THE BEHAVIOR AND ENDOCRINOLOGY OF DOMINANCE IN FEMALE WHITE-FACED CAPUCHIN MONKEYS (*CEBUS CAPUCINUS IMITATOR*) IN SECTOR SANTA ROSA, ÁREA DE CONSERVACIÓN GUANACASTE, COSTA RICA

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ABSTRACT

The relationship between behavior, hormones and the environment has long been of interest to evolutionary biologists and biological anthropologists. Hormone levels vary between individuals, seasonally, and affect behavior. Research in male mammals shows dominance rank is related to androgen and cortisol levels, both of which vary with breeding season. However, even though females also produce androgens and they play a crucial role in regulating the female reproductive system, the role of androgens in the behavior of females is not well understood. White-faced capuchins (*Cebus capucinus imitator*) are female philopatric, medium-sized Neotropical monkeys. We characterize dominance in female white-faced capuchins, examine how rates of agonism vary with social and environmental change, and investigate the hormonal underpinnings of behavior in Sector Santa Rosa, Área de Conservación Guanacaste, Costa Rica.

We find that females demonstrate only moderately linear dominance hierarchies, likely due to high kin-relatedness between females. We determined nearly the same hierarchy despite the methodology used to determine the rank order. Rates of agonism varied with dominance rank and fruit availability and we suggest that females inherit their rank from their mother, but use agonism to maintain this rank throughout their lives. Females adjust their rates of agonism such that they exhibit greater rates of agonism when ripe fruit availability is low. We propose that females need to increase agonism in order to gain access to sufficient resources to sustain themselves and their reproductive requirements. We also suggest that higher fruit availability leads to fewer bouts of agonism because there is enough fruit to

occupy most group members. Higher-ranking females exhibit higher androgen and cortisol levels. This is inconsistent with the dual-hormone hypothesis, which suggests that higher-ranking individuals have higher androgen, but lower cortisol levels. It is possible that the threat of male takeovers leads to higher stress and thus higher levels of cortisol as the threat of infanticide remains present. Androgen and cortisol levels did not vary seasonally with fruit availability. This work advances our understanding of the relationship of behavior, hormone levels and environmental changes and is especially important for a growing understanding of androgens in female primates.

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1. INTRODUCTION

Berthold (1849), via castrating male chicks, was the first to recognize an agent created in the testes had the ability to affect a male's behavior (Berthold, 1849). We now know Berthold's agents were androgens, one of many types of hormones that act as chemical messengers in vertebrates and are present in both males and females. Androgens, as well as glucocorticoids, the most prevalent of which is cortisol in primates, are steroid hormones released in response to stress, fear, sexual arousal, and affiliation with conspecifics, among other things (Nelson, 2014). Ultimately, hormones influence the likelihood of a specific behavior occurring in response to a particular stimulus (Nelson, 2014). Our understanding of androgens in wild female primates is limited because behaviorally based, wild studies are sparse, especially those examining females. This dissertation examines androgens in a wild, female primate.

Androgens are conventionally considered 'male' hormones, however they also play a crucial role in regulating the female reproductive system. Androgens are produced in the gonads and adrenal glands and affect the morphological, behavioral, and physiological phenotype of both sexes. Androgens play an integral role in regulating the female reproductive system (Arnold and Breedlove, 1985; Liening et al., 2010). Androgens have primarily been studied in males because of their role in sperm maturation and the development of male-typical genitalia and behavior, but recent studies have called attention to the role of androgens in female behavior and the need for increased investigation in females, especially in wild primates (Arnold and Breedlove, 1985; Beehner et al., 2005; Setchell et al., 2015). Our research seeks to answer questions regarding the relationship between androgens and behavior in females and investigate hypotheses historically applied to males.

Hormones affect behavior through organizational and activational effects (Phoenix et al., 1959). Organizational effects take place prenatally or just after birth and permanently organize the internal and external genitalia, as well as the brain, priming these body parts to respond to specific hormones in the future (Arnold and Breedlove, 1985). The focus of this project will be activational effects, which take place when hormones bind to and activate these primed receptors in the brain, gonads, adrenal glands, pituitary, and pancreas and thereby mediate gene expression, which in turn mediates, and is mediated by, behavior (Arnold and Breedlove, 1985). While all vertebrates possess hormones, not all species, nor sexes or individuals, exhibit the same relationship between specific hormones and behaviors, and we are only just beginning to understand this variation. Primates are key species in which to study this relationship due to their complex social behavior, high intelligence, and the inclusion of humans in this order. An investigation of the role of androgens in the socioecology of a female, large-brained, Neotropical primate is integral to furthering our understanding of vertebrate and primate variation and the interplay between behavior and androgens.

A positive link between aggression and androgens in male primates has been well documented (Cavigelli and Pereira, 2000; Muller and Wrangham, 2004; Sannen et al., 2004; Gould and Ziegler, 2007; Nelson, 2014), though the results from limited studies of female aggression and androgens have had mixed results. In the only study to date (to our knowledge) of androgens and behavior in wild female primates, Beehner et al. (2005) found hybrid baboons with higher androgens exhibit higher rates of aggression (Beehner et al., 2005). Several captive studies have documented this same relationship. Female marmosets that are more aggressive towards territorial inturders show greater increases in testoserone (Ross and French, 2011) and in a meta-analysis, heightened aggression is correlated with higher androgens in women (Book et al., 2001). However, rates of aggression were found to be unrelated to androgen levels in captive female bonobos and ring-tailed lemurs (von Engelhardt et al., 2000; Sannen et al., 2004).

The challenge hypothesis has long suggested a link between behavior and androgens. In its original form, it was proposed to explain variable androgens in males within and across species. It suggests, within a species, androgen levels are affected by breeding system and seasonality, as well as the level of paternal care, in ways that serve to maximize male reproductive success. Accordingly, the challenge hypothesis predicts higher androgen levels in times of aggressive male-male encounters over access to mates and lower androgens during times that require paternal care (Wingfield, 1984). Aggression is addressed in the challenge hypothesis specifically regarding breeding season. However, sexual selection theory dictates that males and females will present different adaptations because of the different factors that affect their reproductive success (Darwin, 1871; Trivers, 1972).

Male reproductive success is largely influenced by their access to mates, which they must compete for with other males, while female reproductive success depends more on access to energetic resources, which they may compete for with other females (Trivers, 1972; Clutton-Brock, 2009). Indeed, aggression in primates often arises between females when competing for food, especially at clumped resources (Isbell, 1991). This contest competition allows some individuals to gain preferential access to food resources, just as male-male aggression allows only some to mate. Thus, it might be expected that, for females, androgens are correlated with aggression in the context of resource availability. If so, then one would predict females to exhibit higher androgen levels during periods of low food availability when contest competition is crucial to gain access to high quality foods.

Dominance has increasingly been linked to androgens in humans and non-human primates (Higley et al., 1996; Mazur and Booth, 1998; Josephs et al., 2006). Where an individual falls in a dominance hierarchy can have reproductive consequences and benefits that can affect an individual's lifetime reproductive success (Magee and Galinsky, 2008). Higher-ranking individuals have higher reproductive success in numerous female primates, likely due to greater access to resources (long-tailed macaques (*Macaca fascicularis*): van Noordwijk & van Shaik, 1999; yellow baboons (*Papio cynochephalus*): Altmann & Alberts, 2003; mountain gorillas (*Gorilla beringei beringei*): Robbins et al., 2007). Evidence that higher-ranking individuals have higher androgens has been found in a multitude of male primates (chimpanzees (*Pan troglodytes*): Muller & Wrangham, 2004; Muehlenbein et al., 2004; White-faced capuchins (*Cebus capucinus imitator*): Jack et al., 2014; mandrills (*Mandrillus sphinx*): Setchell et al., 2008; humans (*Homo sapiens*): Mehta & Josephs, 2010), as well as some female primates (hybrid baboons: Beehner et al., 2005; humans: Mehta & Josephs, 2010). However, the relationship is not entirely consistent, such as in female and male chacma baboons, in which androgens and rank were uncorrelated, though androgens were higher in males rising in rank (Beehner et al., 2006; Beehner et al., 2009). The dual-hormone hypothesis addresses these inconsistencies by expanding on the challenge hypothesis and positing that androgens and cortisol work in unison to affect dominance status *and* reactive aggression (Mehta & Josephs, 2010). Those with high androgens and low cortisol generally have higher dominance ratings while those with both high androgens and high cortisol score lower dominance ratings (Denson & Mehta, 2012; Edwards & Castro, 2013; Jimenez et al., 2012; Mehta & Josephs, 2010).

We examine the relationship between androgens, cortisol, dominance, agonism, and food availability in a wild female Neotripical primate, white-faced capuchin monkeys (*Cebus capucinus imitator)*.

White-faced capuchins are a medium-sized Neotropical primate that occupies a range of habitats as far north as Honduras and as far south as Ecuador (Estrada et al., 2006). The species is moderately sexually dimorphic with adult males being approximately 25-35% larger than adult females (Fedigan, 1993). Average group size ranges from 11 to 18 individuals and groups consist of multiple adult females and their immature offspring and, usually, one or more immigrant adult males (Fedigan and Jack, 2012). Females remain in their natal group throughout their lives [though there are rare instances in which females have been known to disperse (Jack and Fedigan, 2008)], and males disperse at a median age of 4.5 years and change groups approximately every four years (Jack and Fedigan, 2004a; Jack and Fedigan, 2004b). White-faced capuchins exhibit slow life histories relative to their size, with females giving birth to their first infant at approximately 6 years of age (Carnegie et al., 2011b; Perry, 2012) and males obtaining full adult body size at approximately 10 years of age (Dixson, 2002).

White-faced capuchins are defined by a number of key social factors that make them an ideal species in which to examine androgens in females and compare these results to males of the same species. Firstly, female white-faced capuchins exhibit linear dominance hierarchies, as do males who are generally dominant to females (Bergstrom & Fedigan, 2010; Ford & Davis, 1992). Female rank, which is relatively stable, is maternally inherited at approximately 6.5 years of age. Thus far, studies have found no correlation between female reproductive success and rank, likely due to the high rates of alpha male replacements and infanticide (Fedigan, 1993; Fedigan et al., 2008). Despite the inconsistent link between dominance and reproductive success for females in this species, consistent with the priority-of-access model of dominance, higher-ranking females have higher energy intake rates in feeding trees and instigate aggression more frequently, at least in some populations (Altmann, 1962; Vogel, 2004). Males, on the other hand, attain rank through intrasexual competition, male rank is unstable, and alpha males sire the majority of offspring (Fragaszy et al., 2004; Jack and Fedigan, 2006). Alpha males exhibit elevated androgen and GCs in comparison with lower-ranking males (Schoof & Jack, 2013). These important differences between female and male social structure make this investigation compelling and purposeful.

Female white-faced capuchins produce a single infant approximately every 2.25 years and carry out the majority of parental care (Fedigan et al., 2008). Females vary considerably in their style of maternal care, with some nursing more frequently and for longer bouts, handling infants more often, and some occasionally hitting or biting an infant during weaning (Manson, 1999; Sargeant et al., 2015). Further, the age at which a mother weans an infant varies between 14 and 23 months (Sargeant et al., 2015). While “personality” differences have been examined in this species (Manson & Perry, 2013), the hormonal basis of this variation between individuals is ripe for investigation.

White-faced capuchins are omnivorous, feeding primarily on fruits (50-80% of their diet [Oppenheimer 1968; Chapman & Fedigan, 1990]), though they adjust their diet based on seasonal availability of ripe fruit, seeds, insect larvae, and nestling mammals (Galetti & Pedroni, 1994; Panger et al., 2002; Rose, 1994). Females depend heavily on fruit to meet the energetic costs of reproduction and lactation (Carnegie et al., 2011). They are able to occupy degraded habitats, though population density increases drastically when human disturbance is eliminated and the forest is allowed to regenerate (Campos et al., 2015). However, upon forest regeneration, white-faced capuchins are still not safe from intermittent population declines. For example, in 2015 infant mortality increased from an average of 28% to nearly 100% due to drought (Perry, 2012, personal observation). Despite their behavioral plasticity, this most recent drought will likely cause a population reduction in white-faced capuchins. Individual maintenance of homeostasis, which is affected by the endocrine system, especially the production of GCs, and the normal reproductive capabilities, which is directly affected by androgens, is key to the survival of white-faced capuchins populations. A deeper understanding of the relationship between forest seasonality, endocrine factors, and social behavior is potentially informative for conservation efforts.

Our study population inhabits Sector Santa Rosa, Área de Conservación Guanacaste, Costa Rica. Santa Rosa National Park was established in 1971 in Northwestern Costa Rica in former cattle grazing pastureland (Allen, 2001). It is now known as Sector Santa Rosa and is part of the broader Área de Conservación Guanacaste. This regenerating tropical dry forest is punctuated by two drastically distinct seasons with the majority of rainfall in the May-December wet season and nearly no rainfall in the January-April dry season (Fedigan, 1993; Melin et al., 2014). Ripe fruit biomass peaks twice yearly, once in May and once in September (Carnegie et al., 2011). The Santa Rosa capuchins have been studied continuously since 1985 and there are currently four habituated groups with ninety-six individuals (Fedigan & Jack, 2012).

For this project, we collect data on three habituated groups of *C. c. imitator* (Admin group [AD], RosaMaria group [RM], Guanacaste group [GN]). All female white-faced capuchins over the age of five years were included (N=23). Individuals were recognizable based on fur and face coloration, scars, broken digits, and peak shape. We collected 525 hours of behavioral focal follows and 324 fecal samples for hormone analysis over seven months.

In this dissertation I investigate the interrelationship of androgens, dominance, agonism, and food availability in female white-faced capuchins. In the first chapter I investigate the different methods for determining dominance hierarchies in female white-faced capuchins and compare four different methods for measuring linearity and determining a hierarchy order as well as apply three additional methods to describe hierarchies. In the second chapter I investigate the affects of fruit availability, dominance, reproductive state, maternal kin, and female group size on rates of aggression. Finally, in the third chapter I explain variation in cortisol and androgen levels based on dominance, rates of agonism, fruit availability, and reproductive state.

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2. DOMINANCE IN FEMALE WHITE-FACED CAPUCHINS (*CEBUS CAPUCINUS IMITATOR*) IN SECTOR SANTA ROSA, COSTA RICA

ABSTRACT

Purpose: We demonstrate the necessity of using multiple methods for resolving dominance hierarchies in order to gain a comprehensive understanding of dominance in social animals using female white-faced capuchins as a model. In female white-faced capuchins, dominance ranking has been characterized as linear in some groups but not others, and dominance is characterized as being intermediate between despotic and relaxed. In this study, we investigate the variability in dominance across groups and examine aspects of dominance that have not previously been measured. Namely, we consider transitivity, hierarchy steepness, and de Vries' test of linearity and compare the rank order using the I&SI method, David's scores, and Elo-rating.

Methods: We recorded dominance interactions between 23 wild adult female white-faced capuchin monkeys (*Cebus capucinus imitator*) in three social groups in the Sector Santa Rosa (SSR) of the Área de Conservación Guanacaste (ACG) in Costa Rica. We applied six different methods for deciphering linear ranking and characterizing the dominance hierarchy in each of the three groups.

Conclusion: White-faced capuchins do not consistently exhibit statistically significant linear dominance hierarchies, though there is strong evidence that groups exhibit an orderliness associated with directional consistency and transitivity. Hierarchy steepness is

generally shallow and the rank order determined using David's Scores, the I&SI method, and Elo-rating are equivalent.

