

STRESS AND AFFILIATION AMONG WILD FEMALE PRIMATES: EFFECTS OF  
GROUP SIZE, RISK, AND REPRODUCTIVE CONDITION IN A DYNAMIC FOREST  
COMMUNITY

By

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To Jim

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## LIST OF ABBREVIATIONS

AA	Aerial alarm
ACTH	Adrenocorticotrophic hormone
BGC	Between-group competition
CRH	Corticotropin-releasing hormone
F	Cortisol
FPS	Proximity score between a focal female and adult females without infants
FWI	Female with infant
FwiPS	Proximity score between a focal female and females with infants
GC	Glucocorticoid
h	Hour(s)
HPA axis	Hypothalamic-pituitary-adrenal axis
m	Meter(s)
min	Minute(s)
MPS	Proximity score between a focal female and adult males
ng/g	Nanograms per gram
RV	Raleighvallen, Suriname (the study site)
SE	Standard error
SPE	Solid-phase extraction
TFPS	Proximity score between a focal female and all adult females (i.e., FPS + FwiPS)
TPA	Terrestrial predator alarm
TPS	Proximity score between a focal female and all troop-mates (adult males, adult females and immatures)
WGC	Within-group competition

Abstract of Dissertation Presented to the Graduate School  
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By

Erin E. Ehmke

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Chair: Sue Boinski  
Major: Anthropology

My research examines the dynamics among social, ecological and reproductive challenges, affiliative behavior, and stress (as measured by fecal cortisol) of wild female brown capuchin monkeys in Raleighvallen, Suriname. In order to better understand if and how social affiliation is used to manage physiological stress, I first identify the socioecological variables that act as primary stressors to females in a high-risk, low-energy environment. Results indicate an adaptive function of differential group size, particularly within an unpredictable ecological landscape where the cost/benefit regime can shift quickly. The study period proved to be a beneficial time for the smaller group observed in that the larger group females experienced increased competition, reduced allogrooming, and higher cortisol levels. Perceived predation risk also varied according to group size and acted as a primary stressor to females.

I also focus on more fine-scaled dyadic social relationships and test the long-held assumption that capuchins are categorically a female-bonded genus. My results show that female bonding is not a static, species-specific characteristic, but rather a labile strategy reflecting ecological and reproductive parameters. Relationships, measured

through grooming and proximity patterns, between females were transient and occurred primarily in response to infant presence. Females were arguably more strongly bonded to adult males, and the alpha male in particular, possibly in an effort to acquire increased predator protection and tolerance at food resources. Finally, I investigate if female cortisol levels co-vary with shifts in their social relationships. Intriguing patterns emerge implicating the potential stress-reducing effects of strengthened relationships, particularly with male conspecifics.

My study explores (1) the interaction of social and ecological parameters that affect the daily lives and decision-making processes of wild primates, contributing to the understanding of emergent variability in social behavior among group-living animals, and (2) the association between stress and social behavior. Since chronic stress is detrimental to health and fitness, behavioral responses aimed at reducing stress, namely social bonding and investment, are adaptive and provide a mechanistic understanding of the evolution of sociality.

## CHAPTER 1 INTRODUCTION AND LITERATURE REVIEW

### **General Research Goal and Specific Objectives**

My research asks, what are the benefits of affiliation? As there are opportunity costs to social behavior, in what social, reproductive, and ecological circumstances do individuals strategically use social relationships? Specifically, I investigate if and how female primates use non-random affiliative behavior (i.e., social bonds) as a means to mediate or circumvent physiological stress.

The concept of social bonds is frequently (and abstractly) referred to, but the topic is rarely a direct focus of empirical study. Additionally, the term 'social bond' is an ambiguous one, further complicating its understanding and undermining its comparative value within biological systems. The goal of my dissertation is three-fold: (1) to provide an operational definition of social bond, one that can be replicated and studied in other systems; (2) to present data of comparative use; and (3) to test hypotheses regarding the proximate mechanisms and subsequent effects of female relationships.

To accomplish these goals, I use brown capuchin monkeys (*Cebus apella*) as my study system. *Cebus* is arguably the best-studied genus of New World non-human primates. The social, ecological, and reproductive lives of wild *C. apella*, however, became largely over-generalized as a result of research based at only a few field sites. My study site represents a little-studied ecosystem for brown capuchins, and as such, preliminary data indicate striking behavioral deviations from the expected norm. Further, there are no published reports regarding the endocrinological basis of (non-sexual) behavior within wild female *C. apella*.

In the following chapters, I examine the relationship between sociality, affiliation, and stress. In this introductory chapter, I review the physiology of stress, synthesize theory regarding primate socioecology, and discuss the prevalence and evolution of mammalian social bonds as well as the biological basis to and social functions of grooming behavior. I then introduce capuchin monkeys and briefly review what is known regarding the behavioral endocrinology of and affiliation among *Cebus* females.

## **Literature Review**

### **The Physiology of Stress and Its Measurement**

Stress is a complex physiological mechanism that integrates physiological and behavioral responses to any threat to homeostasis, whether real or perceived (Tilbrook and Clarke 2006). Over the short term, acute stress response is an adaptive condition whereupon energy is diverted from long-term processes such as digestion, growth, immune function, and reproduction and mobilized to meet short-term needs, thus increasing an individual's likelihood of surviving and re-establishing homeostasis. Over extended periods, however, the metabolic costs of sustained stress rise steeply (Sapolsky et al. 2000), adversely affecting female health and reproductive ability, fetal development and the development of offspring social skills, and stress-coping abilities (Sachser et al. 1998; Bardi et al. 2005; Sapolsky 2005; Shively et al. 2005; Wadhwa 2005). In humans, stress has been linked to numerous adverse conditions, including depression, anxiety, cancer, cardiovascular disease, diabetes and dementia (Charmandari et al. 2005).

When an individual is confronted with a stressor, be it intrinsic or extrinsic, the hypothalamic-pituitary-adrenal (HPA) axis is activated. Within seconds, corticotropin-releasing hormone (CRH) is produced in the hypothalamus and acts on

the central nervous system to signal acute stress; CRH then stimulates the anterior pituitary gland to produce adrenocorticotrophic hormone (ACTH), which in turn signals the adrenal cortex to secrete the glucocorticoids (GCs) - mainly cortisol (in primates, carnivores, and ungulates) or corticosterone (in rodents, birds, and reptiles) (Touma and Palme 2005). These GCs are steroid hormones that coordinate an individual's physiological and behavioral response to the stressor, acting to divert energy from long-term processes (e.g., digestion, growth, immune function and reproduction) into the mobilization of energy necessary to meet the demands of the challenge (Sapolsky et al. 2000). Glucocorticoids then provide a negative feedback mechanism by regulating the secretion of CRH and ACTH, thus down-regulating their own production (Tilbrook and Clarke 2006).

Steroid hormones are released as they are produced into the bloodstream where they then act on their target tissues. While blood plasma concentrations of GCs may be used as a measure or indicator of stress, such sampling is associated with numerous potential problems. Because of the pulsatile nature of GC secretion, plasma GC concentration can vary significantly within a matter of minutes and measure only a single point in time. GC production may also show diurnal rhythm patterns. These factors introduce dramatic inter- and intra-individual variation in plasma hormone concentrations at any given time and make the data difficult to interpret, especially on the individual level. Additionally, the restraint techniques necessary to obtain a blood sample are stressful on the animal, and thus the sampling methodology itself increases the immediate concentration of plasma GCs (Palme et al. 2005).

Fecal sampling is a feasible alternative for measuring GC concentration that offers significant advantages over blood sampling, with comparable results (Boinski et al. 1999b). A non-invasive technique, fecal sampling can be done with minimal disturbance to the animal, and the feces can be collected frequently and with (relative) ease. Further, circulating steroid hormones are metabolized extensively by the liver and excreted as conjugates (Palme et al. 2005), a process that effectively pools hormone levels over several hours and minimizes short-term hormonal fluctuations and rhythmic patterns (Goyman et al. 1999). Therefore, fecal corticosteroid metabolites provide a useful indicator of genuine and prolonged physiological stress responses (Boinski et al. 1999b). This process of metabolization and excretion necessitates a species-specific time lag which is related to the animal's intestinal transit time from duodenum to rectum (Touma and Palme 2005); in non-human primates, this lag time is typically less than 48 hours (Whitten et al. 1998): 22 hours in macaques (*Macaca fascicularis*), 24 hours in common marmosets (*Callithrix jacchus*), 26 hours in chimpanzees (*Pan troglodytes*) (Bahr et al. 2000), and 36 hours in yellow baboons (*Papio cynocephalus*) (Wasser et al. 2000).

Despite the acknowledged relationship between stress hormones and genetic, environmental and social factors (Touma and Palme 2005), variation is often controlled for in a laboratory environment. Thus, our understanding of stress and its relevancy for an animal in its natural environment is limited (Reeder and Kramer 2005). I now turn my focus to a review of the evolutionary relationship between an animal's natural environment and its social behavior.

## **Primate Sociality, Competition, and Social Structure: A Historic Perspective**

Acknowledgement of the inseparable link between an organism's ecological and social environment became widespread in the 1970s when empirical studies demonstrated that social structure varies with local ecological conditions (Eisenberg et al. 1972; Clutton-Brock and Harvey 1977; Lott 1984). At that time, the role of the male primate was emphasized, and female social behavior was largely overlooked. Since then, however, females have taken center stage, as it is generally accepted that the social and sexual strategies of females determine the behavioral strategies of males (Emlen and Oring 1977).

Wrangham (1980) developed the first ecological model of primate social behavior, emphasizing between-group competition (BGC) as the primary mechanism underlying the evolution of primate sociality. Strong BGC favors individuals that develop a social bond, facilitating cooperative displacement of rival groups from resources; this encouraged the development of philopatry, with one sex remaining in its natal group to maintain such cooperation through kinship and familiarity. As such, a female-bonded species was defined as one in which females form cohesive matrilineal groups characterized by affiliative interactions, such as proximity, grooming, and the formation of coalitions.

Van Schaik (1989) revised Wrangham's model of social evolution, arguing that predation is the mechanism by which sociality evolved. An increase in the number of collective individuals progressively increases the number of eyes scanning the environment for predators. Therefore, with an increase in group size, an individual's likelihood of survival improves, and anti-predatory vigilance effort required per individual decreases (Elgar 1989; Quenette 1990). Subsequent to the formation of groups,

within-group competition (WGC) became the determining factor in the development of social relationships, with females alleviating the costs of WGC through the formation of a linear dominance hierarchy and coalitionary support. Further, the term 'bond' was uncoupled from philopatry and became a more general condition characterized by affiliation and the formation of agonistic alliances.

### **Mammalian Social Bonds: A Review**

Fine-scaled analyses of the contextual and functional basis for mammalian social behavior are limited, largely, to primates (Kutsuskake 2009). Possibly because of this, female-bonded social systems are known to occur "only in isolated and rather exceptional cases among non-primates" (Shultz and Dunbar 2007, p. 2435). Further, little attempt has been made to define behavioral measures of social bonds in non-primates (Shultz and Dunbar 2007); for most non-primate taxa, however, the primate measures of allogrooming and proximity are cited and used as indices to signify bondedness.

Non-primate mammalian taxa in which differentiated, affiliative intrasexual adult relationships have been the focus of empirical study is largely limited to hyenas (*Crocuta crocuta*), elephants (*Loxodonta africana*), and horses (*Equus* spp.). Among hyenas, females associate more with same-sexed partners than do males (Smith et al. 2007). High-ranking females are more gregarious than low-ranking females (Holekamp et al. 1997; Smith et al. 2007), and subordinate females initiate associations more often than do dominant females (Smith et al. 2007). Further, *Crocuta* demonstrates potentially costly greeting ceremonies that are thought to serve a socially cohesive function, likened to that of grooming behavior among primates (Drea and Frank 2003), and dyadic greeting behavior follows the same patterns of association (East et al.

1993). In response, dominant females better tolerate those subordinates that initiate social interaction, providing them with more dependable access to food and reduced rates of aggression (Smith et al. 2007). Smith et al. (2007) suggested that female *Crocuta crocuta* minimize the costs of group living by directing affiliative social behavior towards outranking conspecifics that provide return benefits. Female elephants demonstrate stable, non-random patterns of social behavior, particularly within family units. Social relationships of non-kin, however, show temporal shifts, especially in response to seasonal changes in resource availability (Wittemyer et al. 2005). Among feral horses, social relationships between females involve preferred partners who allogroom and maintain proximity (Heitor et al. 2006; Cameron et al. 2009), and social bonds between females may be more important to the social stability of the group than are intersexual pair bonds (Curry et al. 2007). Cameron et al. (2009) found that, among unrelated females in a New Zealand population, more gregarious mares received less harassment from groupmates, which may explain the positive relationship between female social integration and reproductive success. These findings contrast with those of Heitor et al. (2006), who demonstrated that among feral horses in Portugal, mares with stronger affiliative relationships were not less aggressive towards one another, regardless of kinship.

Despite the presence of differentiated, dyadic social relationships in female hyenas, elephants, and horses, there exist fundamental differences in the social structures between these taxa and most primate taxa. Hyenas and elephants both have fission-fusion societies, not stable social groups that characterize the females of most primate species. The dynamics of constantly shifting sub-groups provide more flexibility

in partner choice decisions compared to individuals residing in more stable, cohesive social groups (Smith et al. 2007). In group living species with relatively stable compositions, the history of repeated social interaction between group members shape each dyadic (and polyadic) relationship, producing distinct selective pressures which cannot be observed in species with unstable group membership (Kutsukake 2009). Spider monkeys (*Ateles* spp.), one of the only primates to demonstrate a fission-fusion society, provide an ideal example as to the effects of such an unstable social system on individual social relationships. Female *Ateles* show a high level of association, but little selectivity in their association partners. In fact, females associate with one another no more than randomly expected. Instead of differentiated relationships, females passively aggregate in subgroups in response to ecological variables, such as the size and prevalence of particular food patches (Ramos-Fernandez et al. 2009).

Horses, by contrast, reside in stable social groups; both sexes disperse, however, and so females are not expected to develop and maintain the life-long female associations such as those observed in female-philopatric primates. This likely has profound effects on the mechanisms perpetuating social relationships. In squirrel monkeys (*Saimiri* spp.), for example, inter-specific variation in female dispersal patterns affects the strength and stability of female social relationships. In *S. boliviensis*, females are philopatric and form stable, linear dominance hierarchies and long-term social bonds. In *S. sciureus*, female dispersal is flexible (females may remain in natal group or emigrate), and as such, social behavior is rather erratic. Although females form stable, linear dominance hierarchies, severe aggression occurs more frequently and female-female coalitions are less common in *S. sciureus* than in *S. boliviensis*.

Finally, *S. oerstedii* is characterized by female dispersal. In response, females do not develop a dominance hierarchy, participate in coalitions, or form long-term social bonds (Boinski et al. 2002). In order to better understand the focus on primates in regards to social bonds, I next review the evolutionary and biological mechanisms underlying female bondedness.

### **Mammalian Social Bonds: An Evolutionary Perspective**

The evolutionary basis to social bonds is the mother-infant bond. The ontogeny of mammalian infants, both pre- and post-natally, requires extensive specialization on the part of the mother, e.g., placentation, lactation and intensive maternal care. To ensure successful nurturing of offspring, the maternal brain releases oxytocin, a neuropeptide hormone that facilitates milk let-down and olfactory recognition of offspring, stimulating the process of maternal bonding (Curley and Keverne 2005).

The development of other social relationships seems to be regulated by the pre-existing bonding mechanism (Curley and Keverne 2005). In small-brained monogamous mammals such as prairie voles (*Microtus ochrogaster*), the release of oxytocin also occurs post-mating, enabling the female to form an exclusive olfactory partner preference (i.e., an enduring pair bond) (Getz and Carter 1996; Cho et al. 1999; Sanchez-Andrade and Kendrick 2009). Thus, the biological mechanisms underlying bond formation in small-brained mammals are hormone-dependent and rely heavily on olfactory information; as such, their most significant social relationships are between mother and infant and between mating partners. Haplorhine primates (the monkeys and apes), however, diverged from the ancestral mammalian pattern of olfactory reliance and hormonally-facilitated social relationships (Curley and Keverne 2005).

The shift from a reliance on olfactory to visual cues is an important difference between haplorhine and other mammalian social bonding, and the higher cognitive functioning of primates enables complex social relationships to develop outside of hormonal priming. Even sexual behavior and parental care are less controlled by hormones in primates, as sexual interactions frequently occur in a non-reproductive context and post-partum care extends well beyond the period of lactation dependency. Such a release from hormonal determinants both enables alloparenting behavior and requires social learning of parental and social skills (Curley and Keverne 2005), and also expands the breadth of important adult relationships beyond mating partners (Dunbar 2009).

As the formation of social bonds among primates is more cognitive than physiological, primates must continuously reinforce their social bonds through affiliative group interactions. In order to sustain such a group dynamic, a physiological reward mechanism is required. Just as tactile stimulation (parturition and copulation) in small-brained mammals stimulates the release of oxytocin (Curley and Keverne 2005), the tactile stimulation of primate grooming initiates the release of the opioid neuropeptide,  $\beta$ -endorphin (Keverne et al. 1989). This mechanism of rewarding social interactions promotes the development of individual relationships (i.e., social bonds) among primates (Curley and Keverne 2005).

### **The Biological Basis of Grooming**

All primates groom (Shumaker and Beck 2003). This generalized characteristic of the order Primates, however, applies to hygienic (self) grooming (i.e., removal of ectoparasites, dirt) and not necessarily to grooming that provides a social function. For most primates, however, it is generally accepted that grooming is social (Schino 2001).

Social grooming provides biological and physiological benefits to the recipient in terms of ectoparasite removal (Zamma 2002), beta-endorphin release (Keverne et al. 1989), reduced stress (Schino et al. 1988; Engh et al. 2006a; Crockford et al. 2008; Wittig et al. 2008) and lower heart rate (Boccia et al. 1989; Aureli et al. 1999). Social grooming may also mediate reconciliation following an agonistic event (Leca et al. 2002) or increase tolerance around food resources (Barrett et al. 2002).

Allogrooming is the most commonly observed form of affiliation among primates (Di Bitetti 1997; Henzi and Barrett 1999). There are a few primates that do not commonly groom (aside from self-grooming and mother-infant interactions), such as orangutans (*Pongo* spp.), owl monkeys (*Aotus* spp.), squirrel monkeys (*Saimiri* spp.), muriquis (*Brachyteles arachnoides hypoxanthus*), and to a lesser extent spider monkeys (*Ateles* spp.). Orangutan females do not allogroom, although they may tolerate, rest, and maintain proximity with one another (Tobach and Porto 2006; Vogel 2008); their lack of physical affiliation may stem from their primarily solitary social structure. Owl monkeys, the only nocturnal anthropoid, rarely social groom. Moynihan (1964) described owl monkeys as grooming only before copulation, but Wright (1994) never observed grooming among wild owl monkeys, even before copulation. Owl monkey social behavior appears restricted by darkness, as play and aggression are most frequent during monthly lunar cycles when the moon is at its brightest (Wright 1994). Squirrel monkeys also rarely, if ever, engage in social grooming (Boinski 1994; Boinski et al. 2002), although they do engage in affiliative behavior known as huddling (Saltzman et al. 1991). Muriquis (a.k.a. woolly monkeys) do not groom (Strier 1992a), and the rate of grooming among spider monkeys is low, both in captivity and in the wild

(Ahumada 1992; Schaffner and Aureli 2005). This may be a result of their vestigial thumb, as their hand morphology does not provide the dexterity that primate grooming typically requires (Strier 1992a). Instead, spider monkeys and muriquis demonstrate affiliation by embracing, which is suggested to fulfill the same social functions (e.g., provide access to infants, increase tolerance, and reduce the risk of aggression) that grooming provides for other primate species (Strier 1992a,b; Strier et al. 2000, 2002; Schaffner and Aureli 2005; Slater et al. 2007).

Grooming is not unique to the primates. Hygienic grooming is common throughout the mammalian world and is observed frequently among rodents (Hawlena et al. 2008), felids (Eckstein and Hart 2000), equids (Rubenstein 1981), bovids (Mooring and Samuel 1998a; Hart and Pryor 2004; Kohari et al. 2009), and cervids (Hart and Hart 1992; Mooring et al. 1996; Mooring and Samuel 1998b). Although not as common, a few non-primate animal species demonstrate a social function to grooming as well. For example, among meerkats (*Suricata suricatta*), dominant females groom the dominant males more than subordinates, and thus grooming likely functions to maintain the sexual relationship between dominant (breeding) individuals. In terms of female-female grooming, subordinate meerkats focus on dominant females, and the duration of grooming is positively associated with frequency of aggression received from the dominant; therefore, intrasexual grooming among female meerkats may serve to placate the dominant individuals (Kutsukake and Clutton-Brock 2006; Madden and Clutton-Brock 2009). Grooming has also been shown to reduce social tension in horses (*Equus caballus*) (Feh and de Mazieres 1993). Among vampire bats (*Desmodus rotundus*), rates of social grooming correlate with rates of regurgitation (food sharing),

and thus is it likely that social grooming facilitates food-sharing either through honest indicators of body weight (i.e., identifying which individuals are in need of food and which are able to provide it) (Wilkinson 1986), or through the exchange of services such as ectoparasite removal for food sharing.

### **The Social Functions of Grooming**

Grooming may be used strategically as a commodity to be traded, as suggested above by meerkats, horses, and vampire bats. The grooming-for-aid hypothesis suggests that the benefits of grooming are exchanged directly for coalitionary support during inter- and intra-group competition. Since dominant individuals are expected to be more effective allies and therefore more attractive social partners, it is predicted that grooming should be directed up the hierarchy, with subordinate females competing to groom higher-ranking females (Seyfarth 1977). Empirical evidence supporting this hypothesis, however, is inconsistent and focused more on Old World monkeys (Sade 1972; Seyfarth 1977; Stambach 1978; Silk 1982; Seyfarth and Cheney 1984; Schino 2001). Conversely, several studies report the opposite trend, with grooming directed down the hierarchy, possibly as a means for the dominant female to secure support from subordinate females (O'Brien 1993; Linn et al. 1995; Di Bitetti 1997; Parr et al. 1997; Franz 1998; Henzi et al. 2003). Other studies found no link between dominance and grooming directionality (de Waal and Luttrell 1986; Thierry et al. 1990; Bernstein and Cooper 1999; Matheson and Bernstein 2000; Schino et al. 2009). Further, evidence supporting the direct relationship between grooming investment and coalitionary aid is minimal at best and often deemed circumstantial (Henzi and Barrett 1999; Silk et al. 2004; but see Schino 2007).

Grooming may also be exchanged for grooming itself (i.e., reciprocal grooming) (Silk et al. 1999; Payne et al. 2003; Schino and Aureli 2008; Fedurek and Dunbar 2009), as a means to gain access to infants (O'Brien 1993; Muroyama 1994; Perry 1996; Di Bitetti 1997; Manson et al. 1999; Henzi and Barrett 2002), to promote social and food-related tolerance (Kapsalis and Berman 1996; Ventura et al. 2006), and to establish, maintain, or repair social relationships (Stammbach and Kummer 1982; Dunbar 1996; Lehmann et al. 2007; Fedurek and Dunbar 2009).

The value of grooming as a commodity or currency varies not only by services rendered, but also by the individuals involved and the current socioecological milieu of the biological marketplace. In order to maximize one's return, an individual would be expected to direct affiliation towards those partners that potentially provide the most benefits. The benefits exchanged, however, need not be the same (i.e., animals may trade in different currencies), as individuals may vary in their ability to provide benefits of one type of currency over another.

Additionally, the value of different commodities varies depending on ecological conditions (Schino and Aureli 2008). For example, when the dominance hierarchy of a group is weakly expressed or enforced, grooming (a rank-independent currency) has greater value and is typically exchanged for grooming (Henzi et al. 2003; Schino and Aureli 2008). Under conditions of stronger WGC, however, dominance hierarchies become steeper and grooming reciprocation decreases (Barrett et al. 2002); instead, grooming becomes increasingly directed up the hierarchy (Ram et al. 2003) as other currencies, such as tolerance, become more valuable as exchange commodities for grooming. In a meta-analysis of grooming distribution among various primate taxa,

Schino and Aureli (2008) found a flexible trade-off between the exchange of grooming for rank-related benefits and the need to trade grooming for its more direct biological benefits.

Henzi and Barrett (1999) suggested that primate allogrooming provides great social significance based on evidence that the behavior was conserved in the presence of other demands. Dunbar (1991) determined that the social functions of grooming, however, primarily pertain to Old World primates based on data showing that their grooming rates correlated with group size, whereas grooming rates among New World monkeys were more associated (but not significantly) with body size. As the grooming behavior of New World monkeys has become more thoroughly studied, however, the demonstrated social functions of platyrrhine grooming are indeed comparable to that of catarrhines (O'Brien 1993; Perry 1996; Di Bitetti 1997; Schino 2007; Schino and Aureli 2008). In particular, the capuchin monkey (*Cebus* spp.) provides a study system unique to platyrrhines and more akin to catarrhine monkeys, thus bridging the gap between New and Old World primates (Parr et al. 1997).

### ***Cebus*: Ecologically Diverse, Socially Similar?**

Capuchin monkeys are one of the most widely distributed genera of New World primates, found throughout most of Central and South America. They inhabit a diverse range of habitats including tropical rainforest, swamp forest, and deciduous forest with seasonal, desert-like conditions (Fragaszy et al. 2004). Traditionally, the genus is composed of four species: *C. albifrons*, *C. apella*, *C. capucinus*, and *C. olivaceus* (Hill 1960). In recent years, however, the number of recognized species ranges from five to eleven, with much of the controversy focusing on species versus subspecies distinctions of *C. apella* (Fragaszy et al. 2004). For consistency with the majority of

published literature and to side-step the taxonomic confusion until much of the controversy is settled, I refer to the traditionally recognized species (Table 1-1).

*Cebus* spp. are best described as opportunistic and adaptable; in fact, their habitat-use patterns are so flexible that they defy species-specific characterization (Fragaszy et al. 2004). Adult social relationships, however, are typically described through assumed species norms. For example, all *Cebus* species are classified as strongly female-bonded (Janson and Boinski 1992; Fedigan 1993; O'Brien 1993; Perry 1996; Di Bitetti 1997), perhaps mostly because capuchins are generally female-philopatric but also because of strong female-female grooming patterns observed at a few field sites.

In a genus noted for its ability to adapt to diverse ecological conditions, should capuchin social behavior be generalized at the species level? The short answer: No. Recent findings from Brazil introduced a brown capuchin population that lacked female grooming bonds (Izar 2004), and preliminary observations of female *C. apella* in Suriname suggested both temporal and individual variation in intrasexual relationships (Boinski, unpublished data).

Further, despite a generalized tendency for female capuchins to prefer female grooming partners, there exists no inter- or intra-specific consensus on the value of grooming as a currency or how it is used strategically in the biological marketplace. The females in some groups groom up the hierarchy (Perry 1996), while in other groups females groom down the hierarchy (O'Brien 1993; Parr et al. 1997), and some females demonstrate no relation between grooming partner preference and rank (Manson et al. 1999; Schino et al. 2009). There also exists no clear relation between grooming and

coalitionary support (Perry 1996; Di Bitetti 1997; Manson et al. 1999; Schino et al., 2009), especially after controlling for rank and kinship. Schino et al. (2009) suggested that *Cebus* grooming behavior is so heterogeneous because of differences in group size and the varying number of matrilineal lines between groups. They proposed that grooming could be expected to be exchanged for agonistic support only when the group is comprised of more than two matrilineal lines (i.e., when mean relatedness is lower). Otherwise, in smaller groups, there is no opportunity for the exchange of grooming for support since females preferentially support close kin over nonkin. Therefore, while grooming may serve as a means to ensure agonistic support for some *Cebus* females, empirical data more consistently support the notion that grooming is a commodity to be traded for the benefits of grooming itself (Schino and Aureli 2008) and to gain access to young infants (O'Brien 1993; Perry 1996; Di Bitetti 1997; Manson et al. 1999).

The hormonal correlates of social behavior for wild brown capuchin females remain unknown. Published reports of *Cebus* behavioral endocrinology are scant and limited to *C. apella* males (Lynch et al. 2002), captive *C. apella* females (Linn et al. 1995; Carosi et al. 1999; Carosi and Visalberghi 2002; Lahoz et al. 2007), and wild *C. capucinus* females (Carnegie et al. 2005). In fact, female behavioral endocrinology has been studied only in terms of sexual behavior and reproductive physiology (Linn et al. 1995; Carosi et al. 1999; Carosi and Visalberghi 2002; Carnegie et al. 2005; Lahoz et al. 2007). To date, no report has been published on the dynamics of stress in terms of social and ecological variation for wild female *C. apella*.

### **Dissertation Overview: What Lies Ahead**

In the following four chapters, I empirically examine group- and individual-level hypotheses regarding sociality, affiliation, and physiological stress (Table 1-2). In

Chapter 2, I explore the costs and benefits of sociality in terms of differential group size, specifically addressing how predation risk, a seasonal environment and social behavior vary with group size. In Chapter 3, I examine the intrinsic effects (i.e., cortisol levels) of group size and test group-level hypotheses regarding the relationship between group size, female cortisol levels, predation risk, seasonality, and intragroup agonism. In Chapter 4, I study fine-scaled social relationships on the individual level and test hypotheses regarding the consistency of dyadic relationships between females (i.e., are the females truly bonded?). I also explore the relation between female social behavior, ecological pressures, and reproductive state. Finally, in Chapter 5 I examine the hormonal mechanisms driving sociality. Do individual females moderate incurred social and ecological stress by strategically adjusting their social relationships?

Table 1-1. Socioecological comparison of *Cebus* populations at various field sites.

	<i>C. apella</i> (Nouragues, French Guiana)	<i>C. apella</i> (Brazil)	<i>C. apella</i> (Iguazu, Argentina)	<i>C. apella</i> (Manu, Peru)	<i>C. apella</i> (Raleighvallen, Suriname)	<i>C. capucinus</i> (Lomas Barbudal, Costa Rica)	<i>C. capucinus</i> (Santa Rosa, Costa Rica)	<i>C. olivaceus</i> (Venezuela)	<i>C. albifrons</i> (Colombia)
Site description	Seasonal primary rainforest, mixed-habitat	Atlantic forest	Seasonal subtropical forest with bamboo patches	Seasonal lowland flood-plain	Highly seasonal & variable, mixed-habitat	Seasonal tropical dry deciduous forest	Seasonal tropical dry forest; limited water	Seasonal tropical dry deciduous forest	Gallery forest
Predation risk	n.a.	Low	Low	High	High	n.a.	n.a.	n.a.	n.a.
Resource competition	n.a.	High WGC and BGC	High WGC and BGC	High WGC, low BGC	High BGC; variable WGC	High WGC	n.a.	n.a.	n.a.
♀ dominance hierarchy	n.a.	tolerant	linear	n.a.	weakly linear	linear; stable	n.a.	stable; matrilineal	n.a.
♀-bonded (grooming patterns)	n.a.	no	yes	n.a.	no	yes	yes	yes	n.a.
Hierarchical grooming direction	n.a.	n.a.	down	n.a.	no trend	up	no trend	down	n.a.
♀-♀ grooming competition	n.a.	no	no	n.a.	no	no	no	no	n.a.
Published literature	Zhang 1995a,b; Zhang and Wang 1995, 2000	Izar 2004	Janson 1996; Di Bitetti 1997, 2001; Hirsch 2002	Janson 1985, 1988a,b, 1990a,b; van Schaik and van Noordwijk 1989	current study	Perry 1996; Manson et al. 1999; Vogel and Janson 2007; Vogel et al. 2007; Perry et al. 2008	Fedigan 1993; Manson et al. 1999	O'Brien 1991, 1993	Defler 1982

Notes: WGC: within group competition; BGC: between group competition; n.a.: data not available.

Table 1-2. Overview of dissertation chapters 2 to 5.

Chapter	Hypotheses
<p>2. The effect of group size on the social and ecological milieu of female brown capuchins.</p>	<ol style="list-style-type: none"> <li>1. Daily travel distance increases with group size.</li> <li>2. Individual foraging time in a preferred, monopolizable food tree decreases with increased group size.</li> <li>3. Predator alarm frequency (per individual) is inversely associated with group size.</li> <li>4. Rates of female agonism increase with group size; group size affects the strength of female dominance hierarchies.</li> <li>5. Rates of female grooming increase with group size.</li> <li>6. Female brown capuchins in a large troop demonstrate more seasonal variation in patterns of grooming and agonism than do the females in a small troop.</li> </ol>
<p>3. Group size and stress: The effects of a high risk, low energy environment on female brown capuchins.</p>	<ol style="list-style-type: none"> <li>1. Group size affects the level of stress females incur due to predation risk.</li> <li>2. Group size affects the levels of stress females incur during food shortages.</li> <li>3. Rank-related stress is a factor of group size.</li> </ol>
<p>4. Female-bonded primates? Grooming and proximity patterns of female brown capuchins in Suriname.</p>	<ol style="list-style-type: none"> <li>1. Social bonds between adult female brown capuchins are variable over time.</li> <li>2. Dyadic female relationships vary in response to ecological pressures.</li> <li>3. Relationships among females strengthen with the presence of an infant.</li> </ol>
<p>5. Do female brown capuchin monkeys use affiliative behavior to mediate stress?</p>	<ol style="list-style-type: none"> <li>1. Female cortisol levels are inversely associated with rates of affiliative behavior.</li> <li>2. Female cortisol levels vary with monthly variations in affiliation.</li> <li>3. Female cortisol levels vary with reproductive condition.</li> <li>4. Female reproductive condition affects affiliative behavior.</li> </ol>

## CHAPTER 2 THE EFFECT OF GROUP SIZE ON THE SOCIAL AND ECOLOGICAL MILIEU OF FEMALE BROWN CAPUCHINS

### **Introduction**

There is consensus that the benefits of sociality are accompanied by the costs of group living. Numerous studies of social animals investigate the various costs (e.g., increased intragroup competition, more conspicuous to predators) and benefits (e.g., improved intergroup competition, foraging benefits, better predator detection and defense) associated with group living, typically by comparing differences in behavior and reproductive success among groups of different size (van Schaik 1983; van Schaik and van Hooff 1983; Pulliam and Caraco 1984; Watts 1985; Cheney and Seyfarth 1987; Dunbar 1987; Janson 1988b; Robinson 1988; Isbell and Young 1993; Takahata et al. 1998; van Noordwijk and van Schaik 1999; Chapman and Chapman 2000; Krause and Ruxton 2002; Boinski et al. 2003; Keeling et al. 2003; Pride 2005a; Isvaran 2007; Silk 2007a; van Belle and Estrada 2008). The expectation is that individuals maintain membership in groups of favorable size to maximize fitness (Wrangham 1980); individuals resident to groups that are smaller or larger than optimal size, therefore, will reproduce less successfully than those living in intermediate-sized groups (Silk 2007a). What are the short-term ecological and social variables associated with group size that result in such a long-term fitness differential? This question is especially important for the females of female-philopatric species, as they tend to remain in their natal troop regardless of its size.

In this chapter, I test hypotheses regarding the costs and benefits of disparate group sizes using a familiar female-philopatric study species resident to one of the least studied biogeographic regions of the Neotropics. The brown capuchin monkey (*Cebus*

*apella*) is one of the most geographically diverse New World primates, and the species is well-known from populations studied in Peru and Argentina. Do the established brown capuchin “norms” hold true in an ecosystem characterized by a stringent and highly variable cost/benefit regime? Indeed, the two study groups on which my research is based are not of “optimal” size (i.e., intermediate (Silk 2007a)), but represent opposite ends of the continuum for group size (Table 2-1).

## **Hypotheses**

### **Daily Travel Distance Increases with Group Size**

The ecological constraints model, which predicts group size as a function of travel costs (Snaith and Chapman 2007), is based on the assumption that an increase in group size results in an increase of within-group resource competition (WGC). In response, the group may expand the area that must be searched in order for group members to acquire adequate nutritional intake (Eisenberg et al. 1972; Bradbury and Vehrencamp 1976; van Schaik et al. 1983a; Janson 1988a; Janson and Goldsmith 1995; Chapman and Chapman 2000; Ganas and Robbins 2005) until a point is reached at which travel costs exceed energetic returns from the environment, and smaller group size becomes advantageous (Chapman and Chapman 2000). Specifically for brown capuchins, Janson (1988a) found that of small groups, foraging efficiency (food ingested per unit distance traveled) was up to four times greater than that observed of large groups.

### **Individual Foraging Time in a Preferred, Monopolizable Food Tree Decreases with Increased Group Size**

Food patch size influences the degree to which individual foraging efficiency is affected by group size, as small patches are more quickly depleted with more

individuals feeding. Janson (1988a) found that, in large food patches, individual feeding time was not affected by group size, whereas in small patches, individual feeding time decreased with group size.

### **Predator Alarm Frequency (per individual) is Inversely Associated with Group Size**

Perceived predation risk affects an individual's foraging and social behavior (Chapman and Chapman 2000). Because an increase in group size increases the total amount of vigilance and likelihood of predator detection, individuals in larger groups are able to reduce the amount of time spent vigilant (Isbell and Young 1993; Isvaran 2007; Rieucou and Martin 2008) and spend more time foraging (Isvaran 2007), resting, or engaged in social behavior. The reverse may result, however, as small, cryptic groups may avoid predation more effectively than large, conspicuous groups (Terborgh 1983), and increased travel time and foraging effort characteristic of larger groups results in more occasions for exposure to predators (Janson and Boinski 1992).

### **Rates of Female Agonism Increase with Group Size and Group Size Affects the Strength of Female Dominance Hierarchies**

As intragroup competition is expected to increase with group size, it follows that rates of aggression and displacement increase with group size (van Schaik et al. 1983a) as has been empirically demonstrated (Kondo et al. 1989; Keeling et al. 2003). The presence of a dominance hierarchy, however, is widely believed to reduce intra-group aggression (Hemelrijk 1999), as individuals "know their place" and aggression is ritually, rather than physically, expressed. Among farm animals, for example, aggressive behavior in large groups diminished with the presence of established dominance relationships (Rodenburg and Koene 2007). Perry et al. (2008) showed, however, that among white-faced capuchins (*C. capucinus*), the social behavior of females in small

groups was more affected by dominance rank than was the social behavior of females in large groups.

