RESEARCH ARTICLE

The Association of Intergroup Encounters, Dominance Status, and Fecal Androgen and Glucocorticoid Profiles in Wild Male White-Faced Capuchins (*Cebus capucinus*)

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Androgens play a role in male reproductive competition, frequently via aggression, while glucocorticoids are associated with the stress response. However, the relationships of these hormones with different sources of competition (intra- vs. intergroup) and dominance status are highly variable. Here, we consider the fecal androgen (fA) and glucocorticoid (fGC) profiles of alpha and subordinate male *Cebus capucinus* in the context of intergroup competition during a rare period of low intragroup competition (i.e. all females were either pregnant or lactating). Intergroup encounters (IGEs) are a long-term reproductive strategy in male white-faced capuchins, enabling them to assess the composition of neighboring groups. IGEs pose a threat to resident males as these can result in injury or death, loss of dominance rank, group eviction, and group takeovers that are frequently associated with infanticide. From February to July 2007, fecal samples were collected from eight males in three groups of white-faced capuchins in the Santa Rosa Sector of the Área de Conservación Guanacaste, Costa Rica. IGE rate was positively associated with both fA and fGC levels, indicating that IGEs are perceived as reproductive challenges by resident males, and may be associated with elevated metabolic costs. Alpha males sire the majority of group offspring and, accordingly, the threat of IGEs to both future (via rank loss or eviction) and current (via infanticide) reproductive success is greater than for subordinate males. Consistent with this observation, alpha males had higher fA and fGC levels than subordinate males. Given that all females were either pregnant or lactating and pronounced overt intragroup competition was absent, we interpret the difference in hormone profiles of alpha and subordinate males as being primarily associated with variation in the perceived threats of IGEs according to dominance status. Future studies should focus on the interaction of intra- and intergroup competition by examining hormone levels in the presence of periovulatory females. Am. J. Primatol. 75:107–115, 2013. © 2012 Wiley Periodicals, Inc.

Key words: endocrinology; reproductive competition; infanticide; dominance; reproductive skew

INTRODUCTION

Androgens, including testosterone, are a group of steroid hormones that facilitate reproductive competition [Wingfield et al., 1990], maintain reproductive physiology, develop secondary sexual characteristics, and inhibit paternal behavior in males [reviewed in Fernandez-Duque et al., 2009]. Androgens also have deleterious effects such as immunosuppression and compromised survivability [reviewed in Muehlenbein, 2009], though these costs may be outweighed by the benefits of increased competitive ability during periods of elevated reproductive competition. Glucocorticoids (GCs) are associated with the stress response and short-term GC increases are adaptive because they focus energetic resources to areas relevant to immediate survival needs (e.g. energy release) and temporarily suppress nonvital functions (e.g. growth, reproduction) [Sapolsky, 2004]. However, long-term or chronic expression of the stress response, as observed by high GC levels over extended periods, can be detrimental to health [reviewed in Sapolsky, 2004].

As yet, no single hormonal profile exists that reflects either dominant or subordinate status [Creel, 2001], suggesting that many species-specific or population-based social and environmental factors influence the socioendocrinology of male dominance relationships. Research has primarily focused on the many factors that influence male intragroup competition, and thus the relationship between dominance and hormones. These factors may include breeding seasonality [Bales et al., 2006; Brockman et al., 1998; Lynch et al., 2002; Ostner et al., 2002, 2008, 2011] and the presence of periovulatory females [Muller & Wrangham, 2004a; Setchell et al., 2008, 2010; Vandenberg, 1969], dominance style [Muehlenbein et al., 2004; Muller & Wrangham 2004a; Strier et al., 1999] and group stability [Brockman et al., 2001; Sapolsky, 1993], relative allostatic load or metabolic expenditure [Goymann & Wingfield, 2004; Muller & Wrangham, 2004b; Sapolsky, 2004], as well as kinship, the frequency of being subjected to stress, the ability to avoid overt competition (i.e. via evasion), and the availability of social partners [Abbott et al. 2003; Sapolsky, 2004].

