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# Hormonal correlates of male life history stages in wild white-faced capuchin monkeys (*Cebus capucinus*)

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ABSTRACT

Much attention has been paid to hormonal variation in relation to male dominance status and reproductive seasonality, but we know relatively little about how hormones vary across life history stages. Here we examine fecal testosterone (fT), dihydrotestosterone (fDHT), and glucocorticoid (fGC) profiles across male life history stages in wild white-faced capuchins (*Cebus capucinus*). Study subjects included 37 males residing in three habituated social groups in the Área de Conservacíon Guanacaste, Costa Rica. Male life history stages included infant (0 to <12 months; $N = 3$), early juvenile (1 to <3 years; $N = 10$), late juvenile (3 to <6 years; $N = 9$), subadult (6 to <10 years; $N = 8$), subordinate adult ($\geqslant$10 years; $N = 3$), and alpha adult ($\geqslant$10 years; $N = 4$, including one recently deposed alpha). Life history stage was a significant predictor of fT; levels were low throughout the infant and juvenile phases, doubled in subadult and subordinate adults, and were highest for alpha males. Life history stage was not a significant predictor of fDHT, fDHT:fT, or fGC levels. Puberty in white-faced capuchins appears to begin in earnest during the subadult male phase, indicated by the first significant rise in fT. Given their high fT levels and exaggerated secondary sexual characteristics, we argue that alpha adult males represent a distinctive life history stage not experienced by all male capuchins. This study is the first to physiologically validate observable male life history stages using patterns of hormone excretion in wild Neotropical primates, with evidence for a strong association between fT levels and life history stage.



## 1. Introduction

The term life history refers to the patterns of development organisms pass through on their journey from birth to death. While individual members of a species can vary widely in this regard (e.g., death can occur seconds or years after birth for most mammals), knowledge of species-specific life history stages, such as age at weaning, sexual maturity, and first reproduction, are important to the interpretation and understanding of animal behavior. Growth and development are hormonally regulated in all organisms; therefore, major maturational milestones (i.e., life history stages) are generally marked by changes in hormone profiles (Finch and Rose, 1995). For male mammals, androgens (e.g., testosterone and dihydrotestosterone) and glucocorticoids (e.g. cortisol and corticosterone) vary considerably and somewhat predictably in accordance with life history (e.g., Lincoln, 1998; Nef and Parada, 2000). Primates are known for their extended life histories (see Kappeler et al., 2003 for review), yet data on hormonal correlates of maturational milestones are only available for a limited number of taxa. In the present study, we use cross-sectional analyses to examine whether observable behavioral and/or physical changes across male white-faced capuchin (*Cebus capucinus*) life history stages are associated with hormonal differences. This information will enable us to more clearly understand male development and reproductive strategies in the study species and will inform interspecific comparisons of hormone production across life history stages (e.g., Wobber et al. 2013).

In male primates, testosterone (T) is elevated during the first two to six months of life depending on species-specific life histories (Dixson, 2012; Ginther et al., 2002; Mann et al., 1998; Meusy-Dessolle and Dang, 1985; Winter et al., 1976). This initial post-natal high is thought to promote post-partum maturation of the testes, continued masculinization of the brain, and facilitation of sex-typical behavioral organization via activation of the hypo-

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thalamic–pituitary–testicular axis (Fisher, 1998; Mann et al., 1989). Following this post-natal period, T levels fall and generally remain at basal levels throughout the juvenile stage. Testosterone then increases at puberty in association with the onset of spermatogenesis, playing an activational role in the masculinization of body structures and brain organization (reviewed in Dixson, 2012). Throughout puberty, T levels continue to rise as males approach adulthood, reach sexual maturity, and spermatogenesis becomes well-established (Beehner et al., 2009; Bernstein et al., 2008; Copeland et al., 1985; Gesquiere et al., 2005; Martin et al., 1977; Meusy-Dessolle and Dang, 1985; Plant, 1994; Seraphin et al., 2008; Whitten and Turner, 2009), followed by a gradual decline with advancing age (Altmann et al., 2010; Chen et al., 1994; Hakikinen and Pakarinen, 1993; but see Strier et al., 1999). Interestingly, a phenomenon referred to as a "male-specific pubertal testosterone peak" has been documented in several rodent species, whereby androgen levels at the start of puberty can be higher than those exhibited by adults (Eichmann and Holst, 1998, p. 785). To our knowledge, this phenomenon has not been investigated or documented in male primates, though evidence to date clearly demonstrates that T levels vary throughout a male's life. Additionally, variability in individual T levels has been documented among adult male primates according to ecological seasonality (e.g., Cerda-Molina et al., 2009; Gesquiere et al., 2011a; but see Strier et al., 1999), mating/breeding seasonality (Bales et al., 2006; Brockman et al., 1998; Girard-Buttoz et al., 2009; Gould and Ziegler, 2007; Lynch et al., 2002; Ostner et al., 2002; Ostner et al., 2011; but see Strier et al., 1999; see Place and Kenagy, 2000 for review of non-primates), group demography (Rangel-Negrín et al., 2011), dominance status (Arlet et al., 2011; Kraus et al., 1999; Muehlenbein et al., 2004; Muller and Wrangham, 2004a; Muroyama et al., 2007; Schoof and Jack, 2013; Setchell et al., 2008), and changes in dominance status (Alberts et al., 1992; Beehner et al., 2006; Brockman et al., 1998; Eberhardt et al., 1980; Mendoza et al., 1979; Rose et al., 1975; Schoof et al., 2011; Setchell and Dixson 2001a; Wickings and Dixson, 1992).

Dihydrotestosterone (DHT) is an androgen metabolized from testosterone, and its non-aromatizable nature suggests it is especially potent (Dixson, 2012). DHT is known to play a key role in the development of male external genitalia during embryonic growth, and it may also be involved in behavioral masculinization (Dixson, 2012). Although it has not been widely investigated, DHT is also responsible for many androgen-driven events at male puberty (Plant, 1994; Weiner et al., 1996), including the development of secondary sexual characteristics (Griffin and Wilson, 1998) and behavior required for successful copulation (Ginther et al., 2002; Wallen, 2005). However, the full extent of behavioral potency of DHT and other testosterone metabolites is unknown. In both male cotton-top tamarins (*Saguinus oedipus oedipus*) and long-tailed macaques (*Macaca fascicularis*), DHT follows a trajectory similar to T in that it is elevated during the first few months of life, followed by an abrupt decline until puberty (Ginther et al., 2002; Meusy-Dessolle and Dang, 1985). In contrast to macaques whose levels increase sharply at puberty, DHT levels in tamarins remain low for a prolonged period of time before increasing in later adulthood (i.e., up to 10 years; Ginther et al., 2002). While it has not been widely investigated, an increase in the ratio of DHT to T is indicative of increased 5-alpha-reductase activity, the enzyme that metabolizes T to DHT, and this ratio may serve as a good physiological marker for the onset of puberty. For example, Ginther et al. (2002) found that the onset of puberty in cotton-top tamarins was marked by a significant rise in urinary DHT:T and remained elevated thereafter. In brown capuchin monkeys (*Sapajus[Cebus] apella*), metabolism of T into DHT *in vitro* testicular cells increased at the onset of puberty and continued into adulthood, though overall DHT levels were relatively low in comparison to other androgens (Rey et al., 1995). DHT production in maturing testicular cells and a subsequent increase in sexually mature individuals appears to be common among anthropoids and has been shown via *in vitro* analysis of testicular tissue in olive baboons (*Papio anubis*), rhesus macaques (*Macaca mulatta*), and orangutans (*Pongo pygmaeus*) (Preslock, 1980).

In the few species for which they have been examined in relation to male life history, glucocorticoids (GC) have also been shown to increase with age (baboons: Gesquiere et al., 2005; chimpanzees: Seraphin et al., 2008; cotton-top tamarins: Ginther et al., 2002; humans: Touitou et al., 1983; Copinschi and Van Cauter, 1995; rats: Sapolsky, 1992). Several studies of primates have also found that GCs are high in males during infancy. For example, in their study of male development in savanna baboons (*Papio cynocephalus*), Gesquiere et al. (2005) report the highest GC levels at around six months of age with levels declining by age two and remaining low despite increasing levels of testosterone at puberty (~5 years). Infant baboons begin to forage on their own at approximately three months of age and are usually weaned at around one year (Altmann, 1980). This period of elevated GCs may reflect the social and/or physiological stress associated with this important maturational milestone. Captive studies on several other mammalian species have similarly found an association between elevated GC levels and weaning (cotton-top tamarins: Ginther et al., 2002; squirrel monkeys and rhesus macaques: Levine and Wiener, 1988; piglets: Poletto et al., 2006; rodents: Kikusui and Mori, 2009). Dispersal from the natal group is another stressful event during male life history that has been linked with elevated GC levels (Alberts et al., 1992; Bergman et al., 2005). Like T, individual GC levels can fluctuate according to various socioecological conditions such as ecological seasonality (primates: Gesquiere et al., 2011a; non-primates: Romero, 2002 and Schradin, 2008), mating/breeding seasonality (Fitchel et al., 2007; Lynch et al., 2002; Setchell et al., 2010; see Place and Kenagy, 2000 for review of non-primates), group demography (Alberts et al., 1992; Bergman et al., 2005), individual dominance status (Arlet et al., 2009; Bergman et al., 2005; Gesquiere et al., 2011b; Muller and Wrangham, 2004b; Sapolsky, 1983, 2004, 2005; Schoof and Jack, 2013; Van Belle et al., 2009), and changes in dominance status (Alberts et al., 1992; Beehner et al., 2006; Brockman et al., 1998; Schoof et al., 2011; Wickings and Dixson, 1992).