### **Rates of Female Grooming Increase with Group Size**

Females in larger groups may either intensify grooming in order to maintain social cohesion (Cowlshaw and Dunbar 1991), or (2) be constrained in the time available for grooming due to increased travel and foraging effort necessary to off-set increased intragroup competition within a large group (Dunbar 1988). For Old World primate species, most studies agree that there is a positive correlation between time spent grooming and group size (Dunbar 1988; Cowlshaw and Dunbar 1991; Isbell and Young 1993; Lehmann et al. 2007). For New World monkeys, however, the association between group size and grooming is inconsistent. O'Brien (1993) reported that, similar to catarrhines, grooming frequency among female *C. olivaceus* was affected by group size, with females in a large group involved in more grooming than females in a small group. He suggested that the reduced social complexity (fewer matriline and higher degree of relatedness) of small groups resulted in decreased competition and thereby decreased female grooming. However, Manson et al. (1999) found no relationship between *C. capucinus* group size and dyadic female grooming rates.

### **Female Brown Capuchins in a Large Troop Demonstrate More Seasonal Variation in Patterns of Grooming and Agonism than Do the Females in a Small Troop**

For most New World monkeys, the proportion of time invested in grooming and other social behaviors is seasonally variable (Di Bitetti 1997; Freese and Oppenheimer 1981; Kinzey and Wright 1982; O'Brien 1993), due mostly to variation in food availability and the opportunity cost of increased foraging effort (Terborgh 1983; Janson 1988a). Variation in resource availability is most likely to affect groups characterized by WGC

(i.e., larger groups); therefore, individuals resident to larger groups must vary their social strategies in response to ecological variation.

## Methodology

### Site Description

The Guianan region, comprised of French Guiana, Suriname and Guyana, is a little-studied region of South America. This biogeographic area is a dynamic environment with intense annual and seasonal variation. Additionally, the Guianan soils are nutrient-poor and highly weathered as they are derived from Precambrian bedrock (Norconk et al. 1996). The study site was located in Raleighvallen (RV), Suriname, a 7812 km<sup>2</sup> reserve consisting of primary tropical rain forest in the 1.6 million ha Central Suriname Nature Reserve. The main study site measured approximately 2 km<sup>2</sup> and was covered by an extensive trail system. RV's flora and fauna are effectively undisturbed in the historical period, and an intact array of potential predators and competitors are present (Reichart 1993). Much of RV is composed of expansive bamboo patches and dense liana forest that restricts visibility (Boinski et al. 2003). Fleshy fruits are low in abundance and available fruit resources typically occur in small patches (<5 m diameter) (Boinski et al. 2002). One palm species, *Maximiliana maripa*, is particularly important to the food competition regime of *C. apella* in RV. From December through June, this fruit tree provides a high quality resource (rich in digestible proteins, lipids, and carbohydrates) in dense, small clusters (<1 m diameter) (Boinski 1999). A troop may feed in a single *M. maripa* cluster for several hours, during which intra-group competition intensifies and dominance interactions are prevalent.

## Study Animal

The brown capuchin monkey (*Cebus apella*) is one of the four traditionally recognized species in the genus *Cebus* (Hill 1960). Capuchins live in multi-male, multi-female polygamous groups that are typically female philopatric. Adult males and females maintain separate dominance hierarchies; in general, males are dominant to females. *C. apella* social groups are comprised of 12 to 27 individuals, with an average troop size of 17 members. Troop membership and relationships remain relatively stable, except for subadult males who emigrate from their natal group and may subsequently transfer several times. Brown capuchins reside in a variety of habitats encompassing a large geographic range from Columbia to Argentina (Fragaszy et al. 2004). *C. apella* are omnivores and arguably the most labile generalists of New World monkeys. The bulk of their diet consists of fruit supplemented with seeds, vegetation, arthropods, and vertebrates (Terborgh 1983).

Study troops A and B were two of four brown capuchin groups commonly observed within the study site, and the primary study subjects were the 10 adult females resident to these two groups. For most of the study, Troop A consisted of 27 individuals, seven of which were adult females; Troop B consisted of nine individuals, three of which were adult females. During the study, one pregnant female disappeared from Troop A (her disappearance coincided with her predicted due date, and thus it is possible her death was related to giving birth), and two females disappeared from Troop B (cause unknown) (Table 2-2). Relatedness among the adult troop members is unknown; however, genetic analysis of the brown capuchin population in RV is currently underway. The study troops had been habituated to human observers since 1998, and all individuals were recognized based on body size, color patterns, and other identifying

characteristics such as scars, moles, and ear shape. Throughout the study period, inter-observer reliability tests were conducted monthly to ensure consistent and accurate identification of all troop members.

### **Data Collection**

From January to December 2006, I and/or field assistants followed Troop A for up to 10 h each day, beginning at sunrise. Troop A was followed, on average, 28 days per month, composing a total of 2284 h of observation (not including 'out of view' time). I followed Troop B, on average, 8 days per month, composing a total of 495 h of observation (not including 'out of view' time).

General group characteristics such as troop location, travel distance, foliage cover, dispersion, height in canopy, and diet were collected via group scans at 15-min intervals. These data provided comparison of the troop-level characteristics of the females in Troop A with the females in Troop B. Each group's total daily travel distance was calculated using a grid of 50 m<sup>2</sup> quadrants overlaying a map of the study site.

*Cebus apella* social behavior (agonistic, grooming, and sexual) accounts for a small fraction, 1% (Pollard and Blumstein 2008); <10% (Zhang 1995a), of their daily activity budget. Therefore, *ad libitum* sampling (Altmann 1974) provided a more efficient and complete data collection technique for capturing social interactions than did a more structured sampling regime. To reduce observation bias, I moved constantly through the groups to locate non-visible individuals and record their activities. Due to opportunistic sampling, as well as the reduced visibility within the RV forest, the recorded frequencies of social behavior are likely underestimates of the true frequencies. Because of the large number of hours over which behavioral interactions

were recorded, however, I am confident that the data provide strong indication of underlying patterns.

Grooming and agonistic behaviors (Table 2-3), as well as other opportunistic occurrences such as predator interactions, were noted *ad lib*. Only agonistic and grooming bouts involving at least one female (as actor or recipient) and where both participants could be identified (at least to the age and sex class) were included for analysis. All bouts were counted as dyads: If two monkeys were grooming the same individual concurrently, the episode was scored as two actor-recipient grooming bouts; if agonism involved a coalition against a third party, only the initial instigator and victim were scored. Agonism and grooming involving females in estrus (as actors or receivers) were not included in analysis to preclude confounding a female's interest in social partners with her sexual interests (an obvious bias towards males).

## **Data Analysis**

### **Behavioral rates**

Data were grouped into monthly and seasonal averages, as follows: fruiting season (February to April), wet season (May to July), dry season (August to October), and transition season (November to January). To control for differences in troop size when comparing behavioral rates of the females in Troop A with the females in Troop B, *M. maripa* feeding, alarm calls, grooming, and agonism were expressed as rates per individual, assuming all individuals were equal. Although such an assumption does not reflect reality since dyadic interactions and feeding rates were likely affected by intragroup dominance relationships, the assumption was applied to both troops and simply acted as a control for differences in group size and composition.

*M. maripa* feeding rates (min/h) and alarm call rates (# alarms/h) were expressed at the troop- and individual-level. Alarm calls were often only heard and could not be ascribed to a particular individual; similarly, *M. maripa* feeding sessions were chaotic and characterized by high turn-over rate and discontinuous feeding by individuals. Further, the fruiting clump was often at least partially obscured from view making accurate identification of feeders difficult. Therefore, I calculated rates of alarm calls and *M. maripa* feeding to describe the 'average' individual based on the number of active group members. When calculating the average rate of *M. maripa* feeding per individual (min/h/individual), I included only the number of adults and subadults in the troop to form the denominator, as WGC was likely most intense and reciprocal between these individuals. The alarm vocalizations of *Cebus apella*, aerial alarms (AAs) and terrestrial predator alarms (TPAs), are audibly distinct (Boinski et al. 1999). When calculating the rate of AAs and TPAs per individual (alarms/h/individual), the number of adults, subadults, and juveniles comprised the denominator.

Female agonism and grooming rates, in comparison, were calculated to control for the number of females in each group, assuming all females equally participate in agonistic and grooming interactions. In essence, the 'average' Troop A female was compared to the 'average' Troop B female. Female agonistic rates were expressed as # bouts/h/female, with bouts involving females as actor and females as recipient calculated separately. Female groom rates were expressed as min/h/female, with bouts involving females as actor and females as recipient calculated separately.

### **Dominance hierarchy**

For both troops, female ranks were determined by the outcomes of decided female-female agonistic episodes. All agonistic bouts were categorized as either

'decided' or 'undecided'. I considered an agonistic bout as 'decided' if (1) identities of participants were known, and (2) one individual displayed only aggressive signals whereas the other only displayed submissive behavior, or (3) one individual displayed submissive signals, whereas the other individual displayed no agonistic behavior. All other disputes were considered to be 'undecided' (Silk et al. 2006a). Dyadic agonistic bouts between females were constructed into a dominance matrix to determine the hierarchical nature of female relationships (Ferreira et al. 2006).

### **Statistical analysis**

Non-parametric analyses were used because data failed to meet the assumption of normality, even after logarithmic transformation. Homoscedasticity was tested using Levene's Test for Equality of Variances; if Levene's test indicated heterogeneous variances, I used square root transformations. I used the Mann-Whitney U test when comparing two independent samples (Troops A and B) and the Wilcoxin sign-rank tests for comparing two related (intragroup) samples. When comparing more than two samples, the Kruskal-Wallis one-way ANOVA was used in conjunction with Mann-Whitney U tests as the non-parametric posthoc test. To investigate whether an observed frequency distribution fit an expected one, I used the Chi-square goodness of fit test. Analyses were performed using SPSS 11.0; the significance level for all tests (two-tailed) was set at 0.05. Mean values are presented with standard error values.

## **Results**

### **Group Size, Home Range and Habitat Use**

The RV forest is composed of four habitat types: (1) expansive, dense bamboo patches (the bamboo patch primarily utilized by Troops A and B is approximately 400 m by 200 m, centrally located within Troop A's home range and on the southern border of

Troop B's home range), (2) high forest, (3) liana/low forest, and (4) swamp. The home range of Troop A, roughly 700 m<sup>2</sup> in size, is dominated by high forest (54%) with liana/low forest comprising the secondary habitat type (28%); similarly, the home range of Troop B, roughly 500 m<sup>2</sup> in size, is mostly composed of high forest (44%) and liana/low forest (43%) (Figure 2-1).

Although bamboo forests represent only 13% of Troop A's home range (Figure 2-1), the group spent the most time (37% overall) in this habitat type, significantly more often than did Troop B ( $X^2 = 177.88$ ,  $P < 0.001$ ) (Figure 2-2). Seasonal comparison further demonstrates their heavy use of the bamboo patches: In every season except the fruiting season, Troop A spent the most time in the bamboo, most notably during the dry season (Figure 2-3). Troop B, however, spent most of their time, significantly more often than Troop A ( $X^2 = 63.86$ ,  $P < 0.001$ ) in the liana/low forest (49%) (Figure 2-2), a pattern that holds true for every season except the transition season. Their use of the high forest remained relatively consistent throughout the seasons while their use of the bamboo was more variable, peaking in the transition season (Figure 2-4).

Canopy cover was estimated on a scale from 0 to 3 with 0.5 increments such that the score increased with vegetation density (Boinski et al. 2003). Mean cover ( $\pm$  SE) for Troop A and Troop B during the study period was  $2.41 \pm 0.03$  and  $2.34 \pm 0.02$ , respectively. Seasonal cover was similar between the troops, with the largest differential of 0.20 during the dry season (Figure 2-5); there were no statistically significant differences in seasonal cover within or between troops. Canopy cover varied by habitat, with the bamboo providing the most cover to both troops (Figure 2-6); there were no statistically significant differences in habitat cover within or between troops.

## **Group Size, Density and Variation in Travel Distance**

Troop A maintained an average troop dispersion (mean  $\pm$  SE) of  $52.1 \pm 0.4 \text{ m}^2$  with a density of 0.4 monkeys/m or 2.3 m/individual (not including infants) within their daily range. Troop B maintained an average troop dispersion (mean  $\pm$  SE) of  $36.5 \pm 0.9 \text{ m}^2$  with 0.2 monkeys/m or 4.1 m/individual within their daily range.

Troop A spent approximately 65% of their day traveling (vs. stationary) and traveled, on average, a daily distance (mean  $\pm$  SE) of  $1,370 \pm 29 \text{ m}$  (171 m/h). Troop B spent approximately 55% of their day traveling (vs. stationary) and traveled a daily distance (mean  $\pm$  SE) of  $998 \pm 44 \text{ m}$  (159 m/h). Time of day did not greatly impact either troop's travel activity budget (Figure 2-7). Troop A traveled the most (70%) during the afternoon hours (2 to 5 p.m.) as compared to their morning (7 to 11 a.m.) travel (63%) and mid-day (11 a.m. to 2 p.m.) travel (62%). Troop B traveled the most (68%) during the mid-day as compared to the morning (62%) and afternoon (55%). Both troops traveled the most during the transition season and the least during the wet season. Troop A's daily travel rate (m/h) was significantly higher than Troop B's daily travel rate ( $Z = -2.09$ ,  $P = 0.037$ ,  $n_A = 311$ ,  $n_B = 86$ ). This difference, however, was seasonally based; Troop A's daily travel rate was significantly higher than Troop B's daily travel rate during the fruiting season ( $Z = -3.808$ ,  $P < 0.0001$ ,  $n_A = 79$ ,  $n_B = 21$ ), but not during the wet ( $Z = -1.255$ ,  $P = 0.210$ ,  $n_A = 87$ ,  $n_B = 28$ ), dry ( $Z = -1.125$ ,  $P = 0.261$ ,  $n_A = 88$ ,  $n_B = 27$ ), or transition ( $Z = -0.158$ ,  $P = 0.874$ ,  $n_A = 57$ ,  $n_B = 10$ ) seasons (Figure 2-8).

## **Group Size and Variation in *Maximiliana maripa* Feeding**

During the months in which *Maximiliana maripa* fruited (February to July, with sporadic fruiting clusters in September and November), Troop A spent a total of

127.7 observed hours feeding on *M. maripa* (> 7% of total activity budget), with peak feeding rates in May and June (19% and 13% of monthly activity budget, respectively). On average ( $\pm$  SE), Troop A spent  $4.4 \pm 1.3$  min/h per month in a *M. maripa* tree. Troop B spent a total of 31.2 observed hours feeding on *M. maripa* (> 8% of total activity budget), with a peak feeding rate in June (17% of monthly activity budget). On average ( $\pm$  SE), Troop B spent  $5.7 \pm 1.2$  min/h per month in a *M. maripa* tree. There was no significant difference between Troop A and Troop B in the monthly troop rate (min/h) of *M. maripa* feeding ( $Z = -1.033$ ,  $P = 0.345$ ,  $n_A = 8$ ,  $n_B = 6$ ). After controlling for group size, however, Troop B individuals (adults and subadults) had a significantly higher monthly *M. maripa* feeding rate (mean  $\pm$  SE =  $1.26 \pm 0.27$  min/h per individual) than did Troop A individuals (mean  $\pm$  SE =  $0.37 \pm 0.10$  min/h per individual) ( $Z = -2.324$ ,  $P = 0.02$ ,  $n_A = 8$ ,  $n_B = 6$ ).

### **Group Size and Variation in Alarm Calls**

A Harpy Eagle (*Harpia harpyja*) nest is located within the study site, and the nest's residents are the major aerial predators to the primate population in RV (Boinski et al. in prep). The study period was a non-reproductive year for the Harpy Eagles, however, possibly because of extensive flooding that occurred during the wet season. The adult Harpy Eagles were still present in the area and observed to actively hunt, although at a reduced frequency compared to years when nestlings were present (Boinski et al. in prep). A Harpy Eagle was observed near Troop A 5 times throughout the year and detectable near Troop B on 2 occasions. No successful predation was observed.

On average, Troop A produced AAs at a monthly rate (mean  $\pm$  SE) of  $0.62 \pm 0.06$  alarms/h, while Troop B produced AAs at a rate of  $0.66 \pm 0.14$  alarms/h. There was no significant difference between Troop A and Troop B in their monthly AA rates ( $Z =$

-0.577,  $P = 0.590$ ,  $n_A = 12$ ,  $n_B = 12$ ). After controlling for group size, however, Troop B individuals (adults, subadults and juveniles) produced significantly higher AA rates (AA/h per individual) than Troop A individuals ( $Z = -3.385$ ,  $P=0.00$ ,  $n_A = 12$ ,  $n_B = 11$ ) (Figure 2-9). The increased AA rate produced by Troop B individuals may have been a repercussion of height in canopy, as Troop B had a significantly higher 'upper height limit' as compared to Troop A (mean  $\pm$  SE =  $12.23 \pm 0.29$  m and  $10.97 \pm 0.21$  m, respectively) ( $Z = -3.510$ ,  $P < 0.0001$ ,  $n_A = 228$ ,  $n_B = 78$ ). There were no statistical intra- or inter-group seasonal differences in AA rates; both troops produced AAs at the highest rate during the transition season (Figure 2-10). After controlling for group size, however, the average individual in Troop B produced AAs at a nearly significant ( $P = 0.05$ ) higher rate than did the average (non-infant) individual in Troop A during the fruiting, dry, and transition seasons but not during the wet season (Figure 2-11).

Encounters between terrestrial predators and the *C. apella* study troops were infrequent, possibly due to the presence of human observers. Both Troop A and Troop B produced AAs at a significantly higher monthly rate than TPAs (Troop A:  $Z = -3.059$ ,  $P = 0.002$ ,  $n = 12$ ; Troop B:  $Z = -3.059$ ,  $P = 0.002$ ,  $n = 12$ ). There was one definite instance of a jaguar (*Panthera onca*) within range of Troop A. The cat, however, already had a kill (undeterminable species) and did not appear interested in the capuchins. One jaguar attack on the troop was suspected, but cannot be confirmed as it occurred 'out of view' in a stand of bamboo. There were no observed encounters between Troop B and a terrestrial predator.

Troop A produced significantly higher monthly TPA rates (mean  $\pm$  SE =  $0.17 \pm 0.03$  TPA/h) than Troop B (mean  $\pm$  SE =  $0.07 \pm 0.02$  TPA/h) ( $Z = -2.541$ ,  $P = 0.01$ ,  $n_A =$

12,  $n_B = 12$ ). After controlling for group size, however, there was no significant difference between Troop A's and Troop B's individual rate of TPAs (TPA/h per individual) ( $Z = -0.202$ ,  $P = 0.843$ ,  $n_A = 12$ ,  $n_B = 12$ ) (Figure 2-9). The increased TPA rate produced by Troop A may have been a repercussion of proximity to the ground, as Troop A had a significantly lower 'lower height limit' as compared to Troop B (mean  $\pm$  SE =  $4.95 \pm 0.16$  m and  $6.50 \pm 0.22$  m, respectively) ( $Z = -5.727$ ,  $P < 0.0001$ ,  $n_A = 228$ ,  $n_B = 78$ ). There was an effect of season on group TPA rates: Both troops produced TPAs at the highest rate during the transition season, and Troop A produced TPAs at a (nearly) significant higher rate than Troop B during this time (Figure 2-12). After controlling for group size, however, there were no statistical intra- or inter-group differences in individual TPA rates by season (Figure 2-13).

### **Group Size and Variation in Female Agonism**

I recorded 875 agonistic bouts among Troop A members (0.38 bouts/h), 676 of which (77%) were classified as decided bouts (i.e., a clear 'winner' and 'loser' were differentiated). Adult females were responsible for 137 bouts of agonism towards conspecifics (72% food-related), and females received 129 bouts of agonism (90% food-related) (Table 2-4). I recorded 41 agonistic bouts among Troop B members (0.08 bouts/h), 29 of which (71%) were classified as 'decided' bouts. Adult females were responsible for 4 bouts of agonism towards conspecifics (25% food-related), and females received 3 bouts of agonism (100% food-related) (Table 2-4). For both Troops A and B, there was no significant difference in the daily rate of intragroup agonism that females gave versus received (Troop A:  $Z = -0.755$ ,  $P = 0.450$ ,  $n = 300$ ; Troop B:  $Z = -0.169$ ,  $P = 0.866$ ,  $n = 86$ ). In comparing monthly rates of Troop A female agonism with rates of Troop B female agonism (after controlling for the number of females in

each group), Troop A females gave significantly more agonism (bouts/h per female) than Troop B females ( $Z = -2.906$ ,  $P = 0.004$ ,  $n_A = 12$ ,  $n_B = 12$ ). Similarly, Troop A females received significantly more agonism (bouts/h per female) than Troop B females ( $Z = -3.326$ ,  $P = 0.001$ ,  $n_A = 12$ ,  $n_B = 12$ ) (Figure 2-14).

Within Troop A, agonism between females accounted for 6.8% of aggression, 19.5% of displacements, and 10.5% of submission (Table 2-4). Food-related agonism comprised 82% of ♀-♀ agonism, while 11% were of unknown context and 7% involved the alpha female threatening estrus females near the alpha male. Based on the outcomes of these agonistic bouts, the transitivity property, and anecdotal evidence (Chapter 3), it was possible to extrapolate a linear (although weak) dominance hierarchy for Troop A females (Table 2-5). The hierarchy could not be tested statistically because of small sample size (too few dyadic dominance interactions). Within Troop B, there was no observed agonism between females (Table 2-4). Therefore, it was not possible to derive a dominance hierarchy.

Coalitions among Troop A members that involved at least one female occurred at a rate of 0.02 coalitions/h. The primary target of these coalitions was a human observer (44.7%). Troop-mates were the second most frequent target of coalitions (38.3%), and coalitions involving the mobbing of another animal species (e.g., tayra, tamandua) comprised 17% of coalitions. Coalitions within Troop B that involved at least one female occurred at a rate of 0.07 coalitions/h. The primary target of these coalitions was a human observer (87.9%). Mobbing of another animal species comprised the remainder of the observed coalitions (12.1%); Troop B members were never observed to form a coalition against a troop-mate.

## Group Size and Variation in Female Grooming

I recorded 1574 dyadic grooming bouts (with known direction and participants) between Troop A members (0.69 bouts/h). Of the 1013 bouts that involved at least one female (64% of troop grooming), a female acted as the groomer in 817 bouts (81%) for a total duration of 1937.7 min, and as the recipient in 371 bouts (37%) for a total duration of 755.1 min. Females in Troop A gave a significantly higher rate (min/h) of grooming than they received ( $Z = -3.059$ ,  $P = 0.002$ ,  $n = 12$ ). I recorded 363 dyadic grooming bouts (with known direction and participants) between Troop B members (0.73 bouts/h). Of the 202 bouts that involved at least one female (56% of troop grooming), a female acted as the groomer in 141 bouts (70%) for a total duration of 303.6 min, and as the recipient in 93 bouts (46%) for a total duration of 143.9 min. Females in Troop B gave a significantly higher rate (min/h) of grooming than they received ( $Z = -2.353$ ,  $P = 0.019$ ,  $n = 12$ ).

Overall, Troop A had significantly higher daily rates (min/h) of female grooming (given) than did Troop B ( $Z = -3.448$ ,  $P = 0.001$ ,  $n_A = 300$ ,  $n_B = 86$ ), although there was no significant difference between the troops' daily rates of female grooming received ( $Z = -1.423$ ,  $P = 0.155$ ,  $n_A = 300$ ,  $n_B = 86$ ). After controlling for the number of females in each group, however, there was no difference between Troop A and Troop B in the monthly rate (min/h per female) of female grooming given ( $Z = -0.462$ ,  $P = 0.671$ ,  $n_A = 12$ ,  $n_B = 12$ ) or received ( $Z = -0.058$ ,  $P = 0.977$ ,  $n_A = 12$ ,  $n_B = 12$ ). In fact, although not statistically significant, Troop B females both gave and received higher monthly rates of grooming than did Troop A females (Figure 2-15). Further, of the grooming that occurred among adults (♀-♀ and ♂-♀), 51% of the dyads in Troop B were reciprocal, whereas only 30% of the adult grooming dyads in Troop A were reciprocal.

## Group Size and Seasonal Variation in Social Behavior

Troop A females had the highest average rate of grooming (given and received) during the fruiting season (February to April), the time of year that corresponded not only to fleshy fruit availability but also to the presence of young infants. While there was no significant seasonal variation in the rates at which females groomed troop-mates ( $H = 4.443$ ,  $df = 3$ ,  $P = 0.217$ ), there was significant seasonal variation in the rates at which females received grooming ( $H = 20.089$ ,  $df = 3$ ,  $P < 0.0001$ ). Specifically, females received more grooming during the fruiting ( $Z = -4.161$ ,  $P < 0.0001$ ) and wet ( $Z = -3.722$ ,  $P < 0.0001$ ) seasons than during the dry season.

Females in Troop A had the highest average rate of agonism (given and received) during the wet season (May to July), the time of year that corresponded to the peak fruiting of *M. maripa*. In fact, during the wet season, 55% of the 'decided' agonistic bouts involving at least one female occurred in a *M. maripa* tree. There was significant seasonal variation in the rates at which females gave ( $H = 15.596$ ,  $df = 3$ ,  $P = 0.001$ ) and received ( $H = 23.843$ ,  $df = 3$ ,  $P < 0.0001$ ) agonism. Females both gave and received significantly more agonism during the fruiting ( $Z = -2.480$ ,  $P = 0.013$ ;  $Z = -3.666$ ,  $P < 0.0001$ , respectively) and wet ( $Z = -3.468$ ,  $P = 0.001$ ;  $Z = -4.729$ ,  $P < 0.0001$ , respectively) seasons than during the dry season, and females also gave ( $Z = -2.551$ ,  $P = 0.011$ ) and received ( $Z = -2.094$ ,  $P = 0.036$ ) significantly more agonism during the wet season than during the transition season.

Regarding Troop B, there was no discernable association between seasonality and variation in female social behavior. Only the rate at which females groomed conspecifics significantly varied by season ( $H = 8.326$ ,  $df = 3$ ,  $P = 0.040$ ): The average daily rate that a Troop B female groomed troop-mates was significantly higher during

the transition season than during the wet ( $Z = -2.529$ ,  $P = 0.021$ ) and dry ( $Z = -2.405$ ,  $P = 0.031$ ) seasons, but this difference was due solely to an exaggerated grooming rate (12 times the average) performed by the troop's only remaining female during the month of November.

## **Discussion**

The results of this chapter indicate that, based on the variables studied, the females in the smaller troop received more of the benefits of sociality, while the females in the larger troop incurred more of the costs (Table 2-6). Below I discuss the outcome of each hypothesis, considering each variable of study and how it relates to the cost/benefit regime of sociality for brown capuchins in Raleighvallen, Suriname.

### **Daily Travel Distance Increases with Group Size**

This hypothesis is supported and demonstrates a cost of larger group size. Overall, the daily travel rate (m/h) was significantly higher for Troop A than for Troop B. In response to increased WGC, a social group may increase their spread (thereby reducing the number of animals per unit of foraging space) or foraging effort in time and/or space (daily travel rate) (Snaith and Chapman 2007). Troop A employed both mechanisms, indicating a considerable effect of larger group size on the intensity of WGC. While Troop B maintained an average spread of 37 m<sup>2</sup>, Troop A increased their average spread to 52 m<sup>2</sup>. Despite this increase in area, however, the intragroup density for Troop A was still two-fold that of Troop B. In terms of daily travel rate, Troop A traveled farther and faster and rested less than the smaller Troop B.

In further support of the ecological-constraints model (Chapman and Chapman 2000), the difference between Troops A and B in their daily travel rate was most pronounced during the fruiting season when the production of fleshy fruit was at its

peak. In RV, these fruit resources mostly occur in small clumps (Boinski et al. 2002). In response to increased WGC that comes with larger group size, Troop A must search a larger area to ensure adequate nutritional intake for its members.

In the dry season, however, Troop B actually demonstrated a higher daily travel rate than Troop A. During this time of year, fruit production is low, foliage cover is reduced (increasing the monkeys' exposure to aerial predators) and the monkeys rely heavily on the protection and food resources (bamboo shoots and insects) provided by expansive, dense bamboo patches (Boinski et al. in prep). The importance of the bamboo patches is evident in the increased number and intensity of intergroup encounters that occur within this habitat during the dry season (Ehmke et al. in prep). The primary bamboo patch in the study site is approximately 200 m by 100 m and is centrally located within Troop A's home range. It was not uncommon, especially during the dry season, for Troop A to enter this bamboo patch and remain within its perimeter for the entire day. The same bamboo patch is also accessible to Troop B along the southern border of their home range, but they were often displaced from this resource by the larger Troop A and forced to travel in search of safety and/or food elsewhere. Thus, just as large-group females appear to be at a disadvantage during the fruiting season, small-group female *C. apella* in RV appear to receive a cost of reduced group size during the dry season.

Both troops traveled the most during the transition season, a time of year when food resource availability is unpredictable and highly variable from year to year. Based on the similarity in the troops' daily travel rates during this time, such unpredictability in food supply appears to lessen the effect of differential group size.

### **Individual Foraging Time in a Preferred, Monopolizable Food Tree (*Maximiliana maripa*) Decreases with Increased Group Size**

This hypothesis is supported and demonstrates a cost of larger group size.

Overall, Troop B spent more time than Troop A feeding on *M. maripa* fruits, and Troop B individuals (adults and subadults) had a significantly higher monthly rate of *M. maripa* feeding than did Troop A adults and subadults. As with Hypothesis 1, this finding supports the ecological-constraints model such that individuals in a small group can feed in a single patch for longer periods as patches are more slowly depleted (Chapman and Chapman 2000).

### **Predator Alarm Frequency (per individual) is Inversely Associated with Group Size**

I used alarm calls as a proxy measure of perceived predation risk. In an experimental study of wild baboons (*Papio cynocephalus ursinus*) investigating perceived predation risk (i.e., alarm call rates) as a function of group size, females in small groups appeared to perceive the highest risk (Cowlshaw 1997b). In the current study, however, support for this hypothesis varies according to alarm call type and demonstrates a difference in perceived risk from aerial versus terrestrial predators according to group size. In terms of aerial alarms, the hypothesis is supported and consistent with predictions that larger social groups benefit from overall levels of efficacy in predator detection even as individual effort decreases (Pulliam 1973; Bertram 1978). In terms of terrestrial predator alarms, however, the hypothesis is not supported.

For most diurnal primate species, it is commonly suggested that, controlling for body mass (Janson and Goldsmith 1995), group size should increase as predation risk increases (Dunbar 1988). So what explains such a disparity in group size within a single population? Effects of resource competition aside, divergent group size may be a

response to two different anti-predator strategies. In RV, risk of predation from both aerial and terrestrial predators is strong. The primary aerial threat to capuchin monkeys is the Harpy Eagle (*Harpia harpyja*), the largest raptor in the Americas (Brown and Amadon 1968). Harpy attacks on prey are typically accompanied by a series of vocalizations, and experienced prey are able to use this acoustic signal to initiate an escape response (Gil-da-Costa et al. 2003). Therefore, a small group may be better suited for protection from Harpy Eagles because a cryptic, quiet group is harder to locate from the aerial view of a bird than is a large, conspicuous group, and the Harpy vocalizations somewhat preclude the need for “many-eyes” for early predator detection.

On the other hand, a small group is likely more susceptible to quiet, ambush terrestrial predators, such as the jaguar (*Panthera onca*) and puma (*Puma concolor*) that rely heavily on scent for prey detection. The dense vegetation (in the form of lianas and bamboo) dominating RV is a double-edged sword: It provides a source of protection for the monkeys from aerial predators but also reduces visibility and provides camouflage to predatory cats, increasing the monkeys’ risk of terrestrial predation. As potential prey for such terrestrial threats, a small capuchin troop is at a disadvantage due to their reduced group size (e.g., the dilution effect and many-eyes hypothesis).

Thus while the larger Troop A may be more susceptible to attacks by Harpy Eagles, Troop B may be more susceptible to attacks by large cats. Disparate group size may therefore be a response to an environment with a strong predator population posing risk from both sky and ground. Evidence for this is provided by the troops’ habitat preference, range of height in the canopy (group strategy to reduce vulnerability) and alarm rates (individual response to their group’s strategy). While bamboo

comprises a relatively equivalent portion of the troops' home ranges, the dense bamboo patches were the habitat of choice for Troop A, while Troop B minimally occupied this habitat. Troop B stayed significantly higher in the canopy than did Troop A, and Troop B individuals rarely ventured to the forest floor, a pattern that was found for small groups of other primate species as well, such as *C. olivaceus* (de Ruiter 1986) and *Macaca fascicularis* (van Schaik et al. 1983b). Overall, the data suggest that to reduce predation risk from Harpy Eagles, Troop A stayed lower in the canopy and in thick canopy cover; to reduce predation risk from terrestrial cats, Troop B stayed higher in the canopy and avoided risky habitats. In response to these strategies, individuals in Troop B became more vigilant of aerial threats and produced more AAs than did the individuals in Troop A, while Troop A became more sensitive to terrestrial threats and produced more TPAs than Troop B.

**Perceived versus actual predation risk.** For both troops, the frequency of alarm calls far surpassed the number of actual encounters with predators. In particular, although Harpy Eagle attacks on the study groups occurred relatively infrequently as compared to previous years, the monkeys' perceived risk of predation was a strong indicator of past selective pressure (Isbell 1994).

Differentiating between false and true alarms (i.e., perceived vs. actual risk) requires identification and knowledge of the caller and involves opportunity cost (e.g., vigilance in lieu of foraging, resting or social behavior). In many social birds and mammals, researchers report that false alarms represent a high proportion of all alarm calls (Beauchamp and Ruxton 2007); consistent reaction to these false alarms can become additively costly in terms of time and energy expenditure. Using two different

mathematical models, Proctor et al. (2001) and Beauchamp and Ruxton (2007) predicted how flocking birds should respond to ambiguous alarm calls. Both demonstrated that, in general, birds should always respond to multiple alarms but never to single alarm calls, as single instances of alarm are likely false alarms. However, if flock size is small and/or attack time is short, the models predict that the most appropriate action is to respond to all alarms regardless of the number of calls. This may further explain the increased number of aerial alarm calls per individual in Troop B, many of which were secondary AAs in response to a conspecific's alarm.

### **Rates of Female Agonism Increase with Group Size and Group Size Affects the Strength of Female Dominance Hierarchies**

These hypotheses are supported and demonstrate a cost of larger group size. Among primates in female-philopatric societies with demonstrated within-group competition, females tend to form linear dominance hierarchies, whereas in groups with weak within-group competition, females maintain more egalitarian relationships (Sterck et al. 1997). The females in Troop A exhibited a weakly linear dominance hierarchy, while the relationship among the Troop B females is best described as egalitarian; this further indicates that WGC was stronger within Troop A than it was within Troop B.

Although the presence of a dominance hierarchy likely acts to reduce aggression, females in Troop A still expressed higher rates of agonism (as actors and recipients) than the females in Troop B. This may be a repercussion of increased WGC, as approximately 80% of agonistic bouts involving females were food-related.

Alternatively, increased agonism in Troop A may simply be a result of larger group size in that a greater density of individuals provides more occasion for (intentional and unintentional) interaction (Olsson and Westlund 2007). Based on group size (not

including infants), there were 504 possible dyadic associations within Troop A (45 possible adult dyads) and only 36 possible dyadic associations within Troop B (6 possible adult dyads).

### **Rates of Female Grooming Increase with Group Size**

This hypothesis is not supported and demonstrates a cost of larger group size. Larger group size naturally provides a greater number of potential 'enemies' and 'friends' for any given individual (Olsson and Westlund 2007). The females in Troop A appeared to receive the negative social consequences of increased group size (e.g., increased rates of agonism) but not the benefits (e.g., increased rates of grooming). Although the females in Troop A had double the density of neighbors and 14 times the number of possibly dyadic relationships than Troop B females, the females in the smaller group were actually more invested in grooming.

Given that Troop A females participated in grooming less than Troop B females, despite a threefold increase in troop-mates (and potential grooming partners), it is of interest to understand what socioecological variables were associated with female grooming and possibly acted to limit (or promote) grooming behavior. Is grooming a behavior that is better accommodated by the home range use and travel patterns of Troop B? Posthoc consideration revealed that, for both Troops A and B, the two most common habitats in which grooming occurred were the bamboo (40% and 17% of grooming bouts, respectively) and liana/low forest (31% and 64% of grooming bouts, respectively). These habitats were likely preferred by the monkeys for grooming because they provided the most canopy cover from aerial predators. That Troop A groomed most frequently in the bamboo and Troop B clearly preferred the liana/low forest for grooming is likely a reflection of their habitat use patterns in response to their

respective sources of predation risk (as discussed above). Still, however, the home range and habitat use patterns of the two troops does not explain why Troop A groomed so much less than expected; Troop A actually spent a greater percentage of their time (66%) in the habitats amenable to grooming as compared to Troop B (64%).

A more likely explanation is provided by the groups' activity patterns. Pollard and Blumstein (2008) demonstrated that an evolutionary relationship exists between time allocation to rest and social group size. According to their meta-analysis, time spent resting was the most important time component of group size, such that larger groups allocated less time to rest than did smaller groups. In my study, the females in both troops participated in grooming more than expected when the group was stationary as opposed to traveling (Troop A:  $X^2 = 53.2$ ,  $df=1$ ,  $P < 0.001$ ; Troop B:  $X^2 = 86.2$ ,  $df = 1$ ,  $P < 0.001$ ). Troop A traveled more than Troop B on a daily basis, and the travel budget of Troop A was approximately 10% higher than that of Troop B. Therefore, just as smaller groups are able to allocate more time to resting, Troop B remained more stationary and were provided with more opportunity to groom as compared to the larger Troop A. Decreased grooming time is an opportunity cost of residing in a large group that must travel more in order to feed its many mouths.

### **Female Brown Capuchins in a Larger Troop Demonstrate More Seasonal Variation in Patterns of Grooming and Agonism than Do the Females in a Smaller Troop**

This hypothesis is supported and demonstrates a cost of larger group size. While individuals in a small group are more likely to experience social stability in an ecologically unstable environment, the same small-group individuals, however, are likely more vulnerable to large-scale disruption, especially over the long term. For example, the loss of one of the Troop A females during the study provided no measured reaction

by the remaining group members; the large group seemed to act as a buffer to this individual loss. Troop B, however, simultaneously lost two of its three adult females, and troop reaction was more strongly observed. Anecdotal evidence suggested that the alpha male demonstrated an intense behavioral response in the days following their disappearance, and although I cannot attribute a causal link with any degree of certainty, it is of interest that the remaining female uncharacteristically intensified grooming behavior during the transition season that followed. Therefore, barring large-scale disruption, a small, cohesive group provides stability and likely circumvents the effects of daily and seasonally predictable stress. During large-scale social or ecological upheaval, however, a large social group may buffer the effects of unpredictable stress.