In addition to the role of intragroup reproductive competition (i.e. internal source) on hormone levels in multimale species, the influence of dispersing males, intergroup encounters (IGEs), and group takeovers (i.e. external sources) must also be considered as these may be the greater source of reproductive competition in some species [Strier, 1994; van Hooff, 2000]. Nonresident males can pose a threat to resident male reproductive success via copulations with group females, and via IGEs and takeovers that may result in loss of rank, group eviction, infanticide, injury, or death [Bergman et al., 2005; Brockman et al., 2001, 2009; Cristóbal-Azkarate et al., 2006; Fedigan & Jack, 2004; Hrdy, 1977; Ostner et al., 2008; Van Belle et al., 2009b, 2010; van Schaik et al., 2004]. These external sources of reproductive competition may exert a strong influence on male hormone levels. Variation in the androgen profiles of males may be associated with differences in group composition [*Cercopithecus aethiops*: Whitten & Turner, 2004; *Alouatta pigra*: Rangel-Negrin et al., 2011], challenges from extragroup males [*Propithecus verreauxi*: Brockman et al., 1998; *Callithirx kuhlii*: Ross et al., 2004; *Colobus vellerosus*: Teichroeb & Sicotte, 2008; *A. paliatta*: Cristóbal-Azkarate et al., 2006; but see *Eulemur fulvus rufus*: Ostner et al., 2002, 2008; *Saguinus mystax*: Huck et al., 2005; *A. pigra:* Van Belle et al., 2009a], immigration and emigration [*Papio cynocephalus*: Alberts et al., 1992; *P. verreauxi*: Brockman et al., 1998, 2001], and infanticide risk [*E. fulvus rufus*: Ostner et al., 2002, 2008; *Cer. aethiops*: Whitten & Turner, 2004].

Participation in group defense is likely energetically expensive, such that an increase in metabolic load could be associated with increased GC levels, but evidence in support of this is equivocal.

For example, while male chacma baboons experience elevated GC levels after changes in male group membership [i.e. via immigrations, *P. hamadryas ursinus*: Bergman et al., 2005], male moustached tamarins, mantled howlers, black howlers, and captive male marmosets do not show an increase in GCs after encounters with extragroup males [*C. kuhlii*: Ross et al., 2004; *S. mystax*: Huck et al., 2005; *A. paliatta*: Cristóbal-Azkarate et al., 2007; *A. pigra*: Van Belle et al., 2009a]. It may be that GC levels are associated more with actual changes rather than threats of changes in group membership. It also appears that group males maintain elevated GCs as an anticipatory response to the risk of takeovers and killings of infants by extragroup males [*P. verreauxi*: Brockman et al., 2009; *E. fulvus rufus*: Ostner et al., 2008].

In this study, we examine the association between fecal androgen (fA) and fecal glucocorticoid (fGC) levels and intergroup reproductive competition in alpha and subordinate male white-faced capuchins residing in the Santa Rosa Sector, Costa Rica. By chance, our study took place during an unusually lengthy nonreproductive period in which all group females were either pregnant or lactating. This provided us with the rare opportunity to examine male hormone profiles in the absence of periovulatory females and during a time when male intragroup reproductive competition is expected to be low, though perhaps not completely absent. White-faced capuchins are female philopatric and reside in groups comprised of related adult females, multiple immigrant subadult and adult males, and their offspring. Intragroup male relationships are characterized by affiliative interactions and low agonism in our study population [Jack, 2003], and by cooperation in group defense against predators and extragroup males [Jack, 2003; Perry, 1998]. While intragroup relationships among coresident males are tolerant, at the intergroup level, severe and sometimes lethal male–male agonism occurs in the context of IGEs and group takeovers [Fedigan & Jack, 2004; Perry, 1996]. During IGEs, males are the primary participants, while females only rarely participate and generally flee from encounter locations with immature group members [personal observation; Perry, 1996; Rose & Fedigan, 1995; Rose 1998; but see Crofoot, 2007]. IGEs in white-faced capuchins occur throughout the year, although they are slightly more frequent in the dry season [Perry, 1996].

Overall, IGEs play an important role in male long-term reproductive strategies, especially in terms of assessing the composition of neighboring groups for dispersal opportunities [Crofoot, 2007; Fedigan & Jack, 2004; Perry, 1996]. Adult male white-faced capuchins usually immigrate into groups by aggressively and cooperatively evicting resident males [Fedigan & Jack, 2004] and immigration is the primary way in which they increase their dominance status [Jack & Fedigan, 2004]. In

our long-term study groups, most takeovers (14 of 15) occur during the dry season months of January to April, occur approximately every 4 years [Fedigan & Jack, 2004], and result in the eviction of resident males, infanticides, and the occasional deaths or disappearances of both males and females [Fedigan, 2003; Rose, 1998; see also Gros-Louis et al., 2003; Perry, 1996 for similar observations at Lomas Barbudal, Costa Rica]. While infanticides are most common after takeovers [Fedigan & Jack, 2004], they can also occur during IGEs [Vogel & Fuentes-Jiménez, 2006].