INTRODUCTION

Dominance relationships are a common feature of mammalian social groups and are important for reducing potentially costly conflict and maintaining order within groups. Deciphering dominance relationships is important for understanding how primates mitigate the risks of group living while benefitting in myriad ways, including lessening predation and infanticide risk, and exploiting conspecifics for food. Dominance hierarchies form, often independently, for both sexes and in many species high dominance rank results in higher reproductive success (Fedigan, 1983). Female social relationships in primates are highly variable across taxa as well as within species and populations, and reflect a balance between predation risk, interspecific food competition (Wrangham, 1980; van Shaik, 1989), infanticide risk, intergroup and intragroup competition (Sterck et al., 1997), and there is strong conservation across phylogeny (Di Fiore and Rendall, 1994).

Dominance hierarchies are often linear, meaning individuals can be ranked one after the other based on dominant-subordinate dyadic interactions, and it is suggested that this is due to the fact that hierarchies are self-structuring (Chase & Seitz, 2011) and self-reinforcing (Magee and Galinsky, 2008). Studies examining dominance hierarchies often come to one of two conclusions, "linear" or "not linear". However, in many species dominance hierarchies may not be this straightforward. The advance of a multitude of methods to measure different aspects of dominance makes it possible to gain a more comprehensive understanding of a dominance hierarchy, especially those that are not strictly linear. Each method reveals both distinct and overlapping information about a dominance hierarchy and using more than one method can ultimately lead to a broader understanding of the hierarchy and associated social relationships in a given group of animals.

In a number of species, and even between groups within the same population, hierarchies vary from significantly linear to non-linear. In some cases these are due to differing ecological conditions. In the Tai National park, for example, researchers found greeting behavior in female chimpanzees demonstrated a linear dominance hierarchy (Wittig and Boesch, 2003), however previous research on other populations of chimpanzees had failed to demonstrate linear hierarchies (Pusey et al., 1997). These discrepancies were attributed to differences in feeding competition and predation risk. In contrast, when ecological conditions are held constant, linearity in dominance hierarchies should theoretically remain consistent. However, this does not appear to be true in all cases. For instance, during two separate time periods captive bonobos were found to have linear and non-linear dominance hierarchies, which researchers attributed to differences in group composition (Paoli et al., 2006). This mismatch provides a compelling reason to pursue an in-depth examination of the methods used to decipher and characterize dominance hierarchies.

Methods concerning dominance hierarchies, including directional consistency indices, transitivity, de Vries's test of linearity, the I&SI method, normalized David's scores, and Elo-rating, provide an overall image of the organization of a dominance hierarchy. We apply these methods to a well-studied species, the white-faced capuchin monkey (*Cebus capucinus imitator)* that has previously exhibited both linear and non-linear dominance hierarchies (Fedigan, 1993; Perry, 1996; Manson, 1999; Bergstrom and Fedigan, 2010).

Dominance in female white-faced capuchins

In white-faced capuchin monkeys alpha males are clearly recognizable as they are usually the largest individual in the group, display the most vigilance, and are frequently the primary participant when deterring predators, extra-group males, and during inter-group encounters (Rose and Fedigan, 1995; Fragaszy et al., 2004; Jack and Fedigan, 2018). Alpha females are not as clearly distinguishable from subordinate females, though they do show subtle differences in their phenotypic appearance and behavior. In some groups alpha females are more likely to aid in coalitions against males (Perry, 1996), alpha females can be slightly larger than subordinate females (personal observation), and be vigilant more frequently, though they do not engage in significantly more frequent agonism than subordinate females (Rose, 1994; Fragaszy et al., 2004). Ultimately, it is possible determine the alpha female based on agonistic and submissive interactions even though rates of agonism in the wild are generally low (sometimes less than one bout per hour) (Rose, 1994). However, while alpha females are easy to distinguish from other adult females, it is more difficult to distinguish a subordinate of one rank from another rank (Fragaszy et al., 2004).

Female rank is maternally inherited at approximately 6.5 years of age and remains relatively stable throughout individual lifetimes (Perry, 2008). While high rank for female capuchins does confer foraging benefits (Vogel, 2005), to date studies have found no correlation between female reproductive success and rank. Females benefit from priority of access to food, preferred rest spots, and water, however these do not appear to confer reproductive benefits. This lack of benefit is the result of the high rates of alpha male replacements and infanticide that are thought to override any benefits conferred by high rank (Fedigan, 1993; Fedigan et al., 2008; Kalbitzer et al., 2017). Previous research supports linear dominance hierarchies in both male and female *C. c. imitator* and males are generally dominant over females (Bergstrom & Fedigan, 2010). In one study two groups showed statistically significant linearity and the third was non-significant, potentially due to small sample size (Bergstrom and Fedigan, 2010). Previously in the same population one group demonstrated statistically significant linearity while the other did not (Fedigan, 1993). A single group was found to show statistically significant linearity (Perry, 1996), though in follow up studies subordinates were ranked in pairs due to the inability to separate their ranks (Manson, 1999). Because of these inconsistencies across studies we examine multiple methods for characterizing dominance hierarchies in female white-faced capuchins.

Methods for determining linearity and characteristics of dominance hierarchies

We applied six different methods (directional consistency indices, transitivity, de Vries's test of linearity, the I&SI method, normalized David's scores, and Elo-rating) for characterizing dominance hierarchies in female white-faced capuchins. Each method requires a tabulation of dyadic agonistic dominance interactions. Previous work has demonstrated the accuracy of these methods using artificial datasets (Hemelrijk et al., 2005; Bang et al., 2010; Sánchez-Tójar et al., 2018).

One of the most basic elements of a dominance hierarchy is directional consistency, measured using the **directional consistency index** (van Hoof and Wensing, 1987). This describes the percent of interactions that occur in the expected direction.

Within a dyad, when all or the majority of interactions occur in one direction this is determined to be the expected direction. Directional consistency is frequently used in conjunction with other measures of dominance, such as rates of agonism (Wheeler et al., 2013), and as a justification for tests of linearity and assigning rank-order using a dominance matrix (van Hoof and Wensing, 1987; Stevens et al., 2007; Perry, 2008; Martin et al., 2013).

Transitivity in a hierarchy exists if, when A is greater than B and B is greater than C, then A is greater than C. Transitivity is a component of linearity, and is suggested to be a better indicator of linearity when not all relationships between dyads are known (Shizuka and McDonald, 2012), which is common in wild animal populations.

De Vries' test of linearity, and the associated modified Landau's h-value, is a statistical test often used for examining hierarchal linearity for both male and female primates, as well as other mammalian species (e.g. Surbeck et al., 2011) and has been applied to female chimpanzees (Wittig and Boesch, 2003) and white-faced capuchins (Bergstrom and Fedigan, 2010). It conveniently accounts for both tied and unknown relationships when determining if a hierarchy exhibits statistically significant linearity making it especially useful in wild animals in which not all relationships can be determined (de Vries, 1995).

The **I&SI method** is used to determine a best-fit linear hierarchy while minimizing the number and strength of inconsistent interactions, meaning interactions that do not occur in the expected direction (De Vries, 1998). The I&SI method assumes linearity and determines a linear hierarchy based on this assumption.

Instead of creating a matrix for the entire group and ranking individuals relative to each other, **David's scores** are numerical measures of success of agonistic encounters calculated for each individual (Gammell et al., 2003). Normalized David's Scores standardize the numerical value so that it can be compared across groups of different sizes. Previously David's Scores have been found to reflect the "real" hierarchy when comparing methods using artificial datasets (Hemelrijk et al., 2005). From David's scores we can calculate steepness, which reflects the predictability of the outcome of a dominance interaction. Steeper hierarchies result when higher-ranking individuals win the majority of interactions. Less steep hierarchies result when the outcome of dyadic interactions is less predictable.

Elo-rating was created by Arpad Elo (Elo, 1961, 1978) for ranking chess players. It incorporates an individual's likelihood of winning a given dominance interaction and assigns individual scores that are adjusted with each win and loss. There is no associated significance test, thus ratings can be determined at any given time, independent of the number of dyadic dominance interactions that have been recorded.

Significance of Our Research

Previous research on dominance hierarchies in female white-faced capuchins has resulted in variable findings. This study is important for understanding the intricacies behind this variation in dominance style between groups and explaining the flexibility seen in this species. Further, we demonstrate the necessity for applying more than one method to measure dominance hierarchies in order to gain a more substantial understanding.

Research Question

What is the nature of dominance hierarchies in female white-faced capuchins (linear vs non-linear) and which method is accurate for characterizing them?

Hypothesis 1a) Females exhibit unidirectional dominance interactions

Prediction I) Each dyad will exhibit a consistent winner and loser that remains the same from interaction to interaction

Methods used to test: **Directional consistency, transitivity**

Hypothesis 1b) Females exhibit linear dominance hierarchies

Prediction I) Females can be ranked linearly one after the other in dominant-subordinate dyads

Methods used test: **de Vries' test of linearity**

Prediction II) Across multiple methods that rank females in order either by scores or based on a win-loss matrix, the order will be consistent

Methods used to test: **Normalized David's scores, Elo-rating, I&SI method**

Hypothesis 1c) Females exhibit a steep dominance hierarchy

Prediction I) When a line is fitted to David's score ranks, a slope of 0.5 or greater will result, which suggests a steep dominance hierarchy

Methods: **Normalized David's scores**

METHODS

Study site

Santa Rosa National Park (10°50′30″N, 85°37′0″W) was established in 1971 on former cattle grazing pastureland (Allen, 2001). It is now known as Sector Santa Rosa

(SSR) and is part of the broader Área de Conservación Guanacaste (ACG). The ACG became an UNESCO world heritage site in 1999 and includes approximately 147,000 hectares of tropical ecosystems, including marine, dry forest, cloud forest, and rainforest. The ACG is made up of 18 separate sectors of which SSR was the first to be created. SSR is located in the northwestern corner of Costa Rica, 35 km north of the city of Liberia and 40 km south of the Costa Rican boarder with Nicaragua. SSR is made up of regenerating tropical dry forest and is punctuated by two drastically distinct seasons; the majority of rain falls in the wet season from mid-May to mid-December [mean = 1497 mm/year] and nearly no rainfall in the dry season from mid-December to mid-May dry season (Fedigan, 1993; Melin et al., 2014).

Study Subjects

White-faced capuchins monkeys (*Cebus capucinus imitator)* are a medium-sized Neotropical primate that occupies a range of habitats as far north as Honduras and as far south as Ecuador (Estrada et al., 2006). The species is moderately sexually dimorphic with adult males being approximately 25-35% larger than adult females (Fedigan, 1993). Average group size at Sector Santa Rosa ranges from 11 to 18 individuals and groups consist of multiple adult females, their immature offspring and, usually, one or more immigrant adult male (Fedigan and Jack, 2012). Females remain in their natal group throughout their lives [though there are rare instances in which females have been known to disperse (Jack and Fedigan, 2008)], and males disperse at a median age of 4.5 years and change groups approximately every four years thereafter (Jack and Fedigan, 2004) a and 2004b.

The Santa Rosa capuchins have been studied continuously since 1983. At the time of this study, there were four habituated study groups with ninety-six individuals. All group members were individually recognizable based on fur and face coloration, scars, broken digits or other injuries, and peak shape.

Behavioral Observations

Between January and August 2017 we collected data on three social groups of white-faced capuchins in SSR: Administration group [AD], Rosa Maria group [RM], and Guanacaste group [GN]. All adult (age > 6 years) female group members were included in the study (N = 23). Ages were known based on birthdates or estimated if the group was habituated after the individual was born. All females were known to be greater than 6 years of age, at which time females give birth to their first infant. We logged 1,380 hours of contact (AD: 399h, RM: 515h, GN: 466h).

Every month we followed each study group for a block of two separate three to four day periods. We followed groups in rotation and, when possible, sampled from each group before returning to sample from a group again. Behavioral data were collected from sunrise to sunset and included group scans, individual focal follows, and *ad libitum* dominance interactions. We assessed the dominance rank of female-female dyads based on directed agonistic behaviors categorized as low grade aggression (lunge, chase, threatface) and high grade aggression (bite, hit, wrestle), as well as submissive behaviors, including cower, flee, grimace, cry, and tail bite. The individual who demonstrated submissive behavior at the end of the interaction was labeled the loser and the other individual the winner.

We conducted 10-minute focal follows of all adult females (N = 23). During focals we recorded overall state behaviors as well as events. This included all social behaviors and interactions with other individuals, and their identities (see Ethogram [Appendix 1] for comprehensive list; Altmann, 1974). All effort was made to sequentially sample each subject in a group before returning to sample from an individual again. If an individual could not be located during 10 minutes of searching, we moved to the next subject in order. If an individual was out of sight for more than 60 seconds, the follow was discarded from the dataset (adapted from Carnegie et al., 2005). We extracted dyadic dominance relationships from focal follows based on interactions that included agonistic and submissive behaviors.

We collected 584 hours of focal data for an average of 25.3 hours per individual. In total we recorded 38 dominance interactions during focal follows (AD = 13, RM = 11, GN = 14).

We also used *ad libitum* sampling of dominance interactions that involved adult females. *Ad libitum* dominance interactions were recorded while following the group, but outside of a behavioral focal follow. At the time of the event we recorded the individuals involved, including the winner and loser of the dominance interaction and any partners involved; the contested resource, if it could be determined; the agonistic behavior displayed; the submissive behavior displayed; and a description of the order of events that took place. In total we recorded 113 *ad libitum* dominance interactions (AD = 36, RM = 40, GN = 37).

Analyses

Directional Consistency Index: The directional consistency index demonstrates how often unidirectional dominance interactions occur within each dyad. This number is then averaged across all dyads in a group. The directional consistency index is calculated as the total number of interactions that occurred in the more frequent direction of a dyad minus the number of times the behavior occurred in the less frequent direction, divided by the total number of interactions. The directional consistency index ranges from 0 (interactions occur equally in both directions) to 1 (interactions are completely unidirectional) (van Hoof and Wensing, 1987). A directional consistency index above 85% has been suggested to be a more relevant indicator of linearity than Landau's h (Koenig and Borries, 2006).

Transitivity: A finding of transitivity suggests that a hierarchy is linear, which can thus provide support for other tests of linearity. Transitivity exists when A dominates B, B dominates C, and A dominates C. The expected value for the test statistic associated with transitivity, P_t, is 0.75, meaning 3 out of 4 complete triangles (consisting of A, B, and C) are transitive. If P_t is at least 0.75 the hierarchy is considered statistically significantly transitive. All three relationships in a triad must be known and if relationships are unknown that triad is excluded from the analysis. A group's transitivity is a scaled index based on this expected value and the transitivity of a group can thus range from 0 (none of the triangles are transitive) to 1 (all of the triangles are transitive). P_t is normalized, which allows for comparison across group sizes because the test statistic is simply a percentage.

De Vries test of linearity: de Vries' test of linearity is a test to find if linearity is statistically supported. It determines Landau's h, which factors the number of individuals dominated by the individual of interest. The modified Landau's h is updated to include and interpret dyads in which a dominant-submissive interaction has not been observed, also known as unknown dyads. Landau's h varies from 0 (completely non-linear) to 1 (completely linear) (de Vries, 1995). Previous work on this population of capuchins interpreted results as follows: 0-0.5: weak, 0.5-0.8: moderate, 0.8-1.0: strong linearity (Bergstrom and Fedigan, 2010).

Tests of linearity may underestimate the orderliness of a group due to null dyads, meaning unknown relationships between dyads. While this problem is exacerbated as group size increases, it can also affect smaller groups (Shizuka and McDonald, 2012). Incorporating transitivity into an assessment of social orderliness may combat this issue, as the expected value of transitivity ($P_t = 0.75$) remains the same regardless of group size and number of unknowns.