### **Conclusion**

It is often stated that group size in wild populations is self-regulated as individuals choose to stay in or migrate from a social group depending on the benefits obtained. For the females in a female-philopatric society, however, the situation is typically more of a given than a choice. For these females, philopatry can be viewed as a subtle version of captivity. With the imminent costs associated with emigration and immigration (increased predation risk, lack of competitive ability in acquiring resources, lack of social ties and allies, and risk of infanticide) and the benefits provided by a social network founded in kinship and long-time familiarity, a female is almost certain to choose to remain in her natal group regardless of its size (but see Izar 2004). She is born into a situation where she must endure the challenges of her group. Depending on the local ecology of the environment, as well as intra- and inter-group dynamics, there are inherent trade-offs to living in a small versus a large group (and vice versa).

In this chapter, I tested six hypotheses addressing the costs and benefits of disparate group size. If a group of intermediate size provides, in theory, the best balance of between-group and within-group competition (Price and Stoinski 2007), then how does one go about explaining the successful history (eight years and counting) of these two troops of brown capuchins in RV, Suriname that represent completely opposite ends of the spectrum of *C. apella* group size? The answer is provided by the dynamic nature of their local ecology. With intense ecological variation, both within and between years, and a strong regime of aerial and terrestrial predators, deviation from the norm is most adaptive. When the cost/benefit scale can easily shift, what is best for a small group at one point in time may soon be better for a large group – a cycle of unpredictability that has maintained a drastic differential in group size.

The study period proved to be a beneficial time for the individuals in the small group, Troop B. Based on the variables studied, Troop B members received more of the benefits of sociality while Troop A members received most of the costs. Troop A must travel more in order to acquire sufficient nutrients for its many group members, and because their large size makes them more conspicuous to aerial predators, Troop A tended to spend most of their time in the densely covered bamboo patches. Only during the fruiting season, when fleshy fruits reach peak production, was Troop A lured from the protective bamboo. Troop B was not as constrained by the threat of aerial predation, however, and they utilized bamboo only as a fallback resource. And while the females in Troop A were exposed to higher rates of agonism (i.e., WGC) from their many troop-mates, they were less invested in grooming than were the females in Troop B. This low rate of grooming in Troop A is of particular interest given the number of

potential grooming partners, the presence of infants (which tends to increase female attractiveness to grooming conspecifics (O'Brien 1993; Muroyama 1994; Perry 1996; Di Bitetti 1997; Manson et al. 1999; Henzi and Barrett 2002), their access to safe grooming habitat (primarily the liana/low forest and bamboo), and the presence of a female dominance hierarchy. I examine the fine-scaled grooming relationships of the females in Troop A in greater detail in Chapters 4 and 5.

Table 2-1. Reported (or calculated mean) group size of *C. apella* troops at various sites. The two study groups, Troops A and B, represent opposite ends of the continuum of *C. apella* group size.

Location	$\bar{X}$ group size	Source
El Tuparro, Colombia	10	Defler 1982
Manu, Peru	12	Janson 1990b
Manu, Peru	13	Janson 1985
Manu, Peru	13	Terborgh 1983
Atlantic Forest, Brazil	13	Izar 2004
Nouragues, French Guiana	13	Zhang and Wang 2000
Manu, Peru	15	Janson 1996
Iguazu, Argentina	15	Di Bitetti and Janson 2001
Nouragues, French Guiana	15	Zhang and Wang 1995
La Macarena, Colombia	16	Izawa 1980
Iguazu, Argentina	18	Di Bitetti 1997
Iguazu, Argentina	25	Hirsch 2002
Caratinga, Brazil	26	Lynch et al. 2002
“Optimal” (intermediate) <i>C. apella</i> group size	16	
RV, Suriname: Troop A	27	Current study
RV, Suriname: Troop B	9	

Table 2-2. Composition of the study groups, Troop A and Troop B, from January to December 2006. Parentheses indicate final troop composition at the conclusion of the study. Troop A lost one female in October (death presumed to be related to giving birth) and two subadult males in August (emigrated). Troop B lost two females simultaneously in August (unknown cause).

	Group size	# adult ♂	# adult ♀	# subadult ♂	# subadult ♀	# juv ♂	# juv ♀	# infants (<1yr)
Troop A	27 (24)	3	7 (6)	2 (0)	1	7	3	4
Troop B	9 (7)	1	3 (1)	1	0	3	1	0

Table 2-3. Operational definitions for female *C. apella* agonistic and grooming behavior, recorded *ad libitum*.

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Agonism	All aggressive, displacement, and submissive behaviors
<ul style="list-style-type: none"> <li>• Aggressive</li> <li>• Displacement</li> <li>• Submissive</li> </ul>	<ul style="list-style-type: none"> <li>• Actively antagonistic behaviors such as chase, hit, bite, and threat display.</li> <li>• One individual passively supplanted by another, usually (but not exclusively) at a food source. If an individual aggressively displaced another individual, then the bout was scored as 'aggression' and not 'displacement'.</li> <li>• Any instance in which an individual retreated and/or reacted with acquiescent posture or vocalizations without being aggressed towards or displaced.</li> </ul>
Grooming bout	One individual picking through the hair and/or skin of another individual. The bout concludes when the grooming ends or is interrupted by another behavior for more than five seconds. A new grooming bout begins with a new dyad, or whenever the grooming resumes (after $\geq 5$ seconds) or changes direction within the same dyad.

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Table 2-4. Summary of the observed intragroup agonistic bouts involving females (with determinable ‘winner’ and ‘loser’) for Troop A and Troop B. The females in Troop B rarely experienced agonism, while agonistic bouts occurred more frequently for females in Troop A. Troop A females were most frequently aggressive towards immatures and received the most aggression from adult males. Agonism between the females in Troop A occurred mostly in the form of passivity; agonsim between females in Troop B was never observed.

Actor	Recipient	Troop A			Troop B		
		Aggression	Displacement	Submissive	Aggression	Displacement	Submissive
Female	Male	6	1	0	0	0	0
Female	Juvenile*	59	23	20	0	0	4
Female	Female	8	16	4	0	0	0
Male	Female	41	30	11	1	0	0
Juvenile*	Female	4	12	3	2	0	0

Notes: ‘Aggression’ is action taken by the actor whereas ‘Displacement’ and ‘Submissive’ behaviors are actions taken by the recipient without obvious provocation. ‘Female’ and ‘Male’ denotes adult individuals of the respective sex; ‘Juvenile’ includes all immature individuals of both sexes.

Table 2-5. Troop A female dominance matrix based on the outcomes of dyadic agonism.

	Gina	Banana	Jane	LH	Carol	Kate	Tinkerbelle
Gina		1	1	1	^1	1	1
Banana			*1	1	1	1	^1
Jane				1	1	^1	1
LH					1	^1	*1
Carol						1	*1
Kate							*1
Tinkerbelle							

Note: 1 = row individual is dominant to column individual, based on the outcome of agonistic episodes. ^1 = dominance decided based on transitivity. \*1 = dominance decided based on anecdotal evidence.

Table 2-6. Differential benefits and costs for individual female brown capuchins residing in a large group (Troop A) versus a small group (Troop B) in Raleighvallen, Suriname. Based on the variables studied, Troop B members received more of the benefits of sociality while Troop A members received more of the costs. In terms of the benefits of sociality (represented by check marks), individual females in Troop B experienced greater social cohesion (as indicated by higher rates of grooming, grooming reciprocity, and agonistic coalitions), while members of Troop A were able to be less vigilant of aerial predators. The large group size of Troop A likely provides long-term social stability, albeit less support during daily challenges; the smaller Troop B provides a more supportive system overall, but is more susceptible to large-scale disturbances (such as the loss of troop members). In terms of the costs of sociality (represented by X marks), Troop A females experienced increased within-group food competition (as indicated by increased daily travel distance, presence of dominance hierarchy, and decreased foraging time per individual in clumped food patches) and increased intragroup agonism.

	Troop A (large group)	Troop B (small group)
<b>Benefits of Sociality</b>		
* Reduced predation risk		
< AAs/individual	✓	
< TPAs/individual	-	-
* Social cohesion		
> grooming rates		✓
> grooming reciprocity		✓
> coalitions		✓
* Social stability	Long-term	Short-term
<b>Costs of Sociality</b>		
* Increased WGC		
> daily travel distance	✗	
> dominance hierarchy	✗	
< time/individual in clumped food patches	✗	
* Increased intragroup agonism	✗	

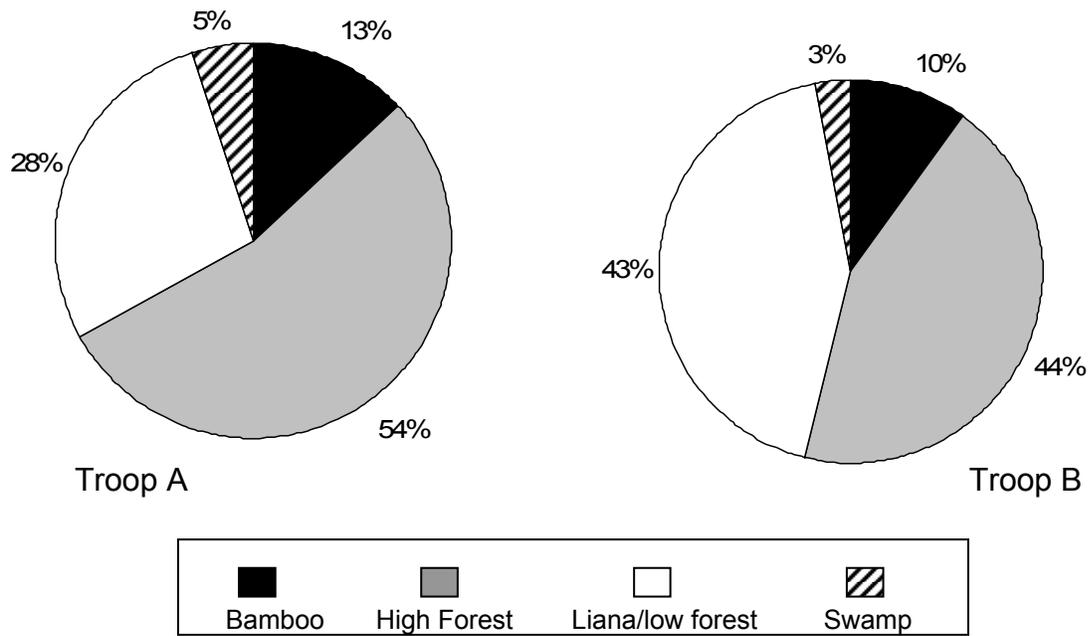


Figure 2-1. Habitat composition of the home ranges of Troop A and Troop B. Troop A's home range was composed primarily of high forest and secondarily of liana/low forest, while Troop B's home range was equally dominated by high forest and liana/low forest.

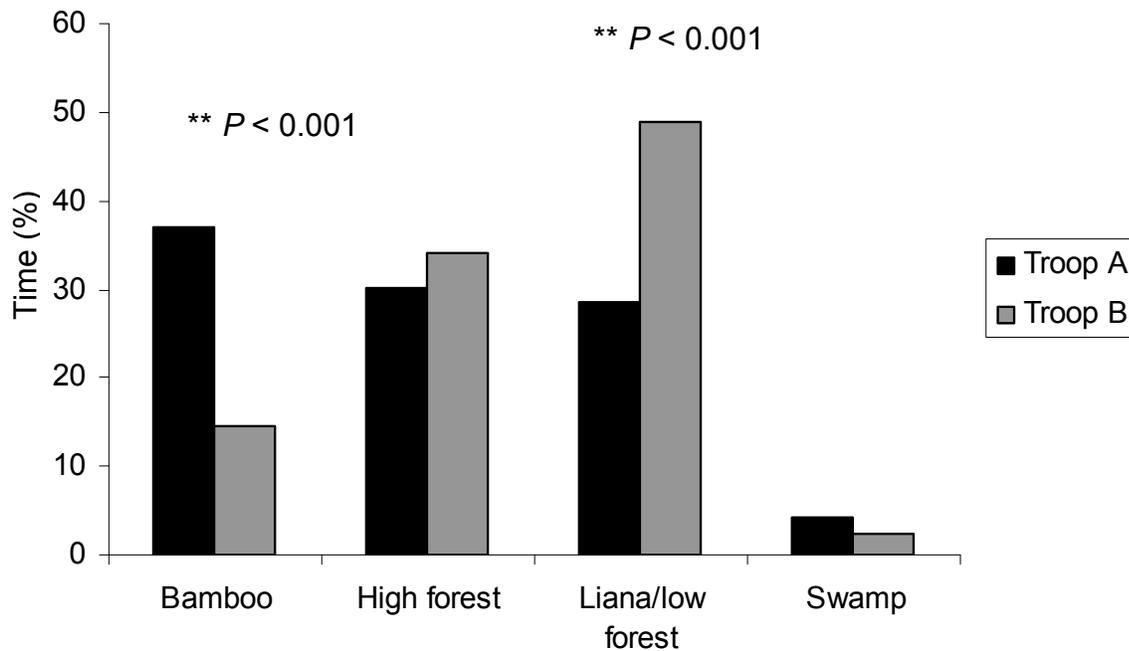


Figure 2-2. Comparison of overall time (%) that Troop A and Troop B spent in each habitat type. Overall, Troop A spent the most time in the bamboo while Troop B spent the most time in liana/low forest. Troop A spent significantly more time in the bamboo than did Troop B ( $\chi^2 = 177.88$ ,  $P < 0.001$ ), while Troop B spent significantly more time in the liana/low forest than did Troop A ( $\chi^2 = 63.86$ ,  $P < 0.001$ ).

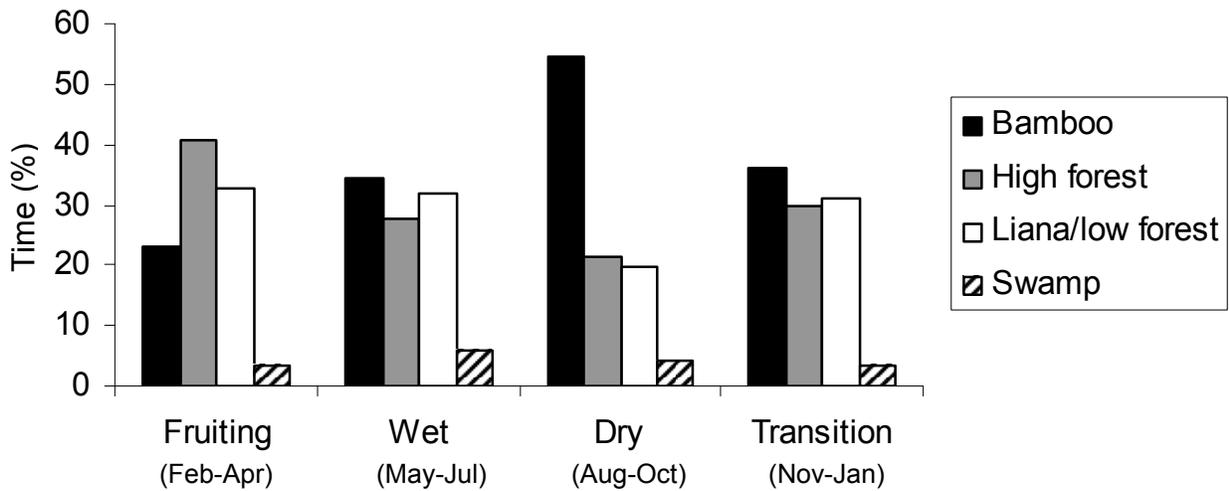


Figure 2-3. Seasonal comparison of Troop A's habitat use (% time). In each season except the fruiting season, the group spent the most time in the bamboo, especially during the dry season. During the fruiting season, the group spent the most time in the high forest. Their use of the liana/low forest, especially in conjunction with the high forest, was relatively consistent.

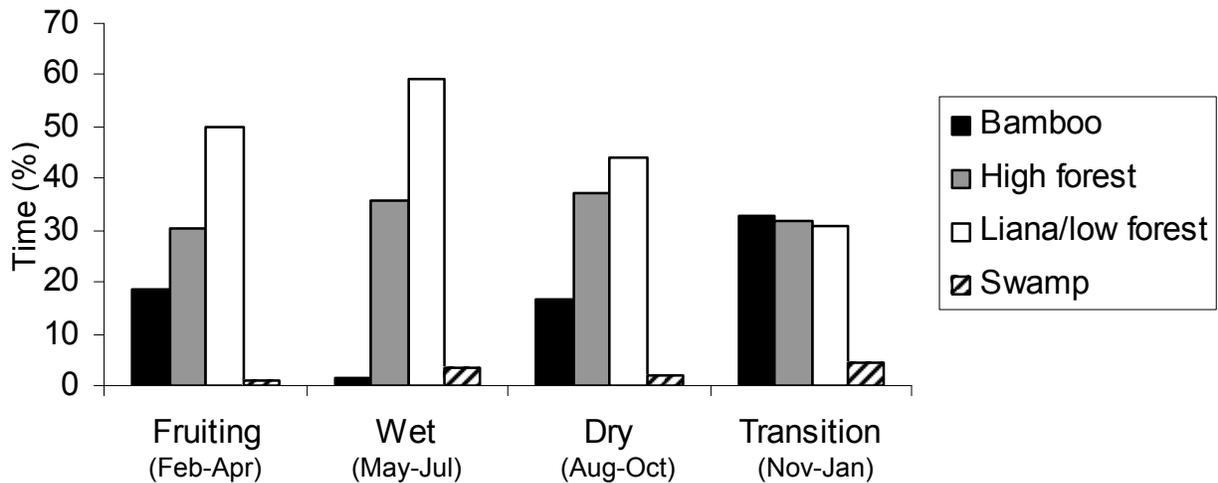


Figure 2-4. Seasonal comparison of Troop B's habitat use (% time). In each season except the transition season, the group spent the most time in the liana/low forest. Their use of the high forest remained relatively consistent throughout the seasons while their use of the bamboo was more variable, peaking in the transition season.

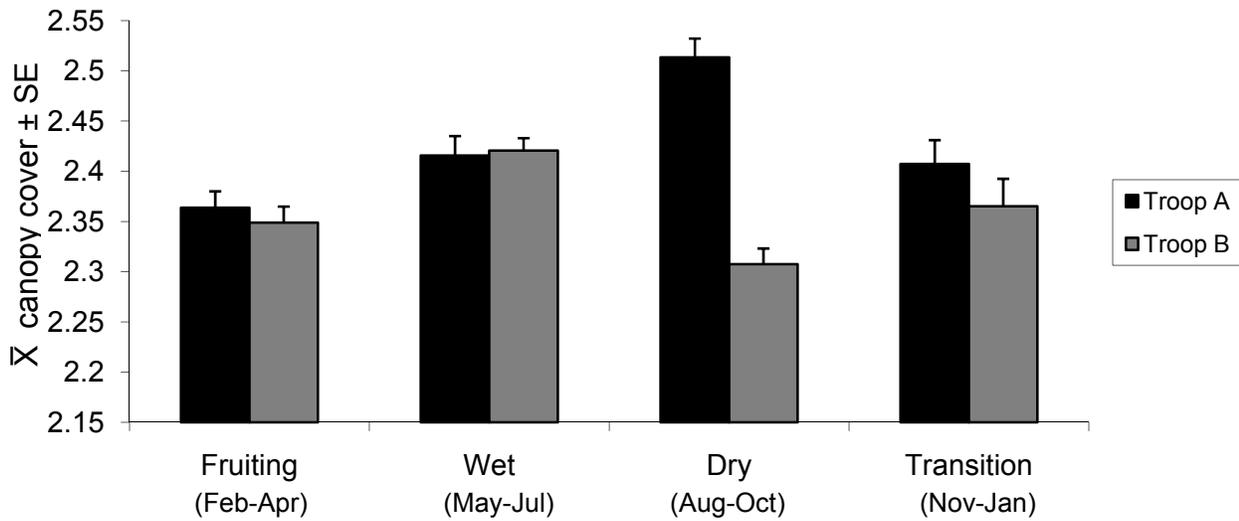


Figure 2-5. Seasonal comparison of average canopy cover (0-3 incremental scale that increases with vegetation density) for Troop A and Troop B. The two troops demonstrated a similar cover score to one another in each season except the dry season. The cover differential between Troop A and Troop B during the dry season, however, was only 0.2 on a three-point scale. There were no statistically significant inter- or intra-group differences in seasonal cover.

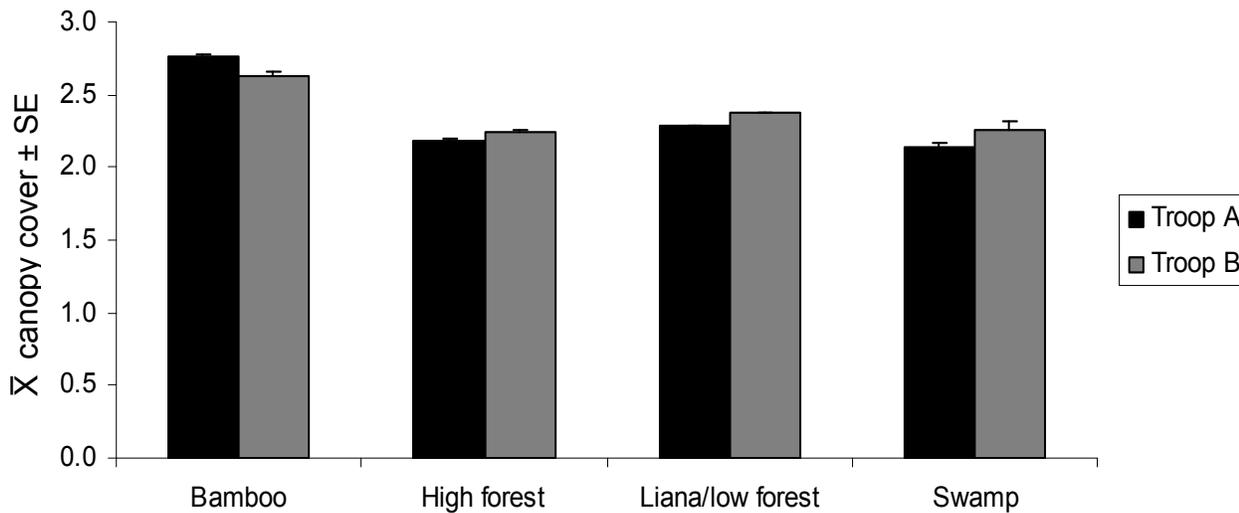


Figure 2-6. Average canopy cover by habitat type for Troop A and Troop B. Both troops were provided the most cover by the bamboo, a condition that reduced exposure to aerial predators but also reduced visibility between conspecifics and increased susceptibility to terrestrial ambush predators. There were no statistically significant inter- or intra-group differences in habitat cover.

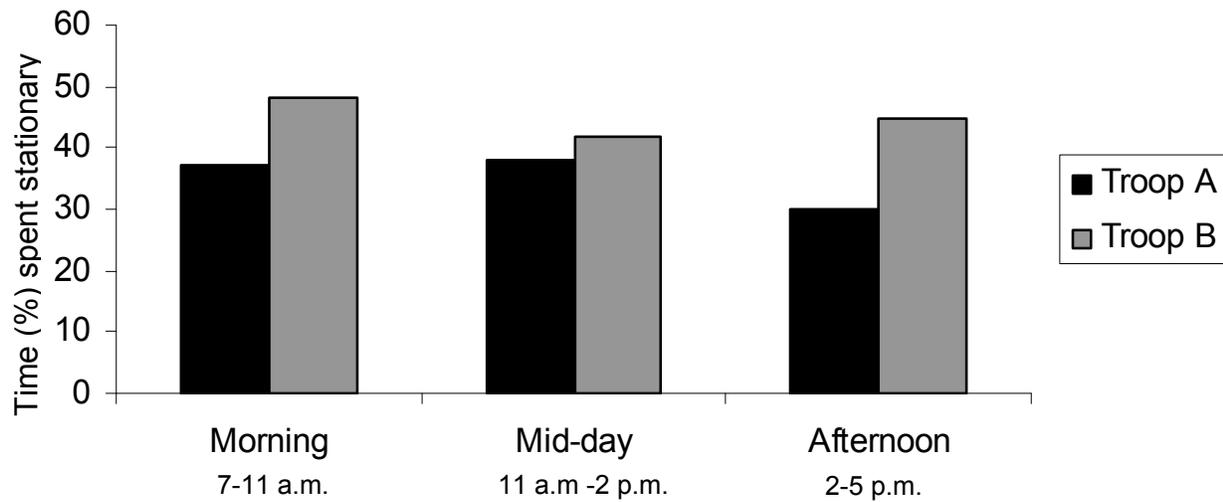


Figure 2-7. Percentage of time Troops A and B remained stationary (vs. travel) during the morning (7:00 to 11:00 a.m.), mid-day (11:00 to 2:00), and afternoon (2:00 to 5:00 p.m.) hours. During each time period, Troop B was more stationary than Troop A. Troop A traveled the most (70%) during the afternoon hours as compared to the morning (63%) and mid-day (62%), while Troop B traveled the most (68%) during the mid-day as compared to the morning (62%) and afternoon (55%).

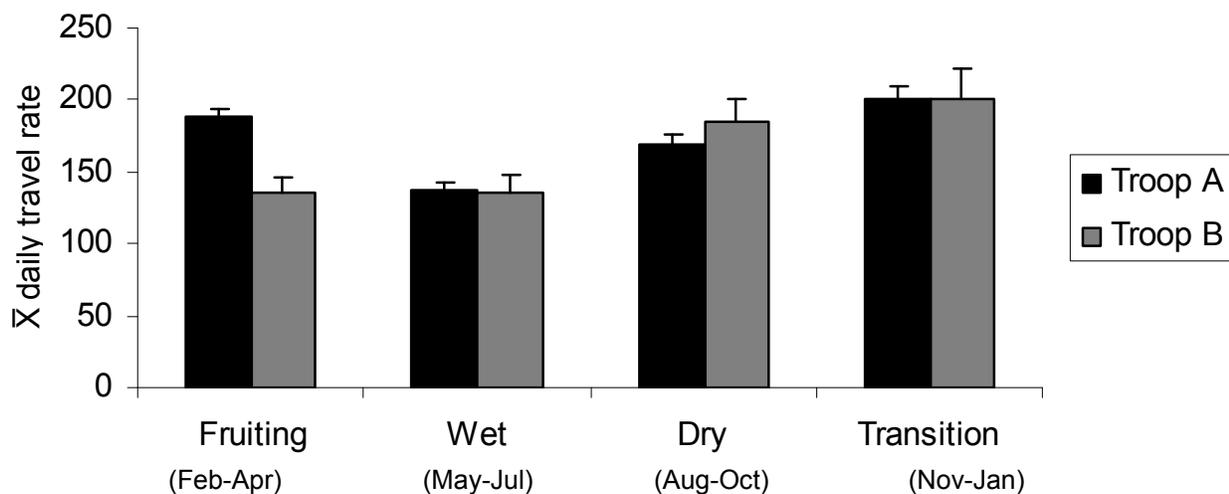


Figure 2-8. Seasonal comparison of daily travel rates (m/h  $\pm$  SE) for Troops A and B. Overall, the daily travel rate of troop A was significantly higher than that of Troop B ( $P = 0.037$ ), but the difference was primarily based on the difference in their travel rates during the fruiting season ( $P < 0.0001$ ).

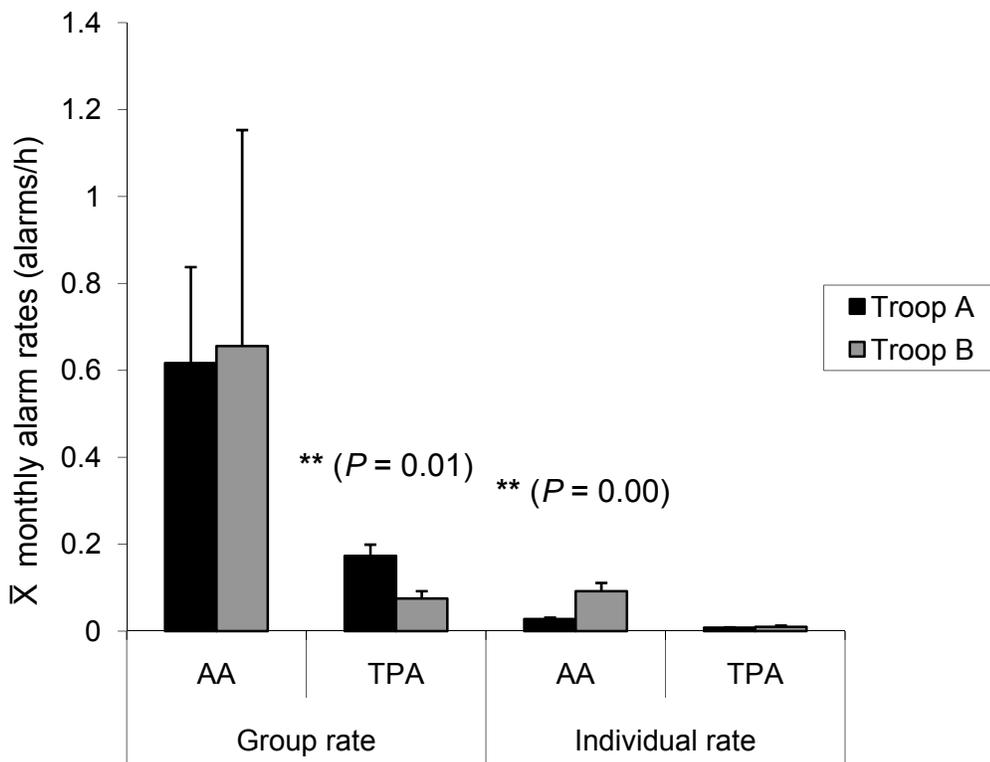


Figure 2-9. Monthly group and individual rates (alarms/h  $\pm$  SE) of aerial alarms (AA) and terrestrial predator alarms (TPA) for Troops A and B. Overall, there was no statistical difference in the monthly rate at which Troop A and Troop B produced AAs, but Troop A produced significantly more TPAs than did Troop B. After controlling for group size, however, Troop B individuals produced AAs at a significantly higher rate than did Troop A individuals while there was no statistical difference in the rate at which Troop A and Troop B individuals produced TPAs.

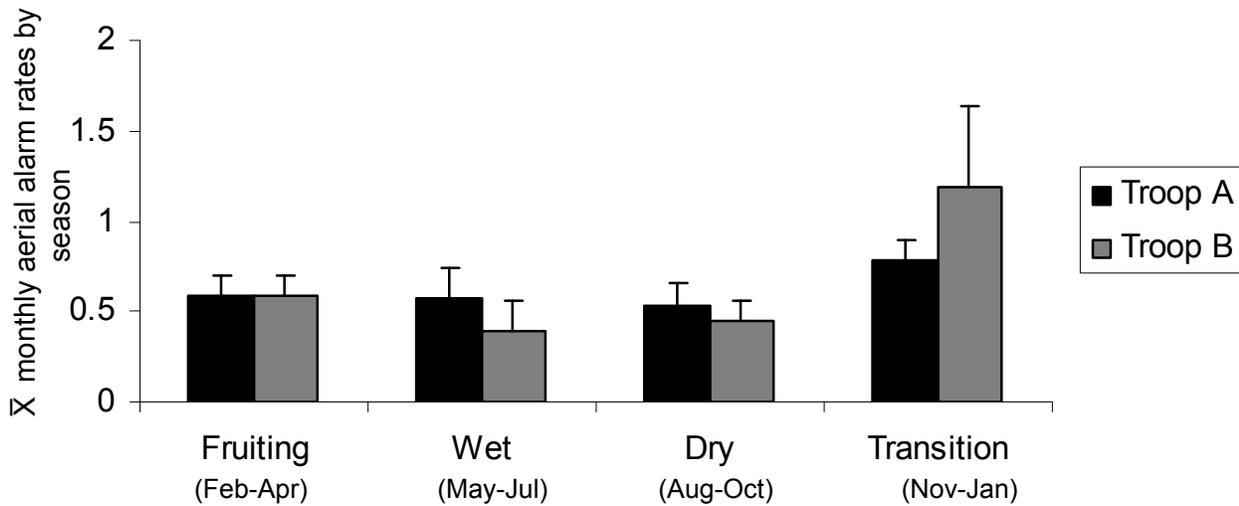


Figure 2-10. Seasonal effect on group rates of aerial alarms (AAs/h  $\pm$  SE) for Troops A ( $n = 23$ ) and B ( $n = 9$ ). Both troops produced the highest rate of AAs during the transition season, although there were no intra- or inter-group statistical differences in seasonal AA rate.

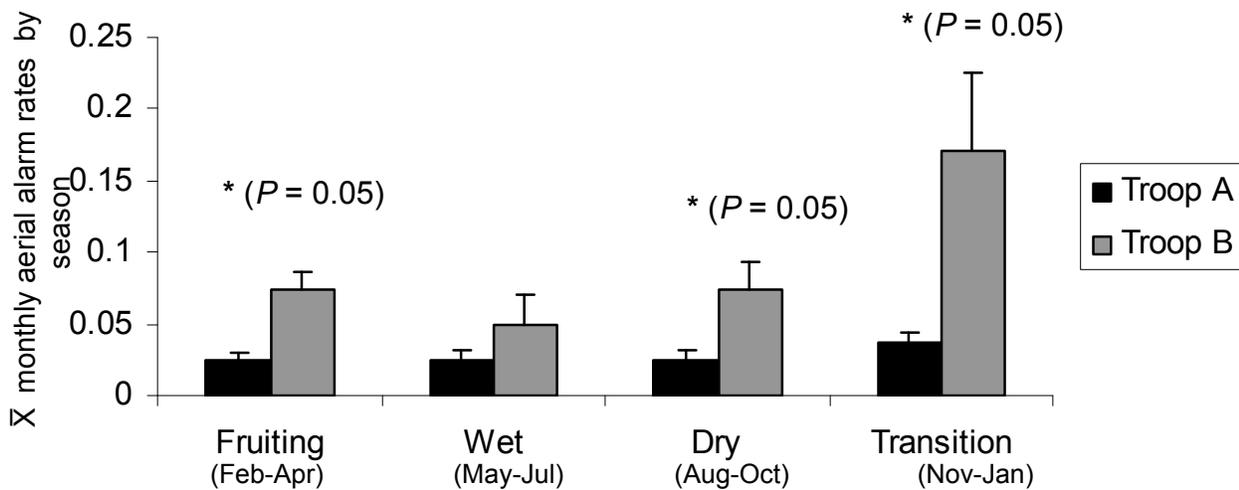


Figure 2-11. Seasonal effect on the rates of aerial alarms (AAs/h  $\pm$  SE) for individuals in Troop A and B. Controlling for troop size, an individual (juvenile, subadult, or adult) in Troop B produced AAs at a nearly significant higher monthly rate (AAs/h) than did an individual in Troop A during the fruiting, dry, and transition seasons.

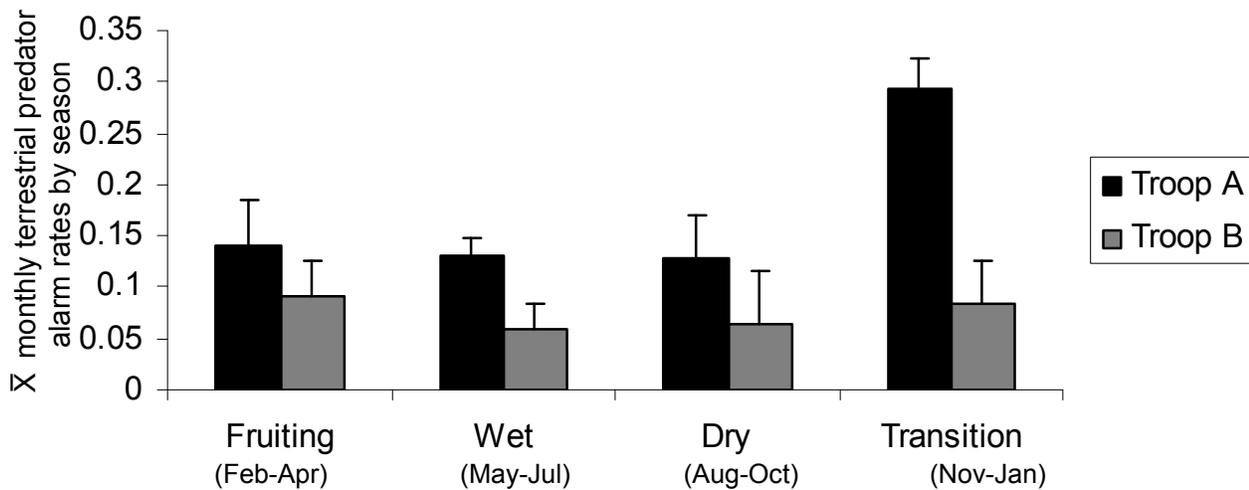


Figure 2-12. Seasonal effect on the group rates of terrestrial predator alarms (TPAs) (TPAs/h  $\pm$  SE) for Troops A ( $n = 23$ ) and B ( $n = 9$ ). Both troops produced the highest rate of TPAs during the transition season. During all seasons, Troop A emitted a higher group rate of TPAs than did Troop B; the difference, however, was (nearly) statistically significant only during the transition season.