In this study we use cross-sectional data to explore patterns of fecal testosterone (fT), dihydrotestosterone (fDHT), and glucocorticoid (fGC) excretion at different life history stages for wild male white-faced capuchin monkeys (*Cebus capucinus*) residing in three social groups. Capuchins reside in multimale, multifemale groups averaging 15 individuals, and are characterized by female philopatry and male dispersal (Fedigan and Jack, 2012). Although births and conceptions occur throughout the year, white-faced capuchins are considered moderate seasonal breeders (*sensu* van Schaik et al., 1999), with 44% of births occurring between May and July (Carnegie et al., 2011a). Male capuchins disperse from the natal group at approximately 4.5 years of age (range = 19 months to 11 years; Jack et al., 2012), after which they continue to disperse throughout their lives at approximately 4-year intervals (Jack and Fedigan, 2004a). Dispersal for non-adult capuchin males is peaceful in nature in that they leave their natal group voluntarily and they do not experience aggression when entering a new group (Jack and Fedigan, 2004a). When adult males join a new group, they usually engage in prolonged antagonistic interactions via multimale coalitions (Fedigan and Jack, 2004). In our long-term study groups, such takeovers occur approximately every four years and often result in the death or eviction of resident males, infanticides, and even the occasional deaths or disappearances of females and juveniles (Fedigan, 2003; Jack and Fedigan, 2004a; Gros-Louis et al., 2003). Following these coalitionary group takeovers, a single male

rises to alpha status with little or no challenge from his coalition partners. Indeed, relationships among our resident males are characterized by affiliative interactions, low rates of aggression, and continued cooperation in group defense (Jack, 2003; Perry, 1998; Schoof and Jack, in press).

White-faced capuchins are medium-sized primates (females are ~2.7 kg and males 3.7 kg) that can live up to 55 years in captivity (Hakeem et al., 1996), and to at least 24 and 26 years of age for wild males and females respectively (Fedigan and Jack, 2012). In general, development in the genus *Cebus* is slow in comparison to other similarly sized primates and capuchins are especially altricial at birth (see Jack, 2011 for review). We recognize male white-faced capuchins as passing through a number of identifiable life history stages based on age, physical appearance, and behavior (see Table 1 for overview). From birth to approximately three months, infants remain in almost constant contact with their mothers and are completely reliant upon them for subsistence (Carnegie, 2011a; MacKinnon, 1995, 2002). At around three months of age, infants begin to experiment with other food sources, and they are fully weaned between 12–14 months (Carnegie, 2011a; MacKinnon, 2002). At weaning, *Cebus* species have typically attained about half of their adult body weight, and do the vast majority of their remaining growth during an extended juvenile period (Fragaszy and Bard, 1997; Fragaszy et al., 2004). In the early juvenile stage, males forage independently but remain close to adult group members; play behaviors also become increasingly important, and often include exploratory sexual behaviors (MacKinnon, 2002). During the late juvenile stage, most male white-faced capuchins disperse from their natal groups (mean 4.5 years; Jack et al., 2012). While white-faced capuchin females are considered juveniles from post-weaning through to the birth of their first offspring (~seven years of age, Fedigan et al., 2008; Fedigan and Jack, 2012), the transition from juvenile to adulthood is not as clearly demarcated for males. After the juvenile stage, males then go through a marked subadult stage (6–10 years), when most males are capable of copulating with ejaculation (Hakeem et al., 1996; pers. obs.). Males as young as 7.8 years have been confirmed to sire offspring in a wild population (Muniz et al., 2010; unpublished), suggesting that at least some males attain sexual/reproductive maturity during subadulthood. It is during this subadult phase that maturing males begin to exhibit behaviors consistent with those of adult males, including active participation in intergroup encounters during which they engage in both vocal and behavioral threats (Jack, 2003; Jack and Fedigan, 2004).

Most sexual and copulatory behavior in white-faced capuchins is, however, reserved for fully adult males (≥10 years), and alpha males sire the majority of offspring in their own social groups (Jack and Fedigan, 2006; Muniz et al., 2010). Agonism among co-resident males is rare, and while there is a clearly identifiable alpha male, linear dominance relationships among subordinates do not appear to exist and/or are difficult to distinguish given the rarity of agonistic interactions (Jack, 2003; Perry, 1998; Schoof and Jack, 2013). Male white-faced capuchins do not attain adult body size until they are 10 years of age, an observation that is consistent with sexually dimorphic patterns of somatic growth in species where males are larger than females (Dixson, 2012). Even as adults, males do not fill out with the entire suite of secondary sexual characteristics (e.g., exaggerated brow ridges, large mandibular girth, broad shoulder girdle) until/if they attain alpha male status within a social group (Schoof et al., 2011). This dormancy in the development of the full suite of secondary sexual characteristics is likely related to androgen levels rather than individual propensities, as androgens are significantly higher in alpha than subordinate adults (Schoof and Jack, 2013, in press) and appear to reach peak levels only after a male attains alpha status (Schoof et al., 2011) (See Figure 1a and b). Given that not all males attain alpha status, and there is considerable age overlap for alpha and subordinate adults, alpha males appear to constitute a distinctive life history phase.

The aim of the present study is to establish a chronology of endocrine function to gain a better understanding of the secretory patterns of androgens and glucocorticoids across life history stages in male white-faced capuchin monkeys. We generally predict that androgens will be lowest in infants and early juveniles, and begin to increase gradually in late juveniles, subadults, and adult males, with peak levels being reached only in alpha males. Similarly, we predict that glucocorticoid levels will be increase in the late juvenile and subadult period, when males engage in natal dispersal, and will be highest in alpha males. Finally, we predict that the deposed alpha male will have hormone levels similar to subordinate adult males.

## 2. Materials and methods

### 2.1. Study site and subjects

This study was conducted in the Santa Rosa Sector of the Área de Conservación Guanacaste, Costa Rica. Santa Rosa, formerly known as Santa Rosa National Park (SRNP), is comprised of over 100 $km^2$ of tropical dry forest. Seasonal effects in this area are marked; an average of 1800 mm of rainfall occurs during the wet season months of May through November, while rainfall is scant or absent and most of the trees lose their leaves during the dry

**Table 1**
Male life history stages in white-faced capuchins and sample collection details, including total number of samples per life history stage, the range of samples collected per individual, and the mean number of samples per individual.

| Life history stage | Descriptors | N (known/estimated age) | Total # of fecal samples(range/mean) |
|---|---|---|---|
| Infant | 0 to <12 months; highly dependent upon mother for food and transport; weaning begins | 3 (3/0) | 10 (2–4/3.3) |
| Early juvenile | 1 to <3 years; fully weaned; independent foraging but maintain close proximity to adults; exploratory sexual behavior | 10 (10/0) | 36 (2–6/3.6) |
| Late juvenile | 3 to <6 years; increased independence; natal dispersal usually occurs | 9 (6/3) | 40 (2–6/4.4) |
| Subadult | 6 to <10 years; transitional body size; participation in intergroup encounters begins; successful ejaculation and ability to sire offspring; subordinate to all adult males | 8 (1/7) | 42 (3–7/5.3) |
| Subordinate adult | ⩾10 years; full adult body size but lack full complement of secondary sexual characteristics | 3 (0/3) | 13 (2–6/4.3) |
| Alpha | ⩾10 years; development of secondary sexual characteristics; dominant to all individuals in the group; sires majority of group offspring | 3 (1/2) | 16 (5–6/5.3) |
| Deposed alpha adult | ⩾10 years; subordinate adult male known to have formerly occupied an alpha position in one or more groups | 1 (0/1) | 6 |

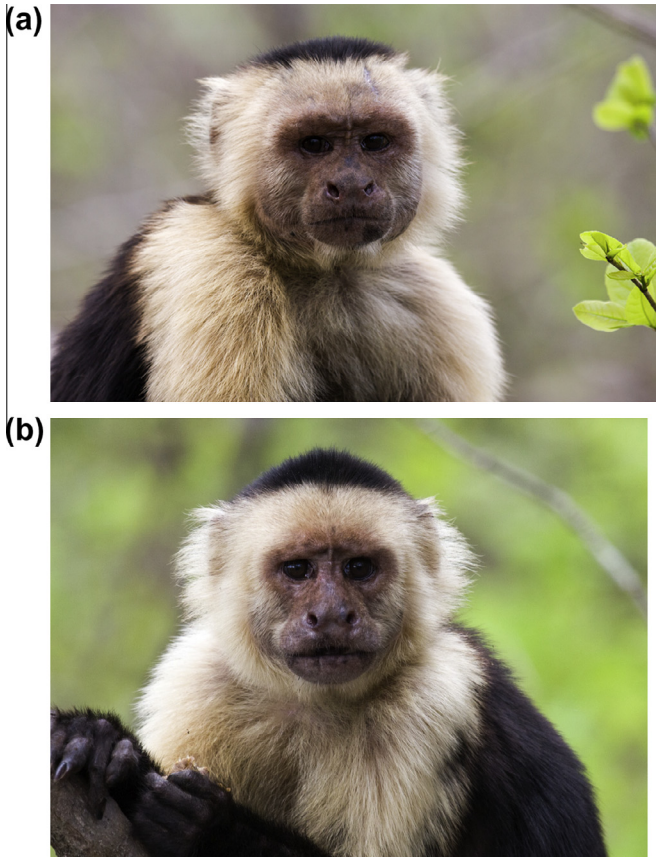


**Fig. 1.** (a) Alpha male and (b) subordinate adult male white-faced capuchins. Note exaggerated brow ridges, broad jawline and shoulder girdle of the alpha male. Photos courtesy of Fernando Campos.

season months of December through April. The white-faced capuchins of Santa Rosa have been under near continuous observation since 1983, and demographic (i.e., deaths, births, emigrations/immigrations) and dominance data are continually recorded (see Fedigan and Jack, 2012 for full description of the field site and history of the capuchin project).

We collected fresh fecal samples from males ($N = 37$) residing in three long-term study groups (CP, LV and GN, see Table 2 for group compositions) between May 29 and July 21, 2010, which coincides with the latter half of the birth peak in this population (Carnegie et al., 2011a). In an earlier study we found that both alpha and subordinate males display higher fecal androgens and fGC levels in the dry season when intergroup interactions (and the threat of takeovers and infanticide) are at their peak (see Schoof and Jack, 2013; Jack et al., 2013). Based on these findings, it is likely that the samples presented here represent hormone levels that are lower than would be encountered during the dry season and the timing of collection works to decrease the effects of differential male response to reproductive effort. CP and LV groups have been the focus of long-term behavioral and ecological study (since 1984 and 1990 respectively) and all natal males are of known age and maternal origins. We began habituating GN in 2006 and reliable demographic data collection began on this group in 2007. Ages for males with unknown birthdates (i.e., those present in the group when observations began and unfamiliar immigrants) were estimated based on body size comparisons with males of known ages. Subjects ranged in age from six months to approximately 18 years and all males were individually identifiable based on natural markings. Given that known birthdates were only available for 21 of the 37 males, we assigned males relative age ranks, with the youngest male being ranked 1 and the oldest ranked 37. We also grouped study subjects into seven recognizable life history stages following MacKinnon (1995, 2002) and Jack et al. (2012): infant (0 to <12 months; $N = 3$), early juvenile (1 to <3 years; $N = 10$), late juvenile (3 to <6 years; $N = 9$), subadult (6 to <10 years; $N = 8$), subordinate adult ($\geqslant$10 years; $N = 3$), alpha adult ($\geqslant$10 years; $N = 3$), and recently deposed alpha adult ($\geqslant$10 years; $N = 1$; see Table 1). The single recently deposed alpha male (6 weeks prior to the start of our study) was also estimated to be the oldest male in our sample. To our knowledge, none of the three subordinate adult males had ever acquired alpha status.

Research protocols for this study were approved by the Área de Conservación de Guanacaste and Tulane University's IACUC. The authors adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates and to the legal requirements of Costa Rica.

### 2.2. Fecal sample collection, hormone extraction, validation and analyses

Fresh fecal samples were collected into plastic vials after defecation, and labeled with the individual male's ID, and the date and time of collection ($N = 163$; mean = 4.4 per individual, range = 2–7 per individual; see Table 1 for details on samples per life history stage). Following Carnegie et al. (2011b), the vials were placed in ice packs until they could be stored in a freezer at the end of the field day. For preliminary field extraction, we weighed out 0.10 g of thawed feces and processed them using Prevail C18 Maxi-Clean 300 mg SPE cartridges (Alltech Associates, Inc., Deerfield, IL) following the methods described in Carnegie et al. (2011b). Samples were analyzed at the Wisconsin National Primate Research Center (WNPRC) by VAMS in August 2010 following the methods described in Schoof et al. (in press). Hormones were eluted from the SPE cartridges with 2 mL of 100% methanol, dried in a hot water bath, reconstituted in 1 mL of 100% ethanol, and stored in a refrigerator. Following Ginther et al. (2001), we used a portion of the sample to separate fT and fDHT fractions by in-house Celite column chromatography. Recoveries were 89.35 ± 3.04% (mean ± SE) for fT fractions and 86.98 ± 3.34% for fDHT fractions ($N = 7$). The fT and fDHT fractions were subsequently analyzed by EIA in which sample volumes of 5–25 uL were dried and resuspended in the assay solution, and 1/3 was aliquoted into each well. fGC was analyzed by EIA without chromatography using 50 uL of the ethanol solution (Carnegie et al. 2011b). All EIAs used antibodies raised in rabbits (for antibody crossreactivities, see

**Table 2**
Composition of study groups in June 2010.

| | CP | LV | GN | Total |
|---|---|---|---|---|
| Adult males | 3 | 1 | 3 | 7 |
| Adult females | 11 | 5 | 11 | 27 |
| Subadult males | 3 | 0 | 5 | 8 |
| Juvenile females (late, early, infant) | 6 (3, 2, 1) | 9 (3, 4, 2) | 4 (0, 3, 1) | 19 (6, 9, 4) |
| Juvenile males* (late, early, infant) | 9 (1, 5, 3*) | 6 (3, 1, 2) | 12 (5, 6*, 1) | 27 (9, 12, 6) |
| Total | 32 | 21 | 35 | 88 |

* The three CP infants and two of the GN early juveniles were not included in this study due to the difficulty of obtaining samples from these young individuals.

Ziegler et al., 1995 and Ginther et al. 2001). All samples and standards (T: 1–250 pg, $N = 8$, 17β-Hydroxy-3-oxo-4-androstene; DHT: 5-alpha-dihydrotestosterone; GC: 3.16–1000 pg, $N = 6$, 11β,17α, 21-Trihydroxypregn-4-ene-3,20-dione; Sigma–Aldrich, St.Louis, MO) were run in duplicate. Concentrations of fT, fDHT, and fGC were measured in ng/g of wet feces.

Mean intra- and inter-assay coefficients of variation (CV) for fT were respectively 3.8 and 5.5 for the low pool, and 3.7 and 6.7 for the high pool. Mean intra- and inter-assay coefficients of variation (CV) for fDHT were respectively 11.8 and 20.3 for the low pool, and 2.0 and 9.9 for the high pool. Mean intra- and inter-assay CVs for fGC were respectively 10.9 and 19.4 for the low pool, and 3.8 and 6.3 for the high pool. Mean percent accuracy was high for all three hormones (fT: 104.69 ± 1.94, $N = 8$; fDHT: 113.21 ± 1.84, $N = 8$; 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 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, $p > 0.05$, $n = 5$; fGC: $t$ (21) = 0.066, $p > 0.05$, $n = 7$).

An ACTH challenge to test the biological validity of the fGC response could not be conducted because the study population is comprised of wild white-faced capuchins. However, prior studies from this population of *C. capucinus* have shown that fGC levels of adult females increase in response to a presumably stressful situation (change in male group composition; Carnegie et al., 2011b). Additionally, individual fGC levels increase with a rise in male dominance rank (Schoof et al., 2011) and decrease with increased habituation levels (Jack et al., 2008), both situations presumably associated with changes in stress. ACTH challenge in the closely related robust tufted capuchin, *Sapajus (Cebus) apella,* results in a cortisol increase (Torres-Farfan et al., 2009).

### 2.3. Data analysis

Slightly more than half of all fecal samples (57%) were collected before noon. There was no diurnal variation for any of the hormone variables (fT: $t$, unequal variances: −1.488, df = 78.443, $p = 0.141$; fDHT: $t$, equal variances = −0.004, df = 160, $p = 0.997$; fDHT:T: $t$, equal variances = 0.392, df = 160, $p = 0.696$; fGC: $t$, equal variances = 0.240, df = 160, $p = 0$ .811); therefore, morning and afternoon samples were pooled for all analyses.

We used Spearman's rank correlation for a preliminary examination of the effects of age (investigated here as a relative age where males were ranked from 1–37 according to known or estimated age, see above) on individual mean levels of fT, fDHT, fDHT:T, and fGC. fT, fDHT, and fGC displayed non-normal distributions even after transformation attempts. Repeated-measures generalized linear mixed models (GLMMs) account for unbalanced repeated measures designs (Cnaan et al. 1997), thereby allowing us to include all fecal samples and avoid averaging hormone levels for individuals (see Muehlenbein et al. 2004 for discussion of this type of mixed-model). Since the distributions for fT, fDHT, and fGC were non-normal, we used GLMMs with gamma regression to test whether these hormones were predicted by male life history stage (gamma distribution with log link used because all values were positive and skewed towards larger values). The square root transformation of fDHT:T was normally distributed so we used a GLMM with a normal distribution and an identity link function. For all GLMMs we employed a scaled identity covariance structure (which assumes that potential correlations between the variables of interest remain stable across the data collection period) with fecal samples (i.e., the repeated measure) nested within each male, and males nested within each social group. We allowed degrees of freedom to vary using the Satterthwaite approximation, and used robust covariances for tests of fixed effects and coefficients. For fT, fDHT and fDHT:fT, we nested males within social group as a random variable. For fGC, however, this combination resulted in an error with the G and Hessian matrices and we therefore included only social group as the random factor in this model. Post-hoc pairwise comparisons of life history stages were conducted only for statistically significant GLMM models. Significance was set at 0.05 and all $p$-levels reported are adjusted for multiple

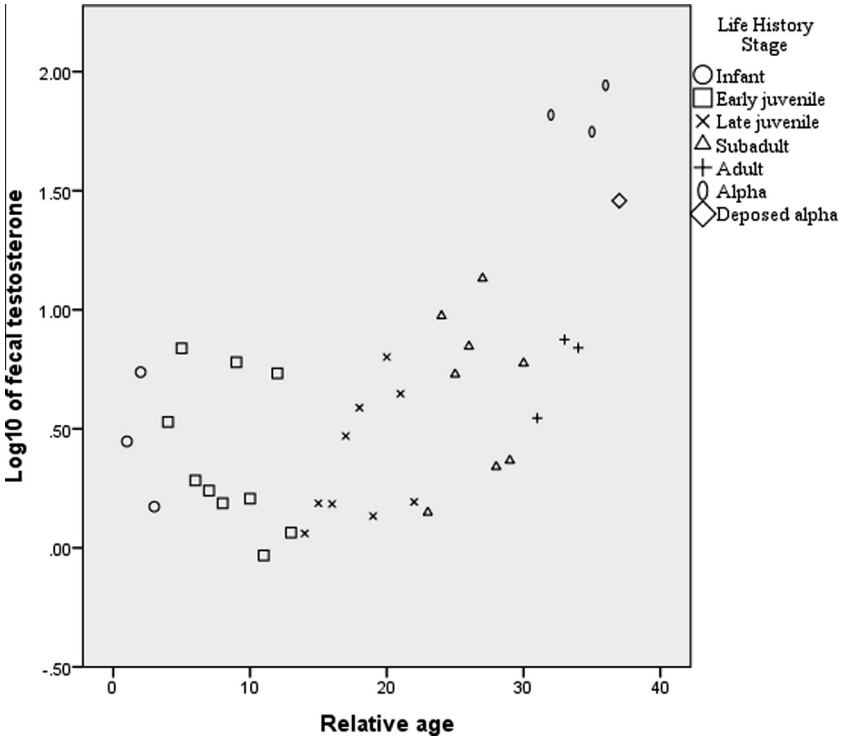


**Fig. 2.** Mean male fecal testosterone level (fT) in relation life history stage and relative male age (with age rank 1 = youngest male [6 months], and age rank 37 = oldest male [estimated at 18 years]).

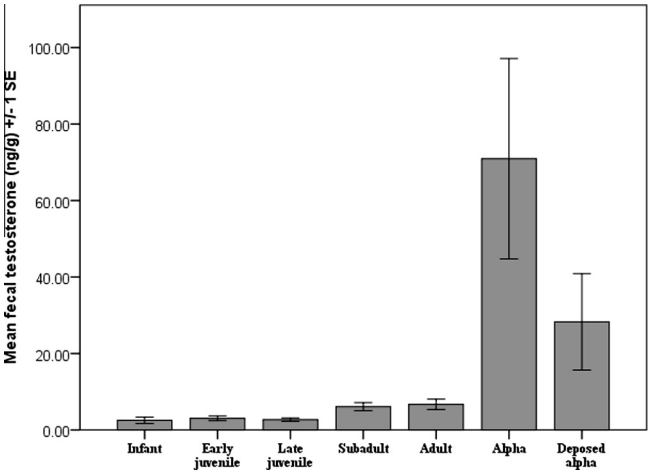


**Fig. 3.** Estimated mean fecal testosterone (fT) ± robust SEM by male life history stage. Summary of significant relationships: Alpha > than all life history stages except deposed alpha; subadult >than late juvenile, early juvenile and infant life history stages.

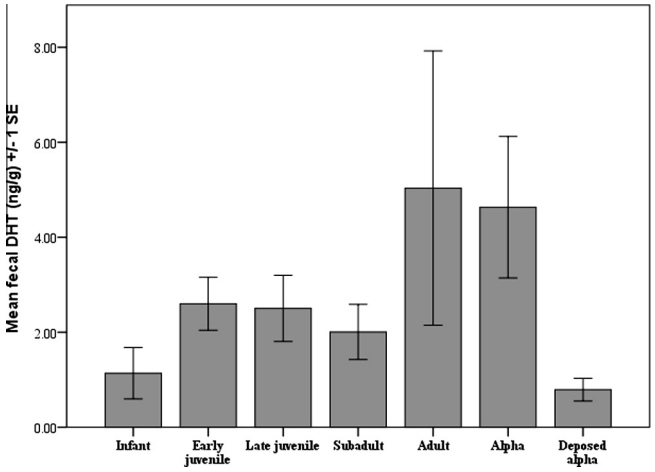


**Fig. 4.** Estimated mean fecal dihydrotestosterone (fDHT) ± robust SEM by male life history stage.

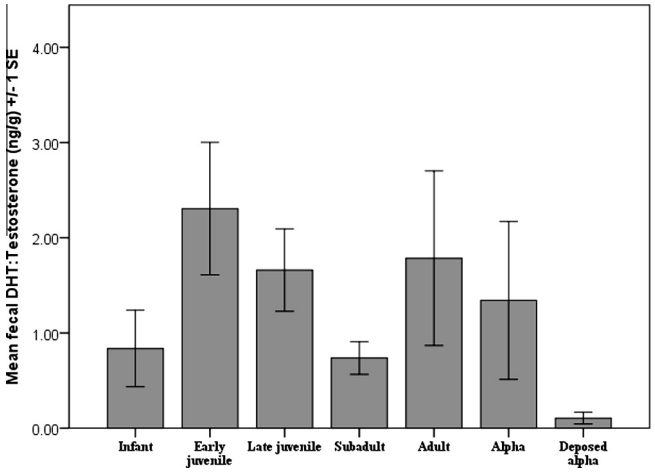


**Fig. 5.** Estimated mean fecal DHT:T ratio ± robust SEM by male life history stage.

comparisons using the least significance difference method. All analyses were conducted in IBM SPSS Statistics 19.0.

## 3. Results

The scatterplot for relative male age rank, life history stage, and fT clearly illustrates that alpha males show the highest fT levels, followed by the sole deposed alpha male (Fig. 2). Given that the mean fT level of the recently deposed alpha male was intermediate to alpha and subordinate adult males, we considered "deposed alpha" as its own life history stage rather than including him with the other subordinate adult males so as to not skew their hormone levels. Male relative age rank was significantly correlated with mean fT levels (Spearman's $\rho = -0.550$, $p < 0.001$).

The GLMM showed that male life history stage was a good predictor of fT ($F$ (6, 26) = 17.234, $p < 0.001$; Fig. 3). Alpha males had significantly higher fT levels than those of all other male life history stages (alpha vs. subordinate adult: $t = 2.830$, $p = 0.010$; alpha vs. subadult: $t = 2.892$, $p = 0.008$; alpha vs. late juvenile: $t = 3.024$, $p = 0.006$; alpha vs. early juvenile: $t = 3.012$, $p = 0.006$; alpha vs. infant: $t = 3.023$, $p = 0.006$), with the exception of the recently deposed alpha male (alphas vs. deposed alpha: $t = 1.550$, $p = 0.136$). The deposed alpha and subordinate adult male fT levels did not differ significantly from any of the other life history stages. Subadult males had significantly higher fT levels than late juveniles ($t = 2.452$, $p = 0.022$), early juveniles ($t = 2.169$, $p = 0.040$), and the difference with infants approached significance ($t = 2.041$, $p = 0.051$). There were no significant differences between late juvenile, early juvenile and infant life history stages.

Male life history stage was not a significant predictor of fDHT ($F$ (6, 28) = 0.966, $p = 0.466$; Fig. 4), fDHT:fT ($F$ (6, 24) = 1.572, $p = 0.198$; Fig. 5), nor fGC ($F$ (6, 147) = 1.598, $p = 0.151$, Fig. 6).

## 4. Discussion

### 4.1. Male hormonal profiles and life history stage

Consistent with previous research in other non-human primates, white-faced capuchin testosterone (fT) levels rose gradually with advancing male age (Fig. 1) and life history stage (Fig. 2). Mean fT levels for infants, early and late juveniles were statistically indistinguishable, while fT levels doubled for males in the subadult and subordinate adult life history stages. Interestingly, hormonal profiles for subordinate adult and subadult males were virtually indistinguishable. In contrast, alpha male testosterone levels (mean = 69.7 ng/g; range = 55.9–87.6 ng/g) were more than eleven times higher than the fT levels of subordinate adult (mean = 5.97;

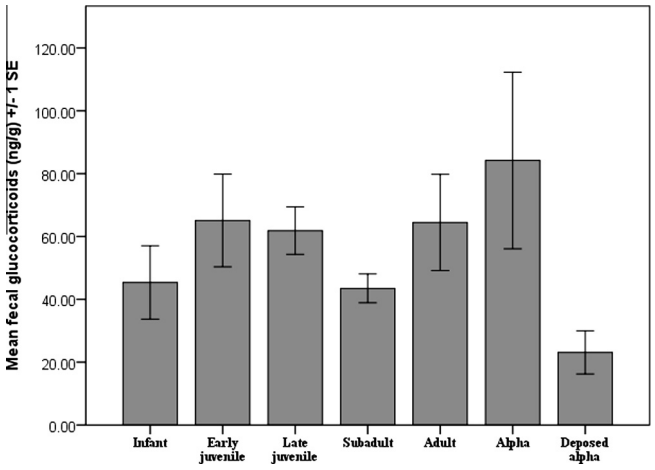


**Fig. 6.** Estimated mean fecal glucocorticoids (fGC) ± robust SEM by male life history stage.

range = 3.5–7.5 ng/g) and subadult males (mean = 5.90 ng/g; range = 1.4–13.5 ng/g), further supporting our contention that these males occupy a distinctive life history stage (see below). We have argued elsewhere that alpha male capuchins maintain high fT levels even in the absence of periovulatory females due to the constant threat of intergroup encounters and takeover attempts as both are associated with infanticide in our study groups (Schoof and Jack, 2013). This may be the case during our study as it took place during the birth peak.

We did not have any males in our sample that were at or near the oldest age estimate for male white-faced capuchins (~24 years) so we are unable to explore the possibility of male fT levels dropping with advancing adult age as has been documented in some mammalian species. It is noteworthy, however, that the oldest male we have documented in our study groups was an alpha male when he disappeared (not included in study sample). In addition, the recently deposed alpha male (referred to as BG herein) was the oldest male in our study sample (at least18 years old) and his fT levels were intermediate to those of alpha and subordinate adult/subadult males in our sample. When BG was alpha male during the same six-week period in 2009 (i.e., also during the birth peak), his mean fT level was 123.84 ng/g compared to 28.70 ng/g in the current study, indicating that fT levels respond to changes in male dominance status. By comparison, mean fT levels of the beta male who deposed BG increased drastically from 7.08 ng/g in the same six-week period in 2009 to 55.93 ng/g as alpha male in the current study. Although the sample size is unquestionably small, these data support our prior finding that androgens increase rapidly following a rise to alpha status (Schoof et al., 2011) and they add to our growing understanding of fT response in relation changes in dominance status in male white-faced capuchins.

Based on the cross-sectional data collected for this study, male life history stage was not a good predictor of fDHT or fDHT:fT, though longitudinal data may uncover a differing pattern of excretion. Of interest in the current data set is our finding that BG, the sole deposed alpha male showed the lowest fDHT and fDHT:T levels (Figs. 3 and 4), indicating decreased 5-alpha-reductase activity and thus lower conversion rates of T to DHT. This may be linked to his recent change in dominance status and/or may be a reflection of the male's increasing age (estimated >18 years), with some research on humans indicating that DHT levels tend to decline with increasing age (Drafta et al., 1982; Matsumoto, 2003; but see Kaufman and Vermeulen, 2005). Increased sampling of aging males is needed to examine the effects of age on male hormone levels. The highest fDHT:T ratios occurred during the early juvenile stage, indicating that relatively more T was being converted to DHT than during the other male life history stages, though these differences were not statistically significant (see Fig. 4).

Life history stage was also not a good predictor of fGC levels, indicating that no single stage is associated with a relatively greater stress response in white-faced capuchins. Although not significant, early and late juveniles display higher fGC levels than infants and subadults, potentially indicative of increased stress associated with important somatic growth, the overall social complexities associated with juvenile life history stages, and dispersal (Pagel and Harvey, 1993). As anticipated, alpha males displayed the highest fGC levels, although the difference was not statistically significant relative to the other life history stages (see Fig. 5). Our previous finding that two of three alpha males had higher fGC levels than their subordinates suggests that fGC excretion may be influenced by the interaction of male dominance status, individual developmental trajectory, and other social and ecological factors, such as the number of coresident males, number of infants, perceived infanticide risk (Schoof and Jack, 2013; Schoof et al., in press), presence of fertile females (Schoof et al., in press), and seasonality (dry vs. wet season; conception vs. birth peak).

### 4.2. Onset of puberty and the development of secondary sexual characteristics

The ratio of fDHT:T peaked in early juvenile male white-faced capuchins (12 months to 3 years). The fDHT:T ratio was slightly lower in late juvenile males (3–6 years), followed by a dramatic drop in subadult males (Fig. 4). A similar pattern has been documented in cotton-top tamarins and the peak in DHT:T is hypothesized to indicate the onset of puberty (Ginther et al., 2002). Although our results were not statistically significant (perhaps owing to the cross-sectional nature of our study and variability among individual males), the observed peak in DHT:T may indicate that the process of sexual maturation is beginning in the early juvenile life history stage. Male juvenile capuchins frequently engage in "exploratory" sexual behavior such as attempted mounting behavior and pelvic thrusting, but these have not been observed to result in intromission (in fact, these are rarely directed towards the genital area). The link between increased DHT metabolism and these sexually dimorphic copulatory behaviors (mainly mounting) is well-established for other species (Wallen, 2005).

Based on the results presented here, male white-faced capuchins appear to enter puberty in earnest during the subadult life history stage (6–10 years), as indicated by the onset of fT elevation above pre-pubertal levels (Plant and Witchell, 2006). Indeed, our finding that several subadults in our sample had higher mean fT levels than subordinate adult males (Fig. 1), may be indicative of the "male-specific pubertal testosterone peak" documented in several rodent species (Eichmann and Holst, 1998). As a group, however, males in the subadult life history stage did not differ significantly from males in the subordinate adult life history stage. Longitudinal data are needed to more fully explore this important life history stage and the role of individual developmental trajectory. While the significant increase in fT observed in subadult over juvenile males likely reflects their impending reproductive maturity (i.e., the gonads are regularly pumping out T in contrast to the endocrine silence associated with juveniles), the somatic growth process is ongoing in white-faced capuchins until full adult body size is reached at around 10 years of age. In human and non-human primates, as well as in non-primate mammalian species, there is a strong association between elevated testosterone levels and the laying down of lean muscle and the promotion of skeletal growth in specific regions (Rogol, 2010; Wiren, 2005).

When comparing the ages of pubertal onset with other primates, capuchins are anomalous for their small size (adult male weight is ~3.7 kg). For example, at approximately 60 kg adult male chimpanzees are nearly 20 times the size of capuchins, yet an increase in plasma T levels occurs around the same age (6–8 years old; reviewed by Plant and Witchell, 2006). While data for platyrrhine species are sparse, pubertal onset occurs much earlier in the few species for which this has been investigated (e.g., ~1 year in cotton-top tamarins: Ginther et al., 2002; ~1 year in marmosets and owl monkeys and 2.5–3 years in squirrel monkeys: Plant and Witchell, 2006), although it should be noted that these species weigh <50% of an adult male capuchin. According to life history theory, the costs of growth and reproduction are such that the two seldom overlap (Charnoz, 1993; Charnov and Berrigna, 1993). In species with high rates of male-male competition, reproductive maturation is often delayed until the male has reached his physical peak and is socially experienced enough to attain and maintain a dominant position in the social hierarchy (Leigh, 1992). In white-faced capuchins, delaying the attainment of adult body size appears to facilitate dispersal by enabling late juvenile males to join new groups with little to no aggression (Jack and Fedigan, 2004a; see van Noordwijk and van Schaik, 2001 for similar observations among long-tailed macaques, *M. fascicularis*). Late juvenile males with lower levels of testosterone do not necessarily

present a direct threat to resident coresident males (especially alpha males), and hence might make the transition into a new social group more easily than adult males, who generally have to takeover groups via aggressive coalitions. By the time a capuchin male reaches full adult body size at around 10 years of age, he is usually well established in his third social group (Jack and Fedigan, 2004b).

However, even after attaining adult body size, not all males develop the full complement of secondary sexual characteristics. We contend that the significantly higher androgen levels found in alpha male white-faced capuchins (present study; Schoof et al., 2011; in press; Schoof and Jack, 2013) are associated with the development and maintenance of their distinctive morphological features (i.e., brow ridge prominence, wider jaws, larger overall size, piloerection). Such dominance-based morphological differences have been reported for several primate species, and while this has been best described for mandrills (*Mandrillus sphinx*: Setchell and Dixson, 2001a, 2001b; Setchell et al., 2010) and orangutans (*P. pygmaeus*: Knott, 2009; Maggioncalda et al., 1999, 2000, 2002), Dixson suggests that "delayed development of masculine secondary sexual traits is a more common reproductive strategy in primates than is currently realized or documented" (2012: 269). We suggest that this is the case in male white-faced capuchins, and that males follow different developmental paths based on physiological and social condition.

## 5. Summary

This is the first study to physiologically validate observable male life history stages using patterns of hormone excretion in wild Neotropical primates. These data provide us with a better understanding of male reproductive potential in this species and will enable us to more succinctly address issues pertaining to how social and demographic processes may influence a male's developmental and social trajectory (i.e., his ability to attain alpha status). An obvious limitation of the cross-sectional nature of this study is that our analyses may not account for variation between individuals within the same life history stage, which may explain why we did not find significant differences in fDHT, fDHT:T and fGC. A longitudinal study would enable us to track individual trajectories through the various life history stages. Nonetheless, given the longevity of our study species and the difficulties inherent in non-invasively studying the dispersing sex throughout their lives (i.e., tracking individuals through multiple dispersal events), the results presented here are significant in that they provide us with a life history snapshot for male white-faced capuchins. It is only through the integration of behavioral, ecological, and endocrine data that we can begin to fully understand and interpret the behavior of wild white-faced capuchins. In concert with the longitudinal life history and demographic data our research team collects on this species (dating back to 1983), the data presented here suggest that male capuchins experience an energy trade-off between growth and reproduction, one that is mediated by frequent dispersal and delayed rank attainment. Collectively these data take us a long way towards understanding the developmental trajectories of male white-faced capuchins and other nonhuman primates, which as whole are characterized by their unusually slow life histories (Kappeler et al., 2003).

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## References

Altmann, J. (Ed.), 1980. Baboon Mothers and Infants. Harvard University Press, Cambridge.
Altmann, J., Gesquiere, L., Galbany, J., Onyango, P.O., Alberts, S.C., 2010. Life history context of reproductive aging in a wild primate model. Ann. N.Y. Acad. Sci. 1204, 127–138.
Alberts, S.C., Sapolsky, R.M., Altmann, J., 1992. Behavioral, endocrine, and immunological correlates of immigration by an aggressive male into a natural primate group. Horm. Behav. 26, 167–178.
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*). Horm. Behav. 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*). Horm. Behav. 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 (*Leotopithecus rosalia*). Horm. Behav. 49, 88–95.
Beehner, J., Bergman, T., Cheney, D., Seyfarth, R., Whitten, P., 2006. Testosterone predicts future dominance rank and mating activity among male Chacma baboons. Behav. Ecol. Sociobiol. 56, 469–479.
Beehner, J., Gesquiere, L., Seyfarth, R., Cheney, D., Alberts, S., Altmann, J., 2009. Testosterone related to age and life-history stages in male baboons and geladas. Horm. Behav. 56, 472–480.
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*). Anim. Behav. 70, 703–713.
Bernstein, R.M., Leigh, S.R., Donovan, S.M., Monaco, M.H., 2008. Hormonal correlates of ontogeny in baboons (*Papio hamadryas anubis*) and mangabeys (*Cercocebus atys*). Am. J. Phys. Anthropol. 136, 156–168.
Brockman, D.K., Whitten, P.L., Richard, A.F., Schneider, A., 1998. Reproduction in free-ranging male *Propithecus verreauxi*: hormonal correlates of mating and aggression. Am. J. Phys. Anthropol. 105, 137–151.
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. Int. J. Primatol. 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*). Am. J. Primatol. 73, 1–9.
Cerda-Molina, A.L., Hernández-López, L., Chavira-Ramirez, R., Cárdenas, M., Mondragón-Ceballos, R., 2009. Seasonality of LH, testosterone and sperm parameters in spider monkey males (*Ateles geoffroyi*). Am. J. Primatol. 71, 427–431.
Charnov, E.L., Berrigan, D., 1993. Why do female primates have such long lifespans and so few babies? *or* Life in the slow lane. Evol. Anthropol. 1, 191–194.
Charnov, E.L. (Ed.), 1993. Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology. Oxford University Press, Oxford.
Chen, H., Hardy, M.P., Huhtaniemi, I., Zirkin, B.R., 1994. Age-related decreased Leydig cell testosterone production in the brown Norway rat. J. Androl. 16, 551–557.
Cnaan, A., Laird, N.M., Slasor, P., 1997. Using the general linear mixed model to analyse unbalanced repeated measures and longitudinal data. Stat. Med. 16, 2349–2380.
Copeland, K.C., Eichberg, J.W., Parker Jr., C.R., Bartke, A., 1985. Puberty in the chimpanzee: somatomedin-C and its relationship to somatic growth and steroid hormone concentrations. J. Clin. Endolinol. Metab. 60, 1154–1160.
Copinschi, G., Van Cauter, E., 1995. Effects of ageing on modulation of hormonal secretions by sleep and circadian rhythmicity. Horm. Res. 43, 20–24.
Dixson, A.F., 2012. Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Humans, Second edition. Oxford University Press, Oxford.
Drafta, D., Schnidler, A.E., Stroe, E., Neacsu, E., 1982. Age-related changes of plasma steroids in normal adult males. J. Steroid Biochem. 17 (6), 683–687.
Eberhardt, J.A., Keverne, E.B., Meller, R.E., 1980. Social influences on plasma testosterone levels in male talapoin monkeys. Horm. Behav. 14, 247–266.
Eichmann, F., Holst, D.V., 1998. Organization of territorial marking behavior by testosterone during puberty in male tree shrews. Physiol. Behav. 65, 785–791.

Fedigan, L.M., 2003. Impact of male takeovers on infant deaths, births and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. Int. J. Primatol. 24, 723–741.

Fedigan, L.M., Jack, K.M., 2004. The demographic and reproductive context of male Replacements in *Cebus capucinus*: How, when and why do male white-faced capuchins take over groups? Behav. 141, 755–775.

Fedigan, L.M., Jack, K.M., 2012. Tracking Monkeys In Santa Rosa: Lessons From A Regenerating Tropical Dry Forest. In: Kappeler, P., Watts, D. (Eds.), Long-term Field Studies of Primates. Springer Press, pp. 165–184.

Fedigan, L.M., Carnegie, S.D., Jack, K.M., 2008. Predictors of reproductive success in female white-faced capuchins (*Cebus capucinus*). Am. J. Phys. Anthropol. 137, 82–90.

Finch, C.E., Rose, M.R., 1995. Hormones and the physiological architecture of life history evolution. Q. Rev. Biol. 70, 1–51.

Fisher, D.A., 1998. Endocrinology of fetal development. In: Williams, R.H., Wilson, J.D. (Eds.), Williams Textbook of Endocrinology, 9th ed. WB Saunders, Philadelphia, pp. 1273–1301.

Fitchel, 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*). Horm. Behav. 51, 640–648.

Fragaszy, D.M., Bard, K., 1997. Comparison of development and life history in *Pan* and *Cebus*. Int. J. Primatol. 18, 683–701.

Fragaszy, D.M., Visalberghi, E., Fedigan, L.M., 2004. The Complete Capuchin: The Biology of the Genus *Cebus*. Cambridge University Press, Cambridge.

Gesquiere, L.R., Altmann, J., Memuna, Z.K., Couret, J., Yu, J.C., Endres, C.S., Lynch, J.W., Ogola, P., Fox, E.A., Alberts, S.C., Wango, E.O., 2005. Coming of age: Steroid hormones of wild immature baboons (*Papio cynocephalus*). Am. J. Primatol. 67, 83–100.

Gesquiere, L.R., Onyango, P.O., Alberts, S.C., Altmann, J., 2011a. Endocrinology of year-round reproduction in a highly seasonal habitat: environmental variability testosterone and glucocorticoids in baboon males. Am. J. Phys. Anthropol. 144, 169–176.

Gesquiere, L.R., Learn, N.H., Simao, C.M., Onyango, P.O., Alberts, S.C., Altmann, J., 2011b. Life at the top: Rank and stress in wild male baboons. Science 333, 357–360.

Ginther, A.J., Ziegler, T.E., Snowdon, C.T., 2001. Reproductive biology of captive male cotton top tamarin monkeys as function of social environment. Anim. Behav. 61, 65–78.

Ginther, A.J., Ziegler, T.E., Carlson, A.A., Snowdon, C.T., 2002. Sexual development in cotton-top tamarin males. Biol. Reprod. 66, 282–290.

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*). Phys. Behav., 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*). Am. J. Primatol. 69, 1325–1339.

Griffin, J.E., Wilson, J.D., 1998. Disorders of the testis and male reproductive tract. In: Wilson, J.D., Foster, D.W., Kronenberg, H.M., Larsen, P.R. (Eds.), Williams Textbook of Endocrinology, 9th ed. Saunders, Philadelphia, pp. 819–875.

Gros-Louis, J., Perry, S., Manson, J.H., 2003. Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). Primates 44, 341–346.

Hakeem, A., Sandoval, R.G., Jones, M., Allman, J., 1996. Brain And Life Span In Primates. In: Birren, J.E., Schaie, K.W. (Eds.), Handbook of the Psychology of Aging, 4th edition. Academic Press, San Diego, pp. 78–104.

Hakikinen, K., Pakarinen, A., 1993. Acute hormonal responses to two different fatiguing heavy-resistance protocols in male athletes. J. Appl. Physiol. 74, 882–887.

Jack, K.M., 2003. Explaining variation in HYPERLINK "http://www.tulane.edu/~kjack/documents/Jack2003-ExplainingVariationinMale.pdf"affiliativeHYPERLINK "http://www.tulane.edu/~kjack/documents/Jack2003-ExplainingVariationinMale.pdf" relationships among male white-faced capuchins (HYPERLINK "http://www.tulane.edu/~kjack/documents/Jack2003-ExplainingVariationinMale.pdf"CebusHYPERLINK "http://www.tulane.edu/~kjack/documents/Jack2003-ExplainingVariationinMale.pdf" HYPERLINK "http://www.tulane.edu/~kjack/documents/Jack2003-ExplainingVariationinMale.pdf"capucinusHYPERLINK "http://www.tulane.edu/~kjack/documents/Jack2003-ExplainingVariationinMale.pdf"). Folia Primatol. 74, 1–16.

Jack, K.M., 2011. The Cebines: Towards an Explanation of Variable Social Structure. In: Campbell, C., Fuentes, A., MacKinnon, K., Bearder, S., Stumpf, R. (Eds.), Primates in Perspective, 2nd edition. Oxford University Press, Oxford, pp. 108–122.

Jack, K.M., Fedigan, L.M., 2004a. Male dispersal patterns in white-faced capuchins, *Cebus capucinus* Part 1: patterns and causes of natal emigration. Anim. Behav. 67, 761–769.

Jack, K.M., Fedigan, L.M., 2004b. Male dispersal patterns in white-faced capuchins, *Cebus capucinus* Part 2: patterns and causes of secondary dispersal. Anim. Behav. 67, 771–782.

Jack, K.M., Fedigan, L.M., 2006. Why be Alpha Male? DOMINANCE and Reproductive Success in Wild White-Faced Capuchins (*Cebus capucinus*). In: Estrada, A., Garber, P., Pavelka, M.A.M., Luecke, L. (Eds.), New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology. Behavior and Conservation, Springer, New York, pp. 367–386.

Jack, K.M., Schoof, V.A., Fedigan, L.M., 2013. Seasonality of alpha male replacements in wild white-faced capuchins (*Cebus capucinus*). Am. J. Primatol. 75 (S1), 79.

Jack, K.M., Sheller, C., Fedigan, L.M., 2012. Social factors influencing natal dispersal in male white-faced capuchins (*Cebus capucinus*). Am. J. Primatol. 74, 359–365.

Jack, K.M., Lenz, B.B., Healan, E., Rudman, S., Schoof, V.A.M., Fedigan, L., 2008. The effects of observer presence on the behavior of *Cebus capucinus* in Costa Rica. Am. J. Primatol. 70, 490–494.

Kappeler, P.M., Periera, M.E., van Schaik, C.P., 2003. Primate life histories. In: Kappelere, P.E., Pereira, M.E. (Eds.), Primate Life Histories and Socioecology. University of Chicago Press, Chicago, pp. 25–40.

Kaufman, J.M., Vermeulen, A., 2005. The decline of androgen levels in elderly men and its clinical and therapeutic implications. Endocrine Rev. 26, 833–876.

Kikusui, T., Mori, Y., 2009. Behavioural and neurochemical consequences of early weaning in rodents. J. Neuroendocrin. 21, 427–431.

Knott, C.D., 2009. Orangutans: Sexual Coercion Without Sexual Violence. In: Muller, M.N., Wrangham, R.W. (Eds.), Sexual Coercion in Primates: An Evolutionary Perspective on Male Aggression against Females. Harvard University Press, Cambridge, MA, pp. 81–111.

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*)? Physiol. Behav. 66, 855–861.

Leigh, S.R., 1992. Patterns of variation in the ontogeny of primate body size dimorphism. J. Human Evol. 23, 27–50.

Levine, S., Wiener, S.G., 1988. Psychoendocrine aspects of mother-infant relationships in nonhuman primates. Psychoneuroendocrinol 13, 143–154.

Lincoln, G.A., 1998. Reproductive seasonality and maturation throughout the complete life-cycle in the mouflon ram (*Ovis musimon*). Anim. Repro. Sci. 53, 87–105.

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 apella nigritus*). Horm. Behav. 41, 275–287.

MacKinnon, K., 2002. Social Development of wild White-Faced Capuchin Monkeys (*Cebus capucinus*) in Costa Rica: An Examination of Social Interactions Between Immatures and Adult Males [Dissertation]. University of California, Berkeley (CA).

MacKinnon, K., 1995. Age Differences in Foraging Patterns and Spatial Associations of the White-Faced Capuchin, (*Cebus capucinus*) in Costa Rica. University of Alberta, Edmonton, MA thesis.

Maggioncalda, A., Sapolsky, R., Czekala, N., 1999. Reproductive hormone profiles in captive male orangutans: Implications for understanding developmental arrest. Am. J. Phys. Anthropol. 109, 19–32.

Maggioncalda, A., Czekala, N., Sapolsky, R., 2000. Growth hormone and thyroid stimulating hormone concentrations in captive male orangutans: implications for understanding developmental arrest. Am. J. Primatol. 50, 67–76.

Maggioncalda, A., Czekala, N., Sapolsky, R., 2002. Male orangutan subadulthood: a new twist on the relationship between chronic stress and developmental arrest. Am. J. Phys. Antropol. 118, 25–32.

Mann, D.R., Gould, K.G., Collins, D.C., Wallen, K., 1989. Blockade of neonatal activation of the pituitary testicular axis: effect on peripubertal luteinizing hormone and testosterone secretion and on testicular development in male monkeys. J. Clin. Endocrinol. Metab. 68, 600–607.

Mann, D.R., Akinbami, M.A., Gould, K.G., Paul, K., Wallen, K., 1998. Sexual maturation in male rhesus monkeys: importance of neonatal testosterone exposure and social rank. J. Endocrinol. 156, 493–501.

Martin, D.E., Swenson, R.B., Collins, D.C., 1977. Correlation of serum testosterone levels with age in male chimpanzees. Steroids 29, 471–481.

Matsumoto, A.M., 2003. Fundamental aspects of hypogonadism in the aging male. Rev. Urol. 5 (Suppl 1), S3–S10.

Mendoza, S.P., Coe, C.L., Lowe, E.L., Levine, S., 1979. The physiological response to group formation in adult male squirrel monkeys. Psychoneuroendocrino 3, 221–229.

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. J. Repro. Fert. 74, 347–359.

Muehlenbein, M.P., Watts, D.P., Whitten, P.L., 2004. Dominance rank and fecal testosterone levels in adult male Chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park. Uganda. Am. J. Primatol. 64, 71–82.

Muller, M.N., Wrangham, R.W., 2004a. Dominance, aggression and testosterone in wild chimpanzee: a test of the 'challenge hypothesis'. Anim. Behav. 67, 113–123.

Muller, M.N., Wrangham, R.W., 2004b. Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). Behav. Ecol. Sociobiol. 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. Am. J. Primatol. 72, 1118–1130.

Muroyama, Y., Shimizu, K., Sugiura, H., 2007. Seasonal variation in fecal testosterone levels in free-ranging male Japanese macaques. Am. J. Primatol. 69, 603–610.

Nef, S., Parada, L.F., 2000. Hormones in male sexual development. Genes Dev. 14, 3075–3086.

Ostner, J., Kappeler, P.M., Heistermann, M., 2002. Seasonal variation and social correlates of androgen excretion in male redfronted lemurs (*Eulemur fulvus rufus*). Behav. Ecol. Sociobiol. 52, 485–495.

Ostner, J., Heistermann, M., Schülke, O., 2011. Male competition and its hormonal correlates in Assamese macaques (*Macaca assamensis*). Horm. Behav. 59, 105–113.
Pagel, M.D., Harvey, P.H., 1993. Evolution of the juvenile period in mammals. In: Pereira, M.E., Fairbanks, L.A. (Eds.), Juvenile Primates: Life History, Development, and Behavior. Oxford University Press, New York, pp. 28–37.
Perry, S., 1998. Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. Behav 135, 139–172.
Place, N.J., Kenagy, G.J., 2000. Seasonal changes in plasma testosterone and glucocorticoids in free-living male yellow-pine chimpmunks and the response to capture and handling. J. Comp. Physiol. B. 170, 245–251.
Plant, T.M., 1994. Puberty in primates. In: Knobil, E., Neill, J.D. (Eds.), The Physiology of Reproduction, Second edition, vol. 2. Raven Press, New York, pp. 453–485.
Plant, T.M., Witchel, S.F., 2006. Puberty in non-human primates and humans. In: Neill, J.D. (Ed.), Knobil and Neill's physiology of reproduction, Third edition, vol. 2. Elsevier Academic Press, St. Louis, pp. 2177–2230.
Poletto, R., Steibel, J.P., Siegford, J.M., Zanella, A.J., 2006. Effects of early weaning and social isolation on the expression of glucocorticoid and mineralocorticoid receptor and 11β-hydroxysteroid dehydrogenase 1 and 2 mRNAs in the frontal cortex and hippocampus of piglets. Brain Res. 1067, 36–42.
Preslock, J.P., 1980. A review of in vitro testicular steroidogenesis in rodents, monkeys and humans. J. Steroid Biochem. 13, 965–975.
Rangel-Negrín, A., Dias, P.A.D., Chavira, R., Canales-Espinosa, D., 2011. Social modulation of testosterone levels in male black howlers (*Alouatta pigra*). Horm. Behav. 59, 159–166.
Rey, R., Campo, S., Ayuso, S., Nagle, C., Chemes, H., 1995. Testicular steroidogenesis in the Cebus monkey throughout postnatal development. Biol. Repro. 52, 997–1002.
Rogol, A.D., 2010. Sex steroids, growth hormone, leptin and the pubertal growth spurt. Endocr. Dev. 17, 77–85.
Romero, L.M., 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. Gen. Compar. Endo. 128, 1–24.
Rose, R.M., Bernstein, I.S., Gordon, T.P., 1975. Consequences of social conflict on plasma testosterone levels in rhesus macaques. Psychosomatic Med. 37, 50–61.
Sapolsky, R., 1983. Individual differences in cortisol secretory patterns in the wild baboon: role of negative feedback sensitivity. Endocrinology 114, 287–296.
Sapolsky, R., 1992. Do glucocorticoid concentrations rise with age in the rat? Neurobiol. Aging 13, 171–174.
Sapolsky, R.M., 2004. Social status and health in humans and other animals. Ann. Rev. of Anthropol. 33, 393–418.
Sapolsky, R.M., 2005. The influence of social hierarchy on primate health. Science 308, 648–652.
Schradin, C., 2008. Seasonal changes in testosterone and corticosterone levels in four social classes of a desert dwelling sociable rodent. Horm. Behav. 53, 573–579.
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 Primatol. 82, 299–307.
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*). Am. J. Primatol. 75, 107–113.
Schoof, V.A.M., Jack, K.M., Ziegler, T. E., in press. Male response to female ovulation in white-faced capuchins (*Cebus capucinus*): variation in fecal testosterone, DHT, and glucocorticoids. Int. J. Primatol.
Schoof, V.A.M., Jack, K.M., in press. Male social bonds: Strength and quality among coresident white-faced capuchin monkeys (*Cebus capucinus*). Behav.
Seraphin, S.B., Whitten, P.L., Reynolds, V., 2008. The influence of age on fecal steroid hormone levels in male Budongo Forest chimpanzees (*Pan troglodytes schweinfurthii*). Am. J. Primatol. 70, 661–669.
Setchell, J., Dixson, A., 2001a. Suppression of the secondary sexual adornments in subordinate adult male mandrills *(Mandrillus sphinx)*. Am. J. Phys. Anthropol. 115, 245–252.
Setchell, J.M., Dixson, A.F., 2001b. Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. Horm. Behav. 39, 177–184.
Setchell, J.M., Smith, T., Wickings, E.J., Knapp, L.A., 2008. Social correlates of testosterone and ornamentation in male mandrills. Horm. Behav. 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. Horm. Behav. 58, 720–728.
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*). Horm. Behav. 35, 125–134.
Torres-farfan, C., Abarzua-catalan, L., Valenzuela, F.J., Mendez, N., Richter, H.G., Valenzuela, G.J., Serón-ferré, M., 2009. Cryptochrome 2 expression level is critical for adrenocorticotropin stimulation of cortisol production in the capuchin monkey adrenal. Endocrinology 150, 2717–2722.
Touitou, Y., Sulon, J., Bogdan, A., Reinberg, A., Sodoyez, J.C., Demey-Ponsart, E., 1983. Adrenocortical hormones, ageing and mental condition: seasonal and circadian rhythms of plasma 18-hydroxy-11-deoxycorticosterone, total and free cortisol and urinary corticosteroids. J. Endorcrinol. 96 (1), 53–64.
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*). Horm. Behav. 56, 355–363.
Van Noordwijk, M.A., van Schaik, C.P., 2001. Career moves: transfer and rank challenge decisions by male long-tailed macaques. Behav 138, 359–395.
van Schaik, C.P., van Noordwijk, M.A., Nunn, C.L., 1999. Sex and Social Evolution in Primates. In: Lee, P. (Ed.), Comparative Primate Socioecology. Cambridge University Press, Cambridge, pp. 204–231.
Wallen, K., 2005. Hormonal influences on sexually differentiated behavior in nonhuman primates. Front. Neuroendocrinol. 26, 7–26.
Weiner, J.S., Marcelli, M., Lamb, D.J., 1996. Molecular determinants of sexual differentiation. World J. Urol. 14, 278–294.
Whitten, P., Turner, T., 2009. Male residence and the patterning of serum testosterone in vervet monkeys (*Cercopithecus aethiops*). Behav. Ecol. Sociobiol. 56, 565–578.
Wickings, E.J., Dixson, A.F., 1992. Testicular function, secondary sexual development, and social status in male mandrills (*Mandrillus sphinx*). Physiol. Behav. 52, 909–916.
Winter, J., Hughes, I., Reyes, F., Faiman, C., 1976. Pituitary-gonadal relations in infancy: 2. patterns of serum gonadal steroid concentrations in man from birth to two years of age. J. Clin. Endocrinol. Metab. 42, 679–686.
Wiren, K.M., 2005. Androgens and bone growth: it's location, location, location. Curr. Opin. Pharma. 5, 626–632.
Wobber, V., Hare, H., Lipson, S., Wrangham, R., Ellison, P., 2013. Different ontogenetic patterns of testosterone production reflect divergent male reproductive strategies in chimpanzees and bonobos. Physiol. Behav. 116–117, 44–53.
Ziegler, T.E., Scheffler, G., Snowdon, C.T., 1995. The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins, *Saguinus oedipus*. Horm. Behav. 29, 407–424.