I&SI method, Best-fit matrix: The I&SI method ranks individuals in a linear order while minimizing the number of reversals, meaning when a lower ranking individual wins over a higher ranking individual. "I" stands for the number of dyads in which the dominance relationship is reversed. "SI" refers to the strength of these inconsistencies, which is the sum of the rank differences of the individuals involved in the inconsistent dyads. The I&SI method works best when linearity is statistically supported, or significant (de Vries, 1995). A small sample size, however, may lead to a non-significant finding of linearity, but still a nearly linear order. Sometimes there are multiple best-fit matrices that have the same I&SI. The matrix with the highest Spearman's correlation coefficient (r_s) is the best-fit matrix.

Normalized David's Scores and Steepness: Steepness is an integral aspect of a dominance hierarchy and compliments findings on linearity (De Vries et al., 2006). Steepness illustrates the absolute difference between adjacently ranking individuals (de Vrie et al., 2006), meaning it demonstrates how closely or distantly individuals are ranked. Each individual in a group has a corresponding David's score, which is the proportion of wins and losses between this individual and all possible partners, summed across all dyads that include that individual. Normalized David's scores, developed by de Vries, are calculated using N (total number of individuals in a hierarchy) and range from 0 to N – 1. Normalized David's scores allow us to calculate the steepness of the hierarchy and compare this measure across groups with different numbers of individuals. The steepness of a hierarchy is found by plotting the normalized David's scores of all individuals from highest to lowest and finding the best-fit line by performing ordinary least fit squares linear regression. Steepness can thus range from 0, the hierarchy is shallow, to 1, the hierarchy is steep.

Elo-rating: Elo-rating adjusts an individual's score with each subsequent dominance interaction. Elo-rating is advantageous because it demonstrates how each interaction affects an individual's score and allows the researcher to view how the hierarchy changes over time. It starts each individual with a score of 1000. The score of an individual is adjusted in response to each dyadic interaction based on the individual's likelihood of winning that interaction. If an individual with the highest rating, A, for example, beats the lowest rated individual, the score of individual A will only change by a small amount because individual A was likely to win. Contrarily, if the highest rated individual, A, wins over the second highest rated individual, individual A's score will increase by a higher amount because individual A was not as favored to win the interaction.

Comparison of Dominance Hierarchy Scoring

We transformed each score, if applicable, to a rank. If an individual ranked equally with another individual they were both given the same rank and the subsequent rank number was skipped. We also categorized each rank as "high" or "low". Individuals ranked one through four were categorized as "High" and the subsequent individuals (3 in AD and 4 in each RM and GN) were ranked as "Low".

Statistical Analyses

We used the R package Compete (Curley, 2017) to calculate the following for each group: directional consistency index, triangle transitivity and an associated *p-value*, modified Landau's h value and an associated *p-value*, David's scores, and best-fit ranking and associated I&SI values and Spearman Rank-Order Correlation Coefficient (R_s).

We used the R package Elo-Rating (Neumann & Kulik, 2014) to calculate Elo-scores for individuals for each month of data collection.

We used SPSS 9 (version 24) for correlations. Results were considered significant at $P < 0.05$.

RESULTS

We observed 151 dominance interactions (49 in AD, 51 in GN, and 51 in RM). 9.23% of dyads were undetermined, meaning we did not observe the dyads in a dominant-subordinate interaction (3 out of 49 (6.12%) in AD, 5 out of 51 (9.80%) in RM, and 6 out of 51 (11.76%) in GN).

Directional consistency Index

The directional consistency index of all three groups (Table 2.1) was above 75%, meaning that at least 3 out of 4 interactions were in the expected direction. It has been suggested that social groups with a directional consistency index above 85% are likely linear, by which definition only 1 of our 3 study groups (GN) showed linearity in the female dominance hierarchy.

De Vries test of linearity, modified Landau's h-value

RM exhibits a statistically significant linear hierarchy (modified Landau's $h = 0.677$, $P = 0.0359$). Both AD and GN did not exhibit a statistically significant linear hierarchies ($P > 0.05$).

I&SI method, Best-fit matrix

For each group there was a single best-fit ranking and associated matrix with the lowest I&SI values and highest r_s value (AD: I = 1, SI = 2, $r_s = 0.893$; RM: I = 1, SI = 3, $r_s = 0.952$; GN: I = 2, SI = 4, $r_s = 0.976$) (Tables 2.2a, 2.2b, 2.2c).

Normalized David's Scores and Steepness

Normalized David's scores ranged from 1.35 to 5.01 across all groups (Tables 2.3a, 2.3b, 2.3c). AD exhibited the steepest hierarchy (range 1.35 to 4.22, steepness slope 0.349), RM exhibited a less steep hierarchy (range 2.10 to 4.67, steepness slope 0.311), and GN had the least steep hierarchy (range 2.39 to 5.01, steepness slope 0.203) (Figures 2.1a, 2.1b, 2.1c). In general, the hierarchies in all three groups are shallow as the slopes are much nearer to 0 than to 1.

Transitivity

Both groups AD and RM exhibited significant transitivity ($P < 0.05$). 81.8% of triadic relationships in AD and 70.4% of relationships in RM were transitive. Group GN did not exhibit significant transitivity as only 50.0% of triadic relationships were transitive.

Elo-rating

Elo-scores ranged from 803 to 1257 in AD, 760 to 1047 in RM, and 692 to 1364 in GN (Tables 2.4a, 2.4b, 2.4c).

Comparison of Dominance Hierarchy Scoring

The numerical rankings based on the I&SI method and David's scores correlated significantly across groups (Spearman's rho, $r_s = 0.953$, $P < 0.0001$). The numerical rankings based on the I&SI method and Elo-rating scores correlated significantly across groups (Spearman's rho, $r_s = 0.588$, $P = 0.003$). The numerical rankings based on David's scores and Elo-rating scores correlated significantly across groups (Spearman's rho, r_s =

0.551, P = 0.006). All three correlations were greater than $r_s = 0.5$, meaning that they are considered strongly correlated (Tables 2.5a, 2.5b, 2.5c).

DISCUSSION

We used six different methods to investigate the linearity of dominance hierarchies and characterize dominance relationships in three groups of white-faced capuchins, including directional consistency indices, transitivity, de Vries's test of linearity, the I&SI method, normalized David's scores, and Elo-rating. We answer our research questions, what is the nature of dominance hierarchies in female white-faced capuchins and which method is accurate for characterizing them by applying these 6 methods and exploring the results.

Hypothesis 1a) Females exhibit unidirectional dominance interactions

Prediction I) Each dyad will exhibit a consistent winner and loser that remains the same from interaction to interaction

Methods used to test: **Directional consistency, transitivity**

Based on previous literature, hierarchies that exhibit greater than 85% unidirectionality are likely linear (Koenig and Borries, 2006). Only GN demonstrates linearity using 85% unidirectionality as a cutoff point. However, white-faced capuchins still appear to exhibit moderately linear hierarchies based on a mean greater than 75% unidirectionality.

Statistically significant transitivity suggests linearity because it means that when A ranks above B and B ranks above C, then A ranks above C. It is also suggested to be a good measure of linearity when the relationship between all dyads is not known, which applies to our study (Shizuka and McDonald, 2012). Two of the three groups, AD and RM, exhibited statistically significant transitivity. The group that did not exhibit transitivity (GN) had the most unknown relationships, meaning that they could not be taken into account for transitivity. It is possible that if more relationships were known it would have exhibited statistically significant transitivity. Rates of agonism in female white-faced capuchins are low thus it is expected that some dyads will not interact in this manner over a relatively short period of time (Rose, 1994).

Hypothesis 1b) Females exhibit linear dominance hierarchies

Prediction I) Females can be ranked linearly one after the other in dominant-subordinate dyads

Methods used test: **de Vries' test of linearity**

Prediction II) Across multiple methods that rank females in order either by scores or based on a win-loss matrix, the order will be consistent

Methods used to test: **Normalized David's scores, Elo-rating, I&SI method**

Our finding that one out of three groups exhibited a statistically significant linear dominance hierarchy is different than previous studies of this same population in which two out of three groups were found to have statistically significant linear dominance hierarchies (Bergstrom and Fedigan, 2010). Slight variation in group size, number of kin, and ecological factors could play a role in shaping dominance hierarchies. All three groups include 7 or 8 adult females, have high kin relatedness, and live in the same national park, however there are microclimates within the park that affect capuchin behavior (Chapman, 1988; Campos and Fedigan, 2009) and cause variability in food sources across the landscape. The de Vries' test of linearity results suggest that these groups have moderately linear hierarchies as even the group that showed statistically significant linearity was only moderately linear (Landau's h = 0.677).

Based on directional consistency indices, transitivity, and de Vries' test of linearity we are confident that this population of white-faced capuchins has at least moderate linearity. We determined rank-orders using the I&SI method, David's scores, and Elo-ratings for each group.

The rank orders determined by all three methods were significantly correlated with each other. Previously David's scores have been shown to be consistent with the "real" hierarchical order (Hemelrijk et al., 2005), thus we conclude that David's scores, the I&SI method, and Elo-rating can be used to confidently decipher the rank order in wild populations in which the hierarchical order is not known.

Elo-rating has the additional advantage of being able to view how rankings change over time as each interaction affects an individuals' rating. We suggest that Elo-rating is useful for visualizing how individual dominance ranks are affected by each interaction, and can also be useful for creating an overall dominance rank that can be applied to the entire study period.

It is possible that the dominance rank determined through the I&SI method and David's Scores is useful only when looking at data averaged across the entire study period, rather than a day-by-day or month-by-month comparison. Elo-rating may is most appropriate and accurate when both pieces of information are sought.

Hypothesis 1c) Females exhibit a steep dominance hierarchy

Prediction I) When a line is fitted to David's score ranks, a slope of 0.5 or greater will result, which suggests a steep dominance hierarchy

Methods: **Normalized David's scores**

Dominance hierarchies were shallow (slope < 0.35) for all three groups. Less steep hierarchies, such as those seen in our study population, are considered more egalitarian, whereas steeper hierarchies are viewed as more despotic (van Shaik, 1989; De Vries et al., 2006). Female white-faced capuchins have previously been classified as having an intermediate to relaxed despotic dominance style due to the combination of unidirectional dominance interactions and high levels of kin-bias (Bergstrom and Fedigan, 2013). Steepness of the dominance hierarchy was not considered in this finding (Bergstrom & Fedigan, 2013). However, our finding that the hierarchies in three groups is shallow and linearity is moderate suggests that females exhibit a more egalitarian or highly relaxed despotic dominance style (de Vries et al., 2006).

CONCLUSIONS

Numerical ranking of dominance hierarchies using the I&SI method, David's scores, and Elo-rating were significantly and highly correlated. Previously David's scores have been demonstrated to best reflect the "real" hierarchy (Hemelrijk et al., 2005) and in our study both the I&SI method and Elo-rating was highly correlated with David's scores. Given that all three methods were consistent, all three methods would be acceptable for ranking individuals, though likely they are best for different purposes. Elo-rating is most reflective of the variable nature of dominance in female white-faced capuchin monkeys. For comparative studies, such as looking at month-by-month comparisons of rank and hormone levels or rates of specific behaviors, such as affiliation or agonism, it would be more relevant to compare ranks based on Elo-ratings. The ranks based on the I&SI method and David's scores are more valuable for comparison purposes when averaging across an entire study period.

Both directional consistency indices and transitivity measures are helpful for understanding the dynamics of a dominance hierarchy as well as supporting rankings, especially if de Vries' test of linearity is not significant. Such as in this population of female white-faced capuchins, if a win-loss dominance matrix appears to support a nearly linear hierarchy yet findings are not significant, the directional consistency index and transitivity lend credence to ranking individuals in a dominance hierarchy. This supports the suggestion that multiple methods should be applied when examining dominance, especially in species in which dominance is flexible, or relaxed, which is further supported by an analysis of steepness. These findings are applicable to social primates as well as other social animals that show dominance relationships, including ibex and elephants, among others.

FUTURE RESEARCH

The value of the resource at hand likely affects whether an individual is willing to engage in more than a peripheral dominance interaction because the potential benefit to winning is worth the risk. Previous research on white-faced capuchins has shown that the perceived value of a resource, based on the abundance of the resource, leads to increased agonsim (Vogel and Janson, 2007; Vogel et al., 2007). Incorporating the type of resource into the dominance interaction to account for how motivated an individual may be in winning the particular interaction would likely be informative, especially if there are reversals that undermine the linearity of the hierarchy.

We also suggest a deeper examination of dominance looking at who the individuals involved are, whether some individuals engage in more dominance interactions, and whether some individuals avoid these interactions. In addition, proximity measurements would illustrate which individuals avoid agonism, especially in a species such as this that displays low rates of agonism. We suggest future studies examine the role of kinship by looking at individual agonistic encounters, determining kinship scores for each encounter, and looking at the relationship between degree of kin relatedness and the outcome of these encounters. Further, future studies that include a broader range of group sizes would be informative of the effect of group size on agonism and dominance hierarchies. Our study included three groups with very similar group sizes, which limited our ability to determine the effect of group size.

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Table 2.1. Directional consistency index by group. All three groups demonstrated directional consistency indices upon 75%, meaning 3 our of 4 dominance interactions demonstrated the expected winner. It has been suggested that a directional consistency index of above 85% suggests that the hierarchy is linear. Using this distinction only GN group demonstrates linear hierarchies in female white-faced capuchins in Sector Santa Rosa.

Group	Directional consistency index
AD	83.7%
RM	76.5%
GN	92.1%

Table 2.2a. Best-fit ranking and associated matrix determined using the I&SI method for AD group.

AD								
		Loser						
Winner		BO	AB	LM	TS	MI	BT	ZA
	BO	NA	0	4	1	0	1	2
	AB	0	NA	4	0	2	0	3
	LM	0	3	NA	1	3	1	2
	TS	0	7	0	NA	3	2	1
	MI	0	0	0	0	NA	3	4
	BT	0	0	0	0	1	NA	1
	ZA	0	0	0	0	0	0	NA

Table 2.2b. Best-fit ranking and associated matrix determined using the I&SI method for RM group

RM									
Loser									
		SI	LU	PR	FT	SH	Ki	ED	LA
Winner	SI	NA	2	0	1	0	2	1	1
	LU	0	NA	1	2	0	1	1	2
	PR	0	0	NA	1	0	1	1	7
	FT	0	1	0	NA	4	3	2	4
	SH	0	0	0	0	NA	1	2	1
	KI	0	0	1	0	0	NA	2	0
	ED	0	0	3	0	1	0	NA	1
	LA	0	0	1	0	0	0	0	NA

Table 2.2c. Best-fit ranking and associated matrix determined using the I&SI method for RM group

GN									
		Loser							
Winner		LL*	PT*	QD	PD	WK	RS	SP	MW
	LL*	NA	1	3	1	3	4	0	1
	PT*	1	NA	3	3	0	2	0	1
	QD	0	0	NA	3	0	4	3	2
	PD	0	0	0	NA	2	3	0	5
	WK	0	0	1	0	NA	1	0	1
	RS	0	0	1	0	0	NA	1	0
	SP	0	0	0	0	1	0	NA	0
	MW	0	0	0	0	0	0	0	NA

* LL and PT are equidominant because they won an equal number of interactions.