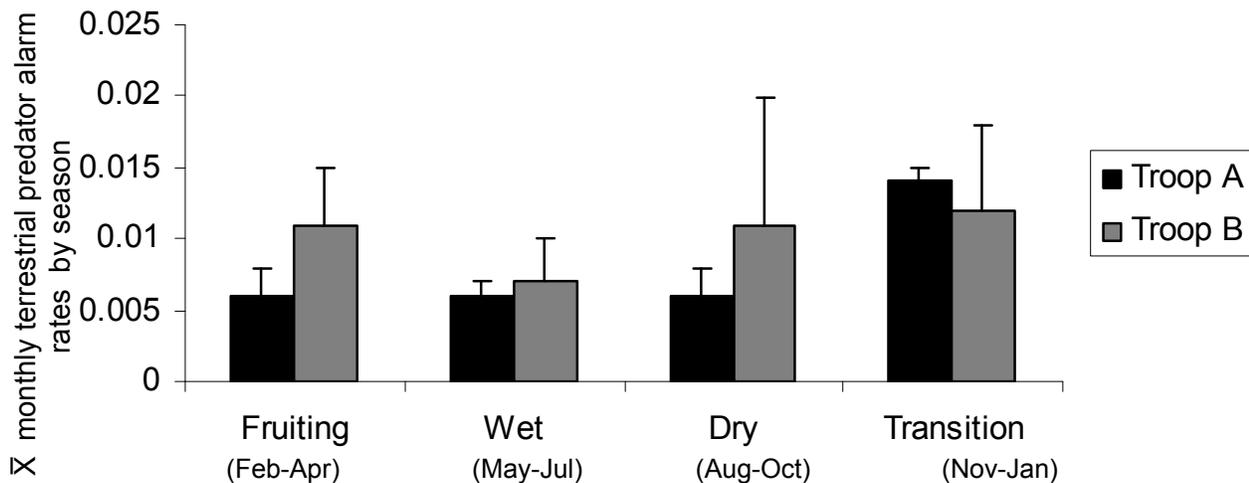


Figure 2-13. Seasonal effect on the rates of terrestrial predator alarms (TPAs/h  $\pm$  SE) for individuals in Troop A and B. Controlling for troop size, an individual (juvenile, subadult, or adult) in Troop B produced TPAs at a higher (non-statistically significant) rate than did a non-infant individual in Troop A during the fruiting, wet, and dry seasons but not during the transition season.

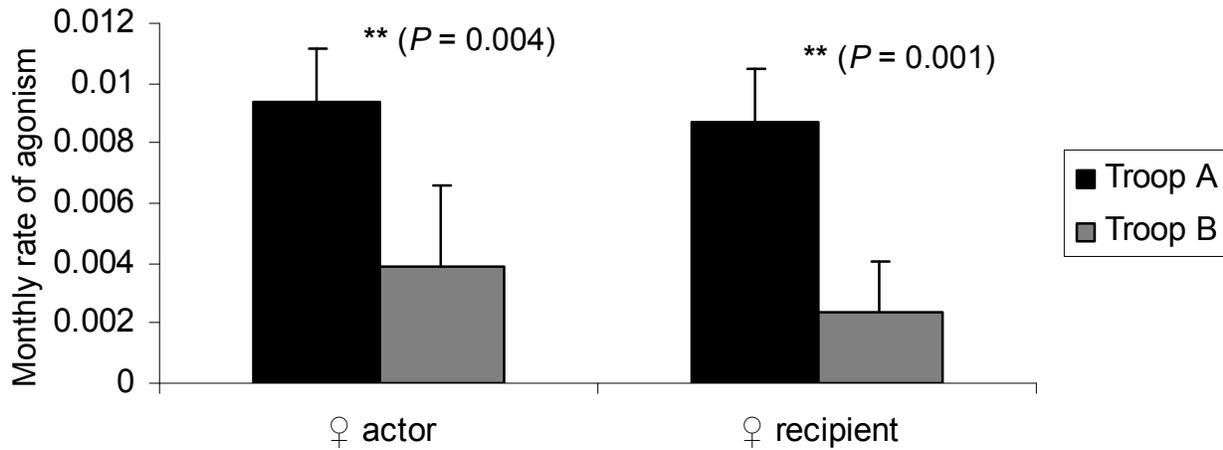


Figure 2-14. Controlling for group size, the monthly rate (bouts/h  $\pm$  SE) at which the average female in Troop A and Troop B experienced agonism (as actor vs. recipient) with troop-mates. The majority of agonism was food-related. The average female in Troop A gave ( $P = 0.004$ ) and received ( $P = 0.001$ ) significantly more agonism than did the average female in Troop B.

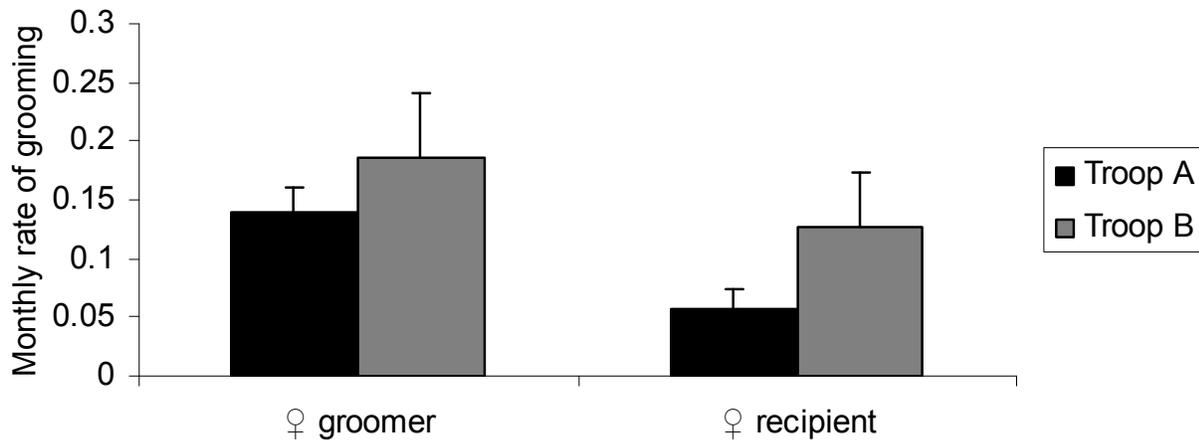


Figure 2-15. Monthly rate (min/h  $\pm$  SE) that the average female in Troop A and Troop B acted as the groomer and as the recipient during grooming. Although not statistically significant, females in Troop B tended to groom and be groomed more than the females in Troop A despite the threefold increase in the number of potential grooming partners for females in Troop A.

CHAPTER 3  
DISPARATE TROOP SIZE AND STRESS: THE EFFECTS OF A HIGH RISK, LOW  
ENERGY ENVIRONMENT ON FEMALE BROWN CAPUCHINS

**Introduction**

Group size is a critical, though relatively dynamic component of social living - a demographic feature dependent on local ecology and social circumstances that is associated with potentially severe fitness consequences. The effects of group size not only have direct and immediate fitness consequences on individuals (e.g., predation risk and access to mates and food resources), but may also indirectly affect individual fitness in terms of physical development and reproductive health. With the benefits of sociality come the costs of group living, and suboptimal group size can exacerbate socioecological stress incurred by individuals. Females in female- philopatric societies are especially impacted by the socioecological and endocrinological consequences of group size, as they tend to remain in their natal troop regardless of its size.

Cortisol, a steroid hormone, is commonly measured as an indicator of stress in wild animal populations (Wingfield et al. 1997). Over the short term, acute stress response is an adaptive physiological condition whereupon energy is diverted from long-term processes such as digestion, growth, immune function and reproduction and mobilized to meet short-term needs ("flight or fight"), thus increasing an individual's likelihood of immediate survival upon encountering a threat. Over extended periods, however, the metabolic costs of sustained stress rise steeply (Sapolsky et al. 2000), adversely affecting female health and reproductive ability, fetal development, and the development of offspring social skills and stress-coping abilities (Sachser et al. 1998; Bardi et al. 2005; Sapolsky 2005; Shively et al. 2005; Wadhwa 2005). Fecal hormones are pooled as they metabolize for a period of time (usually less than 48 h in nonhuman

primates) before elimination (Whitten et al. 1998) and do not capture minute hormonal fluctuations. Therefore, fecal corticosteroid metabolites provide a useful indicator of pronounced or chronic stress (Boinski et al. 1999b).

This chapter investigates the effect of group size on the intensity of socioecological stress incurred by resident females. A population of brown capuchins (*Cebus apella*) in Raleighvallen (RV), Suriname provides a unique opportunity to investigate this relationship: Two study groups are of widely disparate sizes ( $n_1 = 27$ ,  $n_2 = 9$ ) but reside with overlapping home ranges within a high-risk, low energy environment. My study is the first to examine social and ecological stressors of wild female brown capuchins; published reports of *Cebus* behavioral endocrinology are scant and limited to *C. apella* males, captive *C. apella* females and wild *C. capucinus* females. Further, within *Cebus*, female behavioral endocrinology has been studied only in terms of sexual behavior and reproductive physiology (Linn et al. 1995; Carosi et al. 1999; Carosi and Visalberghi 2002; Carnegie et al. 2005).

### **Hypotheses**

Using a combined approach of behavioral observation and hormonal analysis, my study focuses on three hypotheses investigating the effect of disparate group size on the socioecological stress incurred by the groups' resident females.

#### **Group Size Affects the Level of Stress Females Incur Due to Predation Risk**

Predation risk is accepted to be one of the ultimate causes of sociality (van Schaik 1983) and thus is a determinant of group size. Encounters with predators or their cues activate the hypothalamic-pituitary-adrenal (HPA) axis to release epinephrine and glucocorticoids, hormones that prepare and protect the body during stress response (Boinski et al. 1999a; Engh et al. 2006a). Engh et al. (2006a) found that the

glucocorticoid levels of female chacma baboons (*Papio hamadryas ursinus*) increased significantly following a predation event, and Boinski et al. (1999a) demonstrate a positive correlation between the alarm rates of captive brown capuchins and fecal cortisol levels. High cortisol levels have also been found to occur in avian populations facing high predation risk (Scheuerlein et al. 2001). If predation risk is strong enough within a population to promote larger group size (as exhibited within RV by Troop A), then animals facing high predator pressure (those individuals in the same population residing in smaller groups, such as Troop B) should have high cortisol levels (Pride 2005b). I predicted that the females in the smaller group would be more susceptible to increased cortisol levels in response to predation risk.

### **Group Size Affects the Levels of Stress Females Incur During Food Shortages**

Prior studies on various social taxa, e.g. baboons (Sapolsky 1986; Gesquiere et al. 2008), African elephants (Foley et al. 2001), male brown capuchins (Lynch et al. 2002), and ring-tailed lemurs (Pride 2005a), demonstrate increased cortisol levels during periods of harsh environmental conditions and low food availability. Is there a contributing effect of group size on an individual's stress response to cyclical environmental challenges?

Wrangham (1980) suggested that female philopatry is a response to intergroup competition; by this measure, large group size should be preferred over small group size, as larger groups easily supplant small groups during competitive encounters. For most taxa, however, within-group food competition has a greater effect on the dynamics of female relationships than does between-group competition (Janson 1988a; Cheney 1992; Barton and Whiten 1993; Cowlishaw 1995; Silk et al. 1999; Koenig 2000; Boinski et al. 2002), and thus individuals in smaller groups may fare better in terms of access to

resources than do individuals in larger groups. Hormonal measures further indicate the significance of within-group competition for group-living species. Pride (2005a) demonstrated that, during periods of food scarcity, cortisol levels increased for ring-tailed lemurs only in large groups. Similarly, Foley et al. (2001) determined that, for African elephants, cortisol levels increased with group size during the dry season. Therefore, I predicted that (a) the cortisol levels of females would be highest during the dry season (August to October), and (b) during the dry season, mean cortisol concentrations would increase more for females in the large group as compared to females in the small group.

### **Rank-Related Stress is a Factor of Group Size**

Although rank-related stress is a dominant theme in the study of behavioral endocrinology of group-living animals, there remains no consensus on the relationship between social status and cortisol level. Despite the original assumption that subordination induces stress, only a few studies demonstrate that subordinate individuals have higher glucocorticoid levels (Manogue et al. 1975; Virgin and Sapolsky 1997). Other studies demonstrate the opposite trend, with dominant individuals having higher stress levels than subordinates (Saltzman et al. 1998; Cavigelli 1999; Barrett et al. 2002; Cavigelli et al. 2003). A third trend in rank-related stress has actually received the most support, that of no consistent directional relationship between dominance ranking and stress levels (van Schaik et al. 1991; Bercovitch and Clarke 1995; Smith and French 1997; Stavisky et al. 2001; Lynch et al. 2002; Weingrill et al. 2004; Gould et al. 2005; Peel et al. 2005; Pride 2005a).

Predictable stressors induce less of a stress response than do unpredictable and uncontrollable situations (Wingfield et al. 1998), and since a stable social system

produces predictable relationships with dominance interactions that do not require overt aggression, hierarchical position does not necessarily induce endocrine response (Sascher et al. 1998). Weingrill et al. (2004) and Pride (2005b) demonstrated that in female chacma baboons and ring-tailed lemurs, respectively, social rank was not a predictor of cortisol level; for both species the social hierarchies are stable, usually uncontested for long periods of time, and were characterized by little overt aggression. Similarly, in brown capuchins, females may exhibit a weak-ranked hierarchy (Izar 2004) and even mild overt aggression between *C. apella* females at RV is rare.

Even in the absence of a consistent link between stress and social rank, however, does disparate group size differently affect individuals of disparate rank? If group size affects the intensity of within-group resource competition, then it follows that larger groups may demonstrate a more linear dominance hierarchy with subordinate individuals more susceptible to stress through increased aggression and access to only lower quality food resources. Therefore, I predicted that the cortisol levels of dominant and subordinate females would differ more in the large group than in the small group.

## **Methodology**

### **Site Description**

Raleighvallen (RV), a 7812 km<sup>2</sup> reserve consisting of primary tropical rain forest, is located within the 1.6 million ha Central Suriname Nature Reserve in Suriname. The main study site measured approximately 2 km<sup>2</sup> and was covered by an extensive trail system. RV's flora and fauna are effectively undisturbed in the historical period, and an intact array of potential predators and competitors are present (Reichart 1993). The soils of the Guyanan Shield (including French Guiana, Suriname and Guyana) are nutrient-poor and highly weathered as they are derived from Precambrian bedrock.

Fleshy fruits are low in abundance and available fruit resources typically occur in small patches (< 5 m diameter) (Boinski et al. 2002). Additionally, much of RV is composed of expansive bamboo patches and dense liana forest that restricts visibility (Boinski et al. 2003).

### **Study Animal**

The brown capuchin monkey (*Cebus apella*) is one of the four traditionally recognized species in the genus *Cebus* (Hill 1960). Capuchins live in multi-male, multi-female polygamous groups that are typically female philopatric. Adult males and females maintain separate dominance hierarchies; in general, males are dominant to females. *C. apella* social groups are comprised of 12 to 27 individuals, with an average troop size of 17 members. Troop membership and relationships remain relatively stable, except for subadult males who emigrate from their natal group and may subsequently transfer several times. Brown capuchins reside in a variety of habitats encompassing a large geographic range from Columbia to Argentina (Fragaszy et al. 2004). *C. apella* are omnivores; the bulk of their diet consists of fruit supplemented with seeds, vegetation, arthropods, and vertebrates (Terborgh 1983).

Study troops A and B were two of four brown capuchin groups commonly observed within the study site, and the primary study subjects were the 10 adult females resident to these two groups. For most of the study, Troop A consisted of 27 individuals, seven of which were adult females; Troop B consisted of nine individuals, three of which were adult females. During the study, one pregnant female disappeared from Troop A (her disappearance coincided with her predicted due date, and thus it is possible her (presumed) death was related to giving birth), and two females disappeared from Troop B (cause unknown). Relatedness among the adult troop

members is unknown; however, genetic analysis of the brown capuchin population in RV is currently underway. The study troops had been habituated to human observers since 1998, and all individuals were recognized based on body size, color patterns, and other identifying characteristics such as scars, moles, and ear shape. Throughout the study period, inter-observer reliability tests were conducted monthly to ensure consistent and accurate identification of all troop members.

### **Data Collection**

From January to December 2006, I and/or field assistants followed Troop A for up to 10 hours each day (beginning at sunrise). Troop A was followed, on average, 28 days per month, composing a total of 2284 h of observation (not including 'out of view' time). Troop B was followed, on average, 8 days per month, composing a total of 495 h of observation (not including 'out of view' time).

Behavioral data, including all observed occurrences of social agonism and anti-predator behavior, were collected *ad libitum* (Altmann 1974). To reduce observation bias, I moved throughout the groups to locate non-visible individuals and record their activities. Due to opportunistic sampling, as well as the reduced visibility within the Raleighvallen forest, the recorded frequencies of social behavior are likely underestimates of the true frequencies. Because of the large number of hours over which behavioral interactions were recorded, however, I am confident that the data provide strong indication of actual trends.

### **Hormonal Sampling and Analysis**

Fecal samples were collected opportunistically, with the goal of collecting at least one sample per female ( $n_1 = 7$ ,  $n_2 = 3$ ) per 15-day interval (Lynch et al. 2002; Engh et al. 2006a). Fecal samples were collected only if the female was observed defecating and

her identity ascertained with certainty. Upon collection, each sample was immediately placed in an empty plastic vial and stored inside a thermos with an instant chemical cold pack. Samples were processed within three hours of collection and registered, on average, at 44°F. The samples were processed using Solid Phase Extraction (SPE) according to Ziegler and Wittwer (2005): 0.1 g of fecal material was mixed with 2.5 ml of distilled water and 2.5 ml of ethanol. The mixture was then hand-shaken for 5 min and centrifuged for 10 min. Two ml of the supernatant was removed and passed through an Alltech Prevail C18 Maxi-Clean SPE Cartridge (Alltech, Deerfield, IL) and stored. Samples were shipped to The Wisconsin Regional Primate Research Center for analysis. Using Enzyme ImmunoAssay, each sample was analyzed for cortisol (F) concentration (ng/g); the assays were validated for accuracy and parallelism using internal controls.

### **Statistical Analysis**

Using the individual female as a sampling unit allowed me to assess variation within each group as well as between groups. This is justified by evolutionary theory, as selection is generally strongest at the level of the individual, and biologically sensible, because individuals may respond differently to the same environmental stimuli (Pride 2005a). A baseline fecal cortisol level for each female was established by calculating the mean after removing the highest and lowest 5% of values (Peel et al. 2005). These baseline cortisol levels were used when comparing the two troops' female cortisol concentrations and for establishing the relationship between cortisol and state (long-term) variables, such as female dominance rank and seasonal food availability. When establishing the relationship between female cortisol levels and event

(short-term) variables, such as rates of alarm calls and social agonism, however, all cortisol values ( $n_{\text{Troop A}} = 265$ ,  $n_{\text{Troop B}} = 42$ ) were included in analysis.

Non-parametric analyses were used because data failed to meet the assumption of normality. Mann-Whitney U and Kruskal-Wallis tests were performed using SPSS 11.0. Correlations between parameters were evaluated using Spearman's  $r_s$  (Excel's Analyse-It statistical package). The significance level for all tests (two-tailed) was set at 0.05. Mean values are presented with standard error values, unless otherwise noted.

## Results

### Fecal Cortisol Profiles

A total of 265 fecal samples were collected from Troop A females, and 42 samples were collected from Troop B females. Baseline fecal cortisol concentrations ranged from 28.75 to 75.41 ng/g for the seven Troop A females ( $n = 237$ ) and from 25.34 to 48.58 ng/g for the three Troop B females ( $n = 34$ ) (Table 3-1). Troop A females had, on average, higher baseline cortisol concentrations (mean  $\pm$  SE =  $70.45 \pm 4.58$  ng/g) than Troop B females (mean  $\pm$  SE =  $41.13 \pm 6.40$  ng/g), but the difference was not statistically significant ( $Z = -0.442$ ,  $P = 0.658$ ). Over the course of the year, the two groups demonstrated similar patterns of monthly variation in their females' baseline cortisol profiles (Figure 3-1).

### Diurnal Variation in Female Cortisol Levels

While time of day affects plasma and urinary cortisol concentrations (Coe and Levine 1995; Sousa and Ziegler 1998), this effect is less evident in measures of fecal cortisol due to the 1 to 2 day accumulation time in hormone content (Campbell et al. 2001). In my study, there was no discernable relationship between troop-level female baseline cortisol values and time of day. No significant difference existed between

morning versus afternoon female cortisol concentrations for either Troop A ( $Z = -0.401$ ,  $n = 237$ ,  $P = 0.688$ ) or Troop B ( $Z = -0.248$ ,  $n = 34$ ,  $P = 0.804$ ), and while the females in Troop A demonstrated both higher morning and afternoon averages than the Troop B females, the difference was not statistically different ( $Z_{\text{morning}} = -0.435$ ,  $n = 98$ ,  $P = 0.664$ ;  $Z_{\text{afternoon}} = -0.237$ ,  $n = 173$ ,  $P = 0.813$ ) (Figure 3-2). Further, when opportunity allowed, I collected multiple samples per female per day. Evaluation of these samples revealed no consistent increase or decrease in cortisol with time.

Similarly, there was no discernable pattern between diurnal variation in individual female cortisol concentration and seasonality. Only one Troop A female, Gina, had a significantly higher mean morning F value ( $Z = -2.854$ ,  $n = 29$ ,  $P = 0.003$ ), and the difference was significant only in the dry season ( $Z = -2.191$ ,  $n = 14$ ,  $P = 0.022$ ). On the other hand, one Troop A female, Tinkerbelle, had a nearly significant higher mean F value in the afternoon than in the morning ( $Z = -1.907$ ,  $n = 32$ ,  $P = 0.058$ ), and this difference approached significance only in the fruiting season ( $Z = -2.121$ ,  $n = 7$ ,  $P = 0.057$ ).

### **Troop Size, Female Cortisol Levels and Predation Risk**

As discussed in Chapter 2, after correcting for differences in troop size, Troop B individuals produced significantly higher monthly rates of aerial alarms (AA) (mean  $\pm$  SE =  $0.09 \pm 0.02$  AA/h per individual) than Troop A individuals (mean  $\pm$  SE =  $0.03 \pm 0.003$  AA/h per individual) ( $Z = -3.385$ ,  $P = 0.00$ ,  $n_A = 12$ ,  $n_B = 11$ ). No correlation existed, however, between the monthly AA rates of Troop B and the females' monthly F levels ( $r_s = -0.30$ ,  $P = 0.431$ ), while a strong, positive correlation existed between the monthly AA rates of Troop A and the females' monthly F levels ( $r_s = 0.74$ ,  $P = 0.009$ ). Further, an even stronger correlation existed between Troop A's monthly female F

levels and the monthly frequency with which a Harpy Eagle was observed to attack and/or be in proximity (within a 50 m radius) to the group ( $r_s = 0.80$ ,  $P = 0.002$ ) (Figure 3-3), while no correlation resulted between the same variables for Troop B ( $r_s = -0.25$ ,  $P = 0.517$ ).

As was shown in Chapter 2, no significant difference existed between the monthly rates of terrestrial predator alarms (TPA) of Troop A and Troop B after controlling for group size (mean  $\pm$  SE =  $0.008 \pm 0.001$  and  $0.010 \pm 0.003$  TPA/h per individual, respectively) ( $Z = -0.202$ ,  $P = 0.843$ ,  $n_A = 12$ ,  $n_B = 12$ ). However, while no correlation resulted between the monthly TPA rates of Troop A and the females' monthly F levels ( $r_s = -0.01$ ,  $P = 0.983$ ), there was a strong, positive correlation between the monthly TPA rates of Troop B and the females' monthly F levels ( $r_s = 0.74$ ,  $P = 0.022$ ).

Further, anecdotal evidence suggests that four of seven Troop A females produced their highest cortisol values 1 to 2 days following an encounter with a predator. The alpha female, Gina, produced her highest F level (84 times baseline) two days subsequent to a Harpy Eagle attack; Jane's highest F level (9 times baseline) resulted two days following an (out of view) encounter with a terrestrial predator in the bamboo; and Carol's and Kate's highest F levels (13 and 26 times baseline, respectively) occurred the day after a close encounter with a jaguar.

### **Troop Size, Stress, and Seasonality**

Troop A female cortisol levels were highest (mean  $\pm$  SE =  $71.60 \pm 13.46$  ng/g) during the transition season and lowest (mean  $\pm$  SE =  $44.96 \pm 5.60$  ng/g) during the dry season, while Troop B female cortisol levels were highest (mean  $\pm$  SE =  $59.73 \pm 48.00$  ng/g) during the transition season and lowest (mean  $\pm$  SE =  $21.63 \pm 8.50$  ng/g)

during the wet season. There were no statistical differences in seasonal intra-group F concentrations (Figure 3-4).

Troop A females had a higher mean F concentration than Troop B females during the fruiting (mean  $\pm$  SE = 60.92  $\pm$  10.77 and 30.73  $\pm$  5.43 ng/g, respectively), wet (mean  $\pm$  SE = 46.16  $\pm$  9.50 and 21.63  $\pm$  8.50 ng/g, respectively) and transition (mean  $\pm$  SE = 71.60  $\pm$  13.46 and 59.73  $\pm$  48.00 ng/g, respectively) seasons, but Troop B females had a higher mean F concentration than Troop A females during the dry season (mean  $\pm$  SE = 57.44  $\pm$  12.33 and 44.96  $\pm$  5.60 ng/g, respectively). There were no statistical differences in seasonal inter-group F concentrations (Figure 3-4).

### **Troop Size, Stress, and Social Rank**

As described in Chapter 2, the females in Troop A demonstrated a linear (although weak) dominance hierarchy. While the alpha female, Gina, had one of the lowest baseline cortisol values, and the most subordinate female, Tinkerbell, had the highest baseline value, there was no linear correlation between Troop A's female baseline F concentrations and social rank ( $r_s = 0.14$ ,  $P = 0.7599$ ). In fact, with the exception of Tinkerbell, graphical representation demonstrates a bell-shaped curve. A dominance hierarchy for the Troop B females could not be derived (Chapter 2), and thus I was unable to analyze the relationship between their social ranks and cortisol levels (Figure 3-5).

Troop A females were involved in a significantly higher rate of intragroup agonism, both as actors and recipients, than were the females in Troop B (Chapter 2). For neither troop, however, did the monthly rates of female agonism given or received correlate with average monthly female cortisol values (Troop A:  $r_{s \text{ receive}} = 0.06$ ,  $P = 0.863$ ;  $r_{s \text{ give}} = 0.03$ ,  $P = 0.914$ ; Troop B:  $r_{s \text{ receive}} = 0.18$ ,  $P = 0.638$ ;  $r_{s \text{ give}} = 0.05$ ,

$P = 0.8994$ ). For Troop A, however, the seasonal rate of agonism directed towards females displayed a strongly positive (although not significant) relationship to female seasonal cortisol concentrations ( $r_s = 0.80$ ,  $P = 0.20$ ) (Figure 3-6).

## Discussion

The results of my study indicate that overall, the females in the large group (Troop A) were more stressed (i.e., had higher cortisol levels) than the females in the small group (Troop B). Below I discuss the outcome of each hypothesis, considering each variable of study and how it relates to the physiological effects of disparate group size.

### Group Size Affects the Level of Stress Females Incur Due to Predation Risk

Support for this hypothesis varies according to the source of predation risk and verifies that (1) alarm calls are effective as extrinsic indicators of intrinsic stress (Boinski et al. 1999) and (2) individuals perceive their risk from aerial versus terrestrial predators differently according to group size, as discussed in Chapter 2. In support of Cowlshaw's (1997a) study that found that female desert baboons in small groups perceived the highest risk of predation, female *C. apella* in the small group were more stressed by the threat of terrestrial predators. In terms of aerial predation, however, it was the females in the large group that were most stressed by their perceived risk.

It is of interest to note that while female cortisol concentrations in Troop A strongly correlated with both the physical presence of a Harpy Eagle (actual predation risk) and the monthly rate of aerial alarms (perceived predation risk), there was no correlation between Harpy Eagle presence and aerial alarm rates ( $r_s = -0.04$ ,  $P = 0.904$ ). This is likely because a Harpy Eagle attack was often not accompanied by an outburst of alarm calls; instead, the monkeys' typical anti-predator response to a Harpy Eagle is to suddenly drop lower in the canopy, often to the ground, and remain still and silent.

The distinction between actual and perceived predation risk directly relates to a distinction between short- and long-term stress. An encounter with a predator induces an acute stress response whereby energy is diverted to the physiological functions most attuned to escape and survival. This adaptive stress response can become chronic (and thus maladaptive), however, when an individual perceives her overall risk of predation to be high, even in the absence of a predator. If perceived risk accurately predicts the actual risk of predation, even if high, then the risk would be predictable and the stress response would likely be mediated by the down-regulation of glucocorticoid receptors in the brain (i.e., producing low cortisol levels) (Sapolsky et al. 2000), as was found to occur in Belding's ground squirrels (*Spermophilus beldingi*) (Mateo 2007). The fact that Troop A females consistently had higher cortisol levels than their Troop B counterparts, and that their cortisol metabolite concentrations were highly associated with monthly rates of predator alarms, even during a year of reduced Harpy Eagle activity, indicates that predation in RV is both strong *and* unpredictable enough to warrant a continued long-term stress response.

### **Group Size Affects the Level of Stress Females Incur During Food Shortages**

This hypothesis is supported. It was the transition season, however, and not the dry season that was the most stressful time of year for both troops, and the females in the larger Troop A were significantly more stressed than the Troop B females during this time. I overlooked the importance of (un)predictability on the impact of ecological stressors and originally expected the dry season to be the most stressful season for females due to a lack of fleshy fruits. The unpredictable nature of the transition season's food supply, however, evoked more of a stress response than did a predictable lack of fleshy fruits, especially for the Troop A females.

Further, both troops' average daily travel rate was highest during the transition season (Chapter 2), and, as traveling is a noisy and conspicuous behavior, their rates of aerial and terrestrial predator alarms were also the highest during the transition season (Chapter 2). Thus, a cascade of stress was created during the transition season, not only from the variable and unpredictable food supply, but also from the subsequent need to travel further in search of adequate nutrition and the associated increase in perceived predation risk. This supports the 'chronic stress' hypothesis (Boonstra et al. 1998) that predicts synergistic effects of food and predator pressures (Krebs et al. 1995) and indicates that large-group female brown capuchins in RV are more susceptible to chronic stress.

Further validating the importance of predictability in coping with stress is the finding that Troop A was actually the least stressed during the dry season. Posthoc consideration reveals a likely explanation for this unexpected result: The seasonal decrease in fleshy fruit availability was met by the troop's increased use of the expansive bamboo patch centrally located within their home range. In fact, Troop A spent close to 60% of their time in the bamboo during the dry season, nearly double that of other seasons (Chapter 2). This bamboo patch not only provided consistently abundant (albeit lower quality), dispersed food resources (e.g., bamboo shoots and insect larvae) complements of the prior rainy season, but also provided the most protection from Harpy Eagles (a major stressor to Troop A females). Another unexpected finding regarding the dry season is that females in Troop B produced higher cortisol concentrations than the females in Troop A. This uncharacteristically higher stress, however, does not appear to be explained by any of the social or ecological

variables studied, but instead was a likely repercussion of the sudden loss of two of the troop's females during this time. Thus, female cortisol concentrations for Troop B during the dry season were actually only representative of the single remaining female in the months following the disappearance of her two female conspecifics.

The largest differential in cortisol concentrations between the females in Troops A and B occurred during the wet and fruiting seasons. Troop B females were the least stressed during the wet season, the time of year that corresponds to the peak production of *M. maripa* fruits (Boinski et al., in prep). Fruiting *M. maripa* trees provided a large quantity of food in small, dense clusters and therefore reduced the need to travel and forage. Additionally, being a small group, all Troop B individuals were typically observed to feed simultaneously without a substantial increase in agonism. On the other hand, the larger Troop A experienced more stress during the wet season, even with a substantial (*M. maripa*-related) decrease in daily travel rate (Chapter 2). As opposed to Troop B, the females in Troop A experienced an intensified dominance hierarchy and a subsequent increase in tension while feeding in the small clusters of this high-quality fruit. Females were the recipients of significantly more inter- and intra-sexual agonism from adult conspecifics while feeding on *M. maripa* (Chapter 2), and the seasonal rate of agonism directed towards females was positively (although not significantly) related to female cortisol concentrations. I suspect that the increase in stress demonstrated by the Troop A females during the dry season was largely due to the anticipation of agonism, even more so than the actual aggression itself, that can be expected during intensified intragroup competition.

## **Rank-Related Stress is a Factor of Group Size**

This hypothesis is supported, primarily due to the fact that a dominance hierarchy was determinable only among the Troop A females. The alpha female had one of the lowest basal cortisol levels while the most subordinate female had the highest basal cortisol level, and it is of interest to note that no female's basal cortisol concentration differed significantly from that of the female directly above or below her in the hierarchy. However, no linear relationship was found between female rank and basal cortisol level, and the largely bell-shaped relationship may actually indicate a cost of being a middle-ranked female in such a large troop. Establishing linearity to the hierarchy, however, was most difficult for the three middle-ranking females and seemed rather moot, and so I suspect that the bell-shaped curve is an artifact of individual variation rather than indicative of rank-related stress. Chapman et al. (2006) predicted that high variance in cortisol levels indicates stress and is in some way a function of dominance. My study provides support for this assumption, as the most subordinate female (Tinkerbelle) not only produced the highest basal cortisol level but also the most variance in her cortisol measures.

The females in the large troop were clearly more susceptible to the effects of a dominance hierarchy than were the females in the small troop; these effects, however, were most evident when the food supply was unpredictably available and/or distributed in small clumps. Otherwise, rank-related interactions did not appear to be a major source of stress for females, as was shown in rodents (Tamashiro et al. 2005) and other female-bonded species such as baboons (*Papio* spp.) and macaques (*Macaca* spp.) (Sapolsky 2005). The (weakly) linear hierarchy among Troop A females was rarely enforced, with little overt aggression between females.

## Conclusion

Optimal group size for a species is theoretically assumed to be of intermediate size (Silk 2007a). So how does one explain the long-term maintenance of suboptimal (and disparate) group size, as demonstrated by these two troops of brown capuchins? Just as females in female-philopatric societies tend to remain in their (sometimes suboptimally-sized) natal troop because the benefits of staying outweigh the costs of migration, a group is not likely to bear the costs of adjusting size (e.g., re-establishing territories and dominance relationships) in order to better fit environmental challenges when the environment is so dynamic and the challenges so unpredictable (Pride 2005a).

In this chapter, I demonstrated that group size and ecological context interact to affect an animal's internal state, which may be a critical proximate factor linking these environmental pressures to individual fitness (Pride 2005a). In particular, cortisol data suggest:

- Females incur a cost-benefit tradeoff of disparate group size. A large group may provide a more stable system for coping with major socioecological fluctuations over the long-term, but incur increased stress in day-to-day life, as demonstrated by the high cortisol values of the Troop A females. A small group, such as Troop B, is less dynamic; individual group members better endure the daily challenges of ecological variation, but are vulnerable to any major social upheaval or environmental shift. The sensitivity of small-group females to large-scale social disruption occurs in rodents (Haller et al. 1999) and was evident in my study through the increase in cortisol concentration and the prolonged increase in the variance of cortisol of the only remaining female in Troop B in the months following the disappearance of her two female conspecifics.
- In a high risk, low energy environment such as RV, female brown capuchins in large groups are susceptible to chronic stress, particularly in response to predation risk and an unpredictable food supply. These females are assumed to be "physiologically challenged" (Chapman et al. 2006) and may face long-term fitness consequences. In the following chapters, I investigate in further detail the nature of the fine-scaled social relationships of females in Troop A to determine

the social, ecological and reproductive factors most closely associated with their stress levels.

Table 3-1. Baseline values of individual female fecal cortisol concentrations. Each female's baseline value is the calculated mean after removing the highest and lowest 5% of values, and was used to analyze the effect of state (long-term) variables, such as troop size, dominance rank and seasonality, on cortisol concentrations. The baseline cortisol concentration (ng/g) of Troop A was (non-statistically significant) higher than that of Troop B.

Troop	Female	<i>n</i>	F baseline range (ng/g)	F baseline value (ng/g ± SE)
A	Kate	34	3.3 - 252.4	28.75 ± 7.46
	Gina	29	7.2 - 200.4	37.21 ± 8.73
	Carol	37	7.3 - 298.0	49.08 ± 10.15
	Little Horns	40	9.9 - 261.5	57.40 ± 9.28
	Banana	38	4.3 - 271.2	61.72 ± 10.30
	Jane	27	10.5 - 286.1	68.04 ± 14.15
	Tinkerbell	32	7.2 - 445.1	75.41 ± 20.88
	TROOP A	237	3.3 – 445.1	53.86 ± 4.58
B	Mrs. Slocum	10	5.4 – 79.9	25.34 ± 7.05
	Luna	5	29.0 – 86.2	44.38 ± 10.61
	Miss Brahms	19	6.1 – 155.7	48.58 ± 10.20
	TROOP B	34	5.4 – 155.7	41.13 ± 6.40

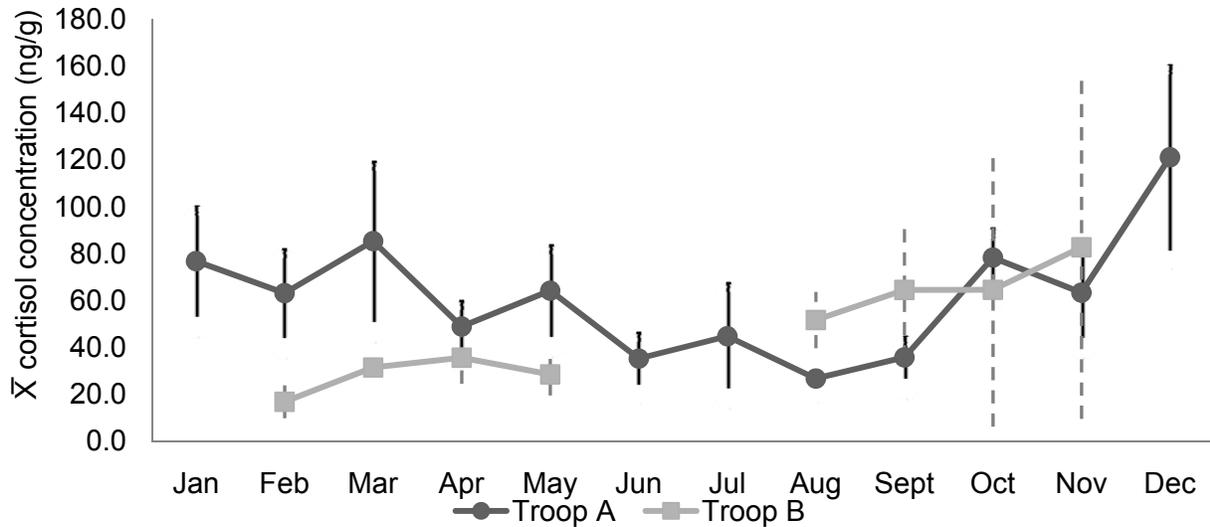


Figure 3-1. Troop-level fecal cortisol (ng/g ± SE) profiles of Group A and Group B females, based on average monthly baseline values. Troop A ♀:  $n=7$  (January to September),  $n=6$  (October to December); Troop B ♀:  $n=3$  (January to July),  $n=1$  (August to December). Values are not included for Troop B in the months of January, June, July and December due to insufficient data. Although Troop A females tended to have cortisol concentrations that were, on average, higher than Troop B female cortisol levels, the two troops demonstrated similar patterns of monthly variation in their females' baseline cortisol profiles.

