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RESEARCH ARTICLE

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Social and demographic correlates of male androgen levels in wild white-faced capuchin monkeys (*Cebus capucinus*)

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The Challenge Hypothesis, designed originally to explain the patterning of competitive behavior and androgen levels in seasonally breeding birds, predicts that males will increase their androgen levels in order to become more competitive in reproductive contexts. Here we test predictions derived from the Challenge Hypothesis in white-faced capuchin monkeys (*Cebus capucinus*), a species that has somewhat seasonal reproduction. We analyzed demographic and hormonal data collected over a 5.25-year period, from 18 males in nine social groups living in or near Lomas Barbudal Biological Reserve, Costa Rica. Alpha males had higher androgen levels than subordinates. Contrary to our predictions, neither the number of breeding-age males nor the number of potentially fertile females was obviously associated with androgen levels. Furthermore, male androgen levels were not significantly linked to social stability, as measured by stability of male group membership or recency of change in the alpha male position. Androgen levels changed seasonally, but not in a manner that had an obvious relationship to predictions from the Challenge Hypothesis: levels were generally at their lowest near the beginning of the conception season, but instead of peaking when reproductive opportunities were greatest, they were at their highest near the end of the conception season or shortly thereafter. This lack of correspondence to the timing of conceptions suggests that there may be ecological factors not yet identified that influence ifA levels. We expected that the presence of offspring who were young enough to be vulnerable to infanticide during an alpha male takeover might influence androgen levels, at least in the alpha male, but this variable did not significantly impact results.

KEYWORDS
challenge hypothesis, dominance, endocrinology, primates, social stability

1 | INTRODUCTION

In many socially living animal species, high dominance rank is associated with higher reproductive success (Bercovitch, 1991; Cowlishaw & Dunbar, 1991; Ellis, 1995). However, the strength of this relationship depends on a variety of social, demographic, and environmental factors, such as the stability of the group (Alberts, Buchan, & Altmann, 2006), alpha male tenure duration (Alberts et al., 2003; Muniz et al., 2010), group composition, that is, the number of males and females co-residing (Alberts et al., 2006; Boesch, Kohou, Néné, & Vigilant, 2006; Charpentier, 2005; Cowlishaw & Dunbar, 1991, 1992; Muniz et al., 2010; Ostner, Nunn, & Schülke, 2008), and the degree of estrous synchrony (Ostner et al., 2008). In species in which dominance rank and reproductive success are positively correlated, traits that are associated with attaining and maintaining high dominance rank should be under positive selection (Ellis, 1995). Such traits include physical strength, fighting abilities, and body mass, all of which are known to be positively related to androgen levels (Bribiescas, 2001). Therefore, in species where gaining and maintaining high dominance rank depend mainly on winning aggressive interactions with male competitors, dominant males are expected to have higher androgen levels than subordinate males (Muller & Wrangham, 2004). Such a positive association between androgen levels and high dominance rank has been confirmed in a number of animal species (carnivores: Creel, Creel, Mills, & Monfort, 1997; primates: Gesquiere et al., 2011; Girard-Buttoz et al., 2015; Rose, Holaday, & Bernstein, 1971; Setchell, Smith, Wickings, & Knapp, 2008; Zucker, 1996; review: Mazur, 1976). Species in which androgen levels were not correlated with dominance were characterized by lacking either: (a) a clear dominance hierarchy (Strier, Ziegler, & Wittwer, 1999); (b) rank related differences in male-male aggression; or (c) aggressive competition over mates (carnivores: Carlson et al., 2004; Dloniak, French, & Holekamp, 2006; primates: Barrett, Shimizu, Bardi, Asaba, & Mori, 2002; Huck, Löttker, Heymann, & Heistermann, 2005; Nieuwenhuijsen, de Neef, Van der Werff ten Bosch, & Slob, 1987; Surbeck, Deschner, Schubert, Weltring, & Hohmann, 2012). This indicates that in species in which high dominance rank does not allow better access to mating opportunities, investing in androgen levels constantly elevated above breeding levels is not beneficial. Within- and between-species variation in androgen levels depends on several variables, such as the social and the mating system, how males achieve and maintain high dominance rank, how males acquire mating access to fertile females, and, finally, on the degree of paternal investment. The most prominent framework addressing drivers of male androgen levels is the “Challenge Hypothesis” (Wingfield, Hegner, Dufty, & Ball, 1990). Originally formulated to describe changes in androgen levels of seasonally breeding birds, it suggests that male androgen levels should be high during territory and mate acquisition (to facilitate aggressive behaviors), but low during periods of paternal investment (to facilitate care behaviors), and that male androgen levels can be elevated to a physiological maximum if needed (e.g., to defend territory, mate, or offspring) (Wingfield et al., 1990). The Challenge Hypothesis was adapted and tested for a variety of vertebrate taxa including primates (Hirschenhauser & Oliveira, 2006; Muller, 2016). In detail, (a) male androgen levels should be increased during the presence of fertile females; (b) elevated male androgen levels should be related to aggressive rather than to copulatory behavior; and (c) higher ranking males should have higher androgen levels (Muller & Wrangham, 2004).

As permanently elevated androgen levels can be energetically costly and suppress immune function, investing in elevated androgen levels should only be done when beneficial (Anestis, 2010). Thus, the relationship between androgen levels should be most pronounced during periods of social instability, that is, when high dominance rank is achieved or must be defended against male competitors. Higher androgen levels during socially unstable periods have been reported for rhesus macaques, *Macaca mulatta* (Higham, Heistermann, & Maestripieri, 2013) and bearded capuchins, *Sapajus libidinosus* (Mendonça-Furtado et al., 2014). Social instability can be a consequence of the threat of new immigrating males or alpha male turnover, which could increase the potential for young infants to be killed. Such situation dependent infanticide can be an adaptive strategy to increase the reproductive success of the infanticidal males (van Schaik & Janson, 2000). Consequently, the need for potential fathers to protect dependent offspring could be accompanied by elevated androgen levels when dependent infants are present, as was shown, for example, in vervet monkeys, *Cercopithecus aethiops* (Whitten & Turner, 2004) and redfronted lemurs, *Eulemur fulvus rufus* (Ostner, Kappeler, & Heistermann, 2002). However, males of many New World monkey species engage in direct paternal care (Wright, 1990), and the Challenge Hypothesis generates the countervailing prediction that androgen levels will be low in males that are directly caring for infants. Some findings from primates (e.g., black tufted-ear marmosets, *Callithrix kuhlii* Nunes, Fite, & French, 2000) support this prediction. In the present study we test predictions from the Challenge Hypothesis in the white-faced capuchin monkey, a highly social primate species.