Table 2.3a. Normalized David's scores for AD group

AD	
Individ.	Score
BO	4.22
LM	3.79
TS	3.74
AB	3.22
BT	2.41
MI	2.27
ZA	1.35

Table 2.3b. Normalized David's scores for RM group

RM	
Individ.	Score
SI	4.67
LU	4.27
FT	3.86
PR	3.84
SH	3.51
ED	2.89
KI	2.85
LA	2.1

Table 2.3c. Normalized David's scores for RM group

GN	
Individ.	Score
LL	5.01
PT	4.75
QD	3.66
PD	3.6
WK	3.24
SP	2.92
RS	2.41
MW	2.39

Figure 2.1a. Normalized David's scores plotted from low to high by individual for AD group. Slope indicates steepness of hierarchy.

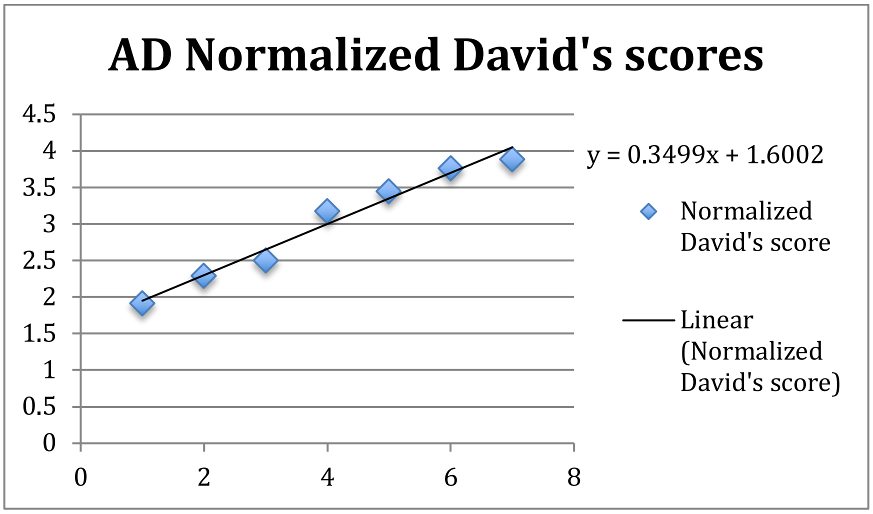

Figure 2.1b. Normalized David's scores plotted from low to high by individual for RM group. Slope indicates steepness of hierarchy.

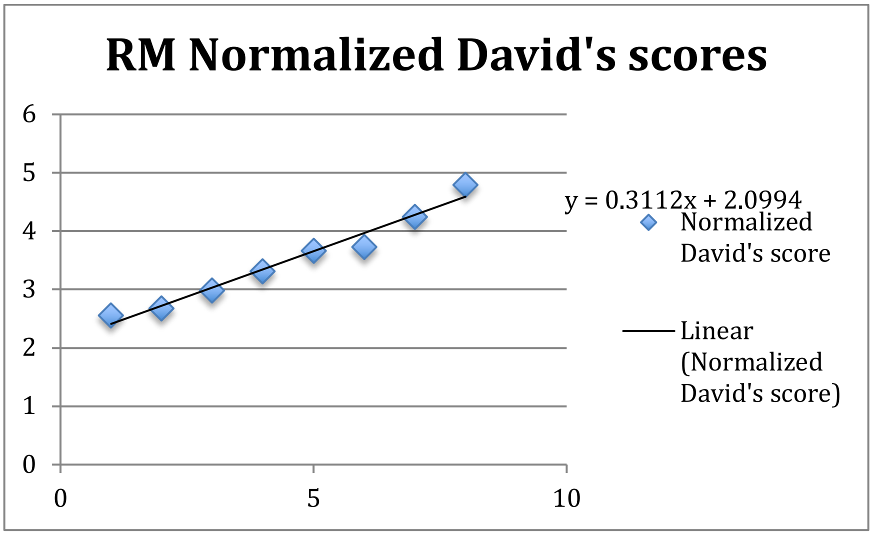

Figure 2.1c. Normalized David's scores plotted from low to high by individual for RM group. Slope indicates steepness of hierarchy

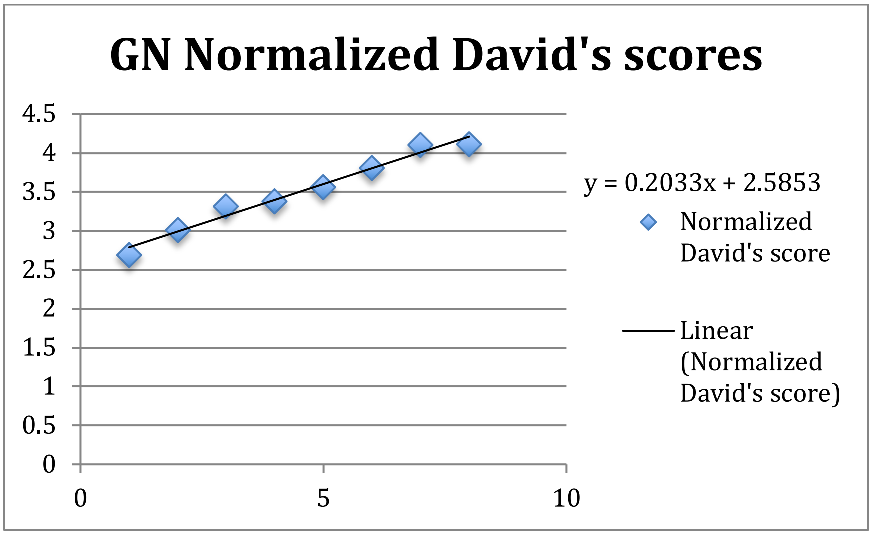

Table 2.4a. The final Elo-rating for each individual ranked highest to lowest for AD group.

Individ.	Elo-score
TS	1257
BO	1199
MI	990
LM	866
ZA	837
BT	826
AB	803

Table 2.4b. The final Elo-rating for each individual ranked highest to lowest for RM group.

Individ.	Elo-score
PR	1047
LU	1041
SH	1041
SI	1039
ED	914
KI	839
LA	815
FT	760

Table 2.4c. The final Elo-rating for each individual ranked highest to lowest for RM group

Individ.	Elo-score
LL	1364
PT	1218
QD	1129
WK	928
SP	871
PD	864
MW	812
RS	692

Figure 2.2a. Elo-scores for AD group plotted across time for the entire study period, demonstrating how dominance scores change in response to each interaction.

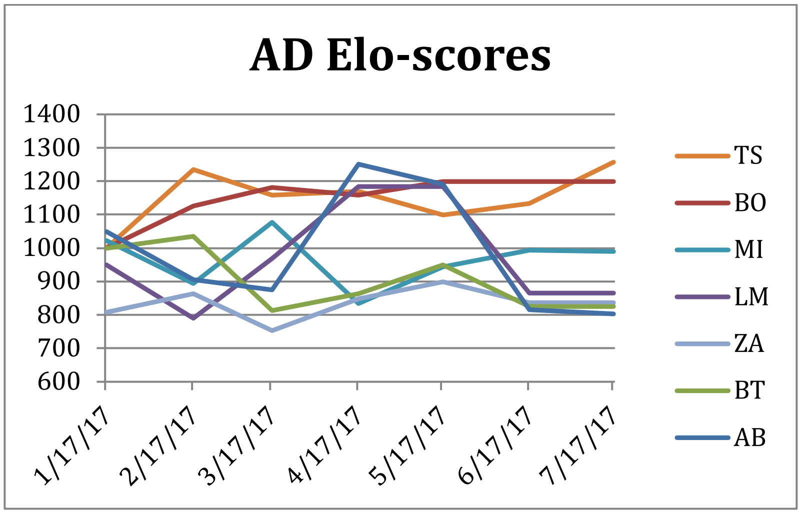

Figure 2.2b. Elo-scores for RM group plotted across time for the entire study period, demonstrating how dominance scores change in response to each interaction.

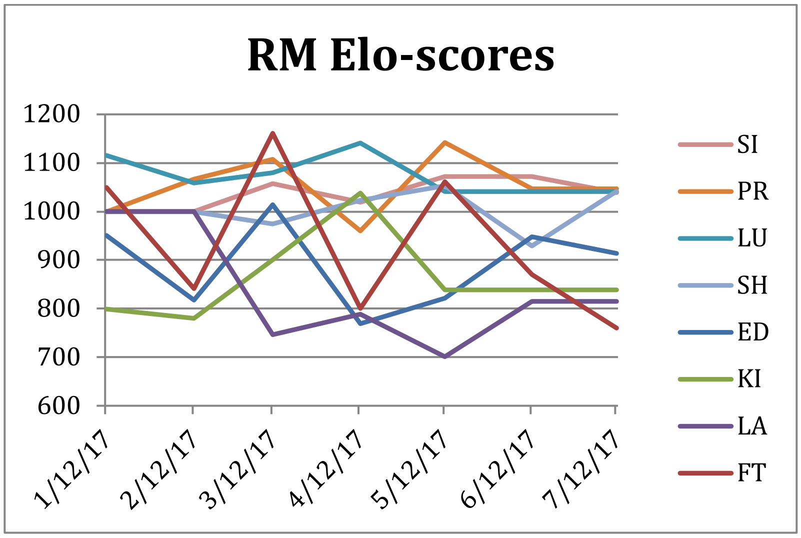

Figure 2.2c. Elo-scores for RM group plotted across time for the entire study period, demonstrating how dominance scores change in response to each interaction.

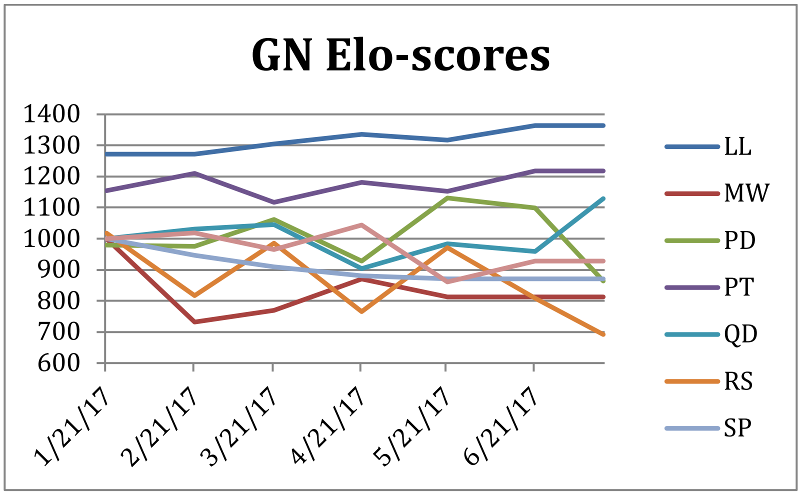

Table 2.5a. Dominance ranks across methods for each individual for AD group.

Individ.	I&SI	David's Score	Elo-Ranking
BO	1	1	2
AB	2	3	7
LM	3	2	4
TS	4	4	1
MI	5	6	3
BT	6	5	6
ZA	7	7	5

Table 2.5b. Dominance ranks across methods for each individual for AD group.

Individ.	I&SI	David's Score	Elo-Rating
SI	1	1	4
LU	2	2	2
PR	3	4	1
FT	4	3	8
SH	5	5	3
KI	6	7	6
ED	7	6	5
LA	8	8	7

Table 2.5c. Dominance ranks across methods for each individual for AD group.

Individ.	I&SI	David's Score	Elo-Rating
LL	1	1	1
PT	1	2	2
QD	3	3	3
PD	4	4	6
WK	5	5	4
RS	6	7	8
SP	7	6	5
MW	8	8	7

3. FRUIT AVAILABILITY AND DOMINANCE RANK PREDICT AGONISM IN WILD FEMALE WHITE-FACED CAPUCHINS (*CEBUS CAPUCINUS IMITATOR*) IN SECTOR SANTA ROSA, COSTA RICA

ABSTRACT

Purpose: To determine if females exhibit different rates of agonism based on group size, reproductive state, kinship, dominance rank, and ripe fruit availability in order to understand what variables affect behavioral changes in female primates.

Methods: We used focal animal sampling to record agonistic interactions in 23 wild adult female white-faced capuchin monkeys (*Cebus capucinus imitator*) in three social groups in the Sector Santa Rosa (SSR) of the Área de Conservación Guanacaste (ACG) in Costa Rica. Using Generalized Linear Mixed Models we determined factors influencing rates of agonism is this population. We included ripe fruit biomass, group size, reproductive state, kinship, and dominance rank as predictor variables based on knowledge of what factors influence female reproductive success and thus, likely, behavior.

Conclusion: Agonism in female white-faced capuchins is correlated with dominance rank and ripe fruit availability as well an interaction between dominance rank and fruit availability. Higher-ranking monkeys engage in more frequent agonism. Monkeys also exhibit higher rates of agonism when ripe fruit availability is low. We propose that when ripe fruit availability is high individuals are preoccupied with foraging and there is

sufficient food such that individuals to do not need to engage in agonism to defend their food sources.

INTRODUCTION

Agonism, which encompasses a suite of behaviors that appear in situations of conflict, is a nearly universal class of behavior displayed by social mammals. Agonism is primarily expected in the context of high value resources that are monopolizable, which makes the risk of injury worthwhile (Wrangham, 1979; Enquist and Leimar, 1987; Sterck et al., 1997; Isbell and Young, 2002). In females, access to food resources is the main limiting factor of reproductive success, as opposed to access to mates for males. It has been demonstrated that agonism in female primates often arises when competing for food, especially at clumped resources (Isbell, 1991). This contest competition allows some individuals to gain preferential access to food resources. When clumped, high quality foods, such as ripe fruit, are plentiful; contest competition is predicted to be high as individuals directly compete for access to these food resources (Isbell, 1991). However, Wheeler et al. (2013) found that diet alone does not predict rates of agonism in a meta-analysis of 23 non-human primate species. There has been limited investigation of what other factors may influence both intra- and inter-individual variation in female non-human primates. Based on an understanding of the determinants of female reproductive success, our research investigates factors that likely influence rates of agonism. Inter-individual variation in agonsim may be affected by number of females in their group and relatedness between females. Intra-individual variation is potentially affected by reproductive state, high value resource availability, and dominance rank.

In some studies, rates of agonism are unaffected by fruit availability, such as in the blue monkey (*Cercopithecus mitis stuhlmanni*) (Pazol and Cords, 2005). Instead, females adjusted their foraging strategies. Subordinate females cope with low fruit abundance by spending more time foraging and all females spend more time foraging for less preferred foods when fruit is scarce (Pazol and Cords, 2005). In the Samango monkey (*Cercopithecus mitis erythrarchus*), female-female agonism for fruit occurs more often than for leaves or other plant parts, however variation in fruit availability as related to rates of agonism was not measured in this study (Payne et al., 2003). Females engage in agonism more frequently over fruit than other plant parts and agonism is affected by preferred food availability (Payne et al, 2003), however, there is likely variation between populations.

The number of females in a group is likely a contributing factor to rates of agonism because as the number of females increases the number of competitive partners also increases. As the number of individuals competing for resources rises, the fewer resources are available per individual, thus increasing competition, which is supported by findings from brown capuchins (Janson, 1988). In a meta-analysis including strepsirrhine and haplorrhine primates, the number of females in a group was significantly positively associated with rates of agonism (Wheeler et al., 2013).

Reproductive state is also likely an influential variable for determining rates of agonism in female non-human primates. Across reproductive states, females undergo shifts in their behavioral repertoire and reproductive success is likely tied to how females alter their behavior across reproductive states. It has been shown that behavior is affected by a female's reproductive state in primates and other animals (e.g. proceptive and receptive behavior, affiliative behaviors (Clement et al., 2005) marking/scenting behaviors (Ferkin et al., 2004), group movement (Fischhoff et al., 2007)). Agonism may also vary as the costs and benefits of gaining access food and other resources changes across a female's reproductive state.

Kinship has been demonstrated to affect agonistic behavior in non-human primates, however the effect on rates of agonism has not been investigated, to our knowledge. In rhesus macaques (*Macaca mulatta*), females directed agonism more frequently at kin than non-kin, particularly younger kin. It is suggested that this is because females are highly involved in the socialization of juveniles (Bernstein and Ehardt, 1986). In vervet monkeys (*Cercopithecus aethiops sabaeus*), females more often aided kin than non-kin in agonistic encounters (Hunte and Horrocks, 1987). Both of these findings suggest that rates of agonism may differ based on the number of kin an individual has in a group.

In primates and other mammals dominance is often a key feature of the social structure. In many species, individuals compete for dominance rank through agonistic interactions in an effort to gain fitness-related benefits. Depending on the species, dominance can have direct and indirect effects on a female's fitness, giving it an important evolutionary role (long-tailed macaques (*Macaca fascicularis*): van Noordwijk & van Shaik, 1999; yellow baboons (*Papio cynochephalus*): Altmann & Alberts, 2003; mountain gorillas (*Gorilla beringei beringei*): Robbins et al., 2007). In a meta-analysis including 25 primate species, including *Cebus capucinus imitator*, dominance was significantly positively related to infant survival to one year and unrelated to fecundity and feeding success (Majolo et al., 2012).

White-Faced Capuchins

White-faced capuchins (*Cebus capucinus imitator*) are medium-sized Neotropical primates and are an ideal study species for investigating variation in rates of agonism. Previously it has been demonstrated that capuchins have variable rates of agonism dependent on foraging factors (Phillips, 1996; Vogel and Janson, 2007), however the affect of additional factors has not been thoroughly examined.

White-faced capuchins are omnivorous, though fruits make up a large portion of their diet (50-80% [Oppenheimer 1968; Chapman & Fedigan, 1990]). In this species, rates of agnoism were found to be higher in trees with higher fruit abundance compared with trees with lower fruit abundance, though this was a not a statistically significant finding (Vogel and Janson, 2007). Additionally, an increase in the number of females in a feeding tree is significantly related to higher rates of agonism (Vogel and Janson, 2007). Congruent with the socioecological model, agonism in feeding trees does not change with the number of adult males or juveniles, only with increasing numbers of females. This is consistent with the idea that food is more important to females due to its limiting effect on reproduction (Vogel and Janson, 2007).

In white-faced capuchins rates of agonsim have previously been found to be related to dominance rank. Higher-ranking females instigate aggression more frequently than lower-ranking females (Vogel, 2004) and lower-ranking females receive higher rates of aggression than higher-ranking females (Perry, 1996). Additionally, higher-ranking females have a higher energetic intake rate at feeding trees (Vogel, 2005).

White-faced capuchins are female-bonded and affiliative behaviors have been demonstrated to be affected by kinship (Perry, 1996). Females associate more frequently with kin (Perry, 1996; Bergstrom and Fedigan, 2013) and the effect of kin bias increases as group size increases (Perry, 2008; Bergstrom and Fedigan, 2013), however kin bias is still considered weak in this species (Perry, 1996; Bergstrom and Fedigan, 2013).

Female white-faced capuchins show limited proceptive behaviors, though males are more interested (e.g. following, sniffing) in females during their fertile phase (Carnegie et al., 2005). Lactating females with new infants receive more grooming than other females (Perry, 1996) and also have higher energy intake rates (McCabe and Fedigan, 2007). Females with male infants receive more attention from group adult males after the birth of their infant than do females who give birth to female infants (Sheller et al., 2009). In white-faced capuchins young infants garner increased attention and thus the mother also receives increased interaction with conspecifics (Perry, 1996).

We studied rates of agonism in a population of white-faced capuchin monkeys at the Sector Santa Rosa of the Área de Conservación Guanacaste, Costa Rica. We quantified ripe fruit biomass, female group size, reproductive state, kinship, and dominance rank.

Research Questions and Predictions

Are rates of agonism correlated with ripe fruit availability, female group, reproductive state, kinship, and dominance rank?

Prediction 1) Ripe fruit availability is positively correlated with rate of agonism. As ripe fruit availability increases, competition, and thus rates of agonsim, will also increase as it would be integral to gain enough resources while they are available.

Prediction 2) As female group size increases, rate of agonism increases due to an a greater number of competitors.

Prediction 3) Lactating females exhibit higher rates of agonism than non-lactating females in order to gain access to enough food to maintain both herself and her growing infant.

Prediction 4) Kinship does not affect rates of agonism due to weak kin-bias in white-faced capuchins.

Prediction 5) Higher-ranking females exhibit higher rates of agonism in order to maintain their high rank.

METHODS

Study Site

Santa Rosa National Park (10°50′30″N, 85°37′0″W) was established in 1971 on former cattle grazing pastureland (Allen, 2001). This area is now known as Sector Santa Rosa (SSR) and is part of the broader Área de Conservación Guanacaste (ACG). The ACG is made up of 18 separate sectors of which SSR was the first to be created. The ACG became an UNESCO world heritage site in 1999 and includes approximately 147,000 hectares of tropical ecosystems, including marine, dry forest, cloud forest, and rainforest. SSR is located in the northwestern corner of Costa Rica, 35 km north of the city of Liberia and 40 km south of the Costa Rican boarder with Nicaragua. SSR is made up of regenerating tropical dry forest and is punctuated by two drastically distinct seasons. The majority of rain falls in the wet season from mid-May to mid-December [mean = 1497 mm/year] with nearly no rainfall in the dry season from mid-December to mid-May dry season (Fedigan, 1993; Melin et al., 2014).

Study Species

White-faced capuchins (*Cebus capucinus imitator*) are a medium-sized Neotropical primate that occupies a range of habitats as far north as Honduras and as far south as Ecuador (Estrada et al., 2006). The species is moderately sexually dimorphic with adult males being approximately 25-35% larger than adult females (Fedigan, 1993). The Santa Rosa capuchins have been studied continuously since 1983. At this site, average group size ranges from 11 to 18 individuals and consist of multiple adult females, their immature offspring and, usually, one or more immigrant adult male (Fedigan and Jack, 2012). Females remain in their natal group throughout their lives [though there are rare instances in which females have been known to disperse (Jack and Fedigan, 2009)], and males disperse at a median age of 4.5 years and change groups approximately every four years thereafter (Jack and Fedigan, 2004).

Between January and August 2017 we collected data on three social groups of white-faced capuchins in SSR: Administration group [AD], Rosa Maria group [RM], and Guanacaste group [GN]. All adult (age > 6 years) female group members were included in the study (N = 23). All group members were individually recognizable based on fur and face coloration, scars, broken digits or other injuries, and cap shape. During our study we logged 1,380 hours of contact (AD: 399h, RM: 515h, GN: 466h).

Field methods

Every month we followed each study group for a block of at least one and usually two separate three to four day periods. We followed groups in rotation and, when possible, sampled from each group before returning to sample from a group again.

Behavioral data were collected from sunrise to sunset and included group scans, individual focal follows, and *ad libitum* dominance interactions.

Focal Follows

We conducted 10-minute focal follows of all study subjects (N = 23), during which we recorded overall state behaviors as well as events (Altmann, 1974). This included all social behaviors and interactions with other individuals, and their identities (see Ethogram for comprehensive list). All effort was made to sequentially sample each subject in a group before returning to sample from an individual again. If an individual could not be located during 10 minutes of searching, we moved to the next subject in order. If an individual was out of sight for more than 60 seconds, the follow was discarded from the dataset (adapted from Carnegie et al., 2005). We extracted dyadic dominance relationships from focal follows based on interactions that included agonistic and submissive behaviors (see below).

Rate of Agonism

Agonism included threat face, vocal threat, lunge, chase, bite, wrestle, and hit. Rates of agonism were determined based on bouts during focal follow observations. Bouts were considered discrete when the participants differed by one or more individual. A bout was considered new if it was separated by at least 1 minute from a previous bout.

Ripe Fruit Biomass

The Santa Rosa Capuchin Project has carried out monthly phenology assessments since 2006 (Melin et al., 2014). Each month, as close as possible to the first of the month, we locate and assess over 450 individual trees from 45 species that are known to be a food source to this population of white-faced capuchins. Each tree is assessed according to the fruit, flower, and leaf maturity and abundance on a five-point scale (0:0%, 1:1-25%, 2:26-50%, 3:51-75%, 4:76-100%). Following Carnegie et al., (2011a), the following formula is used to calculate the estimated grams of fruit produced by a tree (F) of a given diameter at breast height (DBH): F=47*DBH1.9 (Peters et al. 1988). The F for each individual tree was summed for each species and multiplied by the proportion of individuals of that species that had ripe fruit. Finally, the summed values for all species was divided by the total transect area to estimate total grams of fruit/hectare produced each month. There are two phenology trails, one of which is applicable to a single group (RM), the other of which is applicable to the other two study groups (AD, GN).

Female Group Size

Group size was calculated as the number of adult females in a social group. Previous research has demonstrated that rates of agonism do not increase with additional male or juvenile group members (Vogel and Janson, 2007). Each group retained a stable number of adult females throughout the study period [AD = 7, RM = 8, GN = 8].

Reproductive State

We determined reproductive state post hoc based on the appearance or absence of an infant. During our study period all but one female gave birth to an infant or was lactating. This one female subsequently gave birth after the end of the study period. It is clearly visible when female white-faced capuchins are pregnant and the date of conception was calculated based on counting back 158 days from the estimated birth date determined the first observance of an infant (Carnegie et al., 2011b; Schoof et al., 2014).

We classified females as early pregnant (conception to 3 months), late pregnant (3 months to birth), early lactating (infants < 3 months), late lactating (infants > 3 months to 14 months), or other. We divided both pregnancy and lactating into two categories because steroid hormone concentrations, which likely affect behavior, have been shown to change from early to late pregnancy and from early to late lactating in other primates and mammals (Gudermuth et al., 1998; Altmann et al., 2004). "Other" includes adult females that were neither pregnant nor lactating.

Early lactating included females with infants that were less than three months old. At approximately three months of age infants begin traveling more frequently on their own, maternal rates of carrying drastically decrease, and infants begin eating weaning foods (Carnegie et al., 2011; Fedigan et al., 2004; Perry, 2012; Sargeant et al., 2015). Late lactating included females with infants greater than three months of age and less than fourteen months of age, the mean age at which an infant is weaned (Sargeant et al., 2015).

Kinship

Kinship was determined based on birth records and DNA analyses for individual females. Based on these known kin relationships, each female was assigned a single maternal kin-based variable. We only looked at maternal kin because paternal relatives are not generally recognized by non-human primates and maternal relatives are often recognizable for non-human primates, such as has been observed in macaques (Chapais et al., 1997), especially in species with matrilineal dominance hierarchies, such as our study subjects. We calculated this variable by tallying the number of maternal half sibling, mother-offspring, and maternal grandmother-grand offspring relationships and converting it to a proportion in order to standardize across different group sizes. We did not look at more distant relationships because non-human primates have not been shown to recognize or favor more distantly related kin (Silk, 2002; Perry, 2008).

Dominance Rank

We recorded all dominance interactions that involved adult females. Dominance interactions included all instances of conflict that consisted of at least two adult females and both agonistic and submissive behavior was perceptible. Agonistic behaviors included lunge, chase, threat face, bite, hit, wrestle and submissive behaviors included cower, flee, grimace, cry, and tail bite.

Ad libitum dominance interactions were recorded while following the group and not recording a focal follow. At the time of the event we recorded the individuals involved, including the winner and loser of the dominance interaction and any partners involved; the contested resource, if it could be determined; the agonistic behavior displayed; the submissive behavior displayed; and a description of the order of events that took place. The individual that was observed to demonstrate submissive behaviors was deemed the loser. The individual that did not display submissive behaviors was deemed the winner. Dominance ranks were assigned based on David's scores and females were ranked linearly, based on previous findings that these monkeys exhibit moderately linear dominance hierarchies (see Chapter 2).

Statistical Analyses

We used repeated measures Linear Mixed Models (LME4, R version 3.4.3) to determine how predictor variables were associated with rates of agonism. Linear mixed models allow us to account for non-independence, which is inherent in repeated measures. The independent variable, rate of aggression, was nearly normally distributed and this analysis is robust to this assumption, thus we used a normal distribution. We constructed a model with subject ID nested within group as a random effect, and ripe fruit biomass, reproductive state, dominance rank, number of maternal kin, and group size as fixed effects. We visually inspected residual plots and saw no obvious deviations from homoscedasticity or normality. We used likelihood ratio tests of the full model with the effect in question against the model without the effect in question in order to obtain *p-values.*

RESULTS

Rate of Agonism

We collected 584 hours of focal data for an average of 25.3 hours per individual. We recorded 488 bouts of agonism for a mean rate of 0.15 bouts/hour, or one bout every seven hours (Table 3.1). Agonism was most commonly observed as threat faces in which no animals made contact and the agonism was not sustained. Less frequently, agonism consisted of chasing or lunging at an individual. Very infrequently agonism consisted of biting or wrestling with moderate injuries, such as a bloody finger or tail.

Ripe Fruit Biomass

Mean ripe fruit biomass was 35.8 grams/hectar and the ranged from 17.93 to 85.18 grams/hectar (Table 3.2). Ripe fruit availability affected overall rates of agonism ($\chi^2(1) = 14.359$, $P < 0.001$). As ripe fruit biomass decreased, rate of agonism increased by 0.0125 bouts/hour ± 0.00439 (standard errors).

Female Group Size

Two of our study groups had 8 resident females and one group had 7 resident females. Female group composition remained consistent in all three groups throughout the study period. Female group size did not affect rates of agonism ($P > 0.05$).

Reproductive State

Females fell within all 5 categories, which included other, early and late pregnant, and early and late lactating. Reproductive state did not affect rates of agonism ($P > 0.05$) (Table 3.3).

Kinship

The mean proportion of maternal kin was 0.225, meaning that in a group of 8 females approximately 2 females were maternally related to a study subject. Maternal kin relatedness ranged from 0 to 0.428 (Table 3.4), as proportion of maternal kin in the group. Maternal kinship did not affect rates of agonism ($P > 0.05$). However, there was a trend for females with fewer kin to display higher rates of agonism.

Dominance Rank

In total we recorded 113 *ad libitum* dominance interactions (AD = 36, RM = 40, GN = 37) and 38 dominance interactions during focal follows (AD = 13, RM = 11, GN = 14).

Females were ranked linearly using David's scores and all dominance ranks were unique for each individual in a group. Dominance rank affected rate of agonism ($\chi^2(1) = 5.991$, $P = 0.01438$). As rank decreased, rate of agonism decreased by 0.0358 bouts/hour ± 0.01199 (standard errors) (Table 3.5).

Interaction Terms

There was no significant effect of interaction terms ($P > 0.05$).

DISCUSSION

In this study we explored the degree to which rates of agonism in female white-faced capuchin monkeys in Sector Santa Rosa of the Área de Conservación Guanacaste in Costa Rica were explained by social and environmental factors. We found that rates of agonism increased as ripe fruit biomass availability decreased and higher-ranking females exhibited higher rates of agonism than lower ranking females. There was no relationship between rates of agonism, female group size, reproductive state, and number of maternal kin. We suggest that females adjust their rates of agonism during low fruit availability in order to maintain sufficient nutrient intake and higher-ranking females use agonism to maintain their rank.