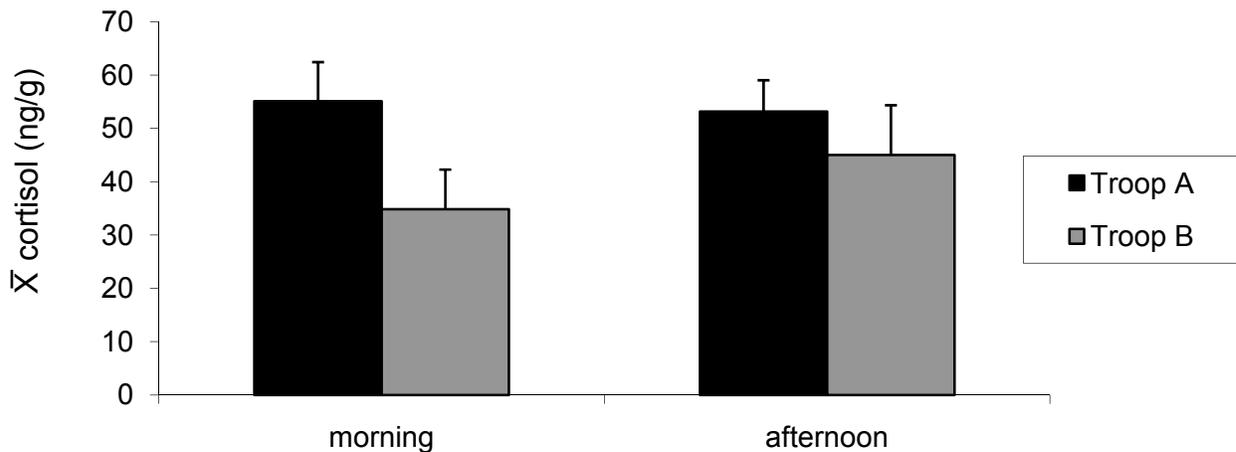


Figure 3-2. Morning versus afternoon cortisol levels (ng/g ± SE) for Troop A and Troop B females. Although the females in Troop A demonstrated higher morning and afternoon averages than the Troop B females, no statistical inter- or intra-troop difference existed in the females' morning and afternoon cortisol levels.

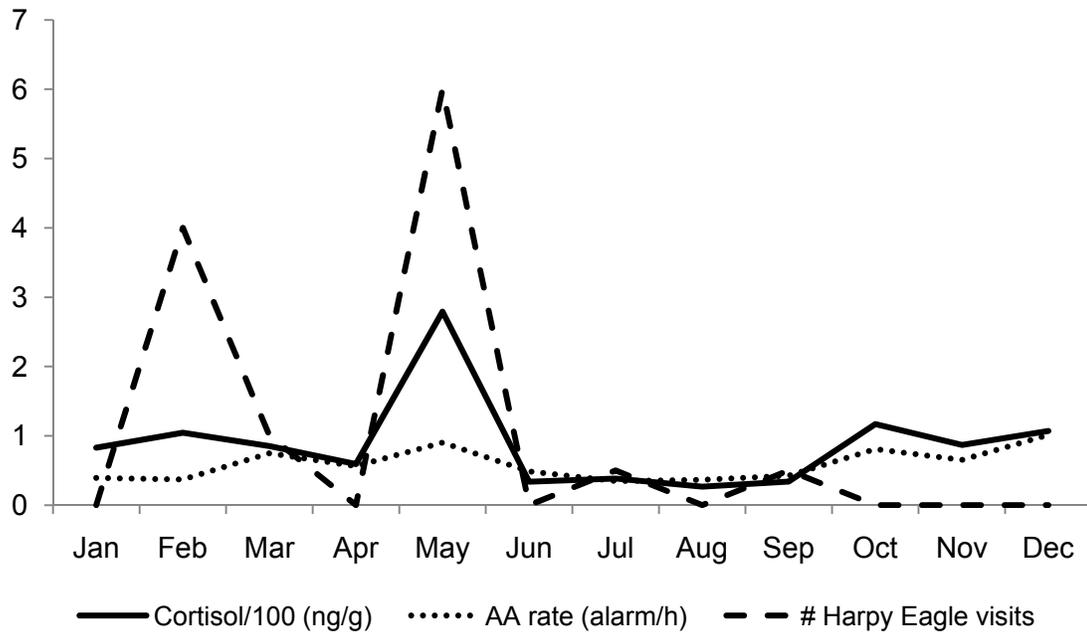


Figure 3-3. Monthly comparison of the rate of aerial alarms (AA/h) produced by Troop A, observed number of Harpy Eagle attacks and/or attendance to the troop within 50 m, and mean cortisol levels of Troop A females. A strong, positive correlation existed between the monthly rates of AAs and the females' monthly cortisol levels ( $r_s = 0.74$ ,  $P = 0.009$ ). An even stronger correlation existed between the monthly presence of Harpy Eagles and the females' cortisol levels ( $r_s = 0.80$ ,  $P = 0.002$ ).

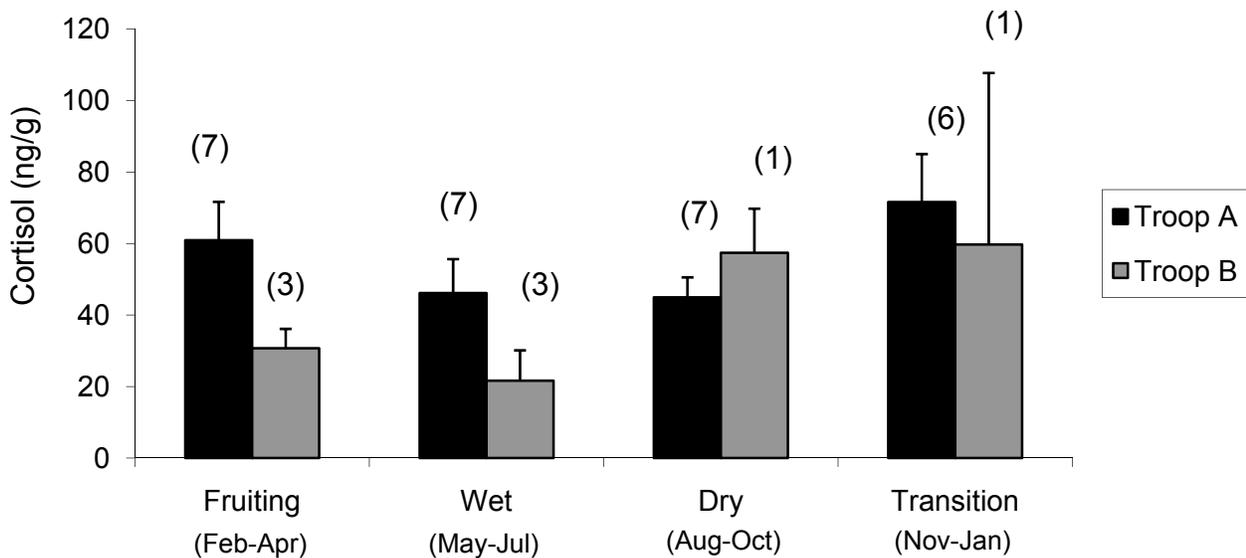


Figure 3-4. Seasonal comparison of average baseline cortisol levels (ng/g  $\pm$  SE) for Troop A and B females. The number of females present in each troop during each season is indicated in parentheses. Troop A female cortisol levels were the highest during the transition season and lowest during the dry season, while Troop B female cortisol levels were highest during the transition season and lowest during the wet season. Troop A females had a higher mean cortisol concentration than Troop B females during all seasons except the dry season, a time confounded by the disappearance of two of the three Troop B females. The largest intergroup differential in female cortisol concentrations occurred in the fruiting and wet seasons when fruits were distributed in small clumps.

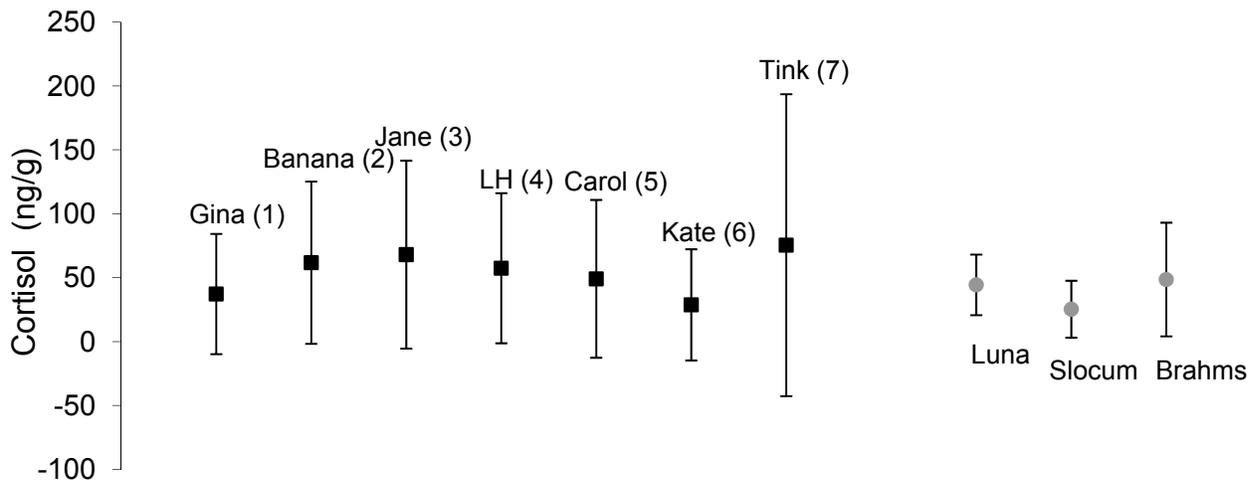


Figure 3-5. Mean baseline cortisol concentrations (ng/g  $\pm$  SD) of individual adult females in Troop A by their respective dominance rank (in parentheses). Mean baseline cortisol concentrations of Troop B females are also shown for comparison, although a dominance hierarchy could not be established among them. The females in Troop A demonstrated a (weakly) linear dominance hierarchy, although their respective baseline cortisol levels did not correlate with rank. Still, however, the alpha female had one of the lowest baseline values while the most subordinate female had the highest baseline value with the most variance. ■ Troop A ♀ ● Troop B ♀

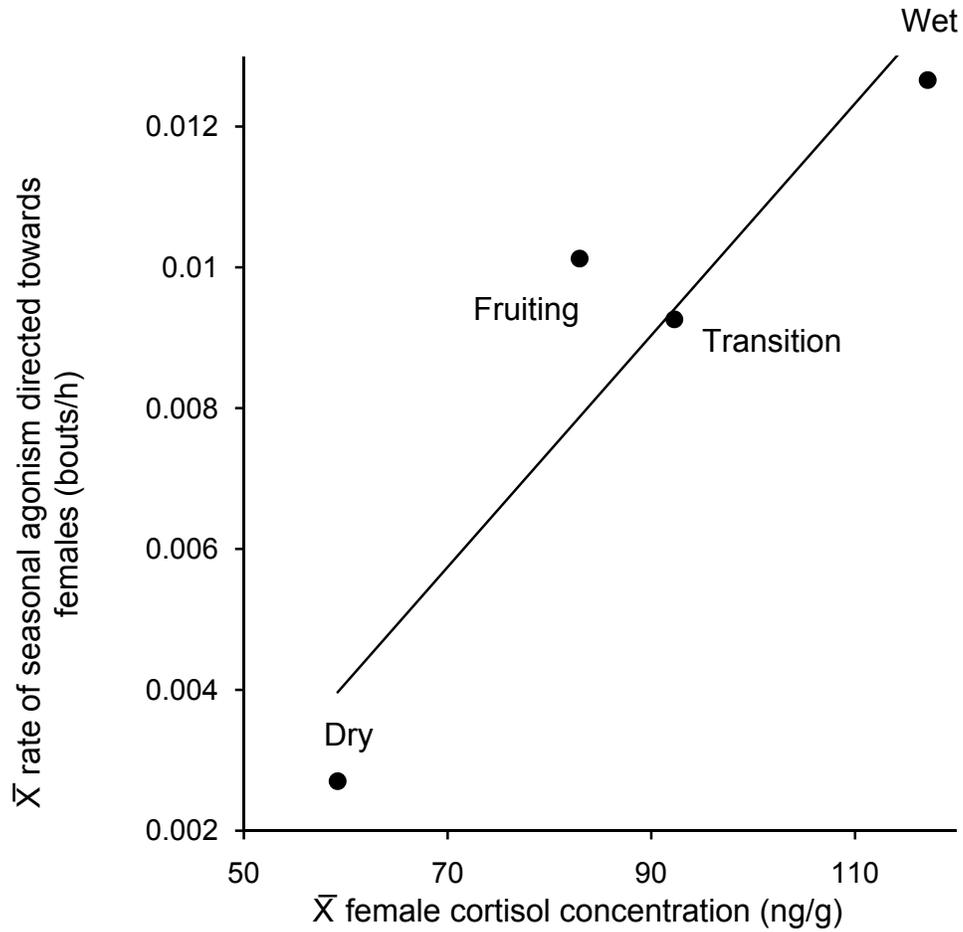


Figure 3-6. Seasonal cortisol concentrations (ng/g  $\pm$  SE) of Troop A females and the rate at which females were the recipients of social agonism from conspecifics (bouts/h). The seasonal rate of agonism directed towards females was strongly and positively (although not significantly) related to female cortisol concentrations ( $r_s = 0.80$ ,  $P = 0.20$ ).

CHAPTER 4  
FEMALE-BONDED PRIMATES? GROOMING AND PROXIMITY PATTERNS OF  
FEMALE BROWN CAPUCHINS IN SURINAME

**Introduction**

Despite the abundant use of the term ‘social bond’ (or one of its many variants) in published articles and the growing literature regarding the functional, adaptive, and theoretical consequences of bonds, there remains a fundamental source of confusion that precludes systematic comparison of related research: What *is* a bond? The term ‘bond’ (a.k.a. social bond, relationship, friendship) is loosely defined, often not operationalized, and used to characterize a variety of social situations (Figure 4-1). For example, ‘bond’ can be synonymous with ‘pair bond’ or ‘cross bond’ between the sexes, in which the term is typically used to describe non-random sexual behavior. For same sex relationships, however, the usage of ‘bond’ becomes more ambiguous, and many authors do not clearly define or consistently apply their use of the term (Figure 4-1). Female-bonded, for example, could indicate either the presence of female philopatry, or differentiated, affiliative relationships between females, which may or may not be kin-based.

**Using Affiliative Behavior as a Proxy Measure of Social Bonds**

When ‘social bond’ is used to describe a highly affiliative relationship between two individuals, relationship strength is typically measured as grooming investment and/or time spent in proximity. Females with the strongest grooming relationships have the strongest and most enduring social bonds (Silk 2007b), and non-random proximity patterns are suggested to indicate indirect affiliation between individuals (Fragaszy et al. 2004). As such, female-bonded primates are expected to groom and spend more time in close proximity with other females than with males.

But are grooming and proximity maintenance equivalent measures of relationship quality, or does use of varying indicators further confound the ambiguity of social bonds? Grooming relationships, by default, include the costs and benefits associated with proximity maintenance; the reverse, however, cannot be said. In fact, Henzi et al. (2003) reported that female baboons did not preferentially groom those females that most frequently maintained nearest neighbor proximity. Is a dyad that demonstrates higher than average time spent in proximity but does not groom considered socially bonded?

Whether or not grooming and proximity are even truly indicative of a bond is also debated. Barrett and Henzi (2002) suggested that both grooming and proximity patterns are labile and therefore not indicative of a long-term bond but rather are currencies to be traded as a short-term strategy. This brings to light another issue of ambiguity concerning social bonds: Just how stable or lasting must a relationship be before the participants are truly bonded? Are long-term bonds (“friendships”) and short-term bonds (“business partnerships”) really so different? There must be some adaptive advantage to the benefits of non-random dyadic affiliation, no matter how fleeting, or else the participants would not invest the time and energy into such behavior. Whether a social group’s relationships are short- or long-lasting is intriguing in itself, and understanding the nature of and variation in bonding patterns, especially variation within-species, will help us to understand the socioecological factors underlying and influencing sociality.

### **A Female-Bonded Primate?**

The distribution of females and female relationships is widely understood to be at the core of primate social groups (Emlen and Oring 1977; Mitchell et al. 1991; van Hooff

and van Schaik 1994); the structure of female social relationships, however, is less understood. While female relationships vary according to local circumstance and in response to the current tradeoffs of the costs and benefits of dyadic association (Barrett et al. 2002), female social bonds are typically presented as a dichotomous, species-level characteristic.

Capuchin monkeys (*Cebus spp.*) present a propitious system to test social evolution models derived largely from Old World monkeys (Parr et al. 1997). Capuchins are unique among platyrrhines in that female philopatry is clearly prevalent throughout the genus, a feature common to catarrhines. Although female philopatry is not a necessary condition for the development of social bonds between females (Byrne et al. 1990; van Schaik 1989), a female philopatric group provides a study system conducive to long-term observation of females with invested relationships and a history of repeated interaction.

Not only are all *Cebus* species female-philopatric, but all are also categorized as strongly female-bonded (Janson and Boinski 1992; Fedigan 1993; O'Brien 1993; Perry 1996; Di Bitetti 1997; Manson et al. 1999). For example, among *C. capucinus*, females spent more time in proximity to other adult females than adult males, and females groomed other females twice as often as they groomed males (Perry 1996). Similarly, Di Bitetti (1997) concluded that female *C. apella* in Argentina established stronger grooming bonds between each other than did males. Do such findings, however, substantiate classification for the entire species, or could such social behavior be site- or time-specific? Recent finding from Brazil introduced a *C. apella* population that lacked female grooming bonds (Izar 2004), and preliminary observations of female

*C. apella* in Suriname suggested both temporal and individual variation in intrasexual relationships (Boinski, unpublished data).

In the previous chapters, I examined troop-level socioecological and endocrinological variables related to the costs and benefits of sociality for female brown capuchins living in groups of disparate size. In this chapter, I focus on fine-scaled within-group variation in female social behavior and quantitatively determine the structure of and temporal shifts within their relationships. For purposes of my study, I defined a social bond as the outcome of similar affiliative strategies between two individuals in a socially cohesive group, and I operationally defined a female bond as one in which a female's primary adult social partner, measured through grooming and proximity, is another female.

## **Hypotheses**

### **Social Bonds among Female Brown Capuchins are Variable Over Time**

Social relationships are identified through the frequency and patterning of interactions over time, and a long-held premise underlying primate sociality is that in stable, coherent groups, strongly differentiated and enduring relationships between females will always be detectable (Henzi et al. 2009). Silk et al. (2006b) measured bond stability as the number of consecutive years in which a female was among another female's top three affiliative partners; they determined that, among savannah baboons (*Papio cynocephalus*), females demonstrated considerable annual stability in their social bonds with some dyads (typically of related females or females of similar age and rank) maintaining close bonds for at least 3 years, and some for more than 5 years. While they acknowledged the presence of more ephemeral social bonds, Silk and her colleagues focused on the longer-lasting relationships that they characterized as 'strong

family ties' and 'friendships'. How much variation was lost, however, when examining dyadic behavior in annual groupings?

The expression of affiliative behavior varies according to ecological conditions (Schino and Aureli 2008), and Barrett et al. (2002) argued that female relationships are more variable than stable, with females exploiting temporary, short-term social relationships. Female chacma baboons (*Papio cynocephalus ursinus*) residing in a seasonal environment were more 'business partners' than 'friends', demonstrating monthly and yearly inconsistencies in their preferred grooming partner and using grooming behavior as a commodity to be bartered for their short-term advantage (Barrett and Henzi 2002).

Preliminary observations of the brown capuchins in RV indicated that female *C. apella* social relationships are more variable than is expected for a 'female-bonded' species. In the years prior to my study, adult females were initially observed to focus their grooming on adult males and only rarely groom other females. A short time later, however, patterns of female-female affiliation shifted, becoming more 'typical' of what is expected of *C. apella* females (Boinski, unpublished data). Thus, both temporal and individual variation in the intensity of female *C. apella* relationships exists at RV. I predicted that females do not *consistently* demonstrate stronger grooming and proximity relationships with other females than with adult males.

### **Dyadic Female Relationships Vary in Response to Ecological Pressures**

Given the premise that individuals form and maintain relationships in response to potential benefits, patterns of social interaction should reflect the desirability of partners and the benefits provided by the relationship (Schino and Aureli 2008). In an environment characterized by social and ecological change, I contend that investment in

relationships should follow a similar pattern – as circumstances change, so do the benefits of particular dyadic interactions. Henzi et al. (2009) provided empirical evidence that female chacma baboons (*Papio hamadryas ursinus*) displayed seasonal changes in social relationships in response to ecological conditions. At times, most notably during the food-scarce season, the females formed short-term companionships with various partners; during the food-abundant season, however, females displayed no particular affiliative partner connections and were best viewed as “simply gregarious”.

Social bonds are suggested to be instrumental in improving access to resources by creating tolerance and securing agonistic support (Henzi and Barrett 1999), and tolerance by dominant individuals may significantly increase feeding success of subordinates, especially in small patches (Janson 1990a). In fact, a meta-analysis of dominance hierarchies, grooming patterns, and ecological conditions determined that steeper dominance hierarchies were associated with more (non-reciprocal) grooming being directed up the hierarchy (Schino and Aureli 2008). Therefore, social bonds can be viewed as a proactive strategy to counteract ecological variation.

As was shown in the previous chapter, the transition season (November to January) was the most stressful time of year for female *C. apella* in RV, presumably due to the unpredictable nature of the food supply; the wet season (May to July), however, was the time of year that Troop A females received the most agonism from troop-mates, presumably due to the peak fruiting of a food resource that is distributed in small, monopolizable clusters. Therefore, I predicted that females non-randomly increase affiliative behavior during the transition and wet seasons, and that the intensified grooming would be directed up the hierarchy more so than in the other seasons.

## **Relationships among Females Strengthen with the Presence of an Infant**

Among baboons (*Papio cynocephalus ursinus*), infants are used as a commodity within a biological marketplace, such that non-mother females groom the mothers of young infants in exchange for access to the infants (Henzi and Barrett 2002). Providing an adaptive explanation for this behavior, Strier (1999) suggested that strong female relationships are vital for primates as their slow-paced developmental patterns encourage cooperative infant rearing that is exemplified by their carrying and nursing of infants other than their own (Fragaszy et al. 2004). Further, Silk et al. (2003) provided empirical evidence that infant survival was significantly associated with the level of social integration of post-partum females. Therefore, I predicted that females with young infants (< 3 months old) would be more socially integrated than non-mothers, and that mothers would be more likely to groom and/or be groomed by other females in response to the physical presence of their infant.

## **Methodology**

### **Site Description**

Raleighvallen Nature Preserve (RV), a 7812 km<sup>2</sup> reserve consisting of primary tropical rain forest, is located within the 1.6 million ha Central Suriname Nature Reserve in Suriname, South America. The main study site measured approximately 2 km<sup>2</sup> and was covered by an extensive trail system. RV's flora and fauna are effectively undisturbed in the historical period, and an intact array of potential predators and competitors are present (Reichart 1993). The forest in RV is ecologically distinct as compared to other areas where brown capuchins are commonly studied. The soils of the Guyanan Shield (including the Guianas and Suriname) are nutrient-poor and highly weathered as they are derived from Precambrian bedrock. Fleshy fruits are low in

abundance and available fruit resources typically occur in small patches (< 5 m diameter) (Boinski et al. 2002). Additionally, much of RV is composed of expansive bamboo patches and dense liana forest that restricts visibility (Boinski et al. 2003).

### **Study Animal**

The brown capuchin monkey (*Cebus apella*) is one of the four traditionally recognized species in the genus *Cebus* (Hill 1960). Capuchins live in multi-male, multi-female polygamous groups that are typically female philopatric. Adult males and females maintain separate dominance hierarchies; in general, males are dominant to females. *C. apella* social groups are typically comprised of 12 to 27 individuals, with an average troop size of 17 members. Troop membership and relationships remain relatively stable, except for subadult males who emigrate from their natal group and may subsequently transfer several times. Brown capuchins reside in a variety of habitats encompassing a large geographic range from Columbia to Argentina (Fragaszy et al. 2004). *C. apella* are omnivores; the bulk of their diet consists of fruit supplemented with seeds, vegetation, arthropods, and vertebrates (Terborgh 1983).

The study troop (Troop A) was one of four brown capuchin groups commonly observed within the study site, and the primary study subjects were the adult females and their relationships to the adult members of the group (Table 4-1). For most of the study, Troop A consisted of 27 individuals, seven of which were adult females. During the study, one pregnant female disappeared; her disappearance coincided with her predicted due date, and thus it is possible her (presumed) death was related to pregnancy or labor-related complications. Relatedness among troop members is unknown; however, genetic analysis of the brown capuchin population in RV is currently underway. The study troop had been habituated to human observers since 1998, and

all individuals were recognized based on body size, color patterns, and other identifying characteristics such as scars, moles, and ear shape. Throughout the study period, inter-observer reliability tests were conducted monthly to ensure consistent and accurate identification of all troop members.

### **Data Collection**

From January to December 2006, I and/or field assistants followed the study troop for up to 10 h each day (beginning at sunrise). Troop A was followed, on average, 28 days per month, comprising a total of 2284 h of observation (not including 'out of view' time). The following behavioral data were collected:

(1) Individual instantaneous scans. In order to determine each female's primary proximity partners and social network shifts over time, I collected instantaneous scans each time a female was in view and her nearest neighbors could be reliably identified. Each scan effectively provided a "snap-shot" of that moment in time, including the female's location in the troop, her behavior, and the identity and behavior of all visible neighbors. Scans were not taken on females involved in direct social behavior such as grooming or aggression; thus, the scans represent an indirect measure of affiliation based on close proximity during travel, feeding, resting, etc. Furthermore, a female was never scanned while she was in estrus, as that would likely bias the data towards male neighbors. Peripheral females were scanned as frequently as were the more central females. A total of 787 scans were collected on Troop A females throughout the study.

(2) Ad libitum notes. *C. apella* social behavior (agonistic, grooming, and sexual) accounts for <10% of their daily activity budget (Zhang 1995a). Therefore, ad libitum sampling (Altmann 1974) provided a more efficient and complete data collection technique for capturing social interactions than did a more structured sampling regime.

Social behavior, such as grooming, play, and agonism, as well as other opportunistic occurrences such as predator interactions, intergroup encounters, and reproductive behavior were noted ad lib. To reduce observation bias, I moved constantly through the groups to locate non-visible individuals and record their activities. Due to opportunistic sampling, as well as the reduced visibility within the Raleighvallen forest, the recorded frequencies of social behavior are likely underestimates of the true frequencies. Because of the large number of hours over which behavioral interactions were recorded, however, I am confident that the data provide strong indication of actual trends.

### **Behavioral Definitions**

A female's social network was defined as the sub-group of conspecifics most frequently observed within a 4 m proximity. A female bond was defined to occur when a female's primary adult social partner (in terms of grooming and/or proximity patterns) is another female. An adult dyad was considered to have a "strong bond" (based on grooming or proximity) if their dyadic grooming duration or proximity score (see below) fell within the top 10% for the group (Silk et al. 2006a).

Grooming bout duration and frequency was recorded for all observed occurrences. A grooming bout involved one individual grooming another, and concluded when the grooming ended or was interrupted by another behavior for more than 5 seconds. A new grooming bout began with a new dyad, or whenever the grooming continued or changed direction within the same dyad. Only grooming bouts involving at least one female (as actor or recipient), and where both participants could be identified (at least to the age and sex class) were included for analysis. All grooming bouts were counted as dyads; thus, if two monkeys were grooming the same individual concurrently, the

episode was scored as two separate actor-recipient grooming bouts. Grooming bouts involving females in estrus (as actors or receivers) were not included in analysis.

Agonism includes all instances of aggressive, displacement, and submissive behaviors. Aggressive behaviors include chase, hit, bite, and threat display. Displacement involved one individual passively supplanted by another, usually (but not exclusively) at a food source; if an individual aggressively displaced another individual, then the bout was scored as 'aggression' and not 'displacement'. Submissive behaviors included any instance in which an individual retreated and/or reacted with submissive posture or vocalizations without being aggressed towards or displaced. Only agonistic bouts involving at least one female (as actor or recipient), and where both participants could be identified (at least to the age and sex class) were included for analysis. All agonistic events were counted as dyads. If the agonism involved a coalition against a third party, only the initial instigator and victim were scored. Agonistic events involving females in estrus (as actors or receivers) were not included in analysis.

## **Data Analysis**

### **Dominance ranks**

Female ranks were determined by the outcomes of decided female-female agonistic episodes. All agonistic bouts were categorized as either 'decided' or 'undecided'. I considered an agonistic bout as 'decided' if: (1) identities of participants were known; and (2) one individual displayed only aggressive signals whereas the other only displayed submissive behavior, or (3) one individual displayed submissive signals, whereas the other individual displayed no agonistic behavior. All other disputes were considered to be 'undecided' (Silk et al. 2006b). Dyadic agonistic bouts between

females were constructed into a dominance matrix to determine the hierarchical nature of female relationships (Ferreira et al. 2006).

### **Proximity scores**

To determine females' primary proximity partners and social network shifts over time, I collated the scan data into monthly patterns of association. A female's social network included those conspecifics most frequently within a 4 m radius (a post-hoc, empirically-based boundary). Monthly proximity scores for each female were calculated (1) for each adult dyad, and (2) by the age/sex class categories of neighbors: adult males (MPS), adult females (TFPS), and all neighbors within 4 m (adult males, adult females, and immatures) (TPS). Additionally, as 4 of the 7 females had dependent infants in the initial months of the study, I was able to investigate the social effect that young infants have on their mothers. I calculated proximity scores separately for the mothers based on the physical presence of their young infants (i.e., while they were and were not carrying their infants) and also differentiated female neighbors that were carrying an infant (FwiPS) from female neighbors that did not have an infant (FPS).

Following Perry (1996), proximity scores were calculated as follows: For each adult dyad (and age/sex class), I tallied (by month) the number of scans that a particular adult male or female individual was within 0 to 1 m, 1 to 2 m, 2 to 3 m, and 3 to 4 m of each female. Neighbor presence was not mutually exclusive, and therefore multiple neighbors could be included in one female scan. Because close neighbors were less likely by chance to be near a female than are more distant neighbors, I multiplied the four scores by weighting factors, such that the closer proximity categories were weighted more heavily. Weighting factors were determined using concentric spheres, with the focal female in the middle, such that the innermost sphere has radius one, the

second sphere has radius two, the third sphere has radius three, and the outer sphere has radius four. The weighting value for the 0 to 1 m category is the reciprocal of the volume of a sphere of radius one; the weighting value for the 1 to 2 m category is the reciprocal of the difference between the volume of a sphere of radius two and the volume of a sphere of radius one, etc. For comparative purposes, these four scores were grouped into a single proximity score. Thus, the equation for calculating the proximity score is:  $\text{Proximity score} = 1,000(0.239a + 0.034b + 0.0126c + 0.0065d)$ , where 'a' is the proportion of a female's total monthly scans in which a neighbor was within 0 to 1 m of the scanned female, 'b' is the proportion of scans in which a neighbor was within 1 to 2 m of the scanned female, and so on. When calculating proportions for female-female dyads, the total number of scans for each of the females in the dyad was summed. The sum of the four weighted values is multiplied by the arbitrary value of 1,000 to make the proximity score more readable. The higher the proximity score, the more time the female spent in close proximity to that individual (or age/sex class).

### **Grooming**

Data were only included in this analysis if the identities (for adults) or age class (for immatures) of the participants were known. All grooming bouts were counted as dyads; thus, if two monkeys were grooming the same individual concurrently, the episode was scored as two actor-recipient grooming bouts within the same grooming session. In order to maintain consistency with the proximity data, grooming bouts involving females in estrus (as actors or recipients) were not included in analysis.

### **Statistical analysis**

Both parametric and non-parametric analyses were used. Non-parametric analyses were used when data failed to meet the assumption of normality.

Homoscedasticity was tested using Levene's Test for Equality of Variances; if Levene's test indicated heterogeneous variances, I used square root transformations. I used the Mann-Whitney U test when comparing two independent samples and the Wilcoxin sign-rank tests for comparing two related samples. When comparing more than two samples, I used either one-way ANOVA in conjunction with Tukey's post hoc tests or, when data remained non-normal even after logarithmic transformation, the Kruskal-Wallis one-way ANOVA in conjunction with Mann-Whitney U tests as the non-parametric alternative to posthoc tests. To investigate whether an observed frequency distribution fit an expected one, I used the Chi-square goodness of fit test. Correlations between parameters were evaluated using Spearman's  $r_s$  (Excel's Analyse-It statistical package). Analyses were performed using SPSS 11.0; the significance level for all tests (two-tailed) was set at 0.05. Mean values are presented with standard error values, unless otherwise noted.

## **Results**

### **Dominance Hierarchy**

Only 27 'decided' agonistic bouts between females were observed (0.01 bouts/h), of which 63% involved displacement, 30% were aggressive, and 7% involved submissive behavior only. Due to low values, the dominance matrix of female-female agonistic frequency was not possible to test statistically. Therefore, dominance relationships among females were not solely determined by the frequencies of dominance interactions. Among the 21 dominance relationships, 13 were decided based on agonistic frequency. Zero-ties accounted for eight dyadic relationships, of which four were decided by applying the transitive property, such that  $a > b$ ,  $b > c$ , therefore  $a > c$  (Izar 2004). The dominance relationship between Banana and Jane,

however, was decided based not on the interactions between them, but on the observation that Banana aggressed towards the dominant female without receiving retaliation. Jane was never observed to challenge the dominant female, and therefore Banana received a higher ranking than did Jane. The remaining unknown relationships (especially between Kate and Tinkerbell) stemmed primarily from Tinkerbell's lack of interaction with other females. Tinkerbell was presumed to be the youngest of the group's adult females, and remained peripheral to the troop throughout the study (except during estrus). In fact, she scored a TFPS near 0.0 and was the female least involved in female-female grooming (see below). Therefore, I ranked Tinkerbell as the least dominant female (Table 4-2).

### **Female Coalitions**

Females were observed to participate in 46 coalitions, 40 of which were dyadic and the remaining six were triadic. Fifty-five percent of dyadic coalitions involved a male-female pair, 35% involved a female-female pair, and 10% involved a female-juvenile pair. The most frequent (26%) coalition partners were the alpha male and the alpha female (Gina). The second most frequent (21%) coalition partners were the two highest ranking females (Gina and Banana). The six triadic coalitions involved various groupings of Gina, Banana, the alpha male, and one of the subordinate males. Coalitions were formed to threaten conspecifics, mob potential dangers (e.g., snakes), and threaten human observers. Females were never observed to form coalitions against another female; three of the female-female coalitions were directed at an adult male.

## **Troop Patterns of Affiliation**

### **Proximity**

Overall, adult female proximity scores with males (MPS) were significantly higher than female-female proximity scores (TFPS), despite a 3:7 male to female sex ratio ( $Z = -2.301$ ,  $P = 0.021$ ). Female MPS scores increased with female rank, while there was no clear pattern between TFPS scores and female rank. The alpha female demonstrated a higher average TFPS score than MPS score while the remaining females had higher average MPS scores than TFPS scores. Statistical comparison of scores, however, yielded only two significant results: Little Horns and Tinkerbell had significantly higher MPS scores than TFPS scores ( $Z_{\text{Little Horns}} = -2.395$ ,  $P = 0.017$ ;  $Z_{\text{Tinkerbell}} = -2.668$ ,  $P = 0.008$ ). On average, the two most dominant females had total proximity scores (TPS), including female, male and immature neighbors, almost three times higher than the subordinate females (Table 4-3).

### **Grooming**

I recorded 1574 dyadic grooming bouts (with known direction and participants) between Troop A members (0.69 bouts/h), 1013 of which (64%) involved at least one female. On average, females spent 1.8% of their monthly activity budget on grooming (as actors and/or receivers). The amount of time females spent grooming adult troop-mates was in (approximate) positive association with female rank. The amount of time that females received grooming from adult members of the troop, however, did not appear associated with rank (Figure 4-2). Females groomed up and down the hierarchy at equal rates; there was no significant difference in the monthly rate (min/h) that subordinate females groomed dominant females (mean  $\pm$  SE =  $0.030 \pm 0.008$ ) and

dominant females groomed subordinate females (mean  $\pm$  SE = 0.029  $\pm$  0.009) ( $Z = -0.11$ ,  $P = 0.909$ ,  $n = 26$ ) (Figure 4-3).

Overall, females gave a significantly higher rate (min/h) of grooming than they received ( $Z = -3.059$ ,  $P = 0.002$ ,  $n = 12$ ). Females acted as the groomer in 817 bouts (81%) and as the recipient in 371 bouts (37%). Females devoted 1937.7 min to grooming conspecifics, with juveniles receiving the largest percentage (36.1%) and females receiving the least (19.1%). Females received a total of 755.1 min of grooming from conspecifics, the largest percentage of which was received from females (49.1%). Not including infants, adult males groomed females the least (17.2%) (Table 4-4, Figure 4-4).

Duration of adult grooming bouts significantly differed by sex ( $F = 5.767$ ,  $P = 0.003$ ,  $df = 2$ ). Females groomed males for a longer duration per bout (mean  $\pm$  SE = 3.1  $\pm$  0.271 min) than females groomed females (mean  $\pm$  SE = 2.1  $\pm$  0.165 min) ( $P = 0.022$ ) (Figure 4-5), and females groomed males longer per bout than males groomed females (mean  $\pm$  SE = 2.1  $\pm$  0.323 min) ( $P = 0.008$ ). Only 30% of the adult grooming bouts were reciprocal. Female-male grooming dyads tended to be slightly more reciprocal than were female-female grooming dyads (26.1% and 24.7%, respectively).