In species where dominant males sire the majority of offspring, the negative impact of lost future reproductive opportunities due to decreased rank or eviction may mean that dominant individuals are disproportionately affected by threats from extragroup males. The additional threat of infanticide, which would result in loss of current offspring, may be especially important. For example, dominant male sifakas, who have priority of access to females [Brockman et al., 1998], appear to respond to challenges from extragroup males and immigration events with elevated testosterone [Brockman et al., 2001] but not fGC levels [Brockman et al., 2009]. Evidence of overt intragroup male reproductive competition in white-faced capuchins is rare [but see Perry, 1998] and alpha males appear to obtain only a slightly disproportionate number of copulations [Rose, 1998]. However, genetic studies demonstrate that alpha males sire the majority of offspring [Jack & Fedigan, 2006; Muniz et al., 2010]. Since alpha males have the highest reproductive success, they have the most to lose during IGEs and group takeovers in terms of future reproductive opportunities due to eviction or rank loss, and current reproductive success due to infanticide. This may explain why alpha males are the most vigilant [Rose & Fedigan, 1995] and the most involved in group defense during IGEs and takeover attempts [Perry, 1996].

Given that IGEs (and, by association, takeovers) may result in loss of rank, group eviction, infanticide, injury, or death, we predict that male fA and fGC levels will be positively associated with IGE rates. We further predict that alpha males will have higher fA than subordinate males because of the disproportional threat of IGEs to alpha male reproductive success. We also predict that alpha males will have higher fGC levels than subordinates because of the presumed higher metabolic costs associated with elevated vigilance and high level of participation in IGEs.

METHODS

Study Site and Subjects

Our study took place in the Santa Rosa Sector of the Área de Conservación de Guanacaste (formerly known as Santa Rosa National Park) from February through July 2007. Located in the northwestern part of Costa Rica, the Santa Rosa Sector is an approximately 108 km^2 protected area made up of a mosaic of dry deciduous, semievergreen, and riparian forest fragments interspersed with regenerating pasture [for additional information on the field site, see Fedigan & Jack, 2012]. Research complied with protocols approved by the Área de Conservación Guanacaste and the Tulane University IACUC, and adhered to the legal requirements of Costa Rica and the United States as well as the American Society of Primatologists principles for the ethical treatment of primates.

We collected hormone data on all male white-faced capuchins (*Cebus capucinus*) aged ≥6 years ($N = 8$) residing in three habituated social groups. Over 940 contact hours were logged in the dry season (EX: 280 hr, GN: 316 hr, LV: 344 hr) and 255 hours in the wet season across all three social groups (EX: 80 hr, GN: 87 hr, LV: 88 hr). With the exception of the only subadult male in our sample (MZ in LV), all males were immigrants and estimated to be ≥10 years of age. As in this and other capuchin species [Fragaszy et al., 2004; Perry, 1998], we were unable to determine male dominance rank below the alpha level due to the rarity of agonistic interactions between male dyads. However, alpha status was clearly identifiable based on physical appearance (i.e. larger brows, jaws, and overall size, and greater piloerection) and behavior.

About half of all IGEs involve chasing and/or physical contact, while the remaining IGEs are characterized by avoidance, fleeing, vocal and ritualized physical threats, or persistent vigilance (Childers, 2008). Alpha males are the most active participants, and participate in the majority of IGEs [Perry, 1996; Rose & Fedigan, 1995]; in groups with multiple males, most subordinates participate, though their participation and intensity is more variable (personal observation). We used handheld digital voice recorders to record *ad libitum* data on the date and time of the encounter, and which groups were involved. IGEs are rare events, and were too infrequently observed during our study period to calculate reliable monthly IGE rates. Therefore, we calculated each group's IGE rate in the dry and the early wet seasons by dividing the number of known IGEs by the total contact hours for each group (Table I). The dry season receives very little, if any, rainfall, and its end is marked by almost daily rainfall beginning in mid-May. Based on rainfall data, the last day of the dry season was May 17, 2007, which we used as the cutoff point between the dry and early wet season.

Collection and Analyses of Fecal Samples

We collected morning fecal samples from all study males at least once per week ($N = 194$). Sample collection, storage, and preliminary field extraction methods followed Carnegie et al. [2011b], using

TABLE I. Rates of IGEs in the Dry Season and Wet Season for Each of the Study Groups

Social group	Dry season			Early wet season		
	IGE	Contact hours	IGE rate*	IGE	Contact hours	IGE rate*
EX	9	280 hr 37 min	0.043	2	80 hr 43 min	0.025
GN	8	316 hr 28 min	0.029	1	87 hr 47 min	0.011
LV	10	344 hr 03 min	0.039	3	88 hr 41 min	0.034

IGE: intergroup encounters
*Events per hour

Prevail C18 Maxi-Clean 300 mg SPE cartridges (All-tech Associates, Inc., Deerfield, IL). Samples were transported and analyzed at the Wisconsin National Primate Research Center (WNPRC) by VAMS. Hormones were washed using 1 ml of 5% methanol, eluted from the SPE cartridges using 2 ml of 100% methanol, dried in a hot water bath, reconstituted in 1 ml of 100% ethanol, and stored in a refrigerator. Samples were subsequently analyzed by in-house enzyme immunoassay for fA [see Ginther et al., 2001] and fGC [Carnegie et al., 2011b], both of which are competitive binding assays that use antibodies raised in rabbits (fA antibody R156, fGC antibody R4866, Munro, University of California, Davis). For fA, sample volumes of 5–25 ul of the ethanol solution were dried and resuspended in the assay solution, and one-third was aliquoted into each well. For fGC, 50 ul of the ethanol solution was used. All samples and standards (1–250 pg, $N = 8$, Δ4-androsten-17β-ol-3-one for fA, and 11β,17α,21-Trihydroxypregn-4-ene-3,20-dione for fGC, Sigma-Aldrich, St.Louis, MO) were run in duplicate. Concentrations of fA and fGC were measured in nanograms per gram (ng/g).

Mean intra- and interassay coefficients of variation (CVs) for fA were 5.5 ng/g and 17.9 ng/g, respectively, for the low pool, and 7.4 ng/g and 12.4 ng/g, respectively, for the high pool. Mean intra- and interassay CVs for fGC were 6.2 ng/g and 14.0 ng/g, respectively, for the low pool, and 2.7 ng/g and 6.0 ng/g, respectively, for the high pool. Mean percent accuracy (the degree to which the assay actually measures the steroid in a known pool) was high for both hormones (fA: 109.05 ± 2.79, $N = 8$; fGC: 115.48 ± 2.27, $N = 6$). Additionally, the percent bound values from the pooled samples paralleled the percent bound values of the standard curve for both hormones, and there were no differences in their slopes (fA: $t(28) = 0.841$, $P > 0.05$, $N = 8$; fGC: $t(21) = 0.066$, $P > 0.05$, $N = 7$).

The validity of the androgen assay is supported by the observation that adult males have higher fecal testosterone than juvenile males [Jack et al., 2011] and fA increased in a subordinate male who became the alpha male [Schoof et al., 2011]. We did not conduct an adrenocorticotropic hormone (ACTH) challenge in our study population to test the biological validity of the fGC response because this would interfere with the naturalistic approach of the research conducted at this field site. However, previous research in this population of *Cebus capucinus* indicates that unhabituated individuals respond to observer presence with high fGC levels than habituated individuals [Jack et al., 2008], females respond to a presumably stressful situation (change in male group composition) with an increase in fGC level [Carnegie et al., 2011b], and a case study indicates that a male had an increase in fGC after he became alpha male [Schoof et al., 2011]. ACTH challenge in *Cebus (Sapajus) apella* results in a cortisol increase [Torres-Farfan et al. 2009].

Statistical Analysis

We used repeated measures generalized linear mixed models (gamma probability distribution, log link function) to analyze the association between IGE rate, male dominance status (alpha vs. subordinate), and hormone levels. Specifically, each model was fitted with the hormone (fA or fGC) as the response variable, fecal sample order (for each male) as the repeated variable, dominance status and IGE rate as fixed effects, and male nested within social group as a random factor. We used a first-order autoregressive (AR1) covariance structure for the repeated measure. A two-tailed t-test revealed no collinearity between the categorical predictor (dominance status) and the continuous predictor (IGE rate; $t = 0.955$, $df = 192$, $P = 0.341$). We used models permitting variation in degrees of freedom across tests (recommended for small sample sizes), and used robust estimation to handle violations of model assumptions about normality and homogeneity of variance of the residuals. All analyses were run in IBM SPSS Statistics for Windows, version 19.0.

RESULTS

Androgens

IGE rate was positively and significantly associated with fA levels ($F = 21.534$, $P < 0.001$, $df = 1, 191$; Fig. 1A), and alpha males had significantly higher fA levels than subordinate males ($F = 13.769$, $P < 0.001$, $df = 1, 191$; Fig. 2A).

Glucocorticoids

IGE rate was positively and significantly associated with fGC levels ($F = 5.693$, $P = 0.018$,
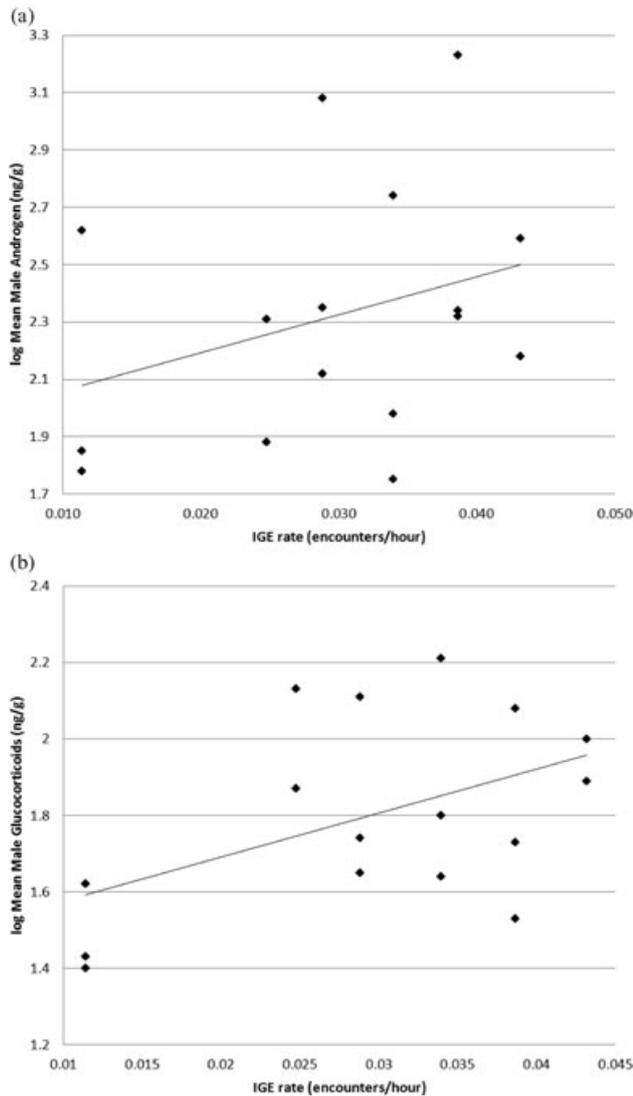
Fig. 1. Log of individual male mean (a) fA and (b) fGC level and seasonal intergroup encounter (IGE) rate (encounters per hour) for each of three social groups.
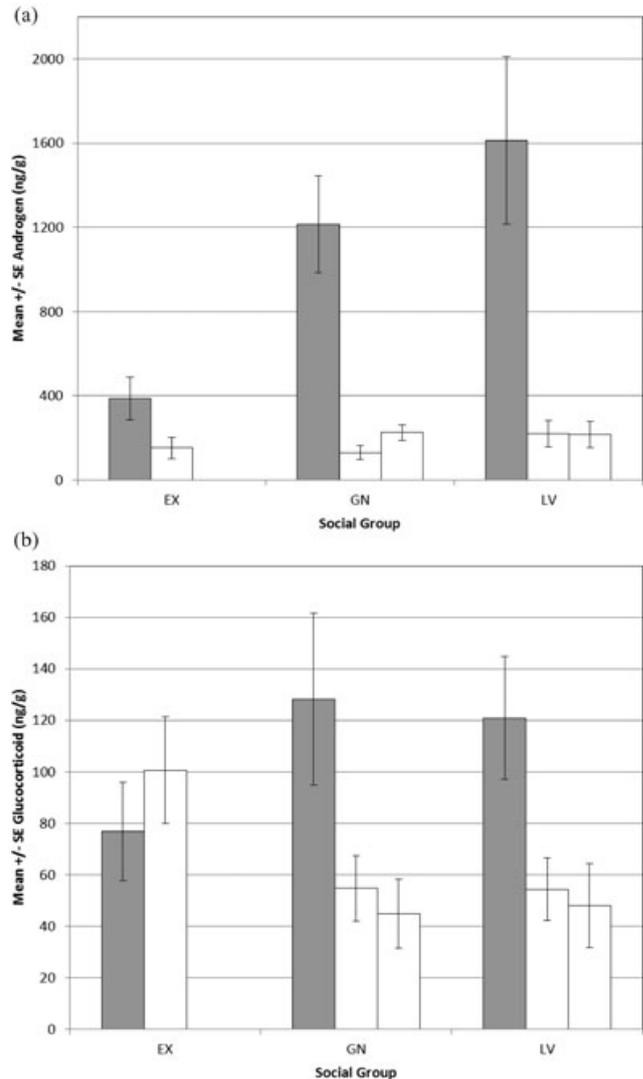

Fig. 2. Mean male (a) fA and (b) fGC levels (nanogram per gram) across three social groups. Alpha males are indicated with solid bars and subordinates are indicated by open bars.

$df = 1$, 191; Fig. 1B), and alpha males had significantly higher fGC levels than subordinate males ($F = 4.441$, $P = 0.036$, $df = 1$, 191; Fig. 2B). Figure 2B indicates that alpha males had higher fGC levels in the two larger groups with multiple subordinates (GN and LV), but not in the smaller group with a single subordinate (EX).

DISCUSSION

White-faced capuchins are classified as moderate seasonal breeders [for classification see van Schaik et al., 1999]; however, sexual behavior, copulations, conceptions, and births can and do occur throughout the year [Carnegie et al., 2011a]. During our study period, all females were either pregnant or lactating (confirmed by progesterone and estradiol assays, unpublished data), and although courtship behavior and copulations (mounts with thrusting) were observed, these were clearly not associated with conceptions. The timing of our study allowed us to examine the influence of intergroup competition on male androgen and GC levels without the possible confound of pronounced intragroup competition, since we can exclude the possibility that males were competing for immediate access to periovulatory females.

Male fA levels were positively and significantly associated with IGE rate. Similar androgen increases have been observed in other species after challenges from extragroup males or bisexual groups [*P. verreauxi*: Brockman et al., 1998; *C. kuhlii*: Ross et al., 2004; *A. paliatta*: Cristóbal-Azkarate et al., 2006; *C. vellerosus*: Teichroeb & Sicotte, 2008;

A. pigra: Rangel-Negrín et al., 2011, but see *E. f. rufus*: Ostner et al., 2008; *S. mystax*: Huck et al., 2005; *A. pigra*: Van Belle et al., 2009a]. Black howler males (*A. pigra*) living in unimale groups have higher androgen levels than males living in multimale groups [Rangel-Negrín et al., 2011]. Given that these males have an increased probability of being challenged for group membership, elevated androgen levels may represent an anticipatory response to reproductive challenges from extragroup males [Rangel-Negrín et al., 2011]. In white-faced capuchins, all males face the threat of group eviction since most takeovers result in the complete replacement of resident males [Fedigan & Jack, 2004]. The positive relationship between fA and IGE rates in white-faced capuchins indicates that resident males perceive IGEs as a form of reproductive competition.

Male fGC levels were also significantly associated with IGE rate. Several studies examining challenges by extragroup males did not observe an increase in fGC levels [*C. kuhlii*: Ross et al., 2004; *S. mystax*: Huck et al., 2005; *A. paliatta*: Cristóbal-Azkarate et al., 2007; *A. pigra*: Van Belle et al., 2009a]. However, previous research on male baboons has demonstrated that immigration events are associated with elevated GC levels, indicating that these are stressful events [*P. h. ursinus*: Bergman et al., 2005]. To our knowledge, however, this is the first study to report a significant relationship between fGC and the rate of IGEs.

In addition to the threats of IGEs mentioned above, infanticide in white-faced capuchins is frequent after group takeovers [Fedigan, 2003; Gros-Louis et al., 2003; Perry, 1996; Rose, 1998] and occurs occasionally during IGEs [Vogel & Fuentes-Jiménez, 2006]. In our study, we calculated IGE rates by season; the observed association between IGE rates and both fA and fGC may be tied to the greater risk of male takeovers (and therefore infanticides) during the dry season [Fedigan & Jack, 2004], which also coincides with the birth peak [Carnegie et al., 2011a]. Reported elevations in fA and fGC levels during the birth season in Verreaux's sifakas and red-fronted lemurs have been linked to the predictable risk of infanticide in these species [*P. verreauxi*: Brockman et al., 2001, 2009; *E. f. rufus*: Ostner et al., 2002, 2008].

Given that alpha male white-faced capuchins are the most active participants during IGEs and takeover attempts and that they direct most of their vigilance toward nonresident males [Rose & Fedigan, 1995; personal observation], we argue that it is not surprising to find that they display significantly higher fA and fGC levels than subordinate males. The observation that alpha males in all three social groups had higher fA than their subordinates supports our contention that IGEs pose a disproportional threat to the reproductive success of alpha males. We also predicted that alpha males would

have higher fGC levels than subordinate males because of the presumed higher metabolic costs associated with elevated vigilance and high level of participation in IGEs. Predicting elevated fGC levels in alpha males is also consistent with the notion that perceived infanticide risk may disproportionately affect them since they sire the majority of offspring [Jack & Fedigan, 2006; Muniz et al., 2010]. Indeed, the two social groups in which alpha males did have higher fGC levels had five and four infants (GN, LV, see Fig. 2B) born during the first four months of the study, which corresponded with the dry season. The third group (EX) had only one infant under the age of 6 months at the start of the study period, and no births occurred during the remainder of the study. Therefore, lower perceived risk of infanticide may account for both lower fGC and fA in the alpha male in EX group compared to the alpha males in the other two groups.

We propose that the difference between alpha and subordinate male fA and fGC during our study is driven primarily by the greater threat of IGEs and takeovers to alpha males, rather than by high intragroup male competition, since no periovulatory females were present. However, chimpanzee and grey-cheeked mangabey males display a similar pattern, where dominant males maintain higher androgens and GC levels than subordinates even in the absence of periovulatory females [*P. troglodytes*: Muehlenbein et al., 2004; Muller & Wrangham, 2004a, b; *L. albigena*: Arlet et al., 2009, 2011]. In these species, dominance status is achieved and maintained aggressively, so the association between persistently elevated androgens levels, status, and aggression are not surprising. Muller and Wrangham [2004a] propose that since estrous females are rare, males maintain high androgens levels due to the unpredictablity of challenges from rivals for access to these females. Furthermore, they suggest that the positive association between dominance status and GC levels are due to relatively higher energetic demands [Muller & Wrangham, 2004b]. Given that white-faced capuchin births occur thoughout the year, females ovulate rarely because of a long interbirth interval (2.2 years), and most (if not all) ovulatory cycles result in conceptions [data not shown; Carnegie et al., 2011a]; therefore, the presence of ovulatory females in this species is also unpredictable. However, previous research shows that within group male–male aggression is extremely rare and that dominance is not aggressively maintained in the studied population [Jack, 2003; but see Perry, 1998 for observations in a different population], making it unlikely that alpha male capuchins maintain higher fA levels due to the unpreditability of aggressive challenges by coresident males. Indeed, in the present study, some males displayed no agonism toward their coresident males, which is why we were unable to assign ranks below the alpha level.

In contrast to chimpanzees and mangabeys, black howler males have low intragroup aggression. Nonetheless, Van Belle et al. [2009a] found that "central" black howler males have higher fA and fGC than "noncentral" males, even in the absence of periovulatory females, a pattern similar to that reported here for white-faced capuchins. Van Belle et al. [2009a] propose that coresident males compete year round, such as chimpanzees and mangabeys, but that they do so covertly by fostering relationships with group females. They propose that the costs of this form of competition may account for higher fA and fGC levels observed in "central" compared to "noncentral" males. As with savannah baboons [*P. cynocephalus*: Gesquiere et al., 2011], costs associated with being an alpha or "central" male may exist even during times when intragroup reproductive competition appears to be low. Previous research has indicated that white-faced capuchin alpha males also generally spend more time affiliating with females than do subordinate males [Carnegie et al., 2005; Jack, 2003; Perry, 1997]. Therefore, we cannot entirely rule out the possibility that covert intragroup competition occurs even in the absence of periovulatory females. To further explore the influence of intragroup reproductive competition on male hormone levels, future work should focus on an examination of male fA and fGC levels during periods when females are ovulating, as well as on male–female interactions.

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