases are adaptive because they mediate energy release to areas needed for immediate survival (e.g., for fight or flight) and temporarily suppress nonvital functions (e.g., growth) in response to transient increases in allostatic load. However, chronic or repeated GC increases can have deleterious effects on health resulting from prolonged and unsustainable elevations in allostatic load (McEwen and Wingfield 2003; Sapolsky 2005). GCs are thus a useful physiological indicator of the relative stress of dominant and subordinate individuals if social status influences allostatic load (Goymann and Wingfield 2004).

The "stress of social subordination" hypothesis reflects the traditional picture of dominance hierarchies, and suggests that subordinate individuals have higher GC levels as a consequence of unequal resource distribution, agonistic behaviors received from dominant individuals, and limited coping opportunities (Abbott *et al.* 2003; Creel 2001; Goymann and Wingfield 2004). Alternatively, the "costs of dominance" hypothesis suggests that dominant individuals have higher GCs due to energetic and/or psychological stress associated with increased sexual activity, mate guarding, challenges from other males, and unstable dominance hierarchies (Abbott *et al.* 2003; Creel 2001; Goymann and Wingfield 2004; Sapolsky 1993, 2005). Reports on primates have yielded equivocal results, with some studies supporting the "stress of social subordination" hypothesis (Ostner *et al.* 2008b; stable periods in *Papio ursinus*: Bergman *et al.* 2005; *Mandrillus sphinx*: Setchell *et al.* 2010), others supporting the "costs of dominance" hypothesis (Gesquiere *et al.* 2011; unstable periods: Setchell *et al.* 2010; *Pan troglodytes*: Muller and Wrangham 2004b; *Lophocebus albigena*: Arlet *et al.* 2009), and several failing to find a relationship between dominance status and GC levels (Bales *et al.* 2006; Girard-Buttoz *et al.* 2009; Lynch *et al.* 2002; Ostner *et al.* 2008a; *Lemur catta*: Gould *et al.* 2005). Goymann and Wingfield (2004) propose that the variable relationship between dominance status and GCs reflects differences in relative allostatic load of high- and low-ranking individuals both across and within species.

In several seasonal and nonseasonal breeders, male GCs increase in the presence of fertile females (Girard-Buttoz *et al.* 2009; Lynch *et al.* 2002; Ostner *et al.* 2008a, b; Setchell *et al.* 2010; Strier *et al.* 1999, 2003; *Propithecus verreauxi*: Fitchel *et al.* 2007; *Pan paniscus*: Surbeck *et al.* 2012; *cf.* Gould *et al.* 2005; Bales *et al.* 2006). The increase in allostatic load in the presence of fertile females may be greater for dominant

males (Fitchel *et al.* 2007; Setchell *et al.* 2010; Surbeck *et al.* 2012), although this does not appear to be the case in species where overt male aggression is rare (Bales *et al.* 2006; Lynch *et al.* 2002; Ostner *et al.* 2008a; Strier *et al.* 1999, 2003; *cf.* Ostner *et al.* 2008b).

Here we examine the fecal metabolites of testosterone (fT) and dihydrotestosterone (fDHT) as androgens reflecting male reproductive effort, as well as fecal glucocorticoid (fGC) excretion as an index of stress in alpha and subordinate male white-faced capuchins (*Cebus capucinus*) in response to female reproductive state. White-faced capuchins are medium-sized Neotropical primates characterized by female philopatry, moderate sexual dimorphism (Fragaszy *et al.* 2004), moderate breeding seasonality (Carnegie *et al.* 2011a, *sensu* van Schaik *et al.* 1999), and the absence of physical or behavioral signs of ovulation (Carnegie *et al.* 2005, 2006). Despite this apparent concealed ovulation, male white-faced capuchins groom and follow periovulatory females more often than nonovulatory females (fertility determined from fecal hormones; Carnegie *et al.* 2005). Though the sample size was very small, the authors also reported that all three observed copulations—and most male courtship behaviors—involved periovulatory females. These data indicate that males modify their behavior and increase reproductive effort toward fertile females, and that males respond to cues of female reproductive status even though ovulation is not conspicuously advertised. As further evidence, alpha males were involved in two of the three copulations observed with periovulatory females (Carnegie *et al.* 2005). They tentatively concluded that alpha males may mate with periovulatory females while subordinate males mate primarily when females are less likely to conceive, an idea consistent with a priority of access model (Carnegie *et al.* 2005, 2006).

Alpha male white-faced capuchins sire the majority of group offspring (*ca.* 68–100%: Jack and Fedigan 2006; Muniz *et al.* 2010), indicating a high degree of reproductive competition, even though they obtain only slightly more copulations than subordinate males (Perry 1997; Rose 1998). Despite high reproductive skew in this species, aggression among coresident male white-faced capuchins is rare, dominance relationships appear relaxed and affiliative, and there is no obvious linear hierarchy among subordinate males (Fedigan 1993; Jack 2003; Perry 1998; Schoof and Jack *in press*). However, alpha males are easily identifiable because they are more robust than subordinate males (large brows and jaws, wide shoulder girdles, and greater overall size; Schoof *et al.* 2011); alpha males are also the most vigilant, the most active in group defense, and the most frequently groomed males by females (Perry 1996; Rose and Fedigan 1995).

In spite of tolerant relationships among coresident male white-faced capuchins, we previously found that alpha males have higher androgen levels than subordinate males even in the absence of fertile females, *i.e.*, all females were either pregnant or lactating (Schoof and Jack 2013). Alpha males may maintain higher baseline androgen levels than subordinates because, despite a conception peak from November to February, nonconceptive mating is common, female fertility is unpredictable, and conceptions occur throughout the year (Carnegie *et al.* 2006, 2011a; Manson *et al.* 1997). Two of three alpha males had higher fGC levels than their subordinates, suggesting that dominance interacts with other social factors, such as group integration or the number of coresident males (Schoof and Jack 2013). Intergroup encounter rates were positively associated with both androgen and fGC levels, indicating that reproductive competition

between groups influences male hormone production. Thus, white-faced capuchins are a good model system in which to examine male androgen response to female ovulation, as they provide novel insight into variation in male reproductive effort in a species in which overt competition is rare and male reproductive skew is high.

In the present study, we examine male androgen and GC levels in relation to dominance status and female reproductive state to examine the costs of dominance in white-faced capuchin monkeys (*Cebus capucinus*).

T and DHT Predictions

First, we test the hypothesis that male reproductive effort increases in the presence of periovulatory females (Hypothesis 1; Table I). Changes in male behavior in the presence of periovulatory females suggest that they can detect female fertility, even though white-faced capuchins have no external signs of ovulation. Therefore, we predict that male reproductive effort, as measured by fT and fDHT, will increase when periovulatory females are present as a result of increased male competition (Prediction 1A; Table I). Given our previous finding that alpha males have higher androgen levels than subordinates, we also test for an interaction between male dominance status and the presence of periovulatory females. Although the roles of female choice and sperm competition are poorly understood, we predict that alpha males will have a disproportionately larger increase, i.e., greater responsiveness, in fT and fDHT than subordinate males in the presence of periovulatory females because they follow and groom females more when they are periovulatory and alpha males sire the majority of group offspring (Prediction 1B; Table I).

Table I Summary of hypotheses, predictions, and support provided by this study of male white-faced capuchins (*Cebus capucinus*, Santa Rosa Sector, ACG, Costa Rica, 2008–2009)

Hypothesis	Prediction	Details	Supported?
1: Reproductive effort increases in the presence of fertile females.	1A: Increased male fT and fDHT in the presence of periovulatory females.	1A: Increased male competition for access to periovulatory females results in greater male reproductive effort.	Yes
	1B: Alpha males have a disproportionate increase in fT and fDHT in the presence of periovulatory females.	1B: Alpha males sire most offspring and may have a greater increase in reproductive effort around periovulatory females.	No
2: Allostatic load increases in the presence of fertile females.	2A: Increased male fGCs in the presence of periovulatory females.	2A: Increased male reproductive effort for access to periovulatory females results in increased allostatic load.	Yes
	2B: Alpha males have a disproportionate increase in fGCs in the presence of periovulatory females.	2B: Competition for access to periovulatory females results in greater increase in allostatic load for alpha males, who have higher reproductive success and thus compete more successfully than subordinate males.	No

GC Predictions

We also test the hypothesis that allostatic load increases in the presence of periovulatory females (Hypothesis 2; Table I). We predict that GCs will be higher in the presence of periovulatory females owing to the costs of increased male reproductive effort (Prediction 2A; Table I). We also test for an interaction with dominance status because we previously found that at least some alpha males have higher fGC levels than their subordinates. In spite of tolerant relationships among coresident male white-faced capuchins, we predict that alpha males will have a disproportionately greater increase in fGC than subordinate males in the presence of periovulatory females as a result of increased reproductive effort (Prediction 2B; Table I).

Methods

We conducted our fieldwork in the Santa Rosa Sector of the Área de Conservación Guanacaste (ACG), Costa Rica between July 2008 and November 2009. The park is made up of *ca.* 108 km² of tropical dry forest consisting of a mosaic of dry deciduous, semi-evergreen, and riparian forest fragments interspersed with regenerating pasture. Seasonal effects are marked, with an average of 1800 mm of rainfall during the wet season months of May through November and almost no rainfall during the dry season months of December through April. Three primate species live in the Santa Rosa Sector (*Cebus capucinus*, *Ateles geoffroyi*, and *Alouatta palliata*); the white-faced capuchins of Santa Rosa have been under near continuous observation since 1983 (see Fedigan and Jack 2012 for full description of the field site and history of the capuchin project). Research complied with protocols approved by the ACG and the Tulane University IACUC and adhered to the legal requirements of Costa Rica and the United States.

Study subjects included all adult (>10 yr, $N = 8$) and subadult males (≥ 6 –10 yr, $N = 6$) residing in three habituated long-term study groups (CP, GN, LV), and all were identifiable based on natural markings, e.g., scars, facial discolorations, missing digits. Each group contained a clearly identifiable adult alpha male, but as with previous studies, a linear hierarchy among subordinate males could not be identified because of the rarity of agonism among coresident males (Fedigan 1993; Jack 2003; Perry 1998). Given that females give birth to their first offspring around 7 yr of age (Fedigan *et al.* 2008), we included all group females >5.5 yr old ($N = 28$) as study subjects.

Hormone Data Collection and Analyses

We opportunistically collected fecal samples once per week from males ($N = 992$, mean = 70.9, range = 66–73) and once every 3 d from females ($N > 2250$). Fresh feces were collected in plastic vials within 5 min of defecation and placed in ice packs until they could be stored in a freezer at the end of the field day (Carnegie *et al.* 2011b). Preliminary field extraction methods using Prevail C18 Maxi-Clean 300 mg Solid Phase Extraction cartridges (Alltech Associates, Deerfield, IL) followed Carnegie *et al.* (2011b), and cartridges were stored at room temperature out of direct sunlight until transported for analyses at the Wisconsin National Primate Research Center (WNPRC) by VAMS. Hormones were eluted with 2 ml of 100% methanol, dried in

a hot water bath, reconstituted in 1 ml of 100% ethanol, and stored in a refrigerator. For male fecal samples, we separated a portion of the sample into fT and fDHT using in-house celite column chromatography (Ginther *et al.* 2001); we found recoveries measured by processing known amounts of each hormone standard through clean chromatography columns to be acceptable (mean \pm SEM, fT: 89.35% \pm 3.37%; fDHT: 86.98% \pm 3.04%). fT and fDHT were subsequently analyzed by in-house enzyme immunoassay (EIA) (Ginther *et al.* 2001); 5–25 μ l of the ethanol solution were dried and resuspended in the assay solution. fGC and fP were analyzed by EIA without chromatography (Carnegie *et al.* 2011b) using 50 μ l of the ethanol solution for fGC and 75 μ l for fP. For fE2, we conducted in-house tritiated radioimmunoassays with 100 μ l of the ethanol solution following the methods developed by Ziegler *et al.* (1987). All samples and standards were run in duplicate. Concentrations of all hormones were measured in ng/g of wet fecal matter.

Taken as a whole, mean intra- and interassay coefficients of variation were within the acceptable range (see Table II). Mean percent accuracy was high for both androgens (fT: 104.69 \pm 1.94, $N = 8$; fDHT: 113.21 \pm 1.84, $N = 8$) and serial dilutions of the pooled samples paralleled the standard curve for each hormone and there were no differences in their slopes (fT: $t(28) = 0.269$, $P > 0.05$, $N = 8$; fDHT: $t(20) = -0.224$, $P > 0.05$, $N = 5$). Hormone assays for fGC (Carnegie *et al.* 2011b), fP, and fE2 (Carnegie *et al.* 2006; 2011b) were previously validated for parallelism and accuracy at the WNPRC.

Interpretation of Female Hormones

Fecal samples collected between parturition and 120 days pre-parturition were excluded as these fall well within the gestation range previously reported for white-faced capuchins (145–166 d; Carnegie *et al.* 2011b). Females that showed little variation and sustained baseline levels of fP were not subsequently analyzed for estradiol (fE2) because they were considered noncycling (Carnegie *et al.* 2006). In some cases, only subsets of female fP profiles were analyzed for fE2.

Carnegie *et al.* (2005, 2011b) operationally defined the periovulatory phase of female white-faced capuchins as being 5 d long (3 d before the rise in fP, the day of the rise, and 1 d after the rise). Because samples were collected from males once per week, we also analyzed our data set using the 7-d periovulatory period used in studies

Table II Hormone intra- and interassay coefficients of variation (CVs) for low pool and high pool (*Cebus capucinus*, Santa Rosa Sector, ACG, Costa Rica, 2008–2009)

Hormone	Low pool CVs		High pool CVs		N
	Intra-assay	Interassay	Intra-assay	Interassay	
fT	3.4	11.8	1.6	6.8	42
fDHT	8.7	22.9	4.3	11.4	41
fGC	7.0	20.4	3.9	10.8	37
fP	6.2	22.7	3.5	18.0	48
fE2	0.5	15.0	0.6	13.6	10

of other New World monkeys (the day of the fP rise ± 3 d; Strier *et al.* 2003, Van Belle *et al.* 2009). We identified 26 periovulatory periods (POPs) based on female hormone profiles (12 of which resulted in conceptions), all of which were included in the analyses. An additional four females conceived during the study, but the hormonal data were insufficient to pinpoint the likely periovulatory period and using the wide range of gestation lengths (current study: 140–171 d) to identify the periovulatory period could have introduced a significant amount of error. Nine of all 16 conceptions occurred during the November–February conception peak, with the remaining seven conceptions occurring outside the conception peak.

Statistical Analyses

All hormone values were log₁₀ transformed because raw data were positively skewed and had high kurtosis. Q–Q plots of the log₁₀-transformed hormone values were examined for normality, and the resulting skew and kurtosis values fell between -1 and $+1$. The minimum sensitivity of the assays was 1.58 ng/g for fGC, and 0.10 ng/g for fDHT and fT. Therefore, the fGC values that fell below the standard curve are recorded as 1.58 ng/g ($N = 4$), while the fDHT ($N = 62$) and fT ($N = 18$) values that fell below the standard curve are recorded as 0.10 ng/g. We did this for two reasons: 1) so as not to artificially lower values for subordinates, who are the ones that primarily had near-0 values, and 2) because 0 values cannot be log₁₀ transformed.

On a few rare occasions, we collected more than one sample per male in a day or week. We included individual samples (not weekly means) if they were collected on >1 d in the week, but if more than one sample was available on any given day, we included only the first sample of the day and excluded any subsequent samples collected on the same day ($N = 3$). One fGC sample was lost during analysis, but we nonetheless included the fT and fDHT values for that sample in the analyses.

We assessed diurnal variation for each male using nonparametric independent (nonpaired) Mann–Whitney U tests because 8.1% of samples were collected after noon (mean collection time = 09:35 h \pm SD 1h49m). Most males had slightly lower fGC and fDHT levels in the afternoon but this difference was not statistically significant (mean morning vs. afternoon fGC \pm SEM: 32.6 \pm 1.8 ng/g vs. 26.0 \pm 3.9 ng/g; mean morning vs. afternoon fDHT \pm SEM: 5.6 \pm 1.5 ng/g vs. 4.4 \pm 1.0 ng/g; $P > 0.05$), whereas 6 of 14 males had higher fT values in the afternoon, but again this difference was not significant (mean morning vs. afternoon fT \pm SEM: 10.7 \pm 4.2 ng/g vs. 10.9 \pm 3.9 ng/g; $P > 0.05$). Adult male BZ had significantly lower fDHT ($U = 38.0$, $z = -2.312$, $P = 0.021$) and fT ($U = 47.0$, $z = -2.069$, $P = 0.039$) values in the afternoon (between 12h05 and 12h40, $N = 4$), and subadult male CR had significantly lower fDHT ($U = 37.5$, $z = -2.363$, $P = 0.018$) and fGC ($U = 36.0$, $z = -2.398$, $P = 0.016$) values in the afternoon (between 12h05 and 13h00, $N = 4$). We excluded the eight afternoon samples from the two males that showed a significant difference between morning and afternoon; we also excluded one fDHT and two fT outliers. Thus, the final data set comprised 983 fT samples, 980 fDHT samples, and 984 fGC samples.

We used repeated measures GLMM with the AR1 first-order autoregressive matrix and a normal identity link function. Male identity was nested within social group, and we used the individual sample number as the repeated measure for each male. Male identity nested within group was included as a random effect for the fT and fDHT

models, but we excluded random effects from the fGC models because the G and Hessian matrices were not positive. The predictor variables were the presence of periovulatory females (0 = absent, 1 = present), male age/status, as well as the interaction between the two. Male age and status were combined into a single variable (age/status) because alpha males are always adults and subordinate subadult males (SADM) are almost invariably lower ranking than subordinate adult males (ADM), though dominance hierarchies among subordinate males are not well defined (Fedigan 1993; Jack 2003; Perry 1998; Schoof *unpubl. data*). Our results are conservative because we kept all predictor variables in the models even if they were not significant, i.e., did not use backwards selection, and we used the residual method for degrees of freedom (fixed for all tests) and robust covariances to handle any violations of model assumptions. The GLMM models using the 7-d periovulatory period were a better overall fit because they had slightly lower AICs than the 5-d periovulatory period models. Because the results did not differ, we report only the results for the models using the 7-d periovulatory period.

We also examined the prediction that fT and fDHT would correlate because they are part of the same metabolic pathway and DHT is metabolized from T. Alternatively, the relationship of fT and fDHT could differ by dominance status and age owing to their different roles in secondary sexual characteristics and puberty, and the metabolism of T to DHT could thus differ by age/status. All analyses were run in IBM SPSS Statistics for Mac, version 20.0, and statistical significance was set at $P < 0.05$ for all tests.

Results

Testosterone (fT)

Mean sample fT was 33.3 ng/g (\pm SEM = 3.09, $N = 983$), while mean individual male fT was 33.03 ng/g (\pm SEM = 12.0, $N = 14$). The presence of periovulatory females and male age/status were significant predictors of log₁₀T, whereas the interaction of the two main effects was not (Table III). Males responded to the presence of periovulatory females with an increase in fT ($\beta = 0.335$, $t = 6.328$, $df = 977$, $P < 0.001$; Fig. 1). Pairwise comparisons indicate that alpha males had significantly higher fT than both subordinate adult ($\beta = 0.944$, $t = 8.472$, $df = 977$, $P < 0.001$) and subadult males ($\beta = 1.180$, $t = 11.300$, $df = 977$, $P < 0.001$); further, subordinate adult males had higher fT than subadult subordinate males ($\beta = 0.236$, $t = 2.945$, $df = 977$, $P < 0.001$; Fig. 1). Although the interaction of the presence of periovulatory females and male age/status was not statistically significant, the greatest increase in estimated mean fT was observed in alpha males, whose fT more than doubled (2.6-fold) in the presence of periovulatory females, followed by adult males with a 2.0-fold increase and subadult males with a 1.9-fold increase in fT.

Dihydrotestosterone (fDHT)

Mean sample fDHT was 25.2 ng/g (\pm SEM = 2.86, $N = 980$), while mean individual male fDHT was 24.9 ng/g (\pm SEM = 7.8, $N = 14$). The presence of periovulatory females and male age/status were significant predictors of log₁₀DHT, whereas the

Table III Generalized linear mixed effects models of log₁₀ fecal testosterone, DHT, and GCs (*Cebus capucinus*, Santa Rosa Sector, ACG, Costa Rica, 2008–2009)

Predictor	F	df	P	Effect
Testosterone	26.760	5, 977	< 0.001	
POP	40.042	1, 977	< 0.001	Present > absent
Age/status	63.923	2, 977	< 0.001	Alpha > ADM > SADM
POP * age/status	0.940	2, 977	0.391	n/a
Dihydrotestosterone	10.122	5, 974	< 0.001	
POP	20.436	1, 974	< 0.001	Present > absent
Age/status	21.981	2, 974	< 0.001	Alpha > ADM = SADM
POP * age/status	2.308	2, 974	0.100	n/a
Glucocorticoids	36.500	5, 978	< 0.001	
POP	35.395	1, 978	< 0.001	Present > absent
Age/status	11.781	2, 978	< 0.001	Alpha > ADM = SADM
POP * age/status	0.510	2, 978	0.601	n/a

POP = periovulatory period, Alpha = alpha adult male, ADM = subordinate adult male, SADM = subordinate subadult male.

interaction of the two main effects was not (Table III). The results indicate that males responded to the presence of periovulatory females with an increase in fDHT ($\beta = 0.249$, $t = 4.521$, $df = 974$, $P < 0.001$; Fig. 2). Pairwise comparisons indicate that alpha males had significantly higher fDHT than both subordinate adult ($\beta = 0.668$, $t = 4.961$, $df = 974$, $P < 0.001$) and subadult males ($\beta = 0.820$, $t = 6.608$, $df = 974$, $P < 0.001$); however, there was no difference among subordinate adult and subadult males ($\beta = 0.152$, $t = 1.486$, $df = 974$, $P = 0.137$; Fig. 2). Although the interaction of periovulatory females and male age/status was not statistically significant, the greatest increase in estimated mean fDHT was observed in alpha males, whose fDHT more than doubled (2.5-fold) in the presence of periovulatory females, followed by subadult males with a 1.6-fold increase and adult males with a 1.4-fold increase in fDHT.

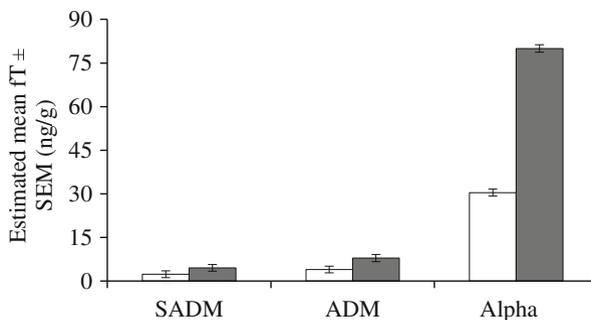


Fig. 1 GLMM estimated mean fecal testosterone \pm robust SEM in ng/g in subordinate subadult (SADM), subordinate adult (ADM), and alpha adult males, in the absence (open bars) and presence (solid bars) of periovulatory females (*Cebus capucinus*, Santa Rosa Sector, ACG, Costa Rica, 2008–2009).

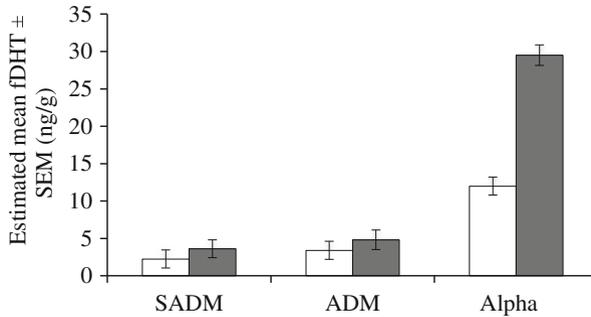


Fig. 2 GLMM estimated mean fecal DHT \pm robust SEM in ng/g in subordinate subadult (SADM), subordinate adult (ADM), and alpha adult males, in the absence (open bars) and presence (solid bars) of periovulatory females (*Cebus capucinus*, Santa Rosa Sector, ACG, Costa Rica, 2008–2009).

Relationship of fT and fDHT

Fecal T and DHT correlated significantly and positively. There was a strong positive correlation between individual male mean log₁₀T and mean log₁₀DHT across the study period (Spearman's $R = 0.960$, $P < 0.001$, one-tailed). Within each fecal sample, there was also a strong and significant positive correlation between log₁₀T and log₁₀DHT after controlling for male age/status category ($R = 0.845$, $df = 976$, $P < 0.001$, one-tailed).

Glucocorticoids (fGC)

Mean sample fGC was 60.3 ng/g (\pm SEM = 3.7, $N = 984$), while mean individual male fGC was 59.7 ng/g (\pm SEM = 4.0, $N = 14$). The presence of periovulatory females and male age/status were significant predictors of log₁₀GC, whereas the interaction of the two main effects was not (Table III). Males responded to the presence of periovulatory females with an increase in fGC ($\beta = 0.255$, $t = 5.949$, $df = 978$, $P < 0.001$; Fig. 3). Pairwise comparisons indicate that alpha males had significantly higher fGC than subordinate adult ($\beta = 0.125$, $t = 2.373$, $df = 978$, $P = 0.018$) and subadult males ($\beta = 0.173$, $t = 4.756$, $df = 978$, $P < 0.001$); however, there was no difference among subordinate adult and subadult males ($\beta = 0.048$, $t = 0.897$, $df = 978$, $P = 0.370$; Fig. 3).

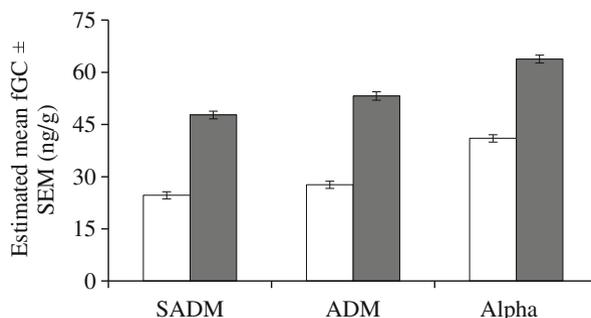


Fig. 3 Estimated mean fecal GCs \pm robust SEM in ng/g in subordinate subadult (SADM), subordinate adult (ADM), and alpha adult males, in the absence (open bars) and presence (solid bars) of periovulatory females (*Cebus capucinus*, Santa Rosa Sector, ACG, Costa Rica, 2008–2009).

The interaction of the presence of periovulatory females and male age/status was not significant, with all males having a 1.6- to 1.9-fold increase in fGC.

Discussion

We found that male androgens and GCs increase in the presence of periovulatory females (Predictions 1A and 2A supported), but that alpha males did not have disproportionate increases (Predictions 1B and 2B not supported). Increases in androgens and GCs during the mating season or in the presence of fertile females are widely reported in primates (Arlet *et al.* 2009, 2011; Bales *et al.* 2006; Bergman *et al.* 2005; Brockman *et al.* 1998; Fitchel *et al.* 2007; Girard-Buttoz *et al.* 2009; Gould and Ziegler 2007; Lynch *et al.* 2002; Miller and Maner 2010; Muller and Wrangham 2004b; Ostner *et al.* 2002, 2008a, b, 2011; Rostal *et al.* 1986; Setchell *et al.* 2008, 2010; Strier *et al.* 1999, 2003). Although such hormonal increases are often associated with concomitant increases in aggression and/or mate guarding, this is not necessarily the case because reproductive effort involves both physiological and behavioral processes (Hirschfield and Tinkle 1975) and are thus not limited to overt male competition. Aggression among coresident male white-faced capuchins is low (current study: 0.10 bouts/focal hour, Schoof *unpubl. data*, following Perry 1998 and based solely on dyadic interactions involving bites, chases, hits, lunges, push/pull, supplants, and threat faces; 0.04–0.14 bouts/focal hour at nearby Lomas Barbudal; Perry 1998), which could be interpreted to indicate low male competition and reproductive effort. However, the high degree of reproductive skew in this species suggests that male intragroup competition is high even if it is not manifested aggressively. Although the role of female choice remains poorly understood (Carnegie *et al.* 2005), it does not preclude male competition. Sperm competition has not been evaluated in this species but seems plausible given that females mate with multiple males, females have been observed removing ejaculate from their vagina, and males sometimes engage in postcopulatory courtship behaviors that may serve to delay sperm removal (Fragaszy *et al.* 2004; Manson *et al.* 1997). Although we cannot rule out the possibility that androgens increase primarily to support basic reproductive physiology, we think this is unlikely given changes in male behavior reported by Carnegie *et al.* (2005), the occurrence of nonconceptive mating in this species (Carnegie *et al.* 2006; Manson *et al.* 1997), and the unpredictability of female fertility, i.e., they are not strict seasonal breeders (Carnegie *et al.* 2011a). Rather, we interpret the androgen increase in the presence of fertile females as indicating that male reproductive effort involves behaviors such as following and grooming (Carnegie *et al.* 2005), which are less conspicuous than overt aggression. The concomitant increase in fGCs further suggests that increased male reproductive effort is associated with costs for all males. The mechanism(s) by which male white-faced capuchins increase their reproductive effort needs to be examined, especially in light of the increase in GCs in the presence of periovulatory females.

We also predicted that the presence of periovulatory females would interact with male dominance status in its effect on fT and fDHT production (Prediction 1B). In a previous study of shorter duration, we found that alpha male white-faced capuchins had higher androgens than subordinate males, even in the absence of fertile females, i.e., all females were pregnant or nursing (Schoof and Jack 2013). Consistent with these

previous findings, the present study indicates that alpha males had higher fT and fDHT levels than subordinates. Given that alpha males sire the majority of group offspring (Jack and Fedigan 2006; Muniz *et al.* 2010), this response is not unexpected. Although alpha males did have a qualitatively greater fT and fDHT, this was not statistically significant (Figs. 1 and 2). In contrast to our prediction, all males—regardless of age and dominance status—experienced a rise in fT and fDHT levels in the presence of fertile females. Among ring-tailed lemurs, only those males most actively engaged in aggressive competition have an increase in androgens (*Lemur catta*: Gould and Ziegler 2007). In species with high mating/reproductive skew and where dominance status correlates positively to androgens, male competition generally involves high levels of aggression, e.g., *Mandrillus sphinx* (Charpentier *et al.* 2005; Setchell *et al.* 2008), *Papio cynocephalus* (Gesquiere *et al.* 2011), and *Pan troglodytes* (Muller and Wrangham 2004a; Wroblewski *et al.* 2009). Reproductive effort associated with aggression may be higher than effort associated with more covert forms of competition. The disproportionate increase in the androgens of alpha male white-faced capuchins reported here may lack statistical significance because they compete primarily through nonaggressive means.

Our prediction that alpha males would have a disproportionate increase in fGC levels in the presence of periovulatory females, i.e., interaction between dominance and female fertility, was also not supported (Prediction 2B). Our previous research indicated that there may be costs associated with dominance, because two of three alpha males had higher fGCs than their subordinates (Schoof and Jack 2013), and in a case study, male fGC levels rose only *after* attaining alpha status (Schoof *et al.* 2011). In the present study, we found that alpha males had higher fGC levels than subordinate males, indicating the higher allostatic load and costs of being an alpha male. However, alpha males did not have a greater fGC increase than subordinate males in the presence of periovulatory females (Fig. 3). To understand better the costs of male reproductive effort and alpha status, variation in sexual behavior, agonism, and affiliation between males of different ranks should be examined in relation to androgens and GCs (Van Belle *et al.* 2009).

We found that the overall patterns of T and DHT were similar, likely due to the strong positive correlation between these androgens. Individual mean male fT and fDHT correlated strongly and positively, as were the intrasample levels of fT and fDHT even after controlling for male age/status, although adult subordinate males had higher fT, but not fDHT, than subadult subordinates. Research on captive male crab-eating macaques, cotton-top tamarins, and juvenile and adolescent—but not adult—male orangutans found that T and DHT follow similar developmental trajectories (Ginther *et al.* 2002; Maggioncalda *et al.* 1999; Meusy-Dessolle and Dang 1985) and follow similar increases during the mating season in Japanese macaques (Rostal *et al.* 1986). Therefore, it is not surprising that the overall patterns of fT and fDHT excretion were similar in white-faced capuchins, but it is not clear how to distinguish differences, if any, in the behavioral effects of T and DHT. The effect sizes for fT were larger than for fDHT, suggesting that two possibilities are likely: 1) the influence of social factors is greater on T, and/or 2) smaller amounts of DHT play larger roles owing to its potency. Future research should focus on variation in the conversion of T to DHT in relation to behavioral differences and developmental milestones (Ginther *et al.* 2002), but are beyond the scope of this article. One particular area of interest is how DHT is associated with the development of secondary sexual characteristics.

Developing adolescent male orangutans have higher DHT levels than arrested males (Maggioncalda *et al.* 1999). Although differences between alpha and subordinate male white-faced capuchins are not as marked as they are in orangutans, alpha males are noticeably more robust than their subordinates. The existence of a correlation between DHT levels and morphometric measurements of robusticity in a wide range of species would allow us to evaluate the hypothesis that the expression of male secondary sexual characteristics occurs along a gradient and is more prevalent than generally acknowledged (Dixson 2012).

Our results also indicate that males respond to female ovulation despite the absence of obvious physical or behavioral signals. This is consistent with Carnegie and colleagues' (2005) report that males followed and groomed periovulatory females more often than nonovulatory females, and that observed copulations involved only periovulatory females. Taken together, these data suggest that males are able to detect ovulation in female white-faced capuchins. Male common marmosets respond to olfactory cues of female ovulation with increased T (*Callithrix jacchus*: Ziegler *et al.* 2005). This effect has also been observed in humans, where ovulatory cues appear to "leak" through and influence male behavior (Gangestad and Thornhill 2008) and T responsiveness (Miller and Maner 2010).

Conclusions

Alpha male white-faced capuchins sire the majority of group offspring; thus, the reproductive benefits of attaining high dominance status are substantial. These reproductive benefits do not, however, come without a cost. In comparison with subordinate males, alpha males invest greater reproductive effort than subordinate males, as measured by fecal T and DHT, and they experience greater stress, as measured by GC levels. All males, regardless of dominance status and age, experience an endocrine response to the presence of fertile females. Specifically, males increased T and DHT production in the presence of periovulatory females, indicating that reproductive effort increased when females are fertile. Furthermore, increased reproductive effort in the presence of fertile females is associated with GC elevations, indicating that allostatic load increases for all males regardless of dominance status. Thus, even in the absence of obvious physical and behavioral signs of ovulation, males produce an endocrine response to fertile females.

Acknowledgments This study was supported by funds from the Fonds Québécois de la Recherche sur la Nature et les Technologies (V. A. M. Schoof), LSB Leakey Foundation (V. A. M. Schoof), National Geographic Society (V. A. M. Schoof, grant 8652-09), National Science Foundation (V. A. M. Schoof, grant 0926039), Tulane University's Stone Center for Latin American Studies (V. A. M. Schoof; K. M. Jack) and Research Enhancement Fund (K. M. Jack), and a grant to the WNPRC from the National Institutes of Health (T. E. Ziegler, grant RR000167). We thank the many field assistants who were involved in data collection: T. Busch, J. Rinderknecht, S. Fatkin, D. Broome, A-S. Pellier, A. Tecza, S. Millus, L. Wilkins, R. Jackson, K. Catanese, and A. Alvarez, and J. Addicott, who provided data management consulting. We are grateful to Dan Wittwer from the WNPRC for hormone assay validations and for guidance and assistance in conducting hormone analyses. We also acknowledge the administrators of the Área de Conservación Guanacaste (especially Roger Blanco Segura) for allowing us to conduct research in the park through the present day. Finally, we thank Alexander Georgiev and Melissa Emery Thompson for inviting us to participate in this special issue, and two anonymous reviewers and the editor-in-chief for their constructive criticisms.

References

- Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Salzman, W., Snowdon, C. T., Ziegler, T. E., Banjevic, M., Garland, T. J., & Sapolsky, R. M. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, *43*, 67–82.
- Arlet, M. E., Grote, M. N., Molleman, F., Isbell, L. A., & Carey, J. R. (2009). Reproductive tactics influence cortisol levels in individual male gray-cheeked mangabeys (*Lophocebus albigena*). *Hormones and Behavior*, *55*, 210–216.
- Arlet, M. E., Kaasik, A., Molleman, F., Isbell, L., Carey, J. R., & Mänd, R. (2011). Social factors increase fecal testosterone levels in wild male gray-cheeked mangabeys (*Lophocebus albigena*). *Hormones and Behavior*, *59*, 605–611.
- Bales, K. L., French, J. A., McWilliams, J., Lake, R. A., & Dietz, J. M. (2006). Effects of social status, age, and season on androgen and cortisol levels in wild male golden lion tamarins (*Leontopithecus rosalia*). *Hormones and Behavior*, *49*, 88–95.
- Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2006). Testosterone predicts future dominance rank and mating activity among male chacma baboons. *Behavioral Ecology and Sociobiology*, *59*, 469–479.
- Bergman, T. J., Beehner, J. C., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2005). Correlates of stress in free-ranging male chacma baboons, *Papio hamadryas ursinus*. *Animal Behaviour*, *70*, 703–713.
- Braude, S., Tang-Martinez, Z., & Taylor, G. (1999). Stress, testosterone, and the immunoredistribution hypothesis. *Behavioral Ecology*, *10*, 345–350.
- Brockman, D. K., Whitten, P. L., Richard, A. F., & Schneider, A. (1998). Reproduction in free ranging male *Propithecus verreauxi*: The hormonal correlates of mating and aggression. *American Journal of Physical Anthropology*, *105*, 137–151.
- Carnegie, S. D., Fedigan, L. M., & Ziegler, T. E. (2005). Behavioral indicators of ovarian phase in white-faced capuchins (*Cebus capucinus*). *American Journal of Primatology*, *67*, 51–68.
- Carnegie, S. D., Fedigan, L. M., & Ziegler, T. E. (2006). Post-conceptive mating in white-faced capuchins, *Cebus capucinus*: Hormonal and sociosexual patterns of cycling, noncycling, and pregnant females. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior, and conservation* (pp. 387–409). New York: Springer Science + Business Media.
- Carnegie, S. D., Fedigan, L. M., & Melin, A. D. (2011a). Reproductive seasonality in female capuchins (*Cebus capucinus*) in Santa Rosa (Area de Conservación Guanacaste), Costa Rica. *International Journal of Primatology*, *32*, 1076–1090.
- Carnegie, S. D., Fedigan, L. M., & Ziegler, T. E. (2011b). Social and environmental factors affecting fecal glucocorticoids in wild, female white-faced capuchins (*Cebus capucinus*). *American Journal of Primatology*, *73*, 861–869.
- Charpentier, M., Peignot, P., Hossaert-McKey, M., Gimenez, O., Setchell, J. M., & Wickings, E. J. (2005). Constraints on control: Factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). *Behavioral Ecology*, *16*, 614–623.
- Creel, S. (2001). Social dominance and stress hormones. *Trends in Ecology and Evolution*, *16*, 491–497.
- Di Fiore, A. (2003). Molecular genetic approaches to the study of primate behavior, social organization, and reproduction. *Yearbook of Physical Anthropology*, *46*, 62–99.
- Dixon, A. F. (2012). *Primate sexuality: Comparative studies of the prosimians, monkeys, apes, and humans* (2nd ed.). Oxford: Oxford University Press.
- Fedigan, L. M. (1993). Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology*, *14*, 853–877.
- Fedigan, L. M., Carnegie, S. D., & Jack, K. M. (2008). Predictors of reproductive success in female white-faced capuchins. *American Journal of Physical Anthropology*, *137*, 82–90.
- Fedigan, L. M., & Jack, K. M. (2012). Tracking monkeys in Santa Rosa: Lessons from a regenerating tropical dry forest. In P. M. Kappeler & D. Watts (Eds.), *Long-term field studies of primates* (pp. 165–184). New York: Springer Science + Business Media.
- Fichtel, C., Kraus, C., Ganswindt, A., & Heistermann, M. (2007). Influence of reproductive season and rank on fecal glucocorticoid levels in free-ranging male Verreaux's sifakas (*Propithecus verreauxi*). *Hormones and Behavior*, *51*, 640–648.
- Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: The biology of the genus Cebus*. Cambridge, U.K.: Cambridge University Press.

- Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society Biological Sciences*, 275, 991–1000.
- Gesquiere, L. R., Learn, N. H., Carolina, M., Simao, M. C. M., Onyango, P. O., Alberts, S. C., & Altmann, J. (2011). Life at the top: Rank and stress in wild male baboons. *Science*, 333, 357–360.
- Ginther, A. J., Ziegler, T. E., Carlson, A. A., & Snowdon, C. T. (2002). Sexual development in cotton-top tamarin males. *Biology of Reproduction*, 66, 282–290.
- Ginther, A. J., Ziegler, T. E., & Snowdon, C. T. (2001). Reproductive biology of captive male cotton-top tamarin monkeys as a function of social environment. *Animal Behaviour*, 61, 65–78.
- Girard-Buttoz, C., Heistermann, M., Krummel, S., & Engelhardt, A. (2009). Seasonal and social influences fecal androgen and glucocorticoid excretion in wild male long-tailed macaques (*Macaca fascicularis*). *Physiology and Behavior*, 98, 168–175.
- Gould, L., & Ziegler, T. E. (2007). Variation in fecal testosterone levels, inter-male aggression, dominance rank and age during mating and post-mating periods in wild adult male ring-tailed lemurs (*Lemur catta*). *American Journal of Primatology*, 69, 1–15.
- Gould, L., Ziegler, T. E., & Wittwer, D. J. (2005). Effects of reproductive and social variables on fecal glucocorticoid levels in a sample of adult male ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Reserve, Madagascar. *American Journal of Primatology*, 67, 5–23.
- Goymann, W., & Wingfield, J. C. (2004). Allostatic load, social status and stress hormones: The costs of social status matter. *Animal Behaviour*, 67, 591–602.
- Griffin, J. E., & Wilson, J. D. (1998). Disorders of the testis and male reproductive tract. In J. D. Wilson, D. W. Foster, H. M. Kronenberg, & P. R. Larsen (Eds.), *Williams textbook of endocrinology* (9th ed., pp. 819–875). Philadelphia: W. B. Saunders.
- Hirschenhauser, K., & Oliveira, R. I. (2006). Social modulation of androgens in vertebrates: meta-analyses of the challenge hypothesis. *Animal Behaviour*, 71, 265–277.
- Hirschfeld, M. F., & Tinkle, D. W. (1975). Natural selection and the evolution of reproductive effort. *Proceedings of the National Academy of Sciences of the USA*, 72, 2227–2231.
- Jack, K. M. (2003). Explaining variation in affiliative relationships among male white-faced capuchins (*Cebus capucinus*). *Folia Primatologica*, 74, 1–16.
- Jack, K. M., & Fedigan, L. M. (2006). Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). In A. Estrada, P. Garber, M. A. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior and conservation* (pp. 367–386). New York: Springer Science + Business Media.
- Kraus, C., Heistermann, M., & Kappeler, P. M. (1999). Physiological suppression of sexual function of subordinate males: A subtle form of intrasexual competition among male sifakas (*Propithecus verreauxi*)? *Physiology and Behavior*, 66, 855–861.
- Lynch, J. W., Ziegler, T. E., & Strier, K. B. (2002). Individual and seasonal variation in fecal testosterone and cortisol levels of wild male tufted capuchin monkeys, *Cebus paella nigrilus*. *Hormones and Behavior*, 41, 275–287.
- Maggioncalda, A., Sapolsky, R., & Czekala, N. (1999). Reproductive hormone profiles in captive male orangutans: Implications for understanding developmental arrest. *American Journal of Physical Anthropology*, 109, 19–32.
- Majolo, B., Lehmann, J., de Bortoli Vizioli, A., & Schino, G. (2012). Fitness-related benefits of dominance in primates. *American Journal of Physical Anthropology*, 147, 652–660.
- Manson, J. H., Perry, S., & Parish, A. R. (1997). Nonconceptive sexual behavior in bonobos and capuchins. *International Journal of Primatology*, 18, 767–786.
- McEwen, B. S., & Wingfield, J. C. (2003). The concept of allostasis in biology and biomedicine. *Hormones and Behavior*, 43, 2–15.
- Meusy-Dessolle, N., & Dang, D. C. (1985). Plasma concentrations of testosterone, dihydrotestosterone, delta 4-androstenedione, dehydroepiandrosterone and oestradiol-17 beta in the crab-eating monkey (*Macaca fascicularis*) from birth to adulthood. *Journal of Reproduction and Fertility*, 74, 347–359.
- Miller, S. L., & Maner, J. K. (2010). Scent of a woman: men's testosterone responses to ovulatory ovulation cues. *Psychological Science*, 21, 276–284.
- Muller, M. N., & Wrangham, R. W. (2004a). Dominance, aggression and testosterone in wild chimpanzees: A test of the “challenge hypothesis”. *Animal Behaviour*, 67, 113–123.
- Muller, M. N., & Wrangham, R. W. (2004b). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, 55, 332–340.
- Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., Gros-Louis, J., & Vigilant, L. (2010). Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. *American Journal of Primatology*, 72, 1118–1130.

- Ostner, J., Kappeler, P. M., & Heistermann, M. (2002). Seasonal variation and social correlates of androgen excretion in male redfronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology*, *52*, 485–495.
- Ostner, J., Kappeler, P. M., & Heistermann, M. (2008a). Androgen and glucocorticoid levels reflect seasonally occurring social challenges in male redfronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology*, *62*, 627–638.
- Ostner, J., Heistermann, M., & Schülke, O. (2008b). Dominance, aggression and physiological stress in wild male Assamese macaques (*Macaca assamensis*). *Hormones and Behavior*, *54*, 613–619.
- Ostner, J., Heistermann, M., & Schülke, O. (2011). Male competition and its hormonal correlates in Assamese macaques (*Macaca assamensis*). *Hormones and Behavior*, *59*, 105–113.
- Perry, S. (1996). Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology*, *17*, 309–330.
- Perry, S. (1997). Male–female relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour*, *134*, 477–510.
- Perry, S. (1998). Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour*, *135*, 139–172.
- Plant, T. M., & Witchel, S. F. (2006). Puberty in non-human primates and humans. In J. D. Neill (Ed.), *Knobil and Neill's physiology of reproduction* (3rd edition, Vol. 2, pp. 2177–2230). St. Louis: Elsevier Academic Press.
- Rose, L. M. (1998). *Behavioral ecology of white-faced capuchins (Cebus capucinus) in Costa Rica*. PhD dissertation, Washington University, St. Louis.
- Rose, L. M., & Fedigan, L. M. (1995). Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. *Animal Behaviour*, *49*, 63–70.
- Rostal, D. C., Glick, B. B., Eaton, G. G., & Resko, J. A. (1986). Seasonality of adult male Japanese macaques (*Macaca fuscata*): Androgens and behavior in a confined troop. *Hormones and Behavior*, *20*, 452–462.
- Sapolsky, R. M. (1993). The physiology of dominance in stable versus unstable social hierarchies. In W. A. Mason & S. P. Mendoza (Eds.), *Primate social conflict* (pp. 171–204). Albany, NY: State University of New York Press.
- Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science*, *308*, 648–652.
- Schoof, V. A. M., & Jack, K. M. (2013). The association of intergroup encounters, dominance status, and fecal androgen and glucocorticoid profiles in wild male white-faced capuchins (*Cebus capucinus*). *American Journal of Primatology*, *75*, 107–115.
- Schoof, V. A. M., & Jack, K. M. (in press). Male social bonds: Strength and quality among coresident white-faced capuchin monkeys (*Cebus capucinus*). *Behaviour*.
- Schoof, V. A. M., Jack, K. M., & Carnegie, S. D. (2011). Rise to power: A case study of male fecal androgen and cortisol levels before and after a non-aggressive rank change in a group of wild white-faced capuchins (*Cebus capucinus*). *Folia Primatologica*, *82*, 299–307.
- Setchell, J. M., Smith, T., Wickings, E. J., & Knapp, L. A. (2008). Social correlates of testosterone and ornamentation in male mandrills. *Hormones and Behavior*, *54*, 365–372.
- Setchell, J. M., Smith, T., Wickings, E. J., & Knapp, L. A. (2010). Stress, social behaviour, and secondary sexual traits in a male primate. *Hormones and Behavior*, *58*, 720–728.
- Stocco, D. M., & McPhaul, J. M. (2006). Physiology of testicular steroidogenesis. In J. D. Neill (Ed.), *Knobil and Neill's physiology of reproduction* (3rd ed., pp. 977–1016). St. Louis: Elsevier.
- Strier, K. B., Lynch, J. W., & Ziegler, T. E. (2003). Hormonal changes during the mating and conception seasons of wild Northern muriquis (*Brachyteles arachnoides hypoxanthus*). *American Journal of Primatology*, *61*, 85–99.
- Strier, K. B., Ziegler, T. E., & Wittwer, D. J. (1999). Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis (*Brachyteles arachnoides*). *Hormones and Behavior*, *35*, 125–134.
- Surbeck, M., Deschner, T., Weltring, A., & Hohmann, G. (2012). Social correlates of variation in urinary cortisol in wild male bonobos (*Pan paniscus*). *Hormones and Behavior*, *62*, 27–35.
- Van Belle, S., Estrada, A., Ziegler, T. E., & Strier, K. B. (2009). Social and hormonal mechanisms underlying male reproductive strategies in black howler monkeys (*Alouatta pigra*). *Hormones and Behavior*, *56*, 355–363.
- van Schaik, C. P., van Noordwijk, M. A., & Nunn, C. L. (1999). Sex and social evolution in primates. In P. Lee (Ed.), *Comparative primate socioecology* (pp. 204–231). Cambridge, U.K.: Cambridge University Press.
- Wallen, K. (2005). Hormonal influences on sexually differentiated behavior in nonhuman primates. *Frontiers in Neuroendocrinology*, *26*, 7–26.
- Weiner, J. S., Marcelli, M., & Lamb, D. J. (1996). Molecular determinants of sexual differentiation. *World Journal of Urology*, *14*, 278–294.

- Wingfield, J. C., Hegner, R. E., Dufty, A. M. J., & Ball, G. F. (1990). The “challenge hypothesis”: Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, *136*, 829–846.
- Wingfield, J. C., Lynn, S. E., & Soma, K. K. (2001). Avoiding the ‘costs’ of testosterone: ecological basis of hormone-behavior interactions. *Brain, Behavior and Evolution*, *57*, 239–251.
- Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, *77*, 873–885.
- Ziegler, T. E., Bridson, W., Snowdon, C., & Eman, S. (1987). Urinary gonadotropin and estrogen excretion during the postpartum estrus, conception, and pregnancy in the cotton-top tamarin (*Saguinus oedipus oedipus*). *American Journal of Primatology*, *12*, 127–140.
- Ziegler, T. E., Schultz-Darken, N. J., Scott, J. J., Snowdon, C. T., & Ferris, C. F. (2005). Neuroendocrine response to female ovulatory odors upon social condition in male common marmosets, *Callithrix jacchus*. *Hormones and Behavior*, *47*, 56–64.