## **Individual Patterns of Affiliation**

### **Proximity**

Following Silk et al. (2006b), I classified the dyads that fell within the top 10% of all proximity scores as having “strong bonds”. Although the 10% subset may seem arbitrary, it was also a clear empirical break in the data: Strong bonds resulted from dyadic proximity scores higher than 100; the next highest proximity score was 83. Of

the 21 possible female-female dyads, only one was represented in the strong bonds, whereas 3.5 female-female dyads fell within the lowest 10% of proximity scores. By contrast, of the 21 possible female-male dyads, four resulted in strong bonds, and none fell within the lowest 10% of scores (Appendix C).

Those strongly bonded dyads included, in descending order: Gina and Boris (272.49); Gina and Banana (233.69); Banana and Gina (233.27); Banana and Boris (151.67); Jane and Boris (114.05); and Tinkerbell and Boris (110.03). Thus, the only strong (proximity) bond observed between females (Gina and Banana) was also an equitable one. The remaining strong bonds were represented by the three highest-ranking females and the alpha male, with one exception. The strong bond between Tinkerbell and Boris was surprising, given her low rank and overall lack of gregariousness (Table 4-5). Tinkerbell's high proximity score with Boris actually resulted from three uncharacteristic occurrences (further confounded by her overall lack of proximity data) and should not be taken at face-value. Monthly measures of her proximity to the alpha male varied drastically, with a mean monthly value of 11.0 and standard deviation of 17.31; thus the mean is an unreliable predictor of Tinkerbell's true proximity-based relationship with Boris.

### **Grooming**

Following Silk et al. (2006b), I classified the dyads that fell within the top 10% of total grooming duration (min) as having "strong bonds". Of the 21 possible female-female dyads, only one was (reciprocally) represented in the strong bonds. Four female-female dyads were never observed to groom, and in four additional female-female dyads, one partner was never observed to groom. Of the 21 possible female-male dyads, five strong grooming bonds occurred: one that was reciprocal within

the dyad, and four that involved unidirectional grooming of the alpha male by females. Five female-male dyads were never observed to groom, interestingly three of which involved the three highest-ranking females (who were strongly bonded to the alpha male through grooming and proximity) and the same subordinate male. Tinkerbelle was the only female that did not groom the alpha male, Boris, and she was the only female that he was not observed to groom. In five additional female-male dyads, one partner was never observed to groom (Appendix D).

The strongly bonded dyads included, in descending order (groomer and recipient): Gina and Boris (86.5 min); Gina and Banana (83.8 min); Banana and Boris (82.5 min); Kate and Boris (51.2 min); Banana and Gina (49.8 min); Little Horns and Darwin (40.6 min); Jane and Boris (36.3 min); and Darwin and Little Horns (30.2 min). The only strong (grooming) bond observed between females (Gina and Banana) was also an equitable one; the only other equitable strong grooming bond was that between Little Horns and Darwin. All other strong grooming bonds involved a female (the three highest-ranking females and a low-ranking female with a young infant) grooming the alpha male, and these grooming relationships were considerably inequitable (Table 4-6).

### **Grooming versus proximity**

Dyadic total proximity scores and grooming durations were modestly correlated ( $r_s = 0.41$ ,  $P = 0.0010$ ,  $n = 63$ ) (Figure 4-6), a pattern that held true when considering female-female ( $r_s = 0.41$ ,  $P = 0.0068$ ,  $n = 42$ ) and female-male ( $r_s = 0.48$ ,  $P = 0.0266$ ,  $n = 21$ ) dyads separately. When only considering those dyads that were strongly bonded through both grooming and proximity (Gina/Boris, Gina/Banana, Banana/Boris,

Jane/Boris), there was a strong association between total proximity score and grooming duration ( $r_s = 0.90$ ,  $P = 0.0374$ ,  $n = 5$ ).

## **Monthly Variation in Affiliation**

### **Proximity**

There was no significant monthly variation in overall TFPS ( $H = 4.453$ ,  $P = 0.879$ ,  $df = 9$ ) or MPS ( $H = 9.386$ ,  $P = 0.402$ ,  $df = 9$ ). Sample sizes were too small to test statistically for monthly variation in each female's dyadic proximity scores. Patterns emerged, however, to suggest that the females' primary adult proximity partners did not remain consistent over time (Table 4-7).

'Strong bonds', i.e., the top 10% of monthly dyadic proximity scores (Silk et al. 2006b), were exhibited within 21 dyads: 6 ♀-♀ and 15 ♀-♂ pairs; 21 dyads failed to exhibit a single strong (monthly) proximity bond during the length of the study. The most consistent and reciprocal of the strong proximity bonds was between Gina and Banana, the two highest ranking females. The remaining majority of strong bonds were demonstrated between a female and a male. Gina and Banana had the most (5) monthly strong bonds with Boris, although those bonds were inconsistent and without discernable pattern. Gina, Banana, Jane, Little Horns, and Carol each had two months of strong bonds with Darwin, the youngest of the adult males. Again, the bonds were expressed rather inconsistently, but it is interesting to note that these monthly strong bonds occurred without much overlap between the females (Tables 4-8, 4-9).

### **Grooming**

There was no significant monthly variation in the rate (min/h) that females groomed troop-mates ( $H = 17.775$ ,  $df = 11$ ,  $P = 0.087$ ). There was, however, monthly variation in the rate at which females received grooming ( $H = 41.689$ ,  $df = 11$ ,

$P < 0.0001$ ). Sample sizes were too small to test statistically for monthly variation in each female's dyadic grooming relationships. Patterns emerged, however, to suggest that the females' primary adult grooming partners did not remain consistent over time (Table 4-10), and were not effective indicators of monthly shifts in primary proximity partners; female primary proximity and grooming partners (or lack thereof) matched only 35% of the time (Table 4-11).

Grooming 'strong bonds' were exhibited within 29 dyads: 14 ♀-♀ and 15 ♀-♂ pairs; only 13 dyads failed to exhibit a single strong (monthly) grooming bond during the length of the study, and nine of those dyads were never observed to groom. The five strongest bonds of the monthly grooming strong bonds occurred between (groomer and recipient), in descending order: (1) Gina and Banana (February), (2) Banana and Gina (February), (3) Gina and Boris (September), (4) Banana and Boris (January), (5) Jane and Boris (May), representing the relationships between the two highest-ranking females and between the three highest-ranking females and the alpha male. The most consistent of the strong grooming bonds was a tie between Gina/Boris and Banana/Boris (each had 7 of 10 months characterized by strong grooming bonds). The most reciprocal of the strong bonds, however, was the grooming relationship between Little Horns and Darwin; the dyad exhibited four months of equitable, strong grooming bonds (Tables 4-8, 4-9).

Of the strong bonds among females, Gina and Banana expressed the most enduring and equitable bond over time; this relationship, however, did not extend beyond June. The majority of the strong bonds among females occurred in February. Of the strong bonds between a male and a female, females (except for Little Horns)

tended to focus their grooming attention on the alpha male. Boris had a strong grooming bond with an average of three females during each month of the study, and these were highly inequitable grooming relationships. In fact, Boris was responsible for only 15% of the monthly strong bonds he held with females. Although Gina and Banana maintained the strongest grooming bonds with Boris, he did not maintain a single strong grooming bond with either of them. Andycap was never observed to invest in a grooming relationship with a female, but Darwin demonstrated at least one strong grooming bond with most of the females. The most enduring and equitable of strong bonds occurred between Little Horns and Darwin. Tinkerbelle was the only female to not express a single strong grooming bond with the alpha male, nor did she invest in a grooming relationship with either of the subordinate males (Tables 4-8, 4-9).

## **Seasonal Variation in Affiliation**

### **Proximity**

There was no significant seasonal variation in overall TFPS ( $H = 2.668$ ,  $P = 0.446$ ,  $df = 3$ ) or MPS ( $H = 0.422$ ,  $P = 0.936$ ,  $df = 3$ ). Female proximity to other females, however, was highest during the fruiting season (mean  $\pm$  SE =  $28.55 \pm 9.81$ ) while female proximity to males was highest during the transition season (mean  $\pm$  SE =  $28.31 \pm 11.20$ ). In comparing seasonal TFPS to MPS, females stayed closer to males than to females in each season except the fruiting season, although the only statistical difference was during the dry season, when females were significantly closer to males than to females ( $Z = -3.702$ ,  $P < 0.0001$ ) (Figure 4-7).

### **Grooming**

In all seasons, females groomed significantly more than they received ( $Z_{\text{fruiting}} = -5.662$ ,  $P < 0.0001$ ;  $Z_{\text{wet}} = -4.008$ ,  $P < 0.0001$ ;  $Z_{\text{dry}} = -5.838$ ,  $P < 0.0001$ ;

$Z_{\text{transition}} = -3.416$ ,  $P = 0.001$ ). The average rate that females groomed troop-mates was greatest (mean  $\pm$  SE =  $1.13 \pm 0.24$  min/h) during the fruiting season (February to April), the time of year that corresponded not only to fleshy fruit availability but also to the presence of young infants. Females groomed troop-mates the least (mean  $\pm$  SE =  $0.51 \pm 0.12$  min/h) during the dry season. There was no significant seasonal variation, however, in the daily rate that females groomed conspecifics ( $H = 4.718$ ,  $df = 3$ ,  $P = 0.194$ ). Similarly, the average rate that females received grooming from troop-mates was greatest (mean  $\pm$  SE =  $0.54 \pm 0.18$  min/h) during the fruiting season and smallest (mean  $\pm$  SE =  $0.12 \pm 0.04$  min/h) during the dry season. There was significant seasonal variation in the daily rate that females received grooming ( $H = 20.364$ ,  $df = 3$ ,  $P < 0.0001$ ), and this variation was wholly attributed to decreased grooming during the dry season. Females received a higher rate of grooming during the fruiting ( $Z = -4.167$ ,  $P < 0.0001$ ) and wet ( $Z = -3.727$ ,  $P < 0.0001$ ) seasons than during the dry season.

Females devoted more grooming to females than to males only during the fruiting season, and this finding was nearly significant ( $Z = -1.964$ ,  $P = 0.05$ ). In the remaining seasons, there was no statistical difference in the rate at which females groomed males versus females (Figure 4-8). There was no significant difference in any season in the rates at which female-female grooming occurred up versus down the hierarchy ( $P = 0.109$  to  $0.786$ ). Grooming up the hierarchy occurred more than the reverse direction only in the dry and transition seasons, with the greatest (up versus down) differential occurring in the transition season (Figure 4-9).

## The Effect of Infants on Female Affiliation

### Proximity

During the months in which infants ( $n = 4$ ) were  $\leq 3$  months old (January to April), there was no significant difference in female proximity to males (MPS) as compared to female proximity to females (TFPS) ( $Z = -0.365$ ,  $P = 0.715$ ). When differentiating between females with infants (FwiPS) and females without infants (FPS), however, females were significantly more likely to be in close proximity to a female with an infant than to a female without an infant ( $Z = -1.979$ ,  $P = 0.048$ ). Further, while MPS was significantly higher than FPS ( $Z = -3.400$ ,  $P = 0.001$ ), there was no significant difference between MPS and FwiPS ( $Z = -1.714$ ,  $P = 0.086$ ). This indicates that females were more likely to be in close proximity to a male than to a female without an infant, but the same did not hold true when an infant was present.

When only considering the proximity scores of the females with infants (Gina, Banana, Carol, and Kate), their total proximity score (TPS), including female, male, and immature neighbors, was significantly higher when they were carrying their young (0 to 3 month old) infants than when they were not with their infants ( $Z = -2.714$ ,  $P = 0.006$ ). More specifically, when carrying their babies, mothers had a significantly higher FwiPS ( $Z = -2.135$ ,  $P = 0.039$ ) and MPS ( $Z = -2.714$ ,  $P = 0.007$ ) than when they were not carrying their babies. Infant presence, however, did not affect their FPS ( $Z = -0.420$ ,  $P = 0.713$ ) (Figure 4-10). Thus, the physical presence of a young infant increased a female's proximity to other females carrying infants and to males, but did not affect her proximity to females without infants. Further, while the mothers were carrying their young infants, their highest average proximity score was with other females with infants (mean  $\pm$  SE =  $32.2 \pm 11.10$ ) as compared to males (mean  $\pm$  SE =  $24.4 \pm 7.19$ ) or

females without infants (mean  $\pm$  SE = 14.30  $\pm$  6.56). On the other hand, when the mothers were not carrying their young infants, their highest average proximity score was with males (mean  $\pm$  SE = 10.43  $\pm$  5.53) as compared to females without infants (mean  $\pm$  SE = 5.58  $\pm$  4.37) and females with infants (mean  $\pm$  SE = 5.00  $\pm$  3.29).

Infants also appeared to affect the strong bonds that females formed with conspecifics. For example, other than Gina and Banana, the only other female dyad to form a strong bond that endured for more than one consecutive month was that of Banana and Kate. Their infants were the youngest and closest in age (two-week age difference), and the strong proximity bonds between Banana and Kate occurred during the months of February and March when their infants were 1 to 2 months old. Infant presence may have also been a factor influencing the strong proximity bond between Gina and Banana that lasted from January to April. Interestingly, Gina, Banana, and Kate each demonstrated a strong proximity bond with Boris when their infants were approximately 0 to 1.5 months old. The relationship between Kate and Boris appeared particularly infant-based, both in their two-month strong proximity bond (the longest (consecutive) strong bond that any of the females with young infants had with the alpha male), and in the observation that Boris participated in the caretaking of Kate's infant. In fact, Boris was the infant's first observed alloparent, and he was regularly seen carrying the baby. Boris was not observed to carry any other infants. Carol was the only female with an infant that did not develop a strong bond with Boris; this may be due to the fact that Carol's infant was the eldest of the group's infants and was nearly two months old at the onset on the study. The strong bonds between Boris and the other mothers occurred when their infants were typically less than two months old, and

therefore it is possible that a similar relationship between Carol and Boris occurred prior to the study (Tables 4-8, 4-9).

### **Grooming**

Females with infants (FWI) [i.e., females carrying and/or nursing an infant, usually but not necessarily, the mother] groomed conspecifics for a total of 324.8 min. The largest percentage (35.7%) of this grooming was devoted to other FWI, while females without infants received the least (5.3%). Adult males received 26.9% of grooming from FWI, all of which was devoted to the alpha male; females carrying infants were never observed to groom a subordinate adult male. Females with infants received 274.2 min of grooming from conspecifics, the majority of which was given by other FWI and females (42.4% and 29.9%, respectively). All females except for Tinkerbelle (the most subordinate female) were observed to groom FWI. Males (the alpha male and one of the subordinate males) least groomed FWI (3%) (Figure 4-11).

During the months in which infants were approximately 0 to 3 months old (January to April), the grooming interactions of the mothers (Gina, Banana, Carol and Kate) were affected by infant presence. When they carried their infants, the frequency and duration of grooming given versus received did not deviate from expected patterns ( $X^2=0.06$ ,  $df = 1$ ,  $P > 0.10$ ;  $X^2= 2.6$ ,  $df = 1$ ,  $P > 0.10$ , respectively); they groomed conspecifics during 76 bouts (177.8 min) and received from troop-mates 79 grooming bouts (209.6 min). When they were not carrying their infants, however, the females groomed troop-mates more than expected (26 bouts, 81.3 min) and received less grooming (7 bouts, 18.5 min) than expected ( $X^2 = 11.0$ ,  $df = 1$ ,  $P < 0.001$ ;  $X^2=39.5$ ,  $df = 1$ ,  $P < 0.001$ , respectively). Although I did not collect data to compare the actual amount of time that females cared for their infants with the amount of time that females spent away from

their infants, the female proximity scans provide such an estimate. From January to April, the mothers were recorded with their infants in 123 total scans and without their infants in 101 scans. Chi-square analysis reveals that the frequency distributions do not significantly differ ( $X^2 = 2.16$ ,  $df = 1$ ,  $P > 0.10$ ), allowing for a direct comparison within the categorical variable of infant presence. The females groomed more than expected when carrying their infants and less than expected when they were without their infants (number of bouts:  $X^2 = 26.75$ ,  $df = 1$ ,  $P < 0.001$ ; duration (min):  $X^2 = 56.48$ ,  $df = 1$ ,  $P < 0.001$ ). Similarly, the females received grooming more than expected when carrying their infants and less than expected when they were without their infants (number of bouts:  $X^2 = 57.36$ ,  $df = 1$ ,  $P < 0.001$ ; duration (min):  $X^2 = 129.05$ ,  $df = 1$ ,  $P < 0.001$ ). In fact, the females gave nearly three times more grooming and received approximately 10 times more grooming when they were carrying their infants (Figure 4-12).

Infants also appeared to affect the strong (grooming) bonds that females formed with conspecifics. For example, all of the grooming comprising Tinkerbell's strong bonds with Banana and Kate in April occurred while she was carrying Banana's infant. Otherwise, Tinkerbell was never observed to groom or be groomed by a female. Additionally, all of the females with infants maintained strong grooming bonds with the alpha male for at least the first month (and generally for the first three months) of their babies' lives, while the females without infants did not typically form strong bonds with Boris during this same time. The only male to invest in a relationship with a FWI was Darwin grooming Kate in the first month of her infant's life (Tables 4-8, 4-9).

## **Discussion**

Are the female brown capuchins in RV truly female-bonded? According to the common indices of grooming and proximity measured on an annual time-scale, the

short answer is no; the females are not female-bonded in the classic sense and instead are better characterized as cross-bonded with males. Despite a 2:1 female to male ratio, females groomed males significantly longer than they groomed females, and female proximity scores with males were significantly higher than female proximity scores with other females. Further, each individual female's highest average proximity score (aside from Banana's) and longest total grooming duration was with a male, and not with a female. For the most part, proximity and grooming measures resulted in similar 'strong bonds' which emphasized female relationships with males. The only exception was the relationship between Gina and Banana, the two highest ranking females, although each of them was more strongly bonded to a male than to each other. Also of interest, proximity to males increased with female rank, while there was no clear pattern between female rank and proximity to females.

Based on this evidence, male *C. apella* in RV can be viewed as a valuable resource to the females, and the social importance of males may be related to the relatively weak relationships between females (Izar 2004). Especially telling is the finding that the strongest bonds between females were through proximity, while the strongest female-male bonds were through grooming. This indicates that the females were not simply grooming troop-mates that were closest or most available to them. Instead, they actively searched out male grooming partners. Females are expected to be affiliative to those individuals that provide the greatest benefits; in my study, patterns of affiliation suggest that males, and in particular the alpha male, provided the most potential benefits to females (O'Brien 1991). O'Brien (1991) suggested that preference for the alpha male is a reflection of breeding preference, while Janson (1985) suggested

that female *C. apella* may preferentially groom the dominant male in exchange for his tolerance. The benefits that female brown capuchins in RV may accrue through intensified grooming interactions with the alpha male are considered below.

In sum, on an annual-time scale, it was clearly evident that, despite being female philopatric, the females in this group were not female-bonded. But was there within-year variation in female relationships? Understanding short-term patterns of affiliation may provide insight into the functional significance of non-random dyadic social behavior.

### **Outcome of Hypotheses**

#### **Social bonds between adult female brown capuchins are variable over time**

This hypothesis is supported. Both measures of grooming and proximity revealed substantial monthly variation in each female's primary partner, and given a larger sample size, affiliative partners likely shift on an even shorter-term basis. Females demonstrated 60% inconsistency in their monthly primary partners (both in terms of proximity and grooming), and 'strong bonds' that were strong through both grooming and proximity typically lasted for only one month. Such a strong bond, however, endured for three consecutive months between Gina and Banana. These two females were the highest-ranking females, and it is speculated that they are a mother-daughter dyad. Silk et al. (2006a) determined that among female baboons, bond strength was a decreasing function of relatedness, with females forming the strongest bonds with mothers and sisters. Once genetic analysis of the females in my study is complete, a story may emerge that is both explanative and puzzling. Maternal relatedness may explain the relationship between Gina and Banana, but the obvious lack of

female-female bonds within most dyads is all the more intriguing given the high degree of relatedness that is expected among the females.

A female's primary proximity partner did not necessarily predict her primary grooming partner for that same month, and vice versa. In fact, only 35% of cases matched, and monthly dyadic grooming rates and proximity scores were only modestly correlated. This brings to light two methodological questions: (1) Are grooming and proximity equivalent measures of a bond? (2) Should a bond be assigned to a dyad only when both measures agree? Grooming and proximity may not necessarily be equitable proxies of a bond, but are likely compatible and together more fully expose the facets of a dyadic relationship. I acknowledge a design flaw in my data collection that did not allow me to assign which member of a dyad was responsible for maintaining proximity to the other. Therefore, for my study, I place more explanative power in grooming behavior as it indicates an individual's willingness to invest in an affiliative relationship with another. The comparative and corroborative patterns that emerged through the proximity data, however, are still worthy of inclusion and cautious consideration.

### **Dyadic female relationships vary in response to ecological pressures**

Support for this hypothesis is tentative. Seasonal differences in social behavior were not consistently supported by statistics, possibly because the generalized diet of capuchins provides them relative independence from ecological constraints (Moura 2007). Suggestive patterns emerged, however, to indicate the potential benefits provided by dyadic association. Female proximity to males and investment in the grooming of males is most evident during the transition season, a time of year characterized by an unpredictable food supply and a subsequent need to increase travel rates, increasing exposure to predators (Chapters 2 and 3). In support of Janson

(1985), this could be viewed as a social strategy whereby the females increase grooming of the males, and particularly the alpha male, in exchange for tolerance at food sources and during travel. Evidence of such a possible exchange was actually provided by female-female grooming patterns. While not statistically significant, females groomed up the hierarchy more than the reverse direction only during the dry and transition seasons. This could be interpreted as a female strategy to groom higher ranking troop-mates during periods of low and/or unpredictable food availability in attempt to procure tolerance at food sources. Direct evidence for such an exchange, however, was not provided by my study.

However, females did not appear to use grooming as a commodity to be exchanged for tolerance when food was readily and, possibly more importantly, predictably, available. For example, females received the most aggression from males, especially the alpha male, during the wet season when feeding on *M. maripa*, a high-quality resource that fruits in monopolizable clusters (Chapter 2). Rates of female-male grooming during this time, however, were virtually the lowest among the four seasons. Therefore, although females do not appear to use grooming as a means to reduce aggression from males, females may utilize the grooming of males as a form of insurance during periods of instability and/or unpredictability, securing better access to resources (tolerance during feeding) and decreasing risk (improving predator protection via closer proximity to males). Hierarchical grooming among females may serve as a commodity to be traded for tolerance at food resources; investigation into such a fine-scaled dyadic transaction deserves further study.

Females stayed closer to females and devoted more grooming to females than to males only during the fruiting season. Upon initial consideration, this increase in female relationships may appear to be in response to the peak production of fleshy fruits, possibly as a means to increase intrasexual tolerance while feeding. If this were the case, however, I would expect grooming during this time to be directed up the hierarchy (Seyfarth 1977), when, in fact, the rate at which females groomed up the hierarchy was slightly lower than the rate at which females groomed down the hierarchy. While the association between female relationships and fruit availability should not be ruled out in entirety, the intensification of female-female behavior during the fruiting season was confounded by the presence of infants, as four of the seven females had infants that were less than three months old during this time.

#### **Relationships among females strengthen with the presence of an infant**

This hypothesis is supported, indicating that young infants were a source of interest to troop-mates, and that, with the presence of an infant, a mother became more socially immersed. In terms of monthly 'strong bonds' between females, especially those that were strong through both grooming and proximity, 78% occurred when at least one of the females had a young infant; the females that did not have infants did not show a tendency to form strong bonds during this time. Therefore, despite the dynamic and seasonally variable environment, infant presence seemed to most affect female-female relationships. For example, other than Gina and Banana, the only other female dyad to form a strong bond that endured for more than one consecutive month was that of Banana and Kate. Their infants were the youngest and closest in age (two-week age difference), and the strong bonds between Banana and Kate occurred during the months of February and March when their infants were 1 to 2 months old.

Infant presence may have also been a factor influencing the strong bonds between Gina and Banana that lasted from January to April, as both females had young infants during this time, and Gina was not observed to groom Banana after May.

Thus it is evident that young infants were the primary catalyst for the intensification of female-female relationships. The question then becomes, Why? Anecdotal evidence suggests that the most subordinate female, Tinkerbelle, exchanged alloparenting services for affiliative behavior from females: All of the grooming comprising Tinkerbelle's strong bonds with Banana and Kate in April occurred while she was carrying Banana's infant; otherwise, Tinkerbelle was never observed to groom or be groomed by a female. However, this occurred only over a two-day period, and the use of alloparenting as a commodity to be traded (for reciprocal alloparenting or for grooming), did not appear to be widespread among the females in this group. For example, Banana frequently 'babysat' Gina's infant, but the reverse was rarely, if ever, observed. In fact, alloparenting among the females (mothers and non-mothers) was not commonly observed; instead it was the juveniles (male and female) that most frequently carried infants.

I find it more likely that the intensification of proximity and grooming relationships among females from February to April was an artifact of mothers becoming more central in the group, as the females were nearly twice as likely, on average, to be located in the center of the group when they had infants that were less than three months old. Whether the females became more central as a means to increase protection from predators and access to higher quality food resources or to socialize their infants is unknown. Often, however, it appeared that new mothers (especially the more

subordinate ones) 'escaped', by choice, to the periphery to forage whenever possible as though overwhelmed by their sudden popularity. As grooming behavior promotes the release of  $\beta$ -endorphins (Keverne et al. 1989) and thus reduces tension, it is my belief that a new mother intensifies grooming behavior, in part, as a means to cope with the social stress she incurs while socializing and protecting her infant (to be empirically examined in the following chapter).

### **Female-Male Relationships**

The results of this chapter indicate that, overall, females were more motivated to bond with males, and in particular the alpha male, than with other females. This general pattern of female-male affiliation resembles that which is demonstrated among some hamadryas baboon populations (*Papio hamadryas*), whereby each female has a stronger bond with the dominant male than with the other adult females (Byrne et al. 1990; Barton et al. 1992; Swedell 2002). Such populations with strong inter-sexual affiliative relationships are characterized as cross-bonded (Byrne et al. 1990), a term that has not previously been used to describe any capuchin group or population.

Among *C. apella* and *C. olivaceus*, it is well-established that, of males, females both sexually and socially prefer the dominant male (Janson 1984; Robinson 1988; O'Brien 1991; Di Bitetti 1997; Izar 2004). Close association with the dominant male, however, is not without its costs. In fact, nearly 70% of the agonism females received in my study came from the alpha male, and the two highest-ranking (and most central) females received approximately 2 to 3 times more agonism from the alpha male than did the other females. The benefits afforded by interaction with the dominant male, then, must be great enough to outweigh the costs. Estrus-cycling females and females

with infants are expected to receive different benefits from their association with the dominant male, and I discuss these differentiated relationships below.

### **Associations between females with infants and adult males**

All of the females with infants maintained strong grooming bonds with the alpha male, Boris, for at least the first month (and generally for the first three months) of their babies' lives. The relationship between Kate and Boris appeared particularly infant-based, both in their two-month strong (grooming and proximity) bond (the longest consecutive strong bond that any of the females with young infants had with the alpha male), and in the observation that Boris participated in the caretaking of Kate's infant. In fact, Boris was the infant's first observed alloparent, and he was regularly seen carrying the baby. Boris was not observed to carry any other infants. Carol was the only female with an infant that did not develop a strong bond with Boris; this may be due to the fact that Carol's infant was the eldest of the group's infants and was nearly two months old at the onset on the study. The strong bonds between Boris and the other mothers occurred when their infants were typically less than two months old, and therefore it is possible that a similar relationship between Carol and Boris occurred prior to the study.

The mothers were clearly responsible for maintaining the close association with the alpha male (as he rarely reciprocated grooming), and it is of interest to note that, of the adult males, females with babies only groomed Boris. In this multi-male, multi-female species, infant paternity is uncertain as estrus females typically mate with more than one male. The alpha male, however, generally has the most access to females in estrus at the time they would be ovulating (Janson 1984) and so likely sires the majority of the group's infants. Preferential mating and post-natal association with

the dominant male may be a strategy to protect infants from infanticide. However, the females did not appear especially wary of the subordinate males and, in fact, Darwin, the youngest adult subordinate male, demonstrated an unreciprocated strong grooming bond with Kate when her infant was less than one-month old (i.e., Darwin's advances were tolerated by the mother of a newborn).

The benefits accrued from a mother's association with the alpha male are not mutually exclusive. As the dominant male occupies a central position in the group and controls access to resources (Janson 1985; Janson 1990a,b), it is likely that a mother's affiliative investment in such a relationship garners a suite of benefits in addition to protection from potentially infanticidal males, such as: increased tolerance at high-quality food resources (especially important for meeting the energetic demands of lactation) and in the center of the group (i.e., increased predator protection), the security of his close proximity (i.e., protection for her and her infant from agonism and/or bothersome conspecifics), and the introduction and socialization of her infant with the dominant male, the most important individual in the group (i.e., preparing for her offspring's future).

### **Associations between reproductively-cycling females and adult males**

Of the three females that did not have infants during the study period, Jane and Tinkerbell demonstrated the strongest and most frequent affiliative relationships with the alpha male. Little Horns, however, was arguably more closely bonded to Darwin than she was to Boris, although she demonstrated four months of strong bonds to both males. The relationships of cycling females with males may be a reflection of their breeding preference; however, as affiliative behavior observed during a female's estrus cycle was not included in analysis, the resulting patterns do not represent a direct

connection between female-male affiliation and mating. Further, among *C. apella*, mate preference occurs through female choice, and so it is unlikely that a female would need to use grooming, for example, to entice a male to mate with her. I find it more likely that these females preferentially associate with the dominant male as a means to acquire the benefits of his tolerance, namely access to high quality resources and improved predator protection.

Males, however, focused their affiliative behavior on the females that did not have infants, a finding that I find particularly interesting given the level of motivation new mothers demonstrated in associating with the dominant male. For example, from January to June when the infants were < 6 months old, the alpha male groomed non-mothers ( $n = 3$ ) more than twice as long as he groomed mothers ( $n = 4$ ), although the females with infants groomed him more than four times longer than did the non-mothers. The relationships between the alpha male and females with infants were decidedly one-sided, with males demonstrating a clear preference for the females that were most likely to conceive – investing in their future reproductive success at the possible expense of their current reproductive output. Again, this preference was quantitatively obvious even after excluding observations made during the females' estrus periods. Because females exercise mate preference, and the females had their choice of three possible mates in the group, males appear to utilize grooming behavior as a means to secure access. The fact that the dominant male was just as, if not more, active than the subordinate males in maintaining affiliative contact with the cycling females suggests that he cannot rely solely on his status to acquire matings.

## Conclusion

The concept of female bonds is at the core of theories of primate social evolution, and compelling evidence suggests that females sharing strong bonds obtain significant survival and reproductive advantages. The obvious benefits of female-female bonds, therefore, make the lack of such relationships all the more intriguing. The results of my study suggest that the females in a female-philopatric species may not necessarily view other females as their most beneficial social partners.

- Female brown capuchins in Raleighvallen were not female-bonded in the classic sense. Instead, the females were arguably cross bonded – especially with the alpha male. This was clearly evident when analyzing the data on a yearly time-scale. Finer-scaled temporal analysis, however, revealed that the females were *sometimes* female-bonded. Long-term social bonds, therefore, may not be necessary, or even beneficial, in a dynamic ecological landscape.
- Female relationships did not appear to be affected by seasonal food availability. Although a hierarchy among the females was weakly evident, there was a noticeable lack of interaction among most females. Because food patches in Raleighvallen are either very small or very large, and the monkeys rely heavily on insects, females generally did not affect each other's access to food, and this may result in a lack of motivation for females to bond.
- Instead, affiliation between females was centered on infants. Lactating females are more sensitive to fluctuations in food availability, and so infants may intensify ecological pressures for their mothers and encourage stronger female relationships. Alternatively, infant presence may encourage a female to bond with conspecifics as a means to socialize or protect the infant, and this may explain the strong bonds that the mothers formed with the alpha male. Mothers may also increase affiliation as a means to cope with the physiological and social burden of caring for, protecting, and socializing their infants.

In sum, I believe that the distinction between 'friends' and 'business partners' is better viewed as the social endpoints on an ecological continuum. In a dynamic environment, dynamic social relationships are most adaptive, with the true value of a social bond possibly within its potential for mobilization (Henzi et al. 2009). As such, relationships between female capuchins in RV can be described, at best, as transient

and seemed to mainly provide dyadic benefit when an infant was born. Instead, relationships with adult males, particularly the alpha male, appeared to provide the females with more long-term benefits likely associated with mediating the costs of high predation risk and an unpredictable food supply.

Table 4-1. Summary of the dominance rank, approximate age, and reproductive history of the adult females in Troop A, as well as general life history notes for the adult males.

	Rank	Est. age (yrs)	Birthing history (most recent birth as of Dec. 2006)	Notes of interest
<b>Females</b>				
Gina	1	> 10	Multiparous (Dec. 24, 2005)	
Banana	2	6	Primiparous (Jan. 21, 2006)	
Jane	3	8	Multiparous, pregnant (Feb. 22, 2005)	Disappeared in October '06. Suspected obstetric-related death (near full term)
Little Horns	4	> 15	Multiparous (Dec. 6, 2004)	
Carol	5	> 10	Multiparous (Nov. 22, 2005)	
Kate	6	> 10	Multiparous (Feb. 5, 2006)	
Tinkerbelle	7	6	Nulliparous, pregnant	Gave birth to 1 <sup>st</sup> infant in December '06
<b>Males</b>				
Boris	alpha	> 10		Alpha male of Troop A since 2003
Andycap		> 15		Immigrated into Troop A in January 2006
Darwin		8-10		Immigrated into Troop A in April 2005; youngest adult male in troop

Table 4-2. Female dominance matrix depicting a (weakly) linear hierarchy based on the outcomes of dyadic agonism, transitivity, and anecdotal evidence.

	Gina	Banana	Jane	Little Horns	Carol	Kate	Tinkerbell
Gina		1	1	1	^1	1	1
Banana			*1	1	1	1	^1
Jane				1	1	^1	1
Little Horns					1	^1	*1
Carol						1	*1
Kate							*1
Tinkerbell							

1 = row individual is dominant to column individual. ^1 = relationship based on transitivity. \*1 = relationship based on anecdotal evidence.

Table 4-3. Average monthly proximity scores ( $\pm$  SE) of Troop A females. The higher the proximity score, the more time the female spent in close proximity (within 4 m) to those conspecifics. Proximity scores were calculated using weighting factors such that proximity of 1 m provided a larger score than did proximity of 4 m (adapted from Perry 1996). Overall, all females except the alpha female, Gina, spent more time in closer proximity to adult males than to adult females despite a 2:1 ratio of potential female and male neighbors, respectively. Two females, Little Horns and Tinkerbell, produced proximity scores with males that were significantly higher than their proximity scores with other females. Female proximity to males increased linearly with female rank.

Female	Rank	Proximity to:		<i>P</i> -value
		Adult females ( <i>n</i> = 6)	Adult males ( <i>n</i> = 3)	
Gina	1	52.7 $\pm$ 15.47	41.1 $\pm$ 11.54	0.721
Banana	2	38.4 $\pm$ 13.10	39.3 $\pm$ 11.83	0.878
Jane	3	5.6 $\pm$ 2.37	21.5 $\pm$ 10.72	0.091
Little Horns	4	1.5 $\pm$ 0.79	14.3 $\pm$ 3.69	0.017*
Carol	5	10.7 $\pm$ 4.91	12.4 $\pm$ 3.64	0.767
Kate	6	11.6 $\pm$ 5.83	12.2 $\pm$ 5.90	0.859
Tinkerbell	7	0.7 $\pm$ 0.68	9.5 $\pm$ 4.96	0.008*

Table 4-4. Frequency and duration of female grooming dyads (by age/sex class), from January to December 2006. Females most groomed juveniles (36% duration) and least groomed females (19% duration). Average bout length was longest when females groomed males. Females received the most grooming from females (49% duration), and not including infants, received the least grooming from males (17% duration).

Groomer	Recipient	Total # bouts	Total duration (min)	$\bar{x}$ bout duration $\pm$ SE (min/bout)
Females	Males	140	429.1	3.1 $\pm$ 0.27
Females	Juveniles	301	700.2	2.3 $\pm$ 0.15
Females	Infants	201	437.7	2.2 $\pm$ 0.16
Females	Females	175	370.8	2.1 $\pm$ 0.17
Males	Females	62	130.0	2.1 $\pm$ 0.32
Juvenile	Females	126	246.0	2.0 $\pm$ 0.16
Infants	Females	8	8.3	1.0 $\pm$ 0.35

Table 4-5. Total proximity scores for adult dyads, January to December 2006. Shaded scores represent 'strong bonds'\* between individuals. The only strong proximity bond observed between females (Gina and Banana, the two highest ranking females) was also an equitable one. The remaining strong bonds occurred between the females and the alpha male, Boris.

	Gina	Banana	Jane	LH	Carol	Kate	Tink	Boris	Andycap	Darwin
Gina	X	233.69	25.55	18.62	23.41	31.77	1.55	272.49	14.10	53.14
Banana	233.27	X	28.16	0.21	10.11	54.40	8.536	151.67	46.41	51.86
Jane	43.93	6.89	X	2.62	4.37	4.27	0.00	114.05	4.30	82.56
Little Horns	6.80	0.70	1.87	X	5.78	1.84	1.70	41.65	23.01	50.60
Carol	21.35	10.11	4.37	5.78	X	46.10	1.36	23.85	49.84	48.46
Kate	31.77	54.40	4.27	1.84	46.10	X	0.73	83.93	3.79	19.97
Tink	1.55	11.15	0.00	1.70	0.50	0.73	X	110.03	14.30	2.56

Notes: Row individual = female for which proximity scores were calculated. Column individual = neighbor; \* Strong bonds are those which comprise the top 10% of average proximity scores among adult dyads.

Table 4-6. Total grooming duration (min) for adult dyads, January to December 2006. Shaded scores represent ‘strong bonds’\* between individuals. The only strong grooming bond observed between females (Gina and Banana, the two highest ranking females) was also an equitable one (i.e., a strong bond for each partner in the dyad). The only other equitable strong grooming bond occurred within a ♀-♂ dyad, Little Horns (LH) and Darwin. All other strong grooming bonds involved a female (inequitably) grooming the alpha male, Boris.