Ripe Fruit Biomass

Fruit biomass varies drastically across the year at Sector Santa Rosa as the majority of rain falls within just seven months and nearly no rain falls in the other five months of the year (Fedigan, 1993; Melin et al., 2014), however ripe fruit biomass does not perfectly track the rainfall pattern. Females show birth seasonality that maximizes maternal survival by timing high fruit availability around early lactating (Carnegie et al., 2011). Our findings that as ripe fruit availability increases, rates of agonism decrease in female white-faced capuchins is inconsistent with theory that as high-quality monopilizeable resources increase in abundance, contest competition increases, which should be visible as increased rates of agonism (Isbell, 1991).

However, we suggest that as ripe fruit, the preferred food of capuchins, becomes more scarce, contest competition increases so that females attain enough food to meet their energetic requirements. Further, we suggest that when ripe fruit availability is high, females are able to spread out, increasing distance between individuals and thus lowering rates of conflict. If enough fruit is available, especially in separate trees or bushes, such that individuals are able to occupy separate food patches, it would not be necessary to defend the food because all or nearly all individuals would be preoccupied with their own food patch.

During our study period, ripe fruit availability was lowest during the dry season and highest during the wet season. White-faced capuchins adjust their activity level in response to changes in temperature, spending more time resting during the dry season (Campos and Fedigan, 2009). If females are spending less time being active during times of low fruit availability, they must make sure to secure enough food to meet their energetic requirements for the day, which would feasibly lead to higher rates of agonism.

Further research examining how capuchins adjust group spread in response to food availability is necessary to fully support our suggestion.

Second, we suggest that possibly higher rates of agonism arise during periods of low fruit availability because the specific species of fruits that are available during this time are more monopolizeable. Fruit availability varies across the year, as does the species of fruit that ripens at any particular time. Some species grow on large trees and are far separated from the next food patch, while others grow on small bushes that are evenly spread over a relatively large area, and others grow on small trees that are dispersed throughout a home range. Which species is fruiting would affect the type of competition (contest versus scramble) and likely the rate of agonism observed. Future research should examine the correlation between the type of fruit available and rates of agonism.

Dominance Rank

Our finding that the rate of agonism is affected by dominance rank is congruent with previous research on white-faced capuchins that reported higher ranking females (alpha position and those closest to the alpha position) instigate agonism more frequently in feeding trees (Vogel, 2004). Our findings suggest that higher-ranking females exhibit higher rates of agonism in all contexts, not just feeding trees. Females inherit their rank from their mother (Perry, 2008), thus agonism in young females likely cements their position in the hierarchy as they reach sexual maturity and are integrated into the hierarchy, and in older females helps to maintain that position.

In female white-faced capuchins thus far there has been no relationship found between dominance rank and reproductive success, likely due to the high rates of alpha male replacements and associated incidents of infanticide (Fedigan, 1993; Fedigan et al., 2008; Brasington et al., 2017). However, females still form moderately linear dominance hierarchies, despite the lack of an established reproductive advantage high rank might garner, and engage in agonism to maintain their rank (see Chapter 2; Fedigan, 1993; Perry, 1996; Manson, 1999; Bergstrom and Fedigan, 2010). Individuals risk injury as well as the opportunity cost of time and energy spent engaging in agonism instead of foraging, resting, or any other behavior necessary for survival and reproduction.

We suggest that there is an as yet undetermined fitness benefit to forming and maintaining dominant-subordinate relationships given the potential costs of agonistic behavior. Continued monitoring of dominance rank and reproductive success are necessary and because these are long-lived animals it may take many more years before this can be evidentially supported.

Group size

Our findings that female group size does not affect rates of agonism in this population of white-faced capuchins is likely due to the very small variation in group size between our three groups, two groups had 8 females and one group had 7 females. Previously it was found that in white-faced capuchins the number of females feeding in a tree affected rates of agonsim (Vogel and Janson, 2007). In addition, it is possible that a group size of approximately 7 or 8 females is an ideal size for limiting agonism and maximizing access to food resources. It has been demonstrated in female macques, who gain little in terms of reproductive success when it comes to high rank, likely maintain an ideal female group size. Group size appears to moderate reproductive success and groups split if too many females are present in a group (Noordwijk and Schark, 1999). In white-faced capuchins, further research, including studies that incorporate groups that consist of fewer and more adult females, would be necessary to test this prediction.

Reproductive State

We found that reproductive state did not affect rates of agonism in this population of white-faced capuchins. Reproductive state has been demonstrated to affect behavior in females of this species with pregnant and lactating females spending more time resting and less time foraging than other females (Rose, 1994). We suggest that females do not adjust rates of agonism based on reproductive state because it does not confer increased acquisition of resources. Lactating and pregnant females have higher energy requirements than other females and in the case of agonism, increased food intake would be the goal of adjusting rates of agonism. However, Rose (1994) found that even though pregnant and lactating females rested more frequently, they did not have a lower energy intake rates. Females instead adjust their foraging effort, likely meaning increased direct competition over resources is not necessary.

Kinship

Our findings that kinship does not affect rates of agonism suggest that females with fewer or greater numbers of kin express the same degree of agonism. Female white-faced capuchins do not exhibit strong kin-bias, however maternal kin are preferred as coalition and grooming partners (Perry, 1996, 2008; Bergstrom and Fedigan, 2013). While higher kin-relatedness in a group might mean more coalition partners and thus higher rates of agonism, females might avoid further agonism after an initial “settling” period in which rank is established based on matrilineal inheritance.

CONCLUSION & FUTURE RESEARCH

In summary, this study presents evidence that rates of agonism change in response to ripe fruit availability and dominance rank in female white-faced capuchins at the Sector Santa Rosa field site. We suggest that female white-faced capuchins increase their rates of agonism in response to low fruit availability in order to meet their energetic requirements. We also demonstrated the effect of dominance rank on rates of agonism. Despite no established relationship between dominance rank and reproductive success for females in this species, individuals engage in dyadic agonistic encounters to determine dominant-subordinate relationships and higher-ranking individual have higher rates of agonism. We suggest that there is an undetermined, likely minor, yet relevant relationship between dominance rank and reproductive success. As data accrue, we encourage future research that employs long-term datasets to examine this link.

Ultimately, our findings suggest that both ecological and social factors influence rates of agonism in female primates.

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Table 3.1. Mean rates of agonism by individual

Individual	Mean Rate of Agonism	Standard Error
AB	0.1219	0.0304
BO	0.1731	0.0671
BT	0.03823	0.0142
ED	0.1063	0.0316
FT	0.1427	0.0532
KI	0.1277	0.0548
LA	0.08007	0.0311
LL	0.2230	0.0671
LM	0.09355	0.0447
LU	0.2183	0.0600
MI	0.1301	0.0450
MW	0.1481	0.0506
PD	0.1552	0.0541
PR	0.3487	0.0861
PT	0.1167	0.0283
QD	0.2472	0.0770
RS	0.01782	0.0128
SH	0.2581	0.0636
SI	0.1861	0.0513
SP	0.04423	0.0174
TS	0.2155	0.0455
WK	0.1348	0.0515
ZA	0.04065	0.0179

Table 3.2. Mean rates of agonism by month and ripe fruit biomass availability

Month	Ripe Fruit Availability (g/hectare)	Mean Rate of Agonism (bouts/hour)	Standard Error of rate of agonism
January	52.78	0.1965	0.0636
February	85.18	0.1272	0.0217
March	23.61	0.1084	0.0142
April	22.02	0.1285	0.0226
May	19.86	0.1526	0.0258
June	34.13	0.1461	.0267
July	25.71	0.2561	0.0387
August	60.56	0.07681	0.0358

Table 3.3. Mean rates of agonism by reproductive state

Reproductive State	Mean Rate of Agonism	Standard Error	N
Other	0.1562	0.0583	18
Early Pregnancy	0.1783	0.0470	30
Late Pregnancy	0.1188	0.0247	48
Early Lactating	0.1682	0.0212	93
Late Lactating	0.1158	0.0139	171

Table 3.4. Mean rates of agonism by maternal kin relatedness

Maternal Kin	Mean Rate of Agonism	Standard Error	N
0	0.219	0.0331	4
0.01-0.25	0.158	0.015	12
0.26-0.428	0.117	0.02	7

Table 3.5. Mean rates of agonism by dominance rank

Dominance Rank	Mean Rate of Agonism	Standard Error
1 (Alpha)	0.1823	0.2016
2	0.1342	0.1215
3	0.1892	0.1511
4	0.1930	0.1257
5	0.1347	0.1903
6	0.08770	0.1474
7	0.06824	0.0524
8	0.08317	0.1396

4. ANDROGENS AND CORTISOL IN RELATION TO THE ECOLOGY AND BEHAVIOR OF FEMALE WHITE-FACED CAPUCHIN MONKEYS

ABSTRACT

Purpose: The role of androgens in the behavior of female non-human primates is not well understood despite the vast body of research that exists relating androgens and behavior in males. We examined the interrelationship of androgens, behavior, and the environment in order to understand how androgens may moderate, and be moderated by, behavior in conjunction with ecological conditions in a female Neotropical primate.

Methods: We collected non-invasive fecal samples from 23 adult female white-faced capuchin monkeys in three social groups in the Sector Santa Rosa of the Área de Conservación Guanacaste in Costa Rica. We conducted focal follows in order to quantify rates of behavior, measured ripe fruit biomass availability using phenology assessments in the population home range, and non-invasively collected fecal samples to quantify androgen and cortisol hormone metabolites via enzyme immunoassay.

Conclusion: In this population of white-faced capuchin monkeys, female androgen and cortisol levels were correlated with each other. Additionally, androgen and cortisol levels were correlated with dominance rank, with higher-ranking females having higher levels of both hormones. Androgen and cortisol levels were not correlated with rates of agonism, ripe fruit availability, and reproductive state. We conclude that androgen and cortisol levels mediate, and are mediated by, dominance rank in female white-faced

capuchins. These results are particularly interesting considering dominance rank and reproductive success are not linked in these monkeys.

INTRODUCTION

The role of androgenic sex hormones in the behavior of females is poorly understood, and based largely on the assumption that they should operate in a similar manner to males. Though conventionally considered ‘male’ hormones, androgens are critical for regulating the female reproductive system and affect female morphological, behavioral, and physiological phenotypes, and mounting evidence links androgens and behavior in females (Nelson, 2011). However, there is a distinct lack of research that has specifically targeted the relationship between androgens and behavior or circumstances that might affect female reproductive success, such as periods of heightened competition for energetic resources. There is evidence that glucocorticoids (stress hormones, including cortisol) act as a moderator of androgens (Mehta and Prasad, 2015) thus making it imperative to consider both families of hormones. To this end, we measured fecal androgen and glucocorticoid metabolite levels in wild female white-faced capuchins (*Cebus capucinus imitator)* at Área de Conservacíon Guanacaste (ACG), Costa Rica and investigated the association between hormone levels and rates of agonism, dominance rank, ripe fruit availability, and reproductive state.

Extensive research has demonstrated that in male primates, androgens play a role in rank, agonism, and paternal care and androgen levels vary between individuals and across life stages (Alberts et al., 1992; Nunes et al., 2000; Schoof and Jack, 2013; Jack et al., 2014). In female primates, there is evidence that androgen levels vary across reproductive stages (Beehner et al., 2005; Davison et al., 2005; Fürtbauer et al., 2013), but only a few studies have examined the role of androgens in female behavior in wild primates (Beehner et al., 2005; Grant et al., 2011; Howlett, 2012; Fürtbauer et al., 2013; Setchell et al., 2015). Two main hypotheses have been proposed to explain variation in androgen levels in males, the challenge hypothesis (Wingfield, 1984) and the dual-hormone hypothesis (Mehta and Josephs, 2010); however to our knowledge the predictions of these hypotheses have not been examined in female non-human primates, who also demonstrate variable androgen levels.

The Challenge Hypothesis

The challenge hypothesis explains variable androgen levels in males, suggesting that heightened levels serve to maximize male reproductive success. Accordingly, the hypothesis predicts higher androgens in times of heightened male-male competition for mates and lower androgens during times that require paternal care (Wingfield, 1984). Studies of male songbirds have provided extensive support for the challenge hypothesis (Chandler et al., 1994; Enstrom et al., 1997; Raouf et al., 1997; Lynn, 2008), and results from a number of male primates support at least some parts (Cavigelli and Pereira, 2000; Muller and Wrangham, 2004a; Girard-Buttoz et al., 2015).

Agonism and parental care, the two main behaviors examined in the challenge hypothesis, are both exhibited by females as well, and can profoundly affect female reproductive success. Rates of agonism are often correlated with dominance rank, including in female white-faced capuchins (Chapter 3) and, in many species, dominance rank and reproductive success are linked (Noordwijk and Schark, 1999; Altmann and Alberts, 2003; Robbins et al., 2007; Majolo et al., 2012).

It has been demonstrated that hybrid baboons with higher androgens exhibit higher rates of agonism (Beehner et al., 2005) and several captive studies have documented this same relationship between agonism and androgens. For example, female marmosets that are more aggressive towards territorial intruders show greater androgen increases (Ross and French, 2011) and a meta-analysis demonstrated a positive correlation between agonism and androgens in women (Book et al., 2001). However, rates of agonism were found to be unrelated to androgen levels in captive female bonobos and ring-tailed lemurs (von Engelhardt et al., 2000; Sannen et al., 2004).

While male reproductive success is limited by access to mates, female reproductive success is limited by access to energetic resources (Darwin, 1871; Trivers, 1972; Clutton-Brock, 2009). Males and females thus present different adaptations that can act to maximize access to the resource limiting their reproductive success. Indeed, agonism in female primates often arises when competing for food, especially at clumped resources (Isbell, 1991). This contest competition allows some individuals to gain preferential access to food resources, just as male-male agonism allows only some to mate. In females it might be expected that androgen levels positively correlate with agonism in the context of food availability. In female hybrid baboons the wet season is associated with higher androgens, a time when food resources are plentiful, however food availability was not directly measured (Beehner et al., 2005).

We examine the relationship between ripe fruit availability and androgens in a female Neotropical primate in order to examine the applicability of the challenge hypothesis to female primates. Based on our findings that rates of agonism increase during times of food scarcity, we expect androgens in females to be higher during times of food scarcity, unlike female hybrid baboons.

The Dual-Hormone Hypothesis

The study of competition and agonism naturally leads to an examination of dominance as dominance hierarchies are often established through agonistic encounters. Dominance is increasingly linked to androgens in human and non-human primates (Higley et al., 1996; Mazur and Booth, 1998; Josephs et al., 2006) and higher-ranking males often have higher androgen levels (Muehlenbein et al., 2004; Muller and Wrangham, 2004b; Setchell et al., 2008; Mehta and Josephs, 2010; Jack et al., 2014). Rank and androgens have also been found to be positively correlated in some female primates (Beehner et al., 2005; Mehta and Josephs, 2010), however, the relationship is not entirely consistent. For example, androgens and rank are not correlated in either female or male chacma baboons, although androgens are higher in males actively rising in rank (Beehner et al., 2006, 2009). The dual-hormone hypothesis addresses these inconsistencies by positing that androgens and glucocorticoids (GCs) work in unison to affect dominance status *and* agonism (Mehta & Josephs, 2010).

The dual-hormone hypothesis proposes that androgens are positively associated with dominance status, but only in individuals with low cortisol. It suggests that GCs block the interaction between androgens and dominance (Mehta & Josephs, 2010). Human studies have provided support for the dual-hormone hypothesis in both men and women; individuals with high androgens and low GCs generally have higher dominance ratings while those with both high androgens and high GCs score lower dominance ratings (Mehta and Josephs, 2010; Jiménez et al., 2012; Denson et al., 2013; Edwards and Casto, 2013). Additionally, individuals with high androgens and high GCs are more prone to agonism in response to appropriate stimuli (i.e., they are considered more reactive to these stimuli; Mehta & Josephs, 2010). Although not specifically addressing the dual hormone hypothesis, Sapolsky (1992) suggests that in nonhuman animals, perceived instability of a dominance hierarchy leads to higher GC and androgen levels in dominant individuals (Sapolsky, 1992). This suggestion has been supported in studies of male Verreaux's sifaka (Brockman et al., 2001), male white-faced capuchins (Schoof et al., 2016), and male and female African wild dogs (Creel et al., 1997).

White-Faced Capuchin Monkeys

We examined androgens and cortisol in a wild, female primate. White-faced capuchins (*Cebus capucinus imitator*) are medium-sized Neotropical primates. White-faced capuchins are omnivorous, feeding primarily on fruits (50-80% of their diet [Chapman and Fedigan, 1990]) and females depend heavily on fruit to meet the energetic costs of reproduction and lactation (Carnegie et al., 2011a). Consistent with the priority-of-access model of dominance, higher-ranking females have higher energy intake rates in feeding trees and instigate agonism more frequently (Carpenter, 1942; Vogel, 2005). Female white-faced capuchins produce a single infant approximately every 2.25 years and carry out the majority of parental care (Fedigan et al., 2008).

In females, reproductive success and rank has not yet been conclusively linked, possibly because of frequent male takeovers and associated incidences of infanticide (Fedigan et al., 2008; Kalbitzer et al., 2017). Females spend most of their adult lives either lactating or pregnant and while intergroup encounters, alpha males replacements, and infanticide are likely one of the biggest limiting factors to their reproductive success, they have little control over these situations. Females may benefit from elevated androgen levels if it aids in gaining increased access to food resources.

Androgens have not previously been measured in female white-faced capuchins. We examine the relationship between dominance, agonism, ripe fruit availability, reproductive state, cortisol, and androgens.

Research Questions

Are androgens and cortisol levels correlated with rates of agonism, dominance rank, reproductive state, and ripe fruit biomass?

METHODS

Study Site

We collected data from May to December 2017 from 3 habituated groups of white-faced capuchins in the Sector Santa Rosa of the Área de Conservación de Guanacaste, Costa Rica.

Santa Rosa is a tropical dry forest that exhibits two drastically distinct seasons with ripe fruit biomass peaking twice yearly, once just prior to the onset of the wet season (May-December) and the other prior to the onset of the dry season (January-April) (Melin et al., 2014). The majority of rain falls in the wet season from mid-May to mid-December [mean = 1497 mm/year] with nearly no rainfall in the dry season from mid-December to mid-May dry season (Fedigan, 1993; Melin et al., 2014).

Study Population

White-faced capuchins occupy a range of habitats as far north as Honduras and as far south as Ecuador (Estrada et al., 2006). The species is moderately sexually dimorphic with adult males being approximately 25-35% larger than adult females (Fedigan, 1993). At SSR the average group size ranges from 11 to 18 individuals and consist of multiple adult females, their immature offspring and, usually, one or more immigrant adult male (Fedigan and Jack, 2012). Females remain in their natal group throughout their lives [though there are rare instances in which females have been known to disperse (Jack and Fedigan, 2009)], and males disperse at a median age of 4.5 years and change groups approximately every four years thereafter (Jack and Fedigan, 2004).

The Santa Rosa capuchins have been studied continuously since 1983 and there are currently five habituated groups with ninety-six individuals (Fedigan and Jack, 2012). All group members are individually recognizable based on fur and face coloration, scars, broken digits or other injuries, and peak shape.

Between January and August 2017 we collected data on three social groups of white-faced capuchins at SSR: Administration group [AD], Rosa Maria group [RM], and Guanacaste group [GN]. All adult (age > 6 years) female group members were included in the study (N = 23). We logged 1,380 hours of contact (AD: 399h, RM: 515h, GN: 466h).

Field Methods

Each month January through August we followed each study group for a block of at least one, and for the majority of months, two separate three to four day periods. We followed groups in rotation and, when possible, sampled from each group before returning to sample from a group again. Behavioral data were collected from sunrise to sunset and included group scans, individual focal follows, and *ad libitum* dominance interactions.

Focal Follows

We conducted 10-minute focal follows of all study subjects during which we recorded overall state behaviors as well as events. This included all social behaviors and interactions with other individuals, and their identities (see ethogram for comprehensive list; Altmann, 1974). All effort was made to sequentially sample all subjects in a group before returning to sample from an individual again. If an individual could not be located during 10 minutes of searching, we moved to the next subject in order. If an individual was out of sight for more than 60 seconds, the follow was discarded from the dataset (adapted from Carnegie et al., 2005). We extracted dyadic dominance relationships from focal follows based on interactions that included agonistic and submissive behaviors.

Fecal Androgens and Cortisol

Between January and August 2017 we collected fecal samples twice monthly from each study subject. Fecal samples were collected within five minutes of defecation. Following Carnegie *et al*. (2011b), samples were stored in Solid Phase Extraction (SPE) cartridges until analysis. Samples were eluted from the SPE cartridges and analyzed using enzyme immunoassay at the Laboratory for the Evolutionary Endocrinology of Primates at the University of Arizona in Tucson.

Mean intra- and inter-assay coefficients of variation (CV) for cortisol were 7.6% and 5.4% respectively for the low pool and 7.1% and 1.9% respectively for the high pool. Mean percent accuracy for cortisol was high (107.02 ± 2.59%, N = 5). The percent bound values from the pooled samples paralleled the percent bound values of the standard curve for cortisol, and there were no differences in the slopes ($F_{(10,11)} = 1.179$, $P > 0.05$, ANOVA).

Mean intra- and inter-assay coefficients of variation (CV) for androgens were 14.4% and 14.2% respectively for the low pool and 7.1% and 14.2% respectively for the high pool. Mean percent accuracy for androgens was high (112.59 ± 2.85%, N = 7). The percent bound values from the pooled samples paralleled the percent bound values of the standard curves for androgens and there were no differences in the slopes ($F_{(12,13)}$ = 0.3031, $p > 0.05$, ANOVA).

Rate of Agonism

All agonism recorded during focal follows was categorized as low grade (no contact made between participants, e.g. threat face, vocal threat, lunge, chase) or high grade (contact made between participants, e.g. bite, wrestle, hit). Rates of agonism were determined based on bouts during focal follow observations. Bouts were considered discrete when the participants differed by one or more individual or wer separated by at least one minute. Rates were determined by dividing bouts by hour.

Dominance Rank

We recorded all dominance interactions that involved adult females. *Ad libitum* dominance interactions were recorded while following the group and not recording a focal follow. At the time of the event we recorded the individuals involved, including the winner and loser of the dominance interaction and any partners involved; the contested resource, if it could be determined; the agonistic behavior displayed; the submissive behavior displayed; and a description of the order of events that took place. We assessed the dominance rank of dyads based on directed agonistic behaviors, as well as submissive behaviors, including cower, flee, grimace, cry, and tail bite. The individual that was observed to demonstrate submissive behaviors was deemed the loser. The individual that did not display submissive behaviors was deemed the winner. We determined dominance rank using David's scores (Gammell et al., 2003) and assigned unique ranks for each individual in a group

Ripe Fruit Biomass

The Santa Rosa Capuchin Project has carried out monthly phenology assessments since 2006 (Melin et al., 2014). Each month, as close as possible to the first of the month, all on-site researchers locate and assess over 450 individual trees from 45 species that are known to be a food source to this population of white-faced capuchins. Upon location of the tree, the researcher judges the fruit, flower, and leaf maturity and abundance on a five-point scale (0:0%, 1:1-25%, 2:26-50%, 3:51-75%, 4:76-100%). The following formula was used to calculate the estimated grams of fruit produced by a tree (F) of a given diameter at breast height (DBH): F=47*DBH1.9 (Peters et al., 1988; Carnegie et al., 2011b). The F for each individual tree was summed for each species and was then multiplied by the proportion of individual trees of that species that had ripe fruit. Finally, the summed values for all species were divided by the total transect area to estimate total grams of fruit/hectare produced each month. We used two phenology trails, one of which is applicable to a single group (RM), the other of which is applicable to the other two study groups (AD, GN).

Reproductive State

We classified females as early pregnant, late pregnant, early lactating, late lactating, or other. We divided both pregnancy and lactating into two categories because steroid hormone concentrations, which likely affect behavior, have been shown to change from early to late pregnancy and from early to late lactating in other primates and mammals (Gudermuth et al., 1998; Altmann et al., 2004). "Other" includes females that were neither pregnant nor lactating.

We determined reproductive state post hoc based on the appearance or absence of an infant. It is possible that some females were pregnant and the pregnancy was spontaneously terminated, however during our study period all but one female gave birth to an infant or was lactating, thus spontaneous termination could only have applied to one female, who subsequently gave birth after the end of the study period. It is clearly visible when female white-faced capuchins are pregnant and the date of conception was calculated by counting back 158 days from the estimated birth date based on the first appearance of an infant (Carnegie et al., 2011a; Schoof et al., 2014).

Females were considered "early lactating" when their infants were less than three months old. At approximately three months of age infants begin travelling more frequently on their own, maternal rates of carrying drastically decrease, and infants begin eating weaning foods (Fedigan et al., 2004; Carnegie et al., 2011a; Perry, 2012; Sargeant et al., 2015). Late lactating included females with infants greater than three months of age and less than fourteen months of age, the mean weaning age (Sargeant et al., 2015).

Statistical Analyses

We used linear regression (LME4, R version 3.4.3) to determine if cortisol and androgen levels were related. Based on visual examination, level of cortisol was not normally distributed and accordingly we natural log transformed the variable and it passed visual examination of normality. Based on visual examination androgen levels were normally distributed. For regression analysis all assumptions were met using visual examination of residual plots and errors.

We used repeated measures Linear Mixed Models (LME4, R version 3.4.3) to construct two different models to determine how predictor variables were associated; cortisol in the first model and androgens in the second model. Linear mixed models allow us to account for non-independence, which is inherent in repeated measures, as well as include nestedness, appropriate for comparison across groups. We assigned group as a random effect with subject ID nested within group. We assigned rate of agonism, ripe fruit biomass, reproductive state, and dominance rank as fixed effects. Rate of agonism was not normally distributed thus we added one and log base 10 transformed the variable. Ripe fruit biomass was not normally distributed consequently we transformed it using log base 10. After transformation all variables passed visual inspection for normality. We performed likelihood ratio tests comparing the full model with all predictor variables with the model without the factor of interest in order to obtain *p-values* (Winter, 2013).

All results were considered significant at $P < 0.05$.

RESULTS

In total we collected 584 hours of focal data for an average of 25.3 hours per individual.

Fecal Androgens and Cortisol

In total we analyzed 351 fecal samples for cortisol and 136 for androgens. Fewer samples were analyzed for androgens due to the large quantity of sample necessary and limited amount of sample available that was needed for measurement of androgens. We only included data for which we had both a cortisol and an androgen sample because we found that each hormone was significant in the other hormone's model.

Fecal androgens ranged from 6.70 to 43.49 ng/g with a median of 30.21 ng/g and mean of 29.63 ng/g. Fecal cortisol ranged from 9.14 to 1738.69 ng/g with a median of 129.15 ng/g and a mean of 220.43 ng/g.

Fecal androgen level and cortisol level were positively correlated (T = 49.91 – 9.834*ln(F), $F_{(1,129)} = 75.6$, $R^2 = 0.358$, $P < 0.0001$, SE = 1.160). As androgen levels increased so did cortisol levels. Because fecal androgen and cortisol were correlated, we included cortisol in our androgen models and androgens in our cortisol models.

In the androgen Mixed Model including rate of agonism, dominance rank, and reproductive state, cortisol was correlated with androgen levels ($\chi^2(1) = 64.677$ $P < 0.0001$). In the cortisol Mixed Model including rate of agonism, dominance rank, and reproductive state, androgen levels were correlated with cortisol levels ($\chi^2(1) = 65.527$ $P < 0.0001$).

Rate of Agonism

In 3,451 focal follows we recorded 488 bouts of agonism for mean rate of 0.15 bouts/hour, or one bout every seven hours. Rate of agonism did not affect the cortisol or androgen model, meaning they were not correlated with either hormone level.

Dominance Rank

In total we recorded 113 *ad libitum* dominance interactions (AD = 36, RM = 40, GN = 37) and 38 dominance interactions during focal follows (AD = 13, RM = 11, GN = 14).

Dominance rank was correlated with cortisol levels ($\chi^2(1) = 6.502$, $P = 0.0108$). As rank decreased, cortisol decreased by 1.230 ng/g ± 1.094 (standard errors). There was no significant interaction between dominance rank and androgen levels in the cortisol model.

Dominance rank was correlated with androgen levels ($\chi^2(1) = 16.069$, $P < 0.0001$). As rank decreased, androgens decreased by 2.457 ng/g ± 0.561 (standard errors). There was no significant interaction between dominance rank and cortisol levels in the androgens model.

Ripe Fruit Biomass

Mean ripe fruit biomass was 35.8 grams/hectar and the range was 17.93 to 85.18 grams/hectar. Ripe fruit biomass did not significantly affect our androgen or cortisol models, meaning ripe fruit biomass was not correlated with either androgen or cortisol levels.

Reproductive State

Females fell within all five categories of reproductive state, including other, early and late pregnant, and early and late lactating. Reproductive state did not significantly affect cortisol or androgen levels.

DISCUSSION

White-faced capuchin monkeys in Sector Santa Rosa, Área de Conservación Guanacaste, Costa Rica exhibited similar androgen and cortisol levels regardless of rates of agonism, ripe fruit availability, and reproductive state. Within individuals, fecal cortisol and androgen levels were related to each other. Dominance rank had a significant, but small correlation with androgen and cortisol levels. Based on these findings we suggest that cortisol and androgen levels do not mediate rates of agonism, nor are they correlated with differential rates of competition over ripe fruit, nor does female reproductive state significantly alter these hormone levels. However, androgen and cortisol levels appear to mediate, and be mediated by dominance rank in these monkeys.

Rate of Agonism & Dominance Rank

Our findings suggest that androgens and cortisol are not related to individual rates of agonism, but *are* associated with dominance rank in female white-faced capuchins. Previously, we demonstrated that rates of agonism are positively associated with dominance rank in female white-faced capuchins and higher-ranking females have higher rates of agonism (Chapter 3). Consistent with the challenge and dual-hormone hypotheses, we propose that mean androgen and cortisol levels are correlated with dominance rank and not agonism because hormone levels would more likely increase in direct response to agonistic encounters, meaning at the time of the encounter, and thus would not correlate with mean rates of agonsim overall.

Contrary to our results, findings from other female primates suggests that androgens mediate agonsim. Androgens are positively correlated with agonism in hybrid baboons (Beehner et al., 2005), captive marmosets (Ross and French, 2011), and women (Book et al., 2001). However, our findings are consistent with results from captive bonobos in which agonism and androgens were unrelated (Sannen et al., 2004). Unlike our current findings with female white-faced capuchins, in bonobos it was demonstrated that dominance rank was unrelated to androgen levels (Sannen et al., 2004). Bonobos exhibit low rates of agonism and egalitarian dominance hierarchies. We found relatively low rates of agonism in female capuchins, especially in comparison to catarrhine primates (Wheeler et al., 2013). We suggest that these low rates of agonism account for a lack of overall correlation between rate of agonism and androgen or cortisol levels.

Previously we found that higher-ranking female capuchins exhibit higher rates of agonism (Chapter 3). It is not intuitive then that higher-ranking monkeys exhibit higher androgens, but higher rates of agonism is not related to androgen levels. Also, there was no significant interaction between cortisol and dominance rank. However, dominance rank is related to cortisol levels, which lends support to the dual-hormone hypothesis (Mehta & Josephs, 2010). Indeed, it appears that in female white-faced capuchins cortisol and androgens are related to dominance, yet contradictory to the dual-hormone hypothesis, these hormones are unrelated to mean rates of agonism.

Our findings are congruent with previous research on dominance and androgens in wild female hybrid baboons and Barbary macaques. In female hybrid baboons that demonstrated that higher-ranking individuals had higher androgen levels (Beehner et al., 2005). In a combination of free-ranging, provisioned and captive, zoo-raised Barbary macaques (*Macaca sylvanus*), non-pregnant female androgen levels were higher in dominant females than in subordinate females (Grant et al., 2011).

Contrary to our findings, in adult female mandrills, Setchell et al. (2015) found no correlation between androgen levels and rank. In female mandrills intense dyadic conflict is rare and rank is highly stable (Setchell et al., 2015), which likely accounts for the lack of relationship between dominance and androgen in this population. In female white-faced capuchins rates of agonism are low, but contested resources do incite competition, which explains why dominance and androgen levels would be related in our study species as compared to mandrills.

In species in which dominance rank is determined through direct competition higher androgen levels should be related to higher rank. Sapolsky (1993) suggests that the stability of the dominance hierarchy affects cortisol and androgens. Female dominance hierarchies in white-faced capuchins are generally stable and during our study period we did not perceive any dramatic changes in the dominance hierarchy.

Ripe Fruit Biomass

Our findings suggest that in this population of female white-faced capuchins, androgen and cortisol levels are not reflective of differential rates of competition due to variation in preferred food availability. As applied to males, the challenge hypothesis suggests that heightened levels of androgen serve to maximize male reproductive success and males should have higher androgen levels during times of frequent aggressive male-male encounters over access to mates (Wingfield, 1984). Male reproductive success is limited by access to mates, while female reproductive success is limited by access to energetic resources (Darwin, 1871; Trivers, 1972; Clutton-Brock, 2009), which would suggest that females may experience higher androgen levels during heightened competition for preferred foods. However, our study does not support this aspect of the challenge hypothesis in female primates. Androgen levels do not appear to mediate competition for resources that limit female reproductive success, such as fruit.

Food availability may not affect androgen and cortisol levels because capuchins have been found to alter their home range and activity patters in response to seasonal changes (Campos and Fedigan, 2009). Females can give birth year round, but there is a strong skew towards births in the months of February through May (Carnegie et al., 2011a). This coincides with high fruit abundance in April and May, which suggests that capuchins maximize maternal survival over infant weaning survival (Carnegie et al., 2011a). Females alter their reproductive and behavioral patterns in response to seasonal changes, perhaps allowing them to maintain stable hormone levels across time.

Reproductive State

We found that female white-faced capuchins do not demonstrate variable androgen and cortisol levels reflective of their reproductive state. Previously in white-faced capuchins pregnant females have been demonstrated to have higher cortisol levels than non-pregnant females (Carnegie et al., 2011b). However, these results were based on a sample size of 8 females, only 7 of which conceived and became pregnant during the study period.

Our findings are counter to research that demonstrates pregnant Ethiopian hybrid baboons have higher androgen than non-pregnant females (Beehner et al., 2005). Androgen levels were measured in a combination of free-ranging, provisioned and captive, zoo-raised Barbary macaques (*Macaca sylvanus*). In non-pregnant females, androgen levels were higher in dominant females than in subordinate females (Grant et al., 2011). Ring-tailed lemurs exhibit elevated androgen levels during pregnancy (Drea, 2011). Androgen is higher in pregnant savannah baboons (*Papio cynocephalus*) than non-pregnant baboons. Androgens are higher in pregnant female mandrills than non-pregnant females (Setchell et al., 2015).

CONCLUSION & FUTURE RESEARCH

In summary, this study presents evidence that androgens and dominance rank are correlated in this population of female white-faced capuchins. Further, this study provides evidence that rates of agonism within individuals are not related to androgens or cortisol. Androgens may be related to individual bouts of agonism, but would need to be measured through blood or urine collected at the time of the interaction, which would only be feasible in a captive population.

We found that dominance was related to cortisol levels, and ripe fruit availability and reproductive state were related to neither androgen nor cortisol levels. Female white-faced capuchins do not appear to demonstrate significantly altered cortisol or androgen levels in response to seasonal variation or changing reproductive state.

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5. CONCLUSION

The white-faced capuchins (*Cebus capucinus imitator*) of Sector Santa Rosa, Área de Conservación Guanacaste, Costa Rica have been studied continuously since 1985. Dominance has previously been investigated in females in this species, however results have been inconsistent between studies (Fedigan, 1993; Perry, 1996; Manson, 1999a; Bergstrom and Fedigan, 2010). We characterize dominance using methods for describing the dominance hierarchy, examining rates of agonism, and measuring androgen and cortisol levels in relation to social and ecological variables.

White-faced capuchins exhibit female philopatry and both males and females have previously been characterized as having linear dominance hierarchies (Fedigan, 1993; Perry, 1996; Manson, 1999b; Bergstrom and Fedigan, 2010). Females assume the rank below their mother upon reaching sexual maturity at approximately six years of age (Perry, 2008).

Our assessment of dominance hierarchies in female capuchins using directional consistency indices, transitivity, steepness, David's scores, Elo-rating, and the I&SI method suggests that they exhibit "moderately linear" dominance hierarchies. All three groups qualified as having linear dominance hierarchies as defined by directional consistency and transitivity. Hierarchies were shallow, meaning that the outcome of dominance interactions is not entirely predictable. The three methods for determining rank order, David's scores, Elo-rating, and the I&SI method, were equivalent and can be used interchangeably. Female white-faced capuchins exhibit relaxed dominance hierarchies and reversals (dominance interactions in which a lower-ranking individual wins over a higher-ranking individual) are not uncommon. Females within groups are generally closely related and inclusive fitness benefits may explain the relaxed nature of dominance hierarchies in this population.

White-faced capuchins exhibit low rates of agonism (0.15 bouts/hour) that a vary with ripe fruit availability and dominance rank. Female group size, reproductive state, and number of maternal kin in the group are not associated with rates of agonism. Higher-ranking females may use agonism to reinforce their inherited position in the dominance hierarchy. Previous research demonstrated no link between reproductive success and rank in this population, however females adjust their rates of agonism based on rank, suggesting that there maybe an as yet undetermined fitness benefit to high rank which makes rank worth fighting for.

Within individuals, androgen and cortisol levels are correlated with each other such that when an individual has high androgen levels it also has high cortisol levels. Androgen and cortisol levels are also related to dominance rank. Higher-ranking females exhibit both higher androgen and cortisol levels. The dual-hormone hypothesis suggests that androgen and cortisol levels are associated in higher-ranking individuals (Mehta and Josephs, 2010), but unlike female capuchins, higher-ranking individuals have higher androgen and lower cortisol levels. In white-faced capuchins, the threat of male takeovers and associated incidences of infanticide may drive higher cortisol levels in female monkeys. Androgens and cortisol levels are unrelated to rates of agonism, fruit availability, and reproductive state. Our findings support the claim that androgens mediate, and are mediated by dominance rank, as has been suggested by the challenge hypothesis, and cortisol and androgen levels are correlated, in support of the dual hormone hypothesis (Wingfield and Hall, 1990; Mehta and Josephs, 2010).

Significance

Research on androgens in females still lags behind that of males. Our research contributes to a broader understanding of the role of androgens in female vertebrates, and more specifically in wild, female primates. Further, this research has implications for the behavioral and ecological endocrinology of female primates. HOW SO?. We have provided added evidence that dominance and androgens are interlinked and expanded this knowledge to a Neotropical primate. While laboratory studies can help guide research on endocrinology, the study of wild populations such as this is imperative to developing a deeper understanding of the relationship between hormones and behavior.

Due to the natural setting of our research we were able to integrate ecology, which is especially important for examining the evolutionary pressures that may have molded these relationships. We found no relationship between androgens, cortisol and fruit availability, which is informative for predicting how populations will respond to variable availability of food resources, both in response to seasonal and climate change.

In addition, we applied hypotheses that have historically principally been applied to males, to a female subject. We highlight the necessity to continue expanding research topics that have initially only investigated males to be applied to females.

Future Directions

We suggest continued research into potential fitness benefits of high rank in female white-faced capuchins. Agonism is costly and establishing a dominance hierarchy can lead to injuries and lead females to lose time feeding, resting, and engaging in essential behaviors for their survival. For this reason, we propose that there is a fitness benefit that has not yet been defined, perhaps because this is a long-lived species and the fitness benefit may only be visible over multiple generations. It is possible that a matriline that occupies higher ranking positions has more successful offspring in the long-term. It would be feasible to track females over multiple generations, however because males disperse and are often not followed for their entire lives determining a fitness benefit to high rank may be based solely on matrilines and not include sons. This could obscure results as reproductive skew in much higher in male white-faced capuchins as alphas sire the majority of offspring.

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APPENDIX

Appendix 1.1. White-faced capuchin ethogram.

A - Actor

R – Recipient

M – Mutual

AFFILIATIVE BEHAVIORS

Approach (A/R) (APP) (event) Focal monkey moves into proximity (within three body lengths) of another monkey.

Leave (A/R) (LEA) (event) Focal monkey moves out of proximity of another monkey.

Rest Proximately (M) (REP) (state) Focal monkey rests within three body lengths of another monkey

Rest in Contact (M) (REC) (state) Focal monkey rests while in contact with another monkey that is not their dependent infant

Play (PLA) (none/M) (state) (Jack 1998) Focal monkey or focal monkey and one or more other monkeys play, including biting, chasing, hitting, bouncing, pushing, and pulling.

Fur Rub (Perry 1995) (M) (KFR) (state) Focal monkey and one or more other monkeys rub plant material on their own fur and each other's fur.

Follow (A/R) (KFL) (event) After receiving a "leave" the focal monkey or other monkey travels closely behind the departing monkey.

Hand Sniff (A/R/M) (KHS) (state) Focal monkey holds another monkeys hand to one's face; digits close to/inserted in the nose, or another monkey does so to the focal monkey.

Groom (A/R) (KGM) (state) Focal monkey uses its hands and mouth, visually inspects and picks through another monkey's fur, or another monkey does so to the focal monkey's fur.

Food Interest (A/R) (CIN) (event) Focal monkey visually inspects, sniffs, or moves to touch the food item of another monkey, or another monkey does so to the food of the focal monkey.

Food Untolerated Theft (A/R) (CUN) (event) Focal monkey's food item is forcefully taken by another monkey or the focal monkey does so to another monkey's food item.

Food Share (A/R) (CSH) (event) (Jack 1998) Focal monkey takes or bites the food of another monkey and the food owner does not react negatively, or the focal monkey is the food owner in the situation.

Food Avoid (A/R) (CAV) (event) Focal monkey moves away or into a position to avoid having food stolen or another monkey does so to the focal monkey.

Food Push (A/R) (CPU) (event) Focal monkey makes forceful physical contact with motion to move other monkey away from one's food item or focal monkey is moved away from food item.

Infant Interest (A/R) (KII) (event) Focal monkey shows interest in an infant monkey by baby talking, putting its face very close to the infant, sniffing the infant, or gently touching the infant. If recipient focal monkey's dorsal infant is of interest to another monkey.

Dorsal (A/R) (KDO) (event) Focal monkey has another monkey in a dorsal position.

Dorsal End (A/R) (KDOX) (event) Focal monkey no longer has a dorsal monkey.

Nurse (A/R) (KNU) (event) Focal monkey nurses an infant.

Nurse End (A/R) (KNUX) (event) Focal monkey no longer nurses.

AGGRESSIVE BEHAVIORS

Threat Face (A/R) (GTF) (event) Focal monkey stares at another individual while opening its mouth to expose the canines or another monkey does so to the focal monkey.

Low Grade Aggression (A/R) (GLG) (event) Focal monkey acts aggressively toward another monkey via lunging or chasing or focal monkey is victim of aggressor. No physical contact is made between the two parties.

High Grade Aggression (A/R) (GHG) (event) Focal monkey acts aggressively toward another monkey via biting, hitting, or wrestling or focal monkey is victim of aggressor.

Physical contact is made between the two parties.

Coalitionary Contact (TCO) (state) <focal><victim><other aggressor> General physical contact between two monkeys acting on the same side of a fight, jointly threatening another monkey, including cheek to cheek and overlord. Focal monkey can be any of the three positions.

Coalitionary threat face (TTF) (state) <focal ><victim><other aggressor> Two monkeys threat face another monkey while not in physical contact. Focal monkey can be any of the three positions.

FEAR AND SUBMISSION

Startle (STA) (event) Focal monkey is interrupted and jumps up when startled - usually in response to a loud noise or sudden movement.

Submissive – (A/R) (ESU) Focal monkey acts lowly towards another monkey, cowering, tail biting, fleeing, crying.

SEXUAL BEHAVIORS

Sex Dance Display (A/R/M) (SDP) (state) Focal monkey makes duck face, paces, turns, or pirouettes, often accompanied by sex squeaks or grunts or anther monkey directs these behaviors toward the focal monkey.

Sex (M) (SEX) (state) Focal monkey engages in intercourse between with another monkey involving mounting and thrusting.

SELF OR GENERALLY DIRECTED BEHAVIORS

Rest (RES) (state) Focal monkey rests alone sitting or leaning against something or lying down.

Fur Rub Solitary (AFU) (state) Focal monkey rubs its own fur with a plant product

Self Groom (SDI) (state) (Jack 1998) Focal monkey uses its hands and mouth to pick through its own hair.

Urinate (URI) (event) Focal monkey urinates, but does not urine wash.

Urine Wash (AUR) (UW) (event) (Jack 1998) Focal monkey urinates and catches the stream of urine with its hand and/or foot on or near the genitals splashes and rubs the urine onto its body.

Vigilant (VIG) (event) Focal monkey scans intently at a long range (not for food).

Travel (TRA) (state) Focal monkey moves through the environment, not actively looking for food or eating.

Visually forage (VFO) (state) Focal monkey looks for food (includes breaking sticks and looking inside); gaze is usually directed to area in immediate vicinity of monkey.

Extractive Forage Insect (EFI) (state) Focal monkey eats insects and grubs from within sticks and bark.

Forage Fruit (FFR) (state) (Jack 1998) Focal monkey ingests/manipulates fruit.

Forage Insect (FIN) (state) Focal monkey ingests/manipulates insects and grubs.

Forage Flower (FFL) (state) Focal monkey ingests/manipulates flowers.

Forage Other (FOT) (state) Focal monkey ingests/manipulates other matter, including wasps nest.

Forage Unknown (FUN) (state) Focal monkey ingests/manipulates an unknown item/substance.

Drink (DRI) (state) - Focal monkey ingests water.

Alarm Call (A/R) (VAL) (event) (Perry 1995) Focal monkey makes alert vocalization in response to aerial predator, ground predator, snake, non-resident conspecifics, or in response to aggression from conspecific.

Lost Call (A/R) (event) Focal monkey vocalizes a lost call.

Alpha Gurgle (A/R) (event) Focal monkey makes a gurgle or grunting noise while near the alpha male.

Out of Sight (state) Focal monkey is out of sight of the observer.

BIOGRAPHY

Gillian King-Bailey was born raised in Petaluma, California. She received a B.S. from Sonoma State University in 2013 and an M.A. from Tulane University in 2016. She has held an Adjunct Instructor position at Tulane University since 2018. She has conducted research on New World primates as well as on native animal populations in California, including the California tiger salamander and the Western pond turtle. When not working, Gillian spends time with her husband and dog, which they adopted when Gillian completed her dissertation fieldwork in 2017.