1.1 | General features of white-faced capuchin monkeys

White-faced capuchins (*Cebus capucinus*) live in social groups of one or more adult males, several females, and their offspring. While mean tenure duration of alpha males at Lomas Barbudal is 0.98 years and therefore comparable to other primate species (chacma baboons, *Papio cynocephalus ursinus*: 0.54 years (Palombit et al., 2000); mantled howling monkeys, *Alouatta palliata*: 2.73 years (Glander, 1992); hanuman langurs, *Presbytis entellus*: 2.2 years (Sommer & Rajpurohit, 1989)), individual males can have extremely long alpha tenures of up to 18 years, leading to a situation in which the alpha male is in place long enough to be co-residing with his adult daughters, and perhaps even grand-daughters—a situation that is quite rare among primates (Perry, 2012). Multi-year periods of alpha male stability and low mortality are punctuated by brief periods of male migration, frequent alpha male turnover, and infanticide, until alpha male stability has once again been achieved. White-faced capuchins do not exhibit sharp breeding seasonality, but births tend to be clustered within a 6-month period (Carnegie, Fedigan, & Melin, 2011; Perry, Godoy, & Lammers, 2012). Although copulations are broadly distributed across males, most of these are non-conceptive, and the majority of offspring (62–79%) are sired by the alpha male (Muniz et al., 2006, 2010). This high degree of reproductive skew is surprising, given the virtual absence of mate guarding and consortship in this species (Jack & Fedigan, 2006; Muniz et al., 2010; Perry, 2012; Perry & Manson, 2008). Overt physical male-male competition over immediate access to estrous females is rare, and alpha males rarely interrupt subordinate males’ copulations (Fedigan & Jack, 2013; Perry & Manson, 2008). Thus, it has been suggested that alpha males might use more subtle forms of mate guarding or that female choice might shape mating patterns (Janson, 1984; Jack & Fedigan, 2006). Although males do not compete directly over copulations, they do compete aggressively for the alpha position, and are often wounded while trying to immigrate into a group (Perry & Manson, 2008). Conflicts with other males are the primary source of mortality in adult males (responsible for 58–83% of adult male deaths) (Perry, 2012), and infanticide occurs in the wake of alpha male turnovers (Fedigan, 2003; Perry et al., 2012). White-faced capuchin monkeys show a high degree of alloparental care, which includes allonursing by other females, but also the carrying of infants by all group members, including males (Perry, 2012).

1.2 | White-faced capuchins and endocrine correlates

Research on white-faced capuchins at Santa Rosa National Park has found that alpha males had higher androgen levels than subordinate males (Jack et al., 2014; Schoof & Jack, 2013; Schoof, Jack, & Carnegie, 2011; Schoof, Jack, & Ziegler, 2013), and in the presence of periovulatory females, androgen levels of all males increased, with alpha male levels rising more (Schoof et al., 2013). Androgen levels correlated with rates of intergroup encounters, but the alpha male had a more pronounced increase of androgen levels than did subordinate males (Schoof & Jack, 2013). However, the effect of the presence of periovulatory females on male androgen levels disappeared when environmental factors (i.e., photoperiod, food availability, temperature, and rainfall) were included in the analysis, suggesting that environmental factors are more influential than social factors (Schoof et al., 2016). In their analysis, the influence of general factors such as group stability, variation in group composition, or alpha male identity, could not be investigated due to the limited number of individuals and groups examined, and the cross-sectional character of the studies. Overcoming the variability in specific patterns of group dynamics, in addition to variation due to seasonality, necessitates the study of a larger number of groups over a long study period. The aim of our study was to investigate how group composition, infanticide susceptibility, dominance rank, and group stability, influence androgen levels of wild adult male white-faced capuchin monkeys, while controlling for individual age, diurnal effects, seasonality, and individual and group identity. Including 18 males over a 5.25-year period, as they migrated in and out of nine social groups, allowed us to control for inter-individual differences across a variety of contexts. Specifically, we made the following predictions:

1. Alpha males will have higher androgen levels than subordinate males.
2. The number of males within a group will be positively correlated with male androgen levels.
3. Males will have higher androgen levels in the presence of potentially fertile females.
4. Male androgen levels will be affected by the stability of the alpha male position, as reflected by the duration the current alpha has held his position (i.e., male androgen levels will be higher in the wake of an alpha male turnover).
5. Androgen levels will be higher in males who have shorter histories of co-residence with their male group-mates, for example, due to immigration.
6. The presence of newborn infants will influence male androgen levels (in this case, it is not clear whether newborns are expected to increase androgen levels to prepare males to defend infants from potentially infanticidal males, or reduce androgen levels, to better prepare males for infant care).

2 | METHODS

2.1 | Study site and subjects

Demographic data and fecal samples were collected by Susan Perry and research assistants at the Lomas Barbudal Monkey Project, a project begun in 1990 (Perry et al., 2012). The site is a highly seasonal tropical dry forest in Guanacaste, Costa Rica, that includes Lomas Barbudal Biological Reserve, Brin d'Amor, and Pelon de la Bajura ranches, and adjacent lands. The wet season extends from mid-May to November, and the dry season from December to May (for further description of the field site see Frankie, Vinston, Newstrom, & Barthell (1988)). The analysis described in this paper was based on fecal samples and demographic and behavioral data, collected from males residing in ten multi-male, multi female social groups. Fecal samples used for hormonal measurements were collected between October 2006 and December 2011, but the analysis used social group composition data from January 2004 to December 2011 (see Supplementary table S1 for detailed information) and data such as birth dates collected from the beginning of the project (1990). All study groups were well habituated to researcher presence and continuously monitored year-round. All data collection procedures were approved by UCLA's Animal Research Committee, protocol 2005–084, and permits were obtained from the relevant Costa Rican authorities (i.e., SINAC and MINAET). The research adhered to Costa Rican laws and to the ASP principles for the ethical treatment of nonhuman primates.

2.2 | Data collection

We measured immunoreactive fecal androgen (ifA) levels in 577 fecal samples from 18 adult males, all of whom were part of Perry's long-term study. Median age was 13.32 years (range: 10–31.31 years). Six samples were discarded from our dataset, as the concentration of the samples was below the sensitivity limit of the assay used. Between January 2004 and December 2011, monkeys were censused at a median rate of 7 days/month (quartiles: 4, 13) (see also Supplementary table S1 for detailed information on group observation hours per day).

2.3 | Hormonal analyses

2.3.1 | Sample processing in the field

Fecal samples were collected immediately following defecation using latex gloves, transported in thermos cans with ice packs for the duration of the day, and immediately stored at −20°C in a freezer after arriving in camp. Within 1 month, samples were thawed, stirred, and dried in an oven for around 3 hr at 95°C. Plant and insect material were removed from the samples, and samples were ground and stored in whirl packs at room temperature until they were shipped to the Max Planck Institute for Evolutionary Anthropology (MPI EVA) in Leipzig, Germany. There, fecal samples were stored at −20°C until further extraction and measurement.

2.3.2 | Sample processing in the lab

Steroid hormones were extracted from dried feces as described by Heistermann, Finke, and Hodges (1995). In brief, 3 ml of 80% methanol were added to 0.1 g dried fecal matter, shaken for 15 min, and centrifuged at 4,400 rpm for 10 min. The supernatant was decanted into a fresh vial, the procedure was repeated with another 3 ml of 80% methanol, and the supernatant was combined with the first one. Subsequently, 500 μl of fecal extract were solvolyzed (Ziegler, 1996), dried in an evaporator at 45°C under a gentle stream of compressed air, reconstituted in 250 μl ethanol (70%), and stored at −20°C until assayed.

2.3.3 | Enzyme immunoassays (EIA)

We used a Testosterone EIA (antibody R156/7) provided by Coralie Munro, UCD, to measure immunoreactive androgens in fecal extracts. Cross-reactivities for this testosterone assay were reported previously by Ginther, Ziegler, and Snowdon (2001), and this assay had previously been used to measure fecal androgen levels in white-faced capuchins (Jack et al., 2014; Schoof et al., 2013, 2016; Schoof & Jack, 2013). Samples and standards were run in duplicates and repeated when the optical densities of duplicates differed by more than 10% or when values were outside the linear range of the assay. Hormonal results were calculated in ng per g dried feces. Inter-assay coefficients of variance (CV) of quality controls of high and low concentrations were 9.33% and 13.35% and intra-assay CV's were 6.60% and 13.00%, respectively. A serially diluted pool sample was assayed and resulted in a curve parallel to the standard curve. Mean extraction efficiency of four sample-pools (each consisting of five different samples) was 89.67% (range: 76.87–100.14%) and mean assay accuracy was 99.37% (range: 90.14–111.41%). An immunogram confirmed the cross-reactivities of the testosterone assay previously given by Ginther et al. (2001).

2.3.4 | Definition of variables

To statistically analyze our data we had to operationalize several of the key predictors in our models. These comprised the co-residence score and the lowest co-residence score (two measures to assess social stability), the number of males and potentially fertile females, the alpha male tenure duration (a log-transformed measure to assess rank stability), and the threat of infanticide. The co-residence score was an individual measure based on the average dyadic duration of co-residence that the male had with each of his other male group-mates who were >7 years old, varying continuously from 0 (for males who were totally unfamiliar with the other males) to 1 (for males who had been in groups with completely stable male membership for at least 135 consecutive days). The lowest co-residence score was the lowest dyadic co-residence score between any two males >7 years old in that same group; this measure was designed to represent the social chaos that might ensue from the immigration of one or more males, even if an individual had multiple long-term relationships with other residents. The infanticide risk measure was basically a measure of the prevalence of young (i.e., infanticide-vulnerable) infants in the group, weighted more heavily toward younger infants; this measure did not take into account paternity of the infants. A more detailed description of each variable is given in the Supplementary information. We defined males to be subadult when between seven and 10 years old and adult when 10 years and older (Fedigan et al., 1996). Male dominance hierarchies were constructed by avoidance and cowering data (Perry, 1996, 1997), collected in both focal observations and ad libitum data. In order to be able to control for individually different slopes when shifting between alpha and subordinate status (modeled by a random slope for dominance status within individual ID), we only included adult males who changed dominance status at least once.

2.3.5 | Statistical analysis

To assess which predictor variables affected fecal androgen levels of males, we fitted a general linear mixed model (LMM; Baayen, 2008), with ifA level (log-transformed) being the response variable. We included dominance status (alpha or subordinate), alpha male tenure duration, the number of males (subadult and adult males) in the group, the number of potentially fertile females present in the group, infanticide susceptibility, individuals' co-residence, and the lowest co-residence score in the group on a given day, as test predictors (Mundry, 2014) with fixed effects.

We included four interactions in the model: (a) the interaction between number of males and potentially fertile females; (b) the interaction between dominance status and infanticide susceptibility; (c) the interaction between dominance status and the lowest co-residence score in the group; and (d) the interaction between dominance status and the alpha male tenure duration (for details see Supplementary table S2). However, including the interaction between infanticide susceptibility and the lowest co-residence score in the group was not possible due to insufficient coverage of the two dimensional parameter space, which means that for most values of both predictors, the magnitude of variation in the respective other predictor was too low to allow for modeling the interaction. To control for their potential effects we included season, time of sampling, and individual age, as control predictors (Mundry, 2014) with fixed effects in the model. Group ID and male ID were included as random effects. The control predictors and all random effects were kept in the null model (see Supplementary information). We included random slopes of all fixed effects and their interactions within monkey ID and group ID to keep type I error rate at the nominal level of 5% (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009). For details of model implementation please see Supplementary information. All models were fitted in R (R Core Team, 2015), version 3.2.3, using the function lmer of the package lme4, version 1.1–12 (Bates, Mächler, Bolker, & Walker, 2015).

3 | RESULTS

3.1 | Impact of demographic factors on fecal androgen levels

Alpha males had higher immunoreactive fecal androgen (ifA) levels than subordinate males (alpha males: median: 5,552 ng/g; quartiles: 2,953, 13,593; subordinate males: median: 1,508 ng/g; quartiles: 672, 3,774). The full model, including all test predictors and interactions, was significant compared to the null model, which lacked all test predictors and interactions ($\chi^2 = 22.12$, df = 11, $p = 0.023$). In the full model, none of the two-way interactions was significant (for details on the full model see Supplementary table S3). All of the two-way interactions were therefore removed from the model. The final model revealed that alpha males had significantly higher ifA levels than subordinate males ($\chi^2 = 13.341$, df = 1, $p < 0.001$, Table 1, Figure 1). Fifteen out of 18 males had higher fecal androgen levels during their time as alpha compared to periods when they were subordinate (Figure 1). None of the demographic test predictors (i.e., the number of males, the number of potentially fertile females, the infanticide susceptibility, the co-residence score, the lowest co-residence score in the group, or the alpha male tenure duration) had a significant effect on male fecal androgen levels (Table 1).

3.2 | Effects of control predictors

We found a highly significant seasonal pattern for ifA levels (Table 1, Figure 2). IfA levels tended to be at their lowest around September, increasing during the peak of conceptions (December and January), and at their highest around March, near the end of the conception season. The time of day the sample was taken and the individual age of adult males had no significant effect on male ifA levels.

4 | DISCUSSION

In this study we found that white-faced capuchin alpha males had significantly higher androgen levels than subordinate males. Specifically, in 15 of the 18 males for which we had data as both alphas and as subordinates, androgen levels were higher during their time as alpha male. None of the other social or demographic factors we investigated in the current study had an effect on male androgen levels. Of the three males who had higher ifA levels when subordinate, one was characterized by an exceptionally low sample size reducing our confidence in the estimates of his androgen levels. In the other two cases, the males seem to have faced more serious competition as subordinates than they did as alphas, which may explain their deviations from the normal pattern of alphas having higher ifA levels than subordinates.

4.1 | General rank-related differences in male androgen levels

Consistent with previous research on this species (Jack et al., 2014; Schoof et al., 2011, 2013; Schoof & Jack, 2013), we found that alpha males had higher androgen levels than subordinate males, even when controlling for individual age and accounting for individual and group identity. This suggests that higher androgen levels in alpha males are not just an artifact of age but related to the change in dominance status. Capuchin alpha males constantly control, monitor, and manipulate relationships of other males in their group (Perry & Manson, 2008), and although male white-faced capuchins do not show direct aggressive competition for access to estrous females within the group (but indirectly through competition over the alpha position), alpha males are highly effective at monopolizing reproduction (Muniz et al., 2010). Presumably, the costs of maintaining higher androgen levels are offset by the reproductive benefits of alpha status.

TABLE 1 Results of the final model of the impact of social and demographic factors on immunoreactive fecal androgen levels in adult males

Term	Estimate	SE	LRT	Df	*p*	Lower CI	Upper CI
Intercept	8.645	0.117	[a]	[a]	[a]	8.411	8.895
Test predictors							
#Potentially fertile females[c]	0.078	0.058	1.713	1	0.19	−0.044	0.198
#Males[c]	0.165	0.105	1.770	1	0.18	−0.077	0.404
Dominance status[b]	**−1.452**	**0.237**	**13.341**	**1**	**< 0.001**	**−1.927**	**−0.978**
Infanticide susceptibility[c]	0.024	0.047	0.088	1	0.77	−0.073	0.129
Lowest co-residence in the group[c]	0.017	0.092	0.032	1	0.86	−0.164	0.212
Log α tenure duration[c]	−0.171	0.108	1.586	1	0.21	−0.393	0.051
Individual co-residence score[c]	0.045	0.094	0.182	1	0.67	−0.166	0.228
Control predictors							
Time at sampling[c]	−0.032	0.046	0.480	1	0.49	−0.128	0.061
Individual age[c]	0.215	0.073	2.214	1	0.14	0.052	0.385
Sine (season)	0.626	0.081	15.503	1	< 0.001	0.468	0.776
Cosine (season)	0.293	0.073	10.806	1	0.001	0.142	0.436

Significant test predictors are indicated in bold.

[a] Not indicated due to lack of meaningful interpretation.

[b] Alpha = 0, subordinate = 1.

[c] Predictors were z-transformed (to mean = 0 and SD = 1); original means (sd) were: # potentially fertile females: 0.87 (1.23); # males: 3.72 (2.61); α tenure duration (in days): 1348.85 (1910.76); Infanticide susceptibility: 0.036 (0.07); Lowest co-residence score in the group: 0.89 (0.26); Individual co-residence score: 0.94 (0.17); Time at sampling (hours:minutes): 11:35 (2.53); Individual age (in years): 15.32 (5.8).

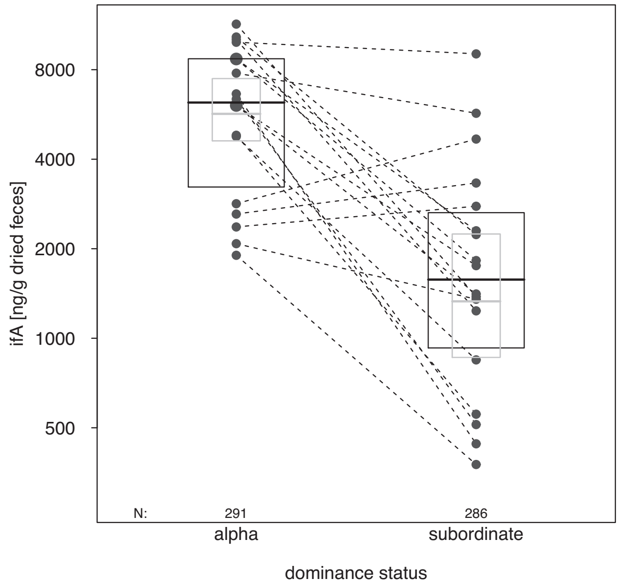

FIGURE 1 Relationship between dominance status and immunoreactive fecal androgen levels (ifA) in male white-faced capuchin monkeys at Lomas Barbudal, Costa Rica. Each point represents the average (geometric mean) of one male (as alpha or subordinate), and points referring to the same male are connected by a dashed line. Black horizontal lines and boxes depict medians and quartiles; gray lines and boxes show the fitted values and their 95% confidence intervals. *N* equals the number of fecal samples measured for alpha and subordinate males. Note that the y-axis is on a log scale

4.2 | Male androgen levels and group structure

In several primate species, male androgen levels increase in the presence of fertile females (Girard-Buttoz et al., 2015; Muller & Wrangham, 2004; Ostner et al., 2002; Xia, Li, Sun, Weed, & Kyes, 2015). In addition, because the potential access to fertile females for each male decreases when more males are present in a group, we hypothesized that a larger number of males in a group would lead to higher male androgen levels due to the greater potential for male-male competition. We found that male androgen levels were unaffected by how many males were present in the group. In a number of other primate species, either the number of males had no obvious effect on male androgen levels (Gould & Ziegler, 2007; Morino, 2014), or males in one-male groups had higher androgen levels than males in multi-male groups (Rangel-Negrín, Dias, Chavira, & Canales-Espinosa, 2011). This was interpreted as being due to a greater risk of extra-group competition (Rangel-Negrín et al., 2011). If, as in white-faced capuchins, overt competition between males over access to females within the group is rare (Fedigan, 1993), one would not necessarily expect a relationship between androgen levels and the operational sex ratio. Furthermore, given the prevalence with which white-faced capuchin males co-migrate with close paternally related kin (Perry, 2012; Wikberg et al., 2014), one might predict that the alpha male's co-migrants would receive enough inclusive fitness benefits from helping him defend his breeding access and progeny, that they would not compete aggressively, though in fact, we have seen some severe aggression between brothers over the alpha male position at Lomas (Perry, unpubl. data).

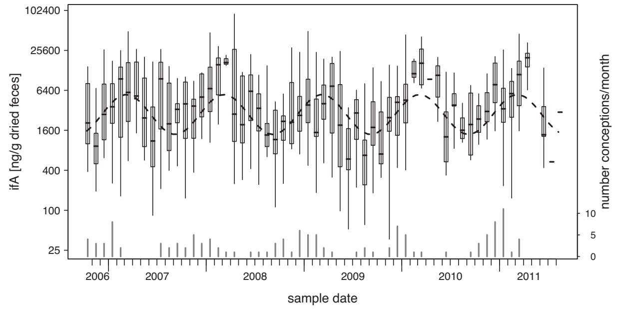

FIGURE 2 Seasonal variation in adult male fecal androgen levels (ifA) of white-faced capuchin monkeys (at Lomas Barbudal, Costa Rica) over the course of the study period (5.25 years). Depicted are monthly medians (horizontal lines), with quartiles (boxes) and percentiles (2.5% and 97.5%, vertical lines). The model is indicated by the dashed line. Note that the *y*-axis is on a log scale. Gray vertical bars at the bottom of the figure indicate the number of conceptions per month (across groups) that resulted in a live birth or stillborn

Male androgen levels at Lomas were also not affected by how many potentially fertile females were present in the group, which is in contrast to what was previously reported for males of this species by a study that used hormonal data to assess female reproductive state (Schoof et al., 2013). These discrepancies in findings may be due to methodological reasons, as assessing female reproductive state using hormonal data would be the more accurate method. Alternatively, actual effects of the presence of potentially fertile females could be overlapping with the effect of environmental factors (e.g., photoperiod, food availability, temperature, and rainfall) on male androgen levels, as previously suggested for this species (Schoof et al., 2016).

4.3 | Seasonality, conception, and changes in male androgen levels

We found a highly significant seasonal effect in male androgen levels over the 5.25 year-long study period. The timing of these changes was not entirely consistent with predictions of the Challenge Hypothesis: ifA levels were lowest shortly after females were starting to conceive and males might be expected to compete for access to them. Rather than peaking at the time when the most fertile females were available, ifA levels peaked at the tail end of the conception season, when most if not all of the females in the group were pregnant or lactating. This is in contrast with results from a 17-month study at Santa Rosa (Schoof et al., 2016), in which the seasonal peak in androgen levels was in December, which was closer to the middle of the conception season at Santa Rosa (which is timed slightly differently from the conception season at Lomas). The timing of conceptions was not always synchronous between groups, and hormone sampling was not entirely even across groups and time periods, so in this pooled data set, male hormone levels for some groups were plotted above conception data for other groups. (Recall that conception data were not part of the model, but were included in the graph to aid interpretation). Therefore, it is possible (though unlikely) that the predictions of the Challenge Hypothesis were supported within each group, but that we obscured these relationships by pooling the data from all groups. Another possible explanation for seasonal variation in male androgen levels in this population is that increased androgen levels might facilitate competition for seasonally varying food sources, rather than mating access. We do not have the ecological data with which to test this hypothesis, which could be explored in future research. Furthermore, post-conception mating, which has been shown to occur in a variety of primate species (e.g., bonobos, *Pan paniscus* (Manson, Perry, & Parish, 1997) and long-tailed macaques, *Macaca fascicularis* (Engelhardt, Hodges, & Heistermann, 2007)), including white-faced capuchins (Manson et al., 1997), might help to explain the peak in male ifA levels at the end of the conception season. However, this would only be an applicable explanation if males are unable to detect early pregnancy, which might indicate paternity confusion (van Schaik et al., 1999). Also, the number of cycling females might be slightly different than the females that successfully conceived. Therefore, future studies should investigate this, for example, by collecting female hormonal data to identify individual cycles and combining it with behavioral data, such as copulation rates.

How do capuchin alpha males benefit by maintaining high androgen levels throughout their tenure that counteract the potential costs of constantly elevated androgen levels? Although there are no actual body mass data available from wild populations of this species, researchers have the impression, based on visual inspection of wild *Cebus capucinus* (Jack et al., 2014; Perry pers. obs.), that the rise to alpha male status is associated with a gain in body mass, as is the case in a related species, *Sapajus libidinosus* (Fragaszy et al., 2016), in which weight changes of ~20% have been associated with acquisition or loss of alpha status in three males. This elevated weight, which is probably related to the observed increase in androgen levels, could be attractive to females and thereby increase alpha male reproductive success via female choice. Perhaps this added body mass helps the alpha male to defend himself against challengers for the alpha position, thereby preserving his breeding access to females and protecting the lives of his infants.

4.4 | Social stability and changes in male androgen levels

The three estimates of social stability investigated in this study did not affect male androgen levels. First, instability in the alpha male position was expected to decrease with increasing alpha tenure duration. Even though we used the log of days since an alpha male turnover event, to account for the possibility that male androgen levels and social stability might be more affected in the first days after the alpha change, this factor did not affect male androgen levels. This finding is somewhat surprising as, in white-faced capuchins, aggression rates increase following rank reversals (Perry, 1998a,b), and males often acquire their alpha positions via aggressive competition (Jack & Fedigan, 2004b; Perry, 1998a; Perry & Manson, 2008) (36 of the 43 alpha male turnovers at Lomas Barbudal during the time period of this study involved aggressive competition (Perry, unpublished data)). In a number of primate species, males have higher androgen levels during periods of rank instability (Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2005; Higham et al., 2013; Morino, 2014; Setchell et al., 2008). However, our result mirrors what has been found for savannah baboons (*Papio cynocephalus*), in which hierarchy stability was not related to androgen levels and did not impact the relationship between rank and androgen levels (Gesquiere et al., 2011). As in savannah baboons (Gesquiere et al., 2011), and in contrast to other primate species, for example, chacma baboons, Papio hamadryas ursinus (Beehner et al., 2005) or rhesus macaques (Higham et al., 2013), alpha male capuchins have permanently higher ifA levels than subordinate males. Therefore, hierarchy instability might not have an obvious additional effect. However, this should be investigated further by adding behavioral data, for example, rates of aggression and denser sampling during periods of rank change events.

Immigration of males from other groups can be a major source of social instability in white-faced capuchins (Jack & Fedigan, 2004a). However, we did not detect an effect of duration of male co-residence on residents' androgen levels. This result was unexpected, as all males of a group usually take part in group defense. Additionally, we predicted that alpha males would show a steeper androgen increase than subordinate males in response to unstable group situations, as they potentially face the threat of losing the alpha position, but this was not the case. Our density of focal animal sampling was not high enough to produce reliable estimates of aggression rates to accompany all of our androgen measurements. This is unfortunate, as detailed behavioral data would inform us about the impact that aggressive interactions during migration and alpha takeovers have on androgen levels, and whether kin relationships and relationship histories between males impact aggression and androgen levels. Further, we found that the duration of co-residence of a male with its subadult and adult male groupmates did not have an impact on male androgen levels. Newly immigrated males are generally the least familiar with other group males and therefore have the lowest co-residence score. Our results contrast with our predictions and with previous results from chacma baboons where new immigrants had increased androgen levels in the month following the dispersal event (Beehner et al., 2005). However, neither of the scores we used to assess social stability captures all of the nuance that is probably involved in immigration events (e.g., differences between single vs. parallel migration, or between peaceful and aggressive immigration).

4.5 | Male androgen levels and the risk of infanticide

In a number of mammalian species, the most striking consequence of males entering a social group is increased risk of infanticide (e.g., carnivores, rodents, and primates (Packer & Pusey, 1984; Parmigiani & Vom Saal, 1994; van Schaik & Janson, 2000)). Males kill dependent offspring of other males in the wake of taking over a group in order to sire their own offspring (Hrdy, 1980). As this reproductive strategy is also common in white-faced capuchins (Fedigan, 2003; Manson, Gros-Louis, & Perry, 2004; Perry & Manson, 2008; Perry et al., 2012), one possible expectation was that males would respond with an increase in androgen levels when dependent offspring were co-resident.

Alternatively, as suggested by the Challenge Hypothesis, male androgen levels may decrease in the presence of young infants to promote paternal investment. Male white-faced capuchins, both fathers and non-fathers, do invest in care of infants, primarily by carrying them around, playing with the infants or allowing them to crawl on them (Perry & Manson, 2008). However, we did not find any effect of the presence of young infants on male androgen levels, perhaps because the effects of direct paternal care and defense against infanticidal males are cancelling one another out. Future studies should investigate this topic by measuring hormonal responses to actual cases of infanticide or stalking, and by linking behavioral measures of paternal care (such as carrying) to male androgen levels.

4.6 | Summary

In summary, in a data set spanning 5.25 years and including nine social groups and 18 males who each contributed samples as both alphas and subordinates, white-faced capuchin males had significantly higher androgen levels when they were alphas than when they were subordinates; this effect was independent of age, and accounted for individual and group identity. None of the other social or demographic factors we investigated in this study had an impact on male androgen levels. However, our finding that season had a highly significant effect on male androgen levels over the 5.25 year study period suggests that seasonal changes in ecological parameters might play a major role in shaping male androgen patterns. We therefore, suggest that future longitudinal studies on male androgen levels investigate the relationship of androgen levels to (a) data on female hormonal status, to more precisely assess the availability of opportunities for direct mate competition; (b) environmental data, for example, on food resources that may vary seasonally; (c) data on changes in body mass in males; and (d) detailed behavioral data on the contexts of physical competition between males.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

REFERENCES

Alberts, S. C., Buchan, J. C., & Altmann, J. (2006). Sexual selection in wild baboons: From mating opportunities to paternity success. *Animal Behaviour*, *72*(5), 1177–1196. https://doi.org/10.1016/j.anbehav.2006.05.001

Alberts, S. C., Watts, H. E., & Altmann, J. (2003). Queuing and queue-jumping: Long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Animal Behaviour*, *65*(4), 821–840. https://doi.org/10.1006/anbe.2003.2106

Anestis, S. F. (2010). Hormones and social behavior in primates. *Evolutionary Anthropology: Issues, News, and Reviews*, *19*(2), 66–78. https://doi.org/10.1002/evan.20253

Baayen R. H. (2008). *Analyzing linguistic data: A practical introduction to statistics using R*. Cambridge, UK New York: Cambridge University Press.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Barrett, G. M., Shimizu, K., Bardi, M., Asaba, S., & Mori, A. (2002). Endocrine correlates of rank, reproduction, and female-directed aggression in male japanese macaques (*Macaca fuscata*). *Hormones and Behavior*, *42*(1), 85–96. https://doi.org/10.1006/hbeh.2002.1804

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2005). Testosterone predicts future dominance rank and mating activity among male chacma baboons. *Behavioral Ecology and Sociobiology*, *59*(4), 469–479. https://doi.org/10.1007/s00265-005-0071-2

Bercovitch, F. B. (1991). Social stratification, social strategies, and reproductive success in primates. *Ethology and Sociobiology*, *12*(4), 315–333. https://doi.org/10.1016/0162-3095(91)90023-J

Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology*, *130*(1), 103–115. https://doi.org/10.1002/ajpa.20341

Bribiescas, R. G. (2001). Reproductive ecology and life history of the human male. *American Journal of Physical Anthropology*, *116*(S33), 148–176. https://doi.org/10.1002/ajpa.10025

Carlson, A. A., Young, A. J., Russell, A. F., Bennett, N. C., McNeilly, A. S., & Clutton-Brock, T. (2004). Hormonal correlates of dominance in meerkats (*Suricata suricatta*). *Hormones and Behavior*, *46*(2), 141–150. https://doi.org/10.1016/j.yhbeh.2004.01.009

Carnegie, S. D., Fedigan, L. M., & Melin, A. D. (2011). Reproductive seasonality in female capuchins (*Cebus capucinus*) in Santa Rosa (Area de Conservación Guanacaste), Costa Rica. *International Journal of Primatology*, *32*(5), 1076–1090. https://doi.org/10.1007/s10764-011-9523-x

Charpentier, M. (2005). Constraints on control: Factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). *Behavioral Ecology*, *16*(3), 614–623. https://doi.org/10.1093/beheco/ari034

Cowlishaw, G., & Dunbar, R. I. (1991). Dominance rank and mating success in male primates. *Animal Behaviour*, *41*(6), 1045–1056.

Cowlishaw, G., & Dunbar, R. I. M. (1992). Dominance and mating success: A reply to Barton & Simpson. *Animal Behaviour*, *44*(6), 1162–1163. https://doi.org/10.1016/S0003-3472(05)80329-X

Creel, S., Creel, N. M., Mills, M. G. L., & Monfort, S. L. (1997). Rank and reproduction in cooperatively breeding African wild dogs: Behavioral and endocrine correlates. *Behavioral Ecology*, *8*(3), 298–306. https://doi.org/10.1093/beheco/8.3.298

Dloniak, S. M., French, J. A., & Holekamp, K. E. (2006). Faecal androgen concentrations in adult male spotted hyaenas, *Crocuta crocuta*, reflect interactions with socially dominant females. *Animal Behaviour*, *71*(1), 27–37. https://doi.org/10.1016/j.anbehav.2005.03.016

Ellis, L. (1995). Dominance and reproductive success among nonhuman animals: A cross-species comparison. *Ethology and Sociobiology*, *16*(4), 257–333. https://doi.org/10.1016/0162-3095(95)00050-U

Engelhardt, A., Hodges, J. K., & Heistermann, M. (2007). Post-conception mating in wild long-tailed macaques (*Macaca fascicularis*): Characterization, endocrine correlates and functional significance. *Hormones and Behavior*, *51*(1), 3–10. https://doi.org/10.1016/j.yhbeh.2006.06.009

Fedigan, L. M. (1993). Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology*, *14*(6), 853–877. https://doi.org/10.1007/BF02220256

Fedigan, L. M. (2003). Impact of male takeovers on infant deaths, births and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. *International Journal of Primatology*, *24*(4), 723–741.

Fedigan L. M., & Jack K. M., (2013). Sexual conflict in white-faced capuchins. In M. L. Fisher, J. R. Garcia, & R. S. Chang (Eds.), *Evolution's empress* (pp. 281–303). New York: Oxford University Press, http://www.oxfordscholarship.com/view/10.1093/acprof:oso/9780199892747.001.0001/acprof-9780199892747-chapter-14.

Fedigan L. M., Rose L. M., & Avila R. M., (1996). See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In M. Norconk, A. Rosenberger, & P. Garber (Eds.), *Adaptive radiations of neotropical primates* (pp. 289–308). New York: Plenum.

Fragaszy, D. M., Izar, P., Liu, Q., Eshchar, Y., Young, L. A., & Visalberghi, E. (2016). Body mass in wild bearded capuchins, (*Sapajus libidinosus*): Ontogeny and sexual dimorphism. *American Journal of Primatology*, *78*(4), 473–484. https://doi.org/10.1002/ajp.22509

Frankie, G. W., Vinston, S. B., Newstrom, L. E., & Barthell, J. F. (1988). Nest site and habitat preferences of *Centris* bees in the Costa Rican dry forest. *Biotropica*, *20*, 301–310.

Gesquiere, L. R., Learn, N. H., 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*(6040), 357–360. https://doi.org/10.1126/science.1207120

Ginther, A. J., Ziegler, T. E., & Snowdon, C. T. (2001). Reproductive biology of captive male cottontop tamarin monkeys as a function of social environment. *Animal Behaviour*, *61*(1), 65–78. https://doi.org/10.1006/anbe.2000.1587

Girard-Buttoz, C., Heistermann, M., Rahmi, E., Agil, M., Fauzan, P. A., & Engelhardt, A. (2015). Androgen correlates of male reproductive effort in wild male long-tailed macaques (*Macaca fascicularis*): A multi-level test of the Challenge Hypothesis. *Physiology & Behavior*, *141*, 143–153. https://doi.org/10.1016/j.physbeh.2015.01.015

Glander, K. E. (1992). Dispersal patterns in Costa Rican mantled howling monkeys. *International Journal of Primatology*, *13*(4), 415–436. https://doi.org/10.1007/BF02547826

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*(12), 1325–1339. https://doi.org/10.1002/ajp.20438

Heistermann, M., Finke, M., & Hodges, J. K. (1995). Assessment of female reproductive status in captive-housed Hanuman langurs (*Presbytis entellus*) by measurement of urinary and fecal steroid excretion patterns. *American Journal of Primatology*, *37*(4), 275–284.

Higham, J. P., Heistermann, M., & Maestripieri, D. (2013). The endocrinology of male rhesus macaque social and reproductive status: A test of the challenge and social stress hypotheses. *Behavioral Ecology and Sociobiology*, *67*(1), 19–30. https://doi.org/10.1007/s00265-012-1420-6

Hirschenhauser, K., & Oliveira, R. F. (2006). Social modulation of androgens in male vertebrates: Meta-analyses of the Challenge Hypothesis. *Animal Behaviour*, *71*(2), 265–277. https://doi.org/10.1016/j.anbehav.2005. 04.014

Hrdy S. B. (1980). *The langurs of Abu: Female and male strategies of reproduction*. Cambridge, Mass: Harvard University Press.

Huck, M., Löttker, P., Heymann, E. W., & Heistermann, M. (2005). Characterization and social correlates of fecal testosterone and cortisol excretion in wild male *Saguinus mystax*. *International Journal of Primatology*, *26*(1), 159–179. https://doi.org/10.1007/s10764-005-0728-8

Jack, K. M., & Fedigan, L. M. (2004a). Male dispersal patterns in white-faced capuchins, *Cebus capucinus* Part 1: Patterns and causes of natal emigration. *Animal Behaviour*, *67*(4), 761–769. https://doi.org/10.1016/j.anbehav.2003.04.015

Jack, K. M., & Fedigan, L. M. (2004b). The demographic and reproductive context of male replacements in *Cebus capucinus*. *Behaviour*, *141*(6), 755–775. https://doi.org/10.1163/1568539042245178

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. A. Garber, M. S. M. Pavelka, & L. Luecke, (Eds.), *New Perspectives in the Study of Mesoamerican Primates: Distribution, ecology, behavior and conservation*. New York: Springer, (pp. 367– 386). http://link.springer.com/chapter/10.1007/0-387-25872-8_18

Jack, K. M., Schoof, V. A. M., Sheller, C. R., Rich, C. I., Klingelhofer, P. P., Ziegler, T. E., & Fedigan, L. (2014). Hormonal correlates of male life history stages in wild white-faced capuchin monkeys (*Cebus capucinus*). *General and Comparative Endocrinology*, *195*, 58–67. https://doi.org/10.1016/j.ygcen.2013.10.010

Janson, C. H. (1984). Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: *Cebidae*). *Zeitschrift für Tierpsychologie*, *65*(3), 177–200.

Manson, J. H., Gros-Louis, J., & Perry, S. (2004). Three apparent cases of infanticide by males in wild white-faced capuchins (*Cebus capucinus*). *Folia Primatologica*, *75*(2), 104–106. https://doi.org/10.1159/000076270

Manson, J. H., Perry, S., & Parish, A. R. (1997). Nonconceptive sexual behavior in bonobos and capuchins. *International Journal of Primatology*, *18*(5), 767–786.

Mazur, A. (1976). Effects of testosterone on status in primate groups. *Folia Primatologica*, *26*(3), 214–226. https://doi.org/10.1159/000155752

Mendonça-Furtado, O., Edaes, M., Palme, R., Rodrigues, A., Siqueira, J., & Izar, P. (2014). Does hierarchy stability influence testosterone and cortisol levels of bearded capuchin monkeys (*Sapajus libidinosus*) adult males? A comparison between two wild groups. *Behavioural Processes*, *109*, 79–88. https://doi.org/10.1016/j.beproc.2014.09.010

Morino, L. (2014). Social correlates of androgen levels in a facultatively monogamous ape (*Symphalangus syndactylus*): A test of the Challenge Hypothesis. *Behavioral Ecology and Sociobiology*, *69*(2), 243–251. https://doi.org/10.1007/s00265-014-1837-1

Muller, M. N. (2016). Testosterone and reproductive effort in male primates. *Hormones and Behavior*, https://doi.org/10.1016/ j.yhbeh.2016.09.001

Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: A test of the "Challenge Hypothesis". *Animal Behaviour*, *67*(1), 113–123. https://doi.org/10.1016/j.anbehav.2003.03.013

Mundry R., (2014). Statistical issues and assumptions of phylogenetic generalized least squares. In L. Z. Garamszegi (Ed.), *Modern phylogenetic comparative methods and their application in evolutionary biology* (pp. 131–153). Berlin, Heidelberg: Springer Berlin Heidelberg, http://link.springer.com/10.1007/978-3-662-43550-2_6

Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., Gros-Louis, J., & Vigilant, L. (2006). Father-daughter inbreeding avoidance in a wild primate population. *Current Biology*, *16*(5), R156–R157.

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*(12), 1118–1130. https://doi.org/10.1002/ajp.20876

Nieuwenhuijsen, K., de Neef, K. J., Van der Werff ten Bosch, J. J., & Slob, A. K. (1987). Testosterone, testis size, seasonality, and behavior in group-living stumptail macaques (*Macaca arctoides*). *Hormones and Behavior*, *21*(2), 153–169.

Nunes, S., Fite, J. E., & French, J. A. (2000). Variation in steroid hormones associated with infant care behaviour and experience in male marmosets (*Callithrix kuhlii*). *Animal Behaviour*, *60*(6), 857–865. https://doi.org/10.1006/anbe.2000.1524

Ostner, J., Kappeler, P., & Heistermann, M. (2002). Seasonal variation and social correlates of androgen excretion in male redfronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology*, *52*(6), 485–495. https://doi.org/10.1007/s00265-002-0532-9

Ostner, J., Nunn, C. L., & Schülke, O. (2008). Female reproductive synchrony predicts skewed paternity across primates. *Behavioral Ecology*, *19*(6), 1150–1158. https://doi.org/10.1093/beheco/arn093

Packer C., & Pusey A. E., (1984). Infanticide in carnivores. In G. Hausfater, & S. B. Hrdy (Eds.), *Infanticide* (pp. 31–42). New York: Aldine.

Palombit R. A., Cheney D. L., Fischer J., Johnson, S., Rendall, D., Seyfarth, R. M., & Silk, J. B. (2000). Male infanticide and defense of infants in chacma baboons. In C. P. Van Schaik, & C. H. Janson, (Eds.), *Infanticide by males and its implications* (pp. 123–152). Cambridge: Cambridge University Press.

Parmigiani S., & Vom Saal F. S. (1994). *Infanticide and parental care. [Chur, Switzerland]*. Langhorne, Pa., USA: Harwood Academic Publishers, (p. 496).

Perry, S. (1996). Female-female social relationships in wild white-faced capuchin monkeys. *Cebus capucinus*, Available from: http://deepblue.lib.umich.edu/handle/2027.42/38432

Perry, S. (1997). Male-female social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour*, 477–510.

Perry, S. (1998a). A case report of a male rank reversal in a group of wild white-faced capuchins (*Cebus capucinus*). *Primates*, *39*(1), 51–70.

Perry, S. (1998b). Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour*, *135*(2), 139–172. https://doi.org/10.1163/156853998793066384

Perry S. (2012). The behavior of wild white-faced capuchins: Demography, life history, social relationships, and communication. In: J. Brockmann, T. J. Roper, M. Naguib, J. C. Mitani, & L. W. Simmons, *Advances in the study of behavior* (pp. 135–181). Burlington: Academic Press Elsevier, Vol. *44*. http://linkinghub.elsevier.com/retrieve/pii/B9780123942883000046

Perry S., Godoy I., & Lammers W., (2012). The Lomas Barbudal monkey project: two decades of research on *Cebus capucinus*. In P. M. Kappeler, & D. P. Watts (Eds.), *Long-Term field studies of primates* (pp. 141–163). Berlin, Heidelberg: Springer Berlin Heidelberg, http://link.springer.com/10.1007/978-3-642-22514-7_7

Perry S., & Manson J. H. (2008). *Manipulative monkeys: The capuchins of Lomas Barbudal* (p. 358). Harvard University Press: Cambridge, Mass.

Rangel-Negrín, A., Dias, P. A. D., Chavira, R., & Canales-Espinosa, D. (2011). Social modulation of testosterone levels in male black howlers (*Alouatta pigra*). *Hormones and Behavior*, *59*(1), 159–166. https://doi.org/10.1016/j.yhbeh.2010.11.005

R Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: http://www.R-project.org

Rose, R. M., Holaday, J. W., & Bernstein, I. S. (1971). Plasma testosterone, dominance rank and aggressive behaviour in male rhesus monkeys. *Nature*, *231*(5302), 366–368. https://doi.org/10.1038/231366a0

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416–420. https://doi.org/10.1093/beheco/arn145

Schoof, V. A. M., Bonnell, T. R., Jack, K. M., Ziegler, T. E., Melin, A. D., & Fedigan, L. M. (2016). Male endocrine response to seasonally varying environmental and social factors in a neotropical primate, *Cebus capucinus*: Seasonal endocrine variation in male capuchins. *American Journal of Physical Anthropology*, *159*(4), 671–682. https://doi.org/10.1002/ajpa.22925

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*(2), 107–115. https://doi.org/10.1002/ajp.22089

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*(6), 299–307. https://doi.org/10.1159/000337220

Schoof, V. A. M., Jack, K. M., & Ziegler, T. E. (2013). Male response to female ovulation in white-faced capuchins (*Cebus capucinus*): Variation in fecal testosterone, dihydrotestosterone, and glucocorticoids. *International Journal of Primatology*, *35*(3), 643–660. https://doi.org/10.1007/s10764-013-9742-4

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*(3), 365–372. https://doi.org/10.1016/j.yhbeh.2008.05.004

Sommer, V., & Rajpurohit, L. S. (1989). Male reproductive success in harem troops of hanuman langurs (*Presbytis entellus*). *International Journal of Primatology*, *10*(4), 293–317. https://doi.org/10.1007/BF02737419

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*(2), 125–134. https://doi.org/10.1006/hbeh.1998.1505

Surbeck, M., Deschner, T., Schubert, G., Weltring, A., & Hohmann, G. (2012). Mate competition, testosterone and intersexual relationships in bonobos, *Pan paniscus*. *Animal Behaviour*, *83*(3), 659–669. https://doi.org/10.1016/j.anbehav.2011.12.010

van Schaik C. P., van Noordwijk M. A., & Nunn C. L., (1999). Sex and social evolution in primates. In P. C. Lee (Ed.), *Comparative primate socioecology* (pp. 204–240). Cambridge: Cambridge University Press.

van Schaik C., & Janson C. H. (2000). *Infanticide by males and its implications* (p. 569). Cambridge, UK: New York: Cambridge University Press.

Whitten, P. L., & Turner, T. R. (2004). Male residence and the patterning of serum testosterone in vervet monkeys (*Cercopithecus aethiops*). *Behavioral Ecology and Sociobiology*, *56*(6), 565–578. https://doi.org/10.1007/s00265-004-0817-2

Wikberg, E. C., Jack, K. M., Campos, F. A., Fedigan, L. M., Sato, A., Bergstrom, M. L., . . . Kawamura, S. (2014). The effect of male parallel dispersal on the kin composition of groups in white-faced capuchins. *Animal Behaviour*, *96*, 9–17. https://doi.org/10.1016/j.anbehav.2014.07.016

Wingfield, J. C., Hegner, R. E., Dufty, A. M., Jr, & Ball, G. F. (1990). The "Challenge Hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, 829–846.

Wright, P. C. (1990). Patterns of paternal care in primates. *International Journal of Primatology*, *11*(2), 89–102. https://doi.org/10.1007/BF02192783

Xia, D.-P., Li, J.-H., Sun, B.-H., Weed, J. L., & Kyes, R. C. (2015). Evaluation of fecal testosterone, rank and copulatory behavior in wild male *Macaca thibetana* at Huangshan China. *Pakistan Journal of Zoology*, *47*(5), 1445–1454.

Ziegler, T. E. (1996). Metabolism of reproductive steroids during the ovarian cycle in two species of callitrichids, *Saguinus oedipus* and *Callithrix jacchus*, and estimation of the ovulatory period from fecal steroids. *Biology of Reproduction*, *54*(1), 91–99. https://doi.org/10.1095/biolreprod54.1.91

Zucker, E. L. (1996). Fecal testosterone values for free-ranging male mantled howling monkeys (*Alouatta palliata*) in Costa Rica. *IPS/ASP Congress Abstracts*, (p. 112).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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