	Gina	Banana	Jane	LH	Carol	Kate	Tink	Boris	Andycap	Darwin
Gina	X	83.8	1.0	2.0	3.5	1.0	0.0	86.5	0.0	0.0
Banana	49.8	X	0.0	3.5	0.0	18.8	4.7	82.5	0.0	3.0
Jane	12.0	12.2	X	17.8	2.3	0.0	0.0	36.3	0.0	0.0
Little Horns	12.0	4.0	3.5	X	8.5	6.0	0.0	7.1	0.5	40.6
Carol	4.5	9.0	3.2	9.2	X	2.0	1.0	24.2	10.0	20.0
Kate	0.0	17.5	0.0	2.0	0.2	X	3.0	51.2	5.3	0.0
Tink	0.0	2.5	0.0	0.0	1.0	0.0	X	0.0	0.0	0.3
Boris	3.7	6.7	18.2	16.2	5.0	6.1	0.0	X	X	X
Andycap	0.0	0.0	0.0	1.3	16.0	0.0	0.0	X	X	X
Darwin	5.3	0.0	2.0	30.2	1.5	5.0	7.0	X	X	X

Notes: Row individual = groomer. Column individual = recipient; \* Strong bonds were those which comprise the top 10% of grooming duration among adult dyads

Table 4-7. Monthly variation in females' primary adult proximity partners, based on the highest dyadic proximity score/month (shown). Female proximity partners did not remain consistent over time.

	Jan	Feb	Mar	Apr	May	Jun	Aug	Sept	Oct	Nov
Gina	Boris 47.34	Banana 44.85	Banana 16.84	Banana 32.79	Boris 24.85	Banana 27.27	Boris 75.75	Boris 37.89	Darwin 17.07	Boris 57.31
Banana	Gina 45.71	Gina 44.85	Boris 28.42	Gina 32.79	Darwin 17.18	Gina 27.29	Gina 25.69	Gina 17.85	Andycape 15.73	Darwin 7.77
Jane	---	---	Gina 19.35	---	Boris 5.06	---	Boris 4.24	Boris 44.62	---	<i>n.a.</i>
Little Horns	---	Darwin 17.88	Boris 14.37	Andycape 3.68	Darwin 7.56	Darwin 16.77	Andycape 4.50	Boris 4.50	Boris 16.77	Carol 3.11
Carol	Kate 1.20	Gina 8.03	Kate 22.41	---	Gina 13.32	---	---	Darwin 31.73	Boris 18.20	Little Horns 3.11
Kate	Carol 1.20	Banana 19.91	Boris 35.51	---	Boris 22.75	Boris 4.00	Gina 16.37	---	Boris 3.33	---
Tinkerbell	---	---	---	---	---	---	Andycape 6.80	---	---	Boris 4.86

Notes: July and December were not included due to insufficient data; only dyads with > 1 instance of proximity (within 4 m) were considered.

Table 4-8. Monthly variation in ♀-♀ proximity (p) and grooming (g) 'strong bonds', comprising the top 10% of monthly proximity scores and grooming durations (such that the focal female is the groomer, dyadic partner the recipient) among adult female dyads. Only 20% of strong proximity bonds matched the strong grooming bonds (indicated by pg). The majority (80%) of bonds that were strong though both grooming and proximity, occurred in the presence of young infants ( $\leq 3$  months old), as indicated by shaded cells. Of the 21 ♀-♀ dyads, only three demonstrated more than one month of reciprocal strong bonds. Notes of interest: Gina and Banana had the most enduring and equitable of strong bonds, but this relationship weakened after April and altogether disappeared after September; Kate and Banana had the next most equitable relationship, but only when their infants were 1 to 2 months old; Jane and Little Horns had a fairly consistent, albeit inequitable, relationship based in grooming.

Focal female	Dyadic partner	Jan	Feb	Mar	Apr	May	Jun	Aug	Sep	Oct	Nov
Gina	Banana	p	pg	pg	pg	g	p	p	p		
Banana	Gina	p	pg	pg	p		pg	p	p		
Gina	Jane						p				
Jane	Gina			pg			p				
Gina	Little Horns										
Little Horns	Gina	g	g								
Gina	Carol		g								
Carol	Gina		g								
Gina	Kate							p			
Kate	Gina							p			
Gina	Tinkerbell										
Tinkerbell	Gina										
Banana	Jane								p		
Jane	Banana		g								
Banana	Little Horns										g
Little Horns	Banana										
Banana	Carol										
Carol	Banana			g							
Banana	Kate		pg	pg					g		
Kate	Banana		pg	p					g		
Banana	Tinkerbell				g						
Tinkerbell	Banana										

Table 4-8. Continued.

Focal female	Dyadic partner	Jan	Feb	Mar	Apr	May	Jun	Aug	Sep	Oct	Nov
Jane	Little Horns				g	g			g	g	↘
Little Horns	Jane		g								
Jane	Carol		g								↘
Carol	Jane		g								
Jane	Kate										↘
Kate	Jane										
Jane	Tinkerbelle										↘
Tinkerbelle	Jane										
Little Horns	Carol					g			g		
Carol	Little Horns					g			g		
Little Horns	Kate					g					
Kate	Little Horns										
Little Horns	Tinkerbelle										
Tinkerbelle	Little Horns										
Carol	Kate			p							
Kate	Carol			p							
Carol	Tinkerbelle										
Tinkerbelle	Carol										
Kate	Tinkerbelle				g						
Tinkerbelle	Kate										

Table 4-9. Monthly variation in ♀-♂ proximity (p) and grooming (g) 'strong bonds', comprising the top 10% of monthly proximity scores and grooming durations among adult dyads. Bonds strong through proximity were only measured from the focal female perspective. Grooming strong bonds are indicated for both dyadic partners, such that the focal individual was the groomer and the dyadic partner the recipient. Only 18% of a female's strong proximity bonds matched her strong grooming bonds (indicated by pg). Of bonds that were strong through both grooming and proximity, 45% occurred between a female with a young infant and the alpha male, Boris, as indicated by shaded cells; 64% occurred between Boris and the two most dominant females (Gina and Banana). Of the 21 ♀-♂ dyads, only two demonstrated more than one month of reciprocal strong grooming bonds. Notes of interest: Gina and Banana maintained the most enduring strong grooming bonds with Boris, although he did not invest in a grooming relationship with either of them. Andycap, the eldest subordinate male, was not observed to invest in grooming relationships with any females. Darwin, on the other hand, demonstrated at least one month of strong grooming bonds with most females. The most enduring and equitable of grooming relationships was that of Little Horns and Darwin.

Focal individual	Dyadic partner	Jan	Feb	Mar	Apr	May	Jun	Aug	Sep	Oct	Nov
Gina	Boris	pg		g	g	pg		p	pg	g	pg
Boris	Gina										
Banana	Boris	pg	g	pg	p	p		pg	g	g	g
Boris	Banana										
Jane	Boris	p	g			g	g	g	p	g	
Boris	Jane		g			g					
Little Horns	Boris			p	g				g	p	
Boris	Little Horns					g					
Carol	Boris	g	g	g	g					p	
Boris	Carol				g						
Kate	Boris	g	pg	pg	g	p					
Boris	Kate					g					
Tinkerbell	Boris		p		p				p		
Boris	Tinkerbell										
Gina	Andycap										
Andycap	Gina										
Banana	Andycap							p		p	
Andycap	Banana										

Table 4-9. Continued

Focal individual	Dyadic partner	Jan	Feb	Mar	Apr	May	Jun	Aug	Sep	Oct	Nov
Jane	Andycap										↘
Andycap	Jane										
Little Horns	Andycap										
Andycap	Little Horns										
Carol	Andycap					p		p		g	
Andycap	Carol										
Kate	Andycap									g	
Andycap	Kate										
Tinkerbell	Andycap										
Andycap	Tinkerbell										
Gina	Darwin									p	p
Darwin	Gina								g		
Banana	Darwin					p		p			g
Darwin	Banana										
Jane	Darwin	p				p					↘
Darwin	Jane								g		
Little Horns	Darwin		pg		g	g	pg				
Darwin	Little Horns		g		g	g	g				g
Carol	Darwin								p	p	g
Darwin	Carol										
Kate	Darwin									p	
Darwin	Kate		g								
Tinkerbell	Darwin										
Darwin	Tinkerbell		g								

Table 4-10. Monthly variation in females' primary adult grooming partner, based on the highest dyadic grooming rate (min/h) per month (shown). Female grooming partners did not remain consistent over time.

	Jan	Feb	Mar	Apr	May	Jun	Aug	Sept	Oct	Nov
Gina	Boris 0.085	Banana 0.387	Banana 0.120	Boris 0.121	Banana 0.042	Banana* 0.018	--	Boris 0.081	Boris 0.038	Boris 0.051
Banana	Boris 0.110	Gina 0.387	Gina* 0.120	Tink 0.034	Gina 0.042	Gina 0.018	Boris 0.049	Kate* 0.044	Boris 0.106	Boris 0.083
Jane	--	Banana 0.060	Gina 0.036	Lit. Horns 0.016	Boris 0.146	Boris 0.025	Boris 0.018	Lit. Horns 0.021	Boris 0.143	n.a.
Little Horns	Gina 0.040	Darwin 0.085	Banana 0.009	Darwin 0.107	Darwin* 0.073	Darwin 0.055	--	Carol 0.032	--	Banana 0.027
Carol	Boris 0.020	Boris 0.055	Banana 0.027	Boris 0.045	Andycap 0.102	Banana 0.009	--	Lit. Horns 0.032	Andycap 0.014	Darwin 0.095
Kate	Boris 0.080	Banana 0.067	Boris 0.059	Boris 0.112	Boris 0.027	--	--	Banana 0.044	Andycap 0.021	Banana 0.011
Tink	--	Darwin* 0.040	--	Banana 0.034	--	--	--	Carol 0.008	--	--

Notes: July and December were not included due to insufficient data; only dyads with > 1 min of grooming were considered. \* Indicates the dyadic grooming relationship was maintained primarily by the partner; otherwise, the dyadic relationship was relatively equitable or maintained primarily by the focal female.

Table 4-11. Females' primary adult partner per month (proximity/grooming). The shaded cells are the months in which a female's primary grooming partner (or lack thereof) was the same as her primary proximity partner. Grooming and proximity partners matched in 35% of cases.

	Jan	Feb	Mar	Apr	May	Jun	Aug	Sept	Oct	Nov
Gina	Boris Boris	Banana Banana	Banana Banana	Banana Boris	Boris Banana	Banana Banana	Boris --	Boris Boris	Darwin Boris	Boris Boris
Banana	Gina Boris	Gina Gina	Boris Gina	Gina Tink	Darwin Gina	Gina Gina	Gina Boris	Gina Kate	AC Boris	Darwin Boris
Jane	-- --	-- Banana	Gina Gina	-- LH	Boris Boris	-- Boris	Boris Boris	Boris LH	-- Boris	n.a.
Little Horns	-- Gina	Darwin Darwin	Boris Banana	AC Darwin	Darwin Darwin	Darwin Darwin	AC --	Boris Carol	Boris --	Carol Banana
Carol	Kate Boris	Gina Boris	Kate Banana	-- Boris	Gina AC	-- Banana	-- --	Darwin LH	Boris AC	LH Darwin
Kate	Carol Boris	Banana Banana	Boris Boris	-- Boris	Boris Boris	Boris --	Gina --	-- Banana	Boris AC	-- Banana
Tink	-- --	-- Darwin	-- --	-- Banana	-- --	-- --	AC --	-- Carol	-- --	Boris --

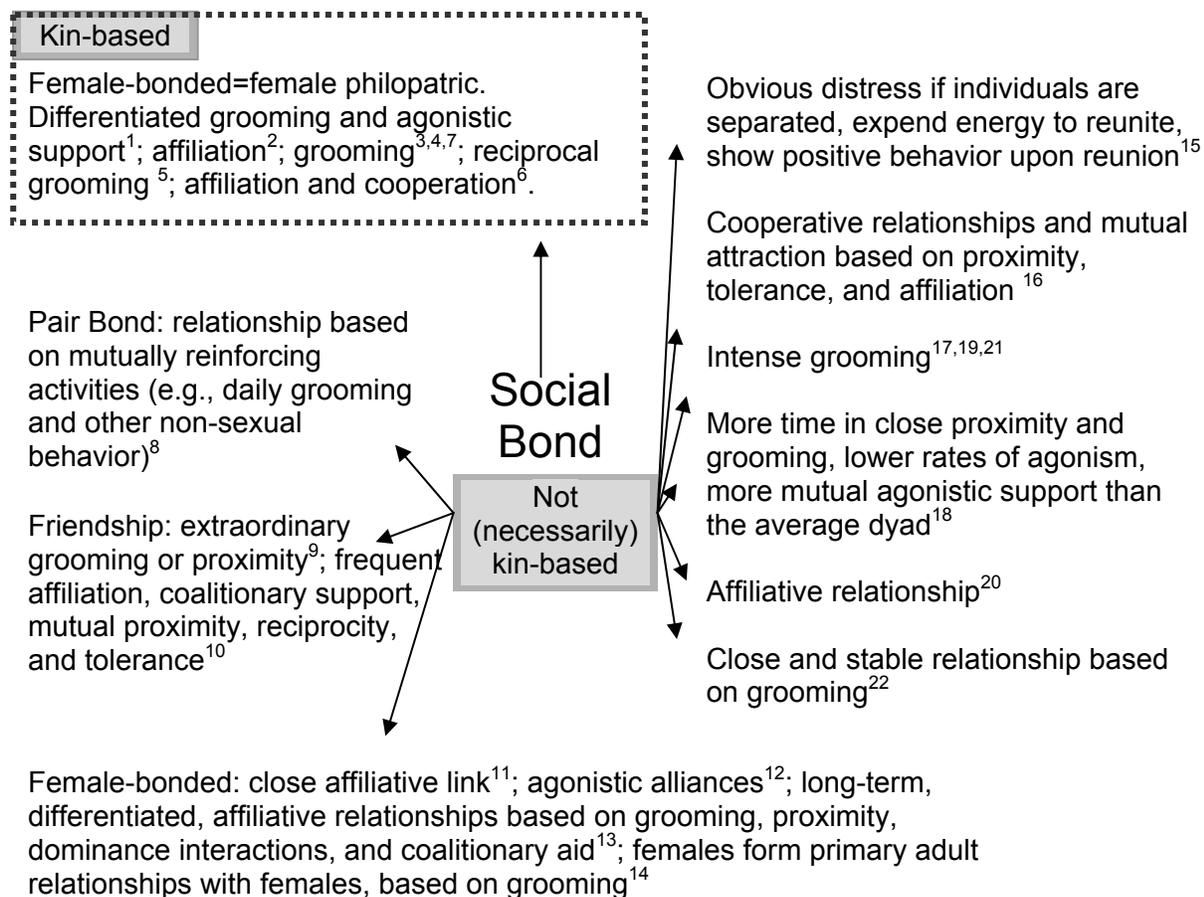


Figure 4-1. Deconstructing intra-sexual social bonds: Various usages of the term 'social bond' and its synonyms, as found in the primate literature. Published usage of a term is included only if a definition or descriptive measure was provided, no matter how vague.

<sup>1</sup>Wrangham 1980; <sup>2</sup>Mitchell et al. 1991; <sup>3</sup>O'Brien 1993; <sup>4</sup>Di Bitetti 1997; <sup>5</sup>Hemelrijk and Luteijn 1998; <sup>6</sup>Manson et al. 1999; <sup>7</sup>Payne et al. 2003; <sup>8</sup>Eisenberg et al. 1972; <sup>9</sup>Palombit et al. 1997; <sup>10</sup>Silk 2002; <sup>11</sup>Byrne et al. 1990; <sup>12</sup>van Schaik 1989; <sup>13</sup>Perry 1996; <sup>14</sup>Henzi et al. 2000; <sup>15</sup>de Waal 1986; <sup>16</sup>van Hooff and van Schaik 1994; <sup>17</sup>Sambrook et al. 1995; <sup>18</sup>van Schaik and Aureli 2000; <sup>19</sup>Nakamichi and Shizawa 2003; <sup>20</sup>Jack 2003; <sup>21</sup>Izar 2004; <sup>22</sup>Silk 2007b

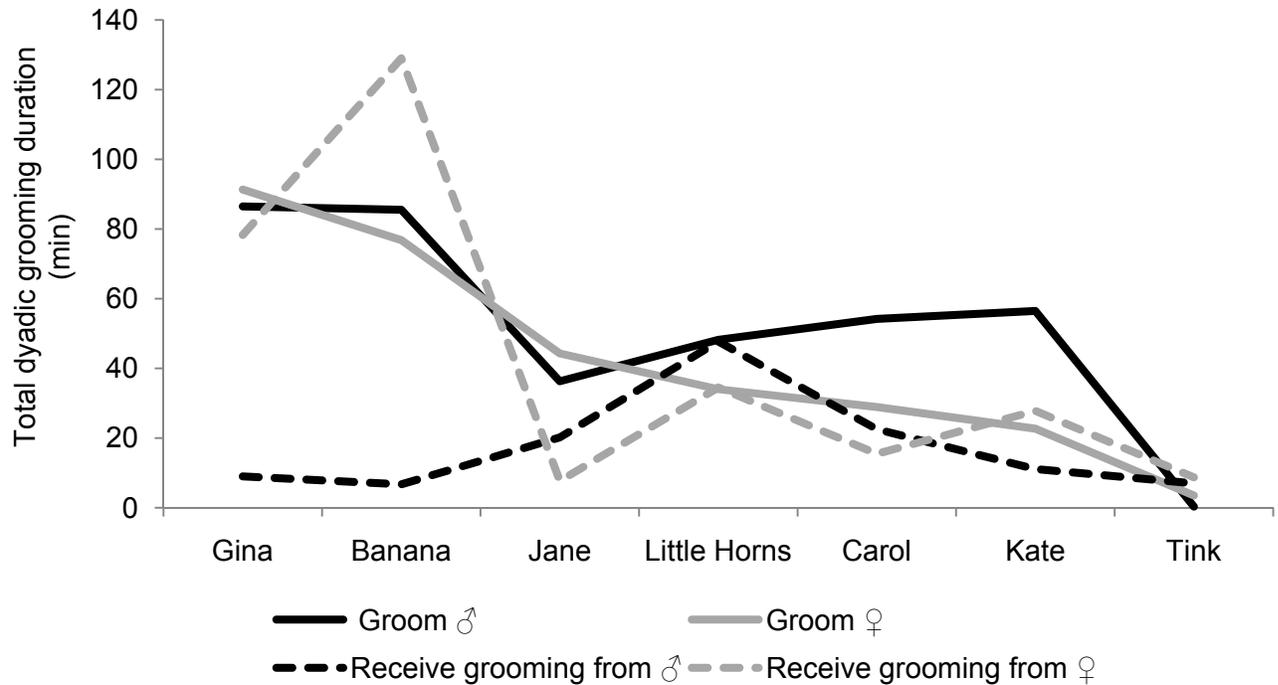


Figure 4-2. Total duration (min) females groomed and received grooming from adult male and female conspecifics. The amount of time females spent grooming females was in positive association with female rank (descending from left to right). Similarly, aside from Jane (who disappeared during the study), the amount of time females invested in grooming males was (approximately) positively associated with female rank. The amount of time that females received grooming from adults, however, does not appear associated with rank.

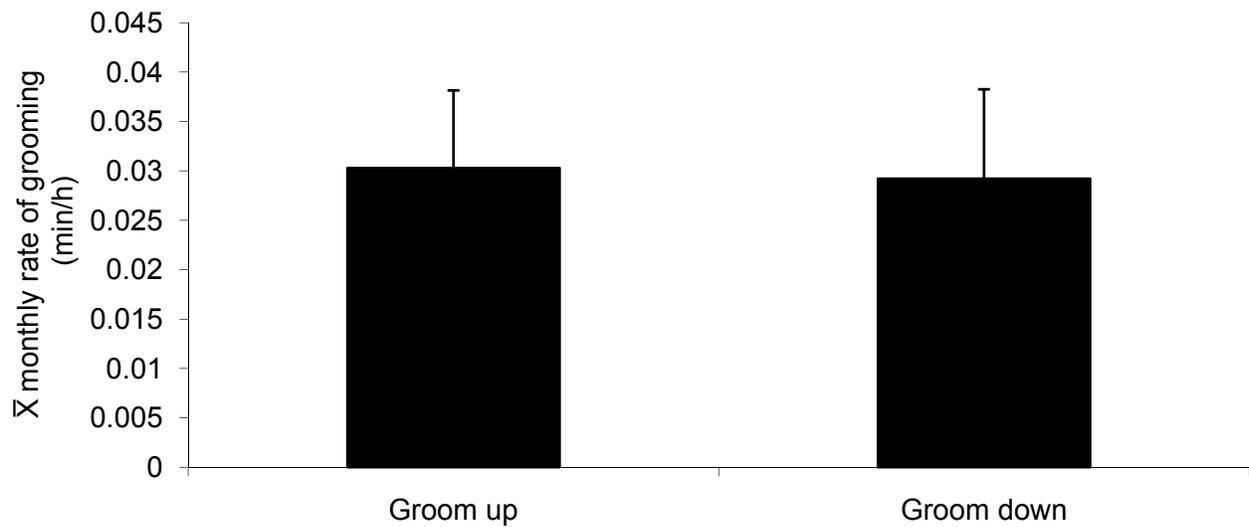


Figure 4-3. The monthly rate (min/h) at which females groomed up the hierarchy as opposed to down the hierarchy. There was no significant difference in the rate at which subordinate females groomed dominant females ( $\bar{x} = 0.030 \pm 0.008$  min/h) and dominant females groomed subordinate females ( $\bar{x} = 0.029 \pm 0.009$  min/h) ( $P = 0.909$ ).

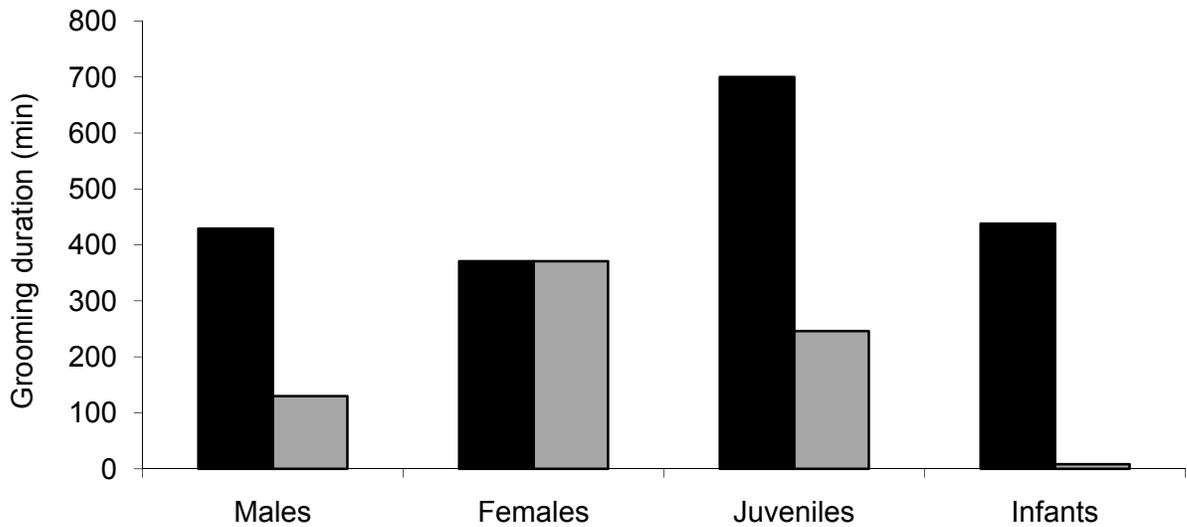


Figure 4-4. Total duration (min) that adult females groomed troop-mates grouped by age/sex class (black bars), and the total duration that adult females received grooming from troop-mates grouped by age/sex classes (grey bars). Females invested the most time in grooming juveniles. Females groomed males more than females groomed females; in general, however, the time investment of female-female grooming was more reciprocal than was female-male grooming.

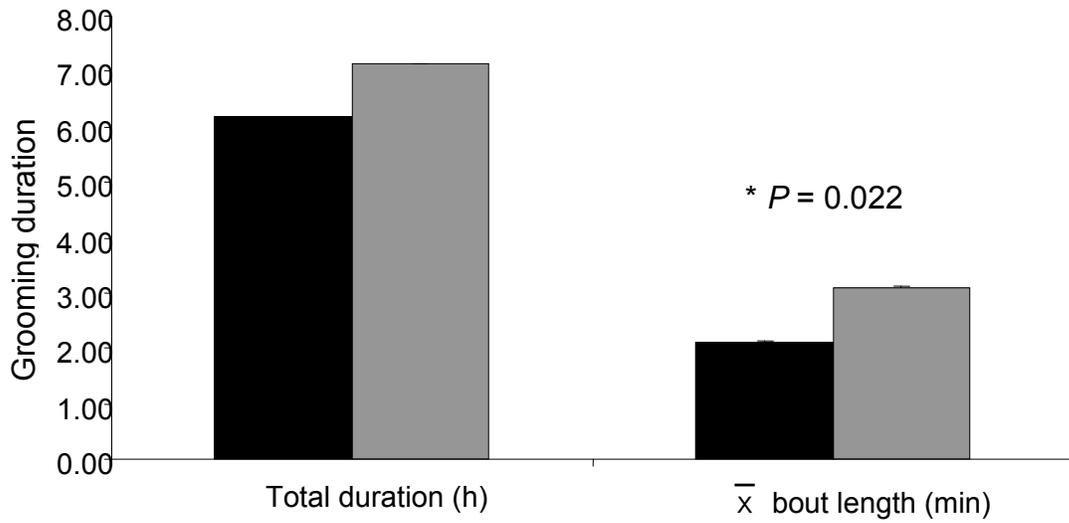


Figure 4-5. Total duration and average bout length of ♀-♀ and ♀-♂ grooming. Females groomed males (grey bars) for a longer total duration than females groomed females (black bars), and grooming bouts were significantly longer ( $P = 0.022$ ) when females groomed males as opposed to female-female grooming bouts.

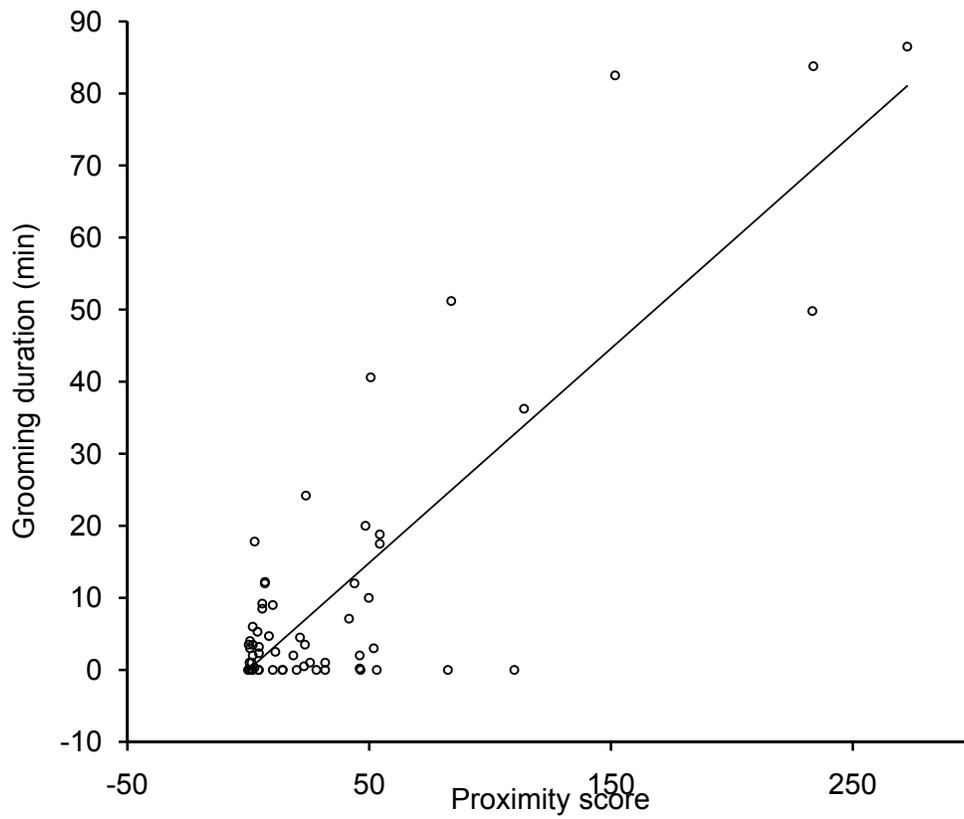


Figure 4-6. Association between total proximity scores and grooming durations (min), including all female-female and female-male dyads ( $r_s = 0.41$ ,  $P = 0.001$ ,  $n = 63$ ).

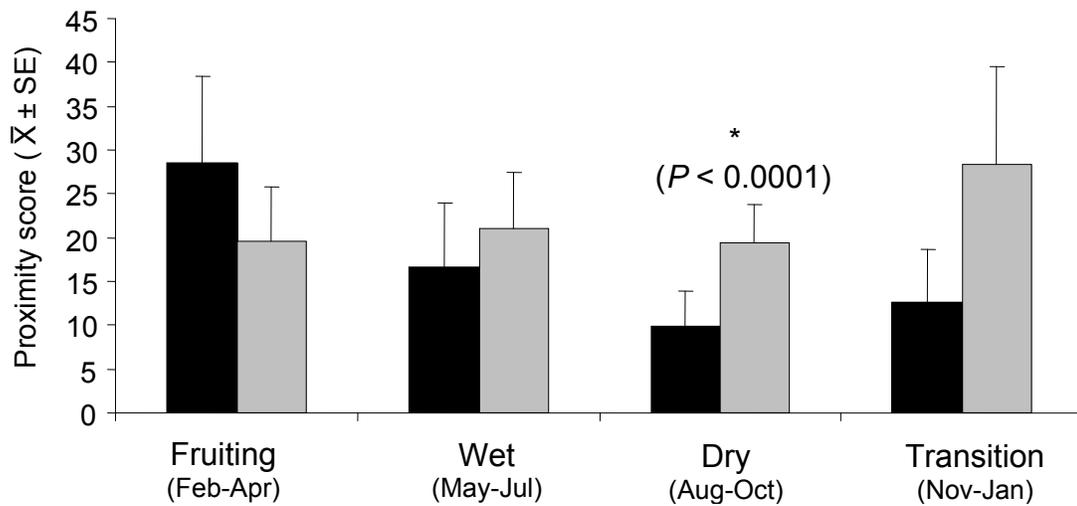


Figure 4-7. Seasonal variation in female proximity to females (black bars) and to males (grey bars). Female proximity to other females was highest during the fruiting season, while female proximity to males was highest during the transition season. Females stayed closer to males than to females in each season except the fruiting season, although the only statistical difference was during the dry season, when females were significantly closer to males than to females ( $P < 0.0001$ ).

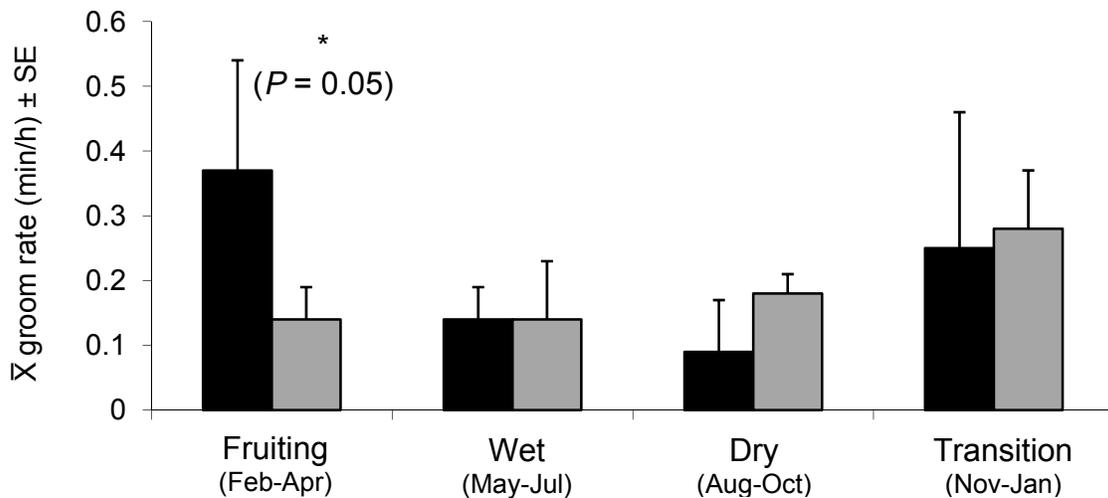


Figure 4-8. Seasonal variation in the rate at which females groomed females (black bars) and females groomed males (grey bars). Females devoted more grooming to females than to males only during the fruiting season, and this finding approached significance ( $P = 0.05$ ). In the remaining seasons, females groomed males more than females although there was no statistical difference in the rate at which females groomed males as opposed to females.

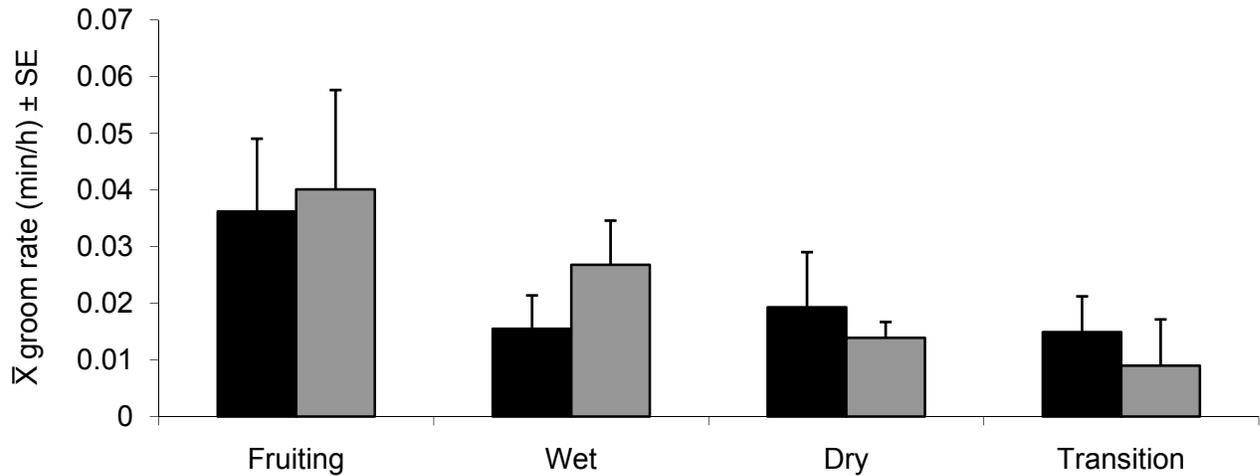


Figure 4-9. The monthly rate (min/h) at which females in each season groomed up the hierarchy (black bars) as opposed to down the hierarchy (grey bars). There was no significant difference in any season in the rates at which female-female grooming occurred up versus down the hierarchy ( $P = 0.109$  to  $0.786$ ). Grooming up the hierarchy occurred more than the reverse direction only in the dry and transition seasons, with the greatest (up versus down) differential occurring in the transition season (Figure 4-9).

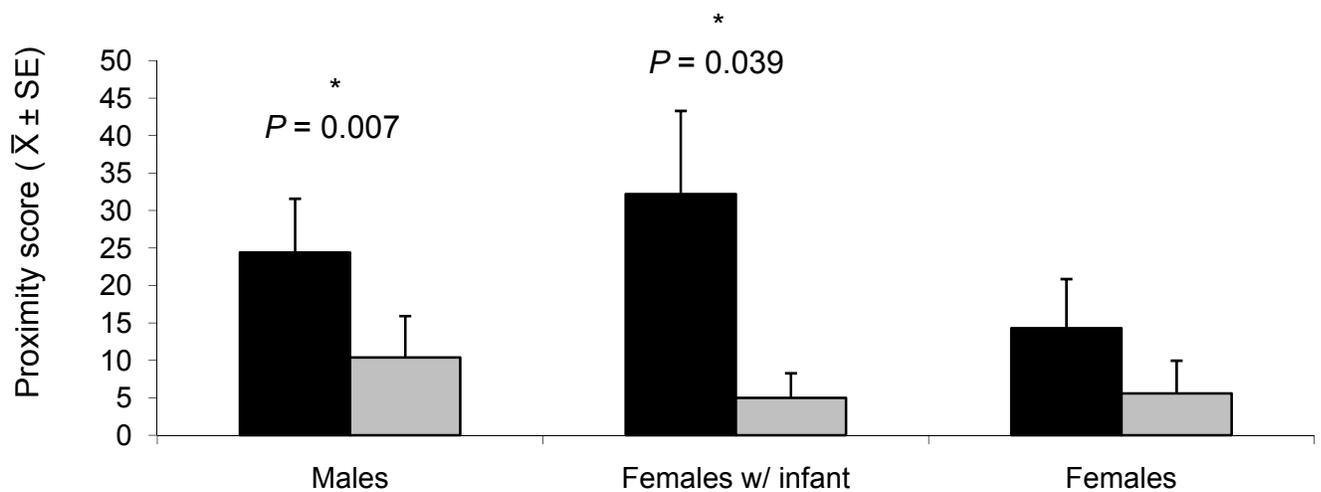


Figure 4-10. Proximity of mothers with (black bars) and without (grey bars) their young infants (<3 months old) to troop-mates during the fruiting season. Mothers carrying their infants (black bars) stayed significantly closer to other females carrying young infants ( $P = 0.039$ ) and to males ( $P = 0.007$ ) than when the mothers were without their infants (grey bars). The physical presence of an infant, however, did not affect a mother's proximity to females without babies.

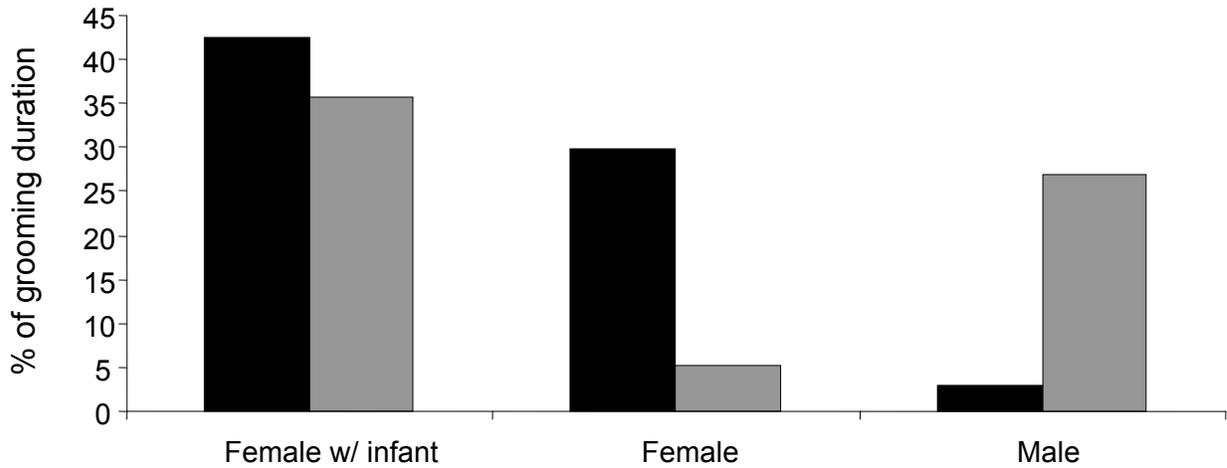


Figure 4-11. Grooming duration (%) between females with infants and adult troop-mates. Black bars represent the % of grooming that females with infants ( $n = 4$ ) received from other females with infants ( $n = 3$ ), females (without infants) ( $n = 3$ ), and males ( $n = 3$ ). Grey bars represent the % of grooming that females with infants groomed females with infants, females (without infants), and males. Females with infants devoted the most grooming to other females with infants, while females without infants received the least. All of the grooming that adult males received from females with infants was directed towards the alpha male. Females with infants received the majority of adult dyadic grooming from females (both with and without infants).

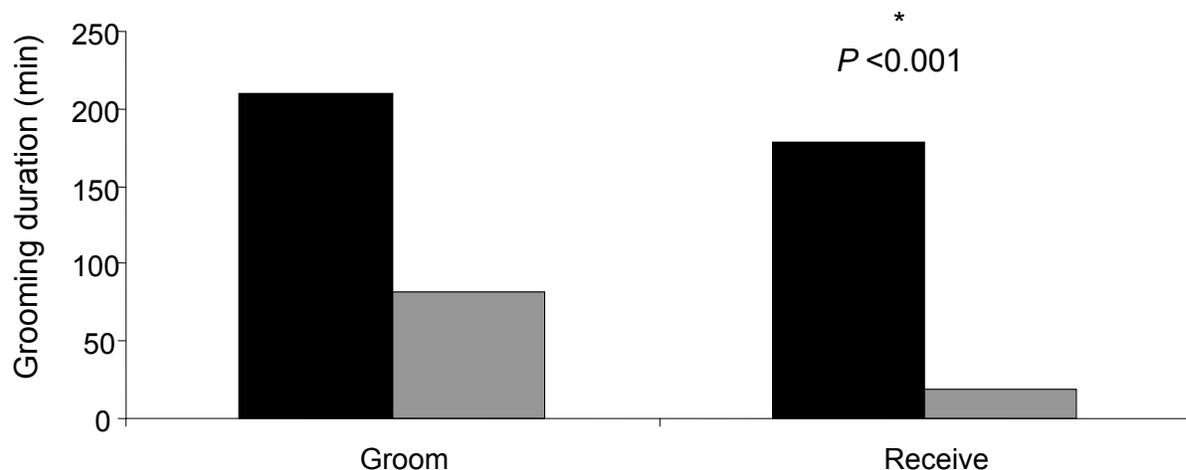


Figure 4-12. Total duration of time (min) that mothers with (black bars) and without (grey bars) their infants (< 3 months old) groomed and received grooming from troop-mates during the fruiting season. Mothers ( $n = 4$ ) both groomed and received grooming significantly more when they were carrying their infants (black bars) than when they were without their infants (grey bars) ( $P < 0.001$  and  $P < 0.001$ , respectively). The difference was not due to a disparity in opportunity, however, as there was no statistical difference in the number of scans that the mothers were observed with ( $n = 123$ ) and without ( $n = 101$ ) their infants during this time ( $P > 0.10$ ).

## CHAPTER 5 DO FEMALE BROWN CAPUCHIN MONKEYS USE AFFILIATIVE BEHAVIOR TO MEDIATE STRESS?

### **Introduction**

This chapter targets the poorly understood nexus that links the dynamics of female stress response (defined as the increase in the stress hormone cortisol) with social behavior and relationships. The glucocorticoid (GC) cortisol, a 'stress hormone', is commonly measured as an indicator of stress. Upon encountering a stressor (i.e., any extrinsic or intrinsic threat to homeostasis), GCs are released into the bloodstream in response to activation of the hypothalamus-pituitary-adrenal (HPA) axis (Wingfield et al. 1997). Over the short term, acute stress response is an adaptive physiological condition, which, upon encountering a threat, regulates the diversion of energy from long-term storage to meet short-term needs, thus increasing prospects of immediate survival. Over extended periods, however, the metabolic costs of sustained stress rise steeply (Sapolsky et al. 2000), adversely affecting female health and reproductive ability, fetal development and the development of offspring social skills, and stress-coping abilities (Sachser et al. 1998; Bardi et al. 2005; Sapolsky 2005; Shively et al. 2005; Wadhwa 2005). Therefore, in order to protect current and future reproductive success, a female should take an active role in managing stress.

Both social (Sapolsky 2005; Soto-Gamboa et al. 2005) and environmental factors contribute to physiological stress in captivity and the wild (Boinski et al. 1999b; Lynch et al. 2002; Pride 2005a,b). While field studies tend to focus on the variables correlated with stress levels of wild animals (Holekamp and Smale 1998; Foley et al. 2001; Lynch et al. 2002; Rogovin et al. 2003; Altmann et al. 2004; Weingrill et al. 2004; Bales et al. 2005; Beehner et al. 2005; Creel 2005; Gould et al. 2005; Pride 2005a,b), experimental

manipulations of captive animals assess the importance of social relationships in the management of stress among a few taxa, specifically and most commonly rodents and non-human primates (Tamashiro et al. 2005). Thus, there is a paucity of data directly investigating how socioecological stress co-varies with social relationships in wild populations.

### **Stress and Sociality**

The social environment of group-living species is a balance of deleterious consequences and adaptive benefits. Specifically in regard to social relationships, individuals may face negative physiological effects as a result of, for example, their dominance status (Chapter 3) but be provided with a (possible) means to reduce neuroendocrine response to stressful situations: In some animals (e.g., guinea pigs (Sachser et al. 1998; Kaiser et al. 2003; Hennessy et al. 2006); prairie voles (Carter et al. 1995); tree shrews (von Holst 1998); squirrel monkeys (Saltzman et al. 1991); marmosets (Norcross and Newman 1999; Rukstalis and French 2005); and rhesus macaques (Gust et al. 1994), including humans (Kirschbaum et al. 1995; Heinrichs et al. 2003; Rosal et al. 2004), the presence of an adult partner provides stress reducing effects. Often referred to as social support (Sachser et al. 1998), the ability to reduce cortisol reactivity to a stressor cannot be provided by any conspecific or group-mate but rather is limited to bonding partners (Mendoza et al. 1991; Carter et al. 1995; Sachser et al. 1998; von Holtz 1998; Rukstalis and French 2005; Hennessey et al. 2006; but see Saltzman et al. 1991; Kaiser et al. 2003).

While the importance of bonding partners is most studied in monogamous species (i.e., male-female pair bonds), the adaptive functions of social bonds are likely provided both inter- and intra-sexually and also within other types of social systems. The

restriction appears to be not the type of social system itself, but rather the affinity of individuals to form strong within-group partner preferences (Hennessy et al. 2008). For example, plasma cortisol levels of male guinea pigs (*Cavia aperea porcellus*), a species with a single male, multi-female social system, similarly increased subsequent to being removed from their social colony and placed in a novel environment either in isolation, with an unfamiliar female, or with a familiar but unbonded female. When placed with a female to whom they were bonded, however, there was a significant decrease in the males' cortisol reactivity (Sachser et al. 1998). Similar results were found when testing the effects of familiar unbonded versus bonded male partners (Kaiser et al. 2003) and bonded versus unfamiliar male partners (Hennessy et al. 2008) on the cortisol response to a novel environment of female guinea pigs. Further, while a harem's female guinea pigs naturally space themselves out and display minimal interaction, there was evidence that captive female-female pairs may demonstrate HPA buffering indicating the ability to, given opportunity, form intrasexual social bonds (Hennessy et al. 2008).

Females are more prone than males to rely on their social network in times of stress, a difference so striking that it is considered to be the primary gender difference in behavioral response to stress, especially among humans. Further, women are not only more likely than men to choose to affiliate during stress, but women choose to affiliate with other women (Taylor et al. 2000). Taylor and colleagues proposed that while the 'fight-or-flight' stress response is adaptive to males, such a response would not address the challenges faced by females; a mother's decision to either fight or flight would similarly endanger her offspring, often rendering them alone and unprotected. As such, the 'tend-and-befriend' pattern evolved in group-living females to protect both the

female and her offspring. Empirical evidence supporting the adaptive significance of female social bonds is provided by a wild population of savannah baboons (*Papio cynocephalus*); females that are more socially integrated within their groups had higher rates of reproductive success (infant survival to year one) than other females, regardless of rank (Silk et al. 2003). Further highlighting the importance of female social networks, female chacma baboons (*Papio hamadryas ursinus*) experienced elevated GC levels when their social bonds were disrupted or became unstable (Engh et al. 2006a) and expanded their social networks when a preferred partner was lost to predation (Engh et al. 2006b).

The presence of non-human primate social bonds is most commonly quantified through measures of grooming and time spent in proximity. The physiological benefits of grooming have been demonstrated empirically in several studies involving captive non-human primates. For example, Boccia et al. (1989) and Aureli et al. (1999) showed that in a female pigtail macaque (*Macaca nemestrina*) and female rhesus macaques (*Macaca mulatta*), respectively, the receipt of grooming lowered heart rate. Similarly, Gust et al. (1993) provided evidence for a negative correlation between affiliative behaviors (including proximity and the receipt of grooming) and cortisol levels in female rhesus macaques. Such evidence lends to the notion that grooming is an effective social outlet for reducing stress (Abbott et al. 2003) and is one of the primary coping mechanisms used by female non-human primates to reduce HPA axis activity (Wittig et al. 2008). The mechanism for such likely stems from the attachment-caregiving system between a mother and infant, and thus is (at least in part) oxytocin-mediated (Taylor et al. 2000). In general, oxytocin both inhibits the release of GCs (Neumann et al. 2000b;

Legros 2001) and promotes affiliative behavior (Martel et al. 1993; McCarthy and Altemus 1997; Carter 1998; Uvnas-Moberg 1998; Insel and Young 2001). The degree to which oxytocin is involved in HPA axis suppression, however, is dependent on both species and reproductive state (Neumann et al. 2000a; Brunton et al. 2008).

## **Stress Hormones and Female Reproductive Condition**

### **Pregnancy and lactation**

Female stress hormone concentration is affected by reproductive condition (Brunton et al. 2008). For example, among baboons, female cortisol levels were significantly higher during pregnancy than during other reproductive stages (Weingrill et al. 2004; Gesquiere et al. 2008), a pattern replicated by several other primate taxa including tamarins (Ziegler et al. 1995; Bales et al. 2005), marmosets (Smith and French 1997), lemurs (Cavigelli 1999), and humans (Lockwood et al 1996). During late pregnancy, especially peripartum, female human and non-human primates experience increased basal GC levels. Such hypercortisolism, however, is not to be viewed as an internal stressor but rather a necessary, adaptive condition of gestation and labor, serving to support fetal growth and development and link fetal organ maturation with parturition (Pepe and Albrecht 1995). This increase in GC concentrations is due to the production of placental corticotropin-releasing hormone (CRH), which increases overall GC concentration (Goland et al. 1994; Lockwood et al. 1996).

Despite the primate pattern of elevated basal GC levels during late pregnancy, it has been shown in various non-human mammals (with research heavily biased towards the rat) that the responsiveness of the HPA axis to physical and psychological stressors decreases during late-pregnancy and is maintained through lactation (Cook 1997; Windle et al. 1997; Shanks et al. 1999; Brunton and Russell 2003; Tu et al. 2005;

Tilbrook et al. 2006). For example, Tilbrook and colleagues (2006) show that, in response to isolation and restraint stress, cortisol levels increased significantly in non-lactating ewes but were not affected in lactating ewes. Additionally, the physical presence of their suckling infants further decreased the mothers' cortisol concentrations as compared to lactating ewes with lambs absent and to non-lactating females. In response to physical stress, a similar pattern was found for human females (Altemus et al. 1995; Kammerer et al. 2002). In response to psychosocial stress (e.g., public speaking), however, the physiological state of lactation did not appear to provide an overall attenuating effect on the human HPA axis, whereas the short-term act of nursing did result in temporary endocrine suppression (Altemus et al. 2001; Heinrichs et al. 2001).

The adaptive benefits of attenuated maternal stress response are well-known, namely to prevent excessive levels of circulating GCs that could impair healthy development of offspring, proper maternal care, adequate and nutritious milk supply, and the physical (e.g., immune function) and psychological well-being of the mother (Altemus et al. 1995; McCormick et al. 1995; Vallee et al. 1997; Weinstock 2001). For example, pregnant and lactating women reported feelings of increased calmness and reduced anxiety and moodiness (Carter et al. 2001; Heinrichs et al. 2001; Glynn et al. 2004), and the abuse of infants by rhesus macaque mothers was linked to elevated HPA axis activity (Maestriperi et al. 2005). Reduced HPA axis activity of the maternal brain, therefore, is a protective mechanism by which reproductive success is improved and mothers are better able to mentally and emotionally cope with hormonal fluctuations (Slattery and Neumann 2008).

The mechanisms underlying suppression of maternal stress-responsivity, however, are yet to be fully understood. Although oxytocin (necessary to stimulate milk let-down and maternal behavior) suppresses GC production, the release of oxytocin during parturition and in response to suckling did not explain the attenuation of stress responsivity observed in pregnant and lactating rats. Rather, oxytocin was an inhibitor of the HPA axis only in virgin females (Neumann et al. 2000a). HPA axis hyporesponsiveness during pregnancy appears to be due to endogenous opioids, whereas low estrogen levels may contribute to reduced GC response during lactation. An alternative, and possibly complementary, explanation for lactation-induced HPA axis hyporesponsiveness may be the neuropeptide prolactin which, like oxytocin, is necessary for milk production and is released in response to suckling (Brunton et al. 2008). In virgin rats, prolactin infusion (which mimics peripartum physiology) reduced anxiety-related behavior and HPA axis activity (Torner et al. 2001; Donner et al. 2007), and prolactin was more effective than oxytocin in reducing cortisol secretion in response to stress in both lactating and non-lactating sheep (Cook 1997).

### **Estrus cycling**

Considerably less has been published regarding the relationship between stress hormones and the female ovarian cycle of estrus and anestrus, likely because of the difficulties in studying such transient conditions. Weingrill and colleagues (2004) reported that, overall, cycling female baboons had lower cortisol values than pregnant and lactating females, a pattern also found among cotton-top tamarins (Ziegler et al. 1995). Because estrogen can stimulate the HPA axis therefore resulting in increased production of GCs (Coe et al. 1986; Altemus et al. 1995), elevated cortisol levels are expected during the periovulatory phase (i.e., the estrus period) when estrogen levels

are high (Weingrill et al. 2004). Support for this prediction comes from studies on the cotton-top tamarin (Ziegler et al. 1995), common marmoset (Ziegler and Sousa 2002), and dairy cow (Lyimo et al. 2000). On the other hand, several studies provide empirical evidence that do not support this prediction. For example, a study of dairy cattle showed no change in cortisol levels between estrus and anestrus females (Walker et al. 2008). Among wild chacma baboons (*Papio hamadryas ursinus*), there were no significant differences in periovulatory cortisol levels as compared to other portions of the female cycle, but the authors acknowledged that the limited number of samples collected during the various phases may have precluded detection of actual patterns (Weingrill et al. 2004). Lahoz and colleagues (2007) reported similar findings for captive *Cebus*: Despite a threefold increase in periovulatory estradiol concentrations, circulating cortisol levels remained unchanged throughout the female cycle.

### **Hypotheses**

Using brown capuchins (*Cebus apella*) as my study system, I investigated the relationship between female cortisol levels, social relationships and reproductive condition, specifically addressing if and how females use affiliative behavior to mediate stress. My study of stress response and management is the first to examine the hormonal correlates of social behavior for female brown capuchins in the wild. Although female *C. apella* are widely accepted to be a female-bonded species, with females dedicating more affiliative behavior (grooming and close proximity) to females rather than to males (Di Bitetti 1997), the results of my study (Chapter 4) indicate deviation from that pattern. Female-female relationships were most evident in the presence of a young infant, and females were generally more closely bonded to males than to females. Further, temporal variation in a female's social network, rather than stable,

long-term relationships, appears to be the norm for this population. Do the shifts in female social networks co-vary with ecological, social and reproductive stressors? While controlled laboratory studies indicate a reciprocal relationship between stress and social support, is such a dynamic empirically evident in a wild population? To address these questions, I studied the following hypotheses:

- Female cortisol levels are inversely associated with rates of affiliative behavior.
- Female cortisol levels vary with monthly variations in affiliation.
- Female cortisol levels vary with reproductive condition.
- Female reproductive condition affects affiliative behavior.

## **Methodology**

### **Site Description**

Raleighvallen (RV), a 7812 km<sup>2</sup> reserve consisting of primary tropical rain forest, is located within the 1.6 million ha Central Suriname Nature Reserve in Suriname. The main study site measured approximately 2 km<sup>2</sup> and was covered by an extensive trail system. RV's flora and fauna are effectively undisturbed in the historical period, and an intact array of potential predators and competitors are present (Reichart 1993). The soils of the Guyanan Shield (including French Guiana, Suriname and Guyana) are nutrient-poor and highly weathered as they are derived from Precambrian bedrock. Fleshy fruits are low in abundance and available fruit resources typically occur in small patches (< 5 m diameter) (Boinski et al. 2002). Additionally, much of RV is composed of expansive bamboo patches and dense liana forest that restricts visibility (Boinski et al. 2003).

## Study Animal

The brown capuchin monkey (*Cebus apella*) is one of the four traditionally recognized species in the genus *Cebus* (Hill 1960). Capuchins live in multi-male, multi-female polygamous groups that are typically female philopatric. Adult males and females maintain separate dominance hierarchies; in general, males are dominant to females. *C. apella* social groups are typically comprised of 12 to 27 individuals, with an average troop size of 17 members. Troop membership and relationships remain relatively stable, except for subadult males who emigrate from their natal group and may subsequently transfer several times. Brown capuchins reside in a variety of habitats encompassing a large geographic range from Columbia to Argentina (Fragaszy et al. 2004). *C. apella* are omnivores; the bulk of their diet consists of fruit supplemented with seeds, vegetation, arthropods, and vertebrates (Terborgh 1983). Female brown capuchins demonstrate a conspicuous behavioral estrus (Janson 1984; Carosi et al. 1999) that is reliably indicative of the periovulatory phase; the length of the female cycle for this species is, on average,  $20.6 \pm 1.6$  days (Carosi et al. 1999).

The study troop (Troop A) was one of four brown capuchin groups commonly observed within the study site; the primary study subjects were the adult females and their relationships to the adult members of the group. For most of the study, Troop A consisted of 27 individuals, seven of which were adult females. The seven females of focus encompassed the spectrum of reproductive conditions: cycling, pregnancy (primiparous and multiparous), and lactating. During the study, one pregnant female disappeared; her disappearance coincided with her predicted due date, and thus it is possible her (presumed) death was related to pregnancy- or labor-related complications (Table 5-1). Relatedness among troop members is unknown; however, genetic analysis

of the brown capuchin population in RV is currently underway. The study troop had been habituated to human observers since 1998, and all individuals were recognized based on body size, color patterns, and other identifying characteristics such as scars, moles, and ear shape. Throughout the study period, inter-observer reliability tests were conducted monthly to ensure consistent and accurate identification of all troop members.

### **Data Collection**

From January to December 2006, I and/or field assistants followed Troop A for up to 10 h each day (beginning at sunrise). The group was followed, on average, 28 days per month, composing a total of 2284 h of observation (not including 'out of view' time). Female proximity data (within a 4 m radius) were collected via 'individual instantaneous scans' ( $n = 787$ ) and converted to quantified proximity scores, abbreviated as MPS (proximity to adult males) and TFPS (proximity to adult females). A detailed description of proximity data collection and proximity score calculations can be found in Chapter 4. Grooming and reproductive behavior were noted *ad libitum* (Altmann 1974).

### **Behavioral and Reproductive Definitions**

I defined a female bond as one in which a female's primary adult social partner (in terms of grooming and/or proximity patterns) was another female. An adult dyad was considered to have a "strong bond" (based on grooming or proximity) if their dyadic grooming duration or proximity score fell within the top 10% for the group (Silk et al. 2006b).

Grooming bout duration and frequency was recorded for all observed occurrences. A grooming bout involved one individual grooming another, and concluded when the grooming ended or was interrupted by another behavior for more than five seconds. A

new grooming bout began with a new dyad, or whenever the grooming continued or changed direction within the same dyad. Only grooming bouts involving at least one female (as actor or recipient), and where both participants could be identified (at least to the age and sex class) were included for analysis. All grooming bouts were counted as dyads; thus, if two monkeys were grooming the same individual concurrently, the episode was scored as two separate actor-recipient grooming bouts. Grooming bouts involving females in estrus (as actors or receivers) were included in analysis only when considering the dynamic between affiliative behavior and reproductive condition.

The focal females encompassed three reproductive conditions: "...cycling (females in any stage of the estrous cycle), pregnant (assigned post hoc from the birth of an infant and starting at the final detumescence of the estrus cycle), and lactating (the period following birth until the resumption of cycling)" (Crockford et al. 2008, p. 257). Lactation and the resumption of cycling following lactation were not mutually exclusive, however, as females tended to resume (at least behavioral) estrus while still nursing; mothers resumed 'estrus-like cycling' when their infants ranged in age from 5 to 10 months. Hormonally, I classified these females as lactating rather than cycling because their cycles were not yet regular and they nursed on a regular basis. Behaviorally, when examining the relationship between reproductive condition and affiliation, I classified these females as being in estrus when they displayed species-typical proceptive behavior. Based on cyclical patterns of behavioral proceptivity common to *C. apella* (e.g., eyebrow raising, grinning, wheez vocalizations, head cocking, chest rubbing, touching (a male) and then running away, backing into the lap of a male, mounting) (Janson 1984; Carosi et al. 1999; Ehmke, personal observation), I was able

to ascertain when a cycling female was in estrous. For purposes of my study, I classified a cycling female as anestrus if she was not in estrus.

### **Hormonal Sampling and Analysis**

Fecal samples were collected opportunistically, with the goal of collecting at least one sample per female ( $n = 7$ ) per 15-day interval (Engh et al. 2006a,b; Lynch et al. 2002). Fecal samples were collected only if the female was observed defecating and her identity ascertained with certainty. Upon collection, each sample was immediately placed in an empty plastic vial and stored inside a thermos with an instant chemical cold pack. Samples were processed within three hours of collection and registered, on average, at 44°F. The samples were processed using Solid Phase Extraction (SPE) according to Ziegler and Wittwer (2005): 0.1 g of fecal material was mixed with 2.5 ml of distilled water and 2.5 ml of ethanol. The mixture was then hand-shaken for 5 min and centrifuged for 10 min. Two ml of the supernatant was removed and passed through an Alltech Prevail C18 Maxi-Clean SPE Cartridge (Alltech, Deerfield, IL) and stored. Samples were shipped to The Wisconsin Regional Primate Research Center for analysis. Using Enzyme ImmunoAssay, each sample was analyzed for cortisol (F) concentration (ng/g); the assays were validated for accuracy and parallelism using internal controls.

A total of 265 fecal samples were collected from Troop A females. A baseline fecal cortisol level for each female was established by calculating the mean after removing the highest and lowest 5% of values (Peel et al. 2005). These baseline cortisol values ( $n = 237$ ) were used when analyzing the relationship between cortisol and reproductive state. When examining the relationship between female cortisol levels and affiliation, however, all cortisol values ( $n = 265$ ) were included in analysis.

## Statistical Analysis

When feasible, data were analyzed using parametric statistical tests; when data failed to meet the assumption of normality, however, non-parametric alternatives were used. When comparing two independent samples (e.g., groom rates of pregnant versus lactating females), I used the independent samples t-test/Mann-Whitney U test; when comparing two related samples (e.g., mean rates at which pregnant females groomed males versus females), I used the paired samples t-test/Wilcoxin signed-rank test. When comparing more than two samples, I used either one-way ANOVA in conjunction with Tukey's post hoc tests or the Kruskal-Wallis one-way ANOVA in conjunction with Mann-Whitney U tests as the non-parametric alternative to posthoc tests. Correlations between parameters were evaluated using either Spearman's  $r_s$  (Excel's Analyse-It statistical package) or, to control for a third variable, partial correlation. Analyses were performed using SPSS 11.0; the significance level for all tests (two-tailed) was set at 0.05. Mean values are presented with standard error values.

## Results

### Association between Social Proximity and Female Cortisol Levels

Overall, there was no troop-wide association between females' mean proximity scores and cortisol levels (TPS:  $r_s = -0.43$ ,  $P = 0.34$ ; TFPS:  $r_s = -0.64$ ,  $P = 0.12$ ; MPS:  $r_s = -0.36$ ,  $P = 0.43$ ) (Table 5-2). Similarly, there were no associations between an individual female's cortisol levels and monthly proximity to males ( $r_s = -0.31$  to  $0.58$ ,  $P = 0.10$  to  $0.73$ ) or to females ( $r_s = -0.06$  to  $0.42$ ,  $P = 0.22$  to  $0.88$ ) (Table 5-3). While most females showed a positive (although not necessarily significant) relationship between proximity scores and time spent in a central position within the troop (Table 5-4), there were no associations between central position and cortisol levels

( $r_s = -0.12$  to  $0.53$ ,  $P = 0.11$  to  $0.90$ ). In regards to monthly proximity strong bonds (the top 10% of females' monthly proximity scores), there were no individual associations between months with versus without such strong bonds and cortisol levels. Further, data did not indicate any directional descriptive trend in female cortisol levels: Two females had higher mean cortisol levels in months with proximity strong bonds as compared to those months without proximity strong bonds; two females had comparably higher mean cortisol levels in months without proximity strong bonds; and the mean cortisol levels of two females were nearly equivalent in months with and without proximity strong bonds (Table 5-5).

### **Association between Grooming (given) and Female Cortisol Levels**

Overall, there was no troop-wide association between female cortisol levels and the monthly rates at which females groomed females ( $r_s = -0.36$ ,  $P = 0.43$ ). The rate at which females groomed males, however, was significantly associated with female cortisol levels ( $r_s = -0.77$ ,  $P = 0.045$ ). While there was a strong correlation between a female's rank and the rate at which she groomed males ( $r = 0.78$ ,  $P = 0.04$ ), there was no association between female rank and overall cortisol level ( $r = 0.39$ ,  $P = 0.38$ ). Further, after controlling for rank, the relationship between female cortisol levels and the grooming of males remains strong and nearly significant ( $r = -0.80$ ,  $P = 0.058$ ). Sample sizes (i.e., grooming rates) were too small and cortisol levels too variable to test statistically for monthly associations between the cortisol levels of an individual female and the rate at which she groomed females and males. For two females, Jane and Carol, however, there was a significant, positive correlation between the number of adult troop-mates they groomed in a month and their monthly cortisol concentrations ( $r_s = 0.823$ ,  $P = 0.01$ ;  $r_s = 0.748$ ,  $P = 0.02$ , respectively); for the remaining five females,

no association existed between monthly grooming network size and cortisol values ( $P = 0.23$  to  $0.92$ ). In regards to monthly grooming strong bonds (the top 10% of adult dyadic grooming durations given by females) and cortisol levels, data did not indicate any directional descriptive trends: Two females had higher mean cortisol levels in months with grooming strong bonds as compared to those months without grooming strong bonds; three females had comparably higher mean cortisol levels in months without grooming strong bonds; and the mean cortisol levels of one female were nearly equivalent in months with and without grooming strong bonds (Table 5-6).

### **Association between Grooming (received) and Female Cortisol Levels**

Overall, there was no troop-wide association between female cortisol levels and the monthly rates at which females received grooming from females ( $r_s = -0.57$ ,  $P = 0.18$ ) or from males ( $r_s = -0.25$ ,  $P = 0.59$ ). Sample sizes (i.e., grooming rates) were too small and cortisol levels too variable to test statistically for monthly associations between the cortisol levels of an individual female and the rate at which she received grooming from females and males. However, there existed no correlation between the number of adult troop-mates that groomed a female each month and her monthly cortisol values ( $P = 0.15$  to  $0.84$ ). In regards to monthly grooming strong bonds (the top 10% of adult dyadic grooming durations received by females), there resulted no significant associations between the presence of monthly grooming strong bonds and cortisol levels for any female. However, a descriptive trend emerged: All females (with the exception of the most subordinate female) had higher cortisol levels in the months characterized by the presence of strong grooming bonds (grooming received) as compared to the months without such bonds (Table 5-7).

## Reproductive Condition, Female Cortisol Levels and Affiliative Behavior

### Cortisol levels

Comparing all females in various states of reproductive condition (anestrous, estrus, pregnancy, and lactation), there was a troop-wide association between reproductive condition and female cortisol levels ( $P = 0.013$ ). Controlling for season, this association remained nearly significant ( $P = 0.067$ ). Overall, pregnant females ( $n = 2$ ) had the highest cortisol levels (mean  $\pm$  SE =  $75.29 \pm 17.01$ ), while lactating females ( $n = 4$ ) had the lowest cortisol levels (mean  $\pm$  SE =  $43.26 \pm 4.90$ ). Posthoc analysis revealed that lactating females had significantly lower cortisol levels than anestrous ( $P = 0.027$ ), estrus ( $P = 0.018$ ) and pregnant ( $P = 0.033$ ) females (Figure 5-1). Due to limited cortisol samples and variable cortisol data, it was not possible to determine statistically whether there existed inter- or intra-individual differences in cortisol levels by reproductive condition.

Pregnant females were represented only by Jane (dominance hierarchy ranking 3 of 7) and Tinkerbelle (ranking 7 of 7), the two females with the highest baseline cortisol levels (Chapter 3). While I cannot rule out the possibility that these individuals were naturally more prone than other females to cortisol reactivity of extrinsic variables, their pregnant condition appears to have been a confounding factor. Tinkerbelle's cortisol levels increased steadily throughout her pregnancy and were strongly and positively correlated with gestation length ( $r_s = 0.94$ ,  $P = 0.005$ ) (Figure 5-2). Jane's cortisol levels, on the other hand, were not associated with gestation length ( $r_s = 0.10$ ,  $P = 0.715$ ), but in her final month of pregnancy (also the month of her presumed death), Jane's mean cortisol level was significantly higher than in all other months in which she was pregnant ( $P = 0.01$  to  $0.03$ ) (Figure 5-3).

Lactating females ( $n = 4$ ) represented the span of the dominance hierarchy (ranks 1, 2, 5, and 6 of 7) and thus provided a natural (troop-level) control for the effect of rank on lactating female cortisol levels. Cortisol levels of lactating females were associated with incremental age groupings of their infants ( $P = 0.005$ ), although in no directional pattern (i.e., the cortisol levels of lactating females did not consistently increase (or decrease) over time as their infants aged and lactation demand lessened). Cortisol levels were highest (mean  $\pm$  SE =  $68.72 \pm 17.26$ ) for lactating females when their infants were  $\leq 3$  months of age and lowest when their infants were 6 to 9 months of age (mean  $\pm$  SE =  $24.34 \pm 3.06$ ) (Figure 5-4). These time spans, however, generally corresponded with the fruiting season (February to April) and dry season (August to October), respectively, and thus introduces seasonality as a confounding variable. Controlling for season, there existed no correlation between female cortisol levels and lactation over time (3-month increments) ( $r = -0.11$ ,  $P = 0.19$ ).

### **Proximity**

In terms of proximity, lactating females (i.e., those with dependent infants) had significantly higher proximity scores with adult females (TFPS) (mean  $\pm$  SE =  $29.02 \pm 6.05$ ) than did cycling (mean  $\pm$  SE =  $1.94 \pm 0.70$ ) ( $P < 0.0001$ ) and pregnant females (mean  $\pm$  SE =  $3.50 \pm 2.18$ ) ( $P = 0.001$ ). The pattern holds true for the proximity to adult males (MPS) of lactating (mean  $\pm$  SE =  $26.88 \pm 4.93$ ), cycling (mean  $\pm$  SE =  $18.11 \pm 5.18$ ), and pregnant (mean  $\pm$  SE =  $7.14 \pm 4.23$ ) females, although the difference is significant only when the MPS of lactating females is compared to the MPS of pregnant females ( $P = 0.023$ ). Further, there was a negative correlation ( $r_s = -0.44$ ,  $P = 0.005$ ) between infant age and the TFPS of mothers ( $n = 4$ ), but no relationship between infant age and mothers' MPS ( $r_s = -0.06$ ,  $P = 0.74$ ) (Table 5-8). Overall, there were no

statistical differences between TFPS and MPS at any 3-month incremental infant age categories ( $P = 0.09$  to  $0.59$ ), but it is interesting to note that for mothers with dependent infants, TFPS remained higher than MPS generally for the first 6 months of their infants lives, after which MPS was higher than TFPS (Table 5-8); individually speaking, this pattern held true for two of the mothers, while the remaining two mothers had TFPS values that were higher than MPS values for only the first 3 months of their infants' lives. For pregnant females ( $n = 2$ ), there was no association between gestation length and proximity to females ( $r_s = -0.09$ ,  $P = 0.81$ ) or males ( $r_s = 0.24$ ,  $P = 0.51$ ). The pregnant females maintained a higher (non-significant) MPS than TFPS during each month of pregnancy (Table 5-9). As proximity data were not collected on estrus females, I was unable to test for the effect of estrus cycling on female proximity scores. Estrus females, however, overwhelmingly dedicated their close attention to following males, and specifically the alpha male. While in anestrus, cycling females ( $n = 3$ ) had significantly higher MPS ( $18.11 \pm 5.18$ ) than TFPS ( $1.94 \pm 0.70$ ) ( $P = 0.001$ ).

### **Grooming (given)**

In terms of grooming behavior, reproductive condition did not have a significant effect on the rates at which females groomed females ( $P = 0.293$ ) or males ( $P = 0.196$ ). Lactating females groomed both females and males at the highest rates ( $0.0201 \pm 0.0057$  min/h,  $0.0357 \pm 0.0062$  min/h, respectively), while pregnant females least groomed both females and males ( $0.0085 \pm 0.0058$  min/h,  $0.0173 \pm 0.0088$  min/h, respectively). In each reproductive condition, females groomed males at a higher (non-significant) rate than they groomed females (Figure 5-5).

The effect of infant age on the rates at which mothers groomed males approached significance ( $P = 0.061$ ), with lactating females most grooming males when their infants

were 0 to 3 months old ( $0.0528 \pm 0.0132$  min/h) and 9 to 12 months old ( $0.0551 \pm 0.0145$  min/h) as compared to when the infants were 3 to 6 and 6 to 9 months old (mean  $\pm$  SE =  $0.0212 \pm 0.0096$ ); infant age did not affect the rate at which mothers groomed females ( $P = 0.249$ ), females groomed mothers ( $P = 0.107$ ), or males groomed mothers ( $P = 0.420$ ). The rate at which mothers groomed females, however, decreased steadily with infant age, and the two variables were modestly correlated ( $r_s = -0.37$ ,  $P = 0.021$ ) (Figure 5-6).

A strong, positive correlation occurred between gestation length and the rate at which Jane, one of the pregnant females, groomed females ( $r_s = 0.95$ ,  $P = 0.05$ ), but there was no such association for the other pregnant female, Tinkerbelle ( $r_s = 0.22$ ,  $P = 0.72$ ). Further, in her final month of pregnancy (October), Jane intensified her grooming effort towards the dominant male and female. In October, Jane dedicated 48% of her grooming duration to the alpha male, whereas in all previous months she dedicated, on average, 35% of her (non-estrus) grooming to him. Similarly, in October, Jane devoted 45% of her grooming duration to the dominant female, whereas previously, this grooming investment averaged 11%. Tinkerbelle's final month of pregnancy occurred after the conclusion of the study, and so I was unable to determine if her peripartum grooming behavior followed a similar pattern.

Cycling females groomed males at nearly two times the rate that they groomed females (Figure 5-5). When in estrus, cycling females devoted 97.9% of their grooming behavior towards the alpha male, whereas during anestrus, only 20.5% of their grooming was directed towards the alpha male.

## **Grooming (received)**

There was a significant effect on the rates at which females of different reproductive condition were groomed by females ( $P = 0.010$ ); this difference was attributable to the low rate of grooming that the pregnant females received from other females ( $0.0004 \pm 0.0004$  min/h). Both lactating and cycling (estrus and anestrus periods combined) females received significantly more grooming from females ( $0.0285 \pm 0.0104$  min/h,  $0.0145 \pm 0.0067$  min/h, respectively) than did pregnant females ( $P = 0.003$ ,  $P = 0.049$ , respectively), while there was no difference between the rates at which females groomed lactating and cycling females ( $P = 0.209$ ). Further, only lactating females received more grooming from females than males, and this difference was significant ( $P = 0.012$ ) (Figure 5-5).

There was a nearly significant difference in the rates at which males groomed females of different reproductive condition ( $P = 0.056$ ), with males focusing their grooming behavior on cycling (estrus and anestrus periods combined) females ( $0.0188 \pm 0.0076$  min/h) as compared to pregnant ( $0.0013 \pm 0.0010$  min/h) and lactating ( $0.0060 \pm 0.0025$  min/h) females (Figure 5-5). When in estrus, cycling females were groomed only by the alpha male; neither subordinate male nor any females were observed to groom estrus females.

## **Discussion**

### **Social Affiliation and Cortisol Levels**

Overall, group-level data did not support the hypothesis that female cortisol levels are inversely associated with affiliative behavior. Specifically, there was no discernable relationship between fecal GC concentration and proximity to adult male and/or female troop-mates, the receipt of grooming from males and/or females, or the grooming of

females. There was, however, an inverse association between female cortisol levels and the rate at which females groomed males, a surprising finding given the evidence that portrays the physiological benefit of the receipt of grooming (Boccia et al. 1989; Gust et al. 1993; Aureli et al. 1999). This unexpected result supports the findings of Shutt et al. (2007), who found that, in female Barbary macaques (*Macaca sylvanus*), it was the giving rather than the receiving of grooming that was associated with reduced stress levels. In the earlier captive studies, the researchers measured the monkeys' immediate physiological response to grooming (via blood collection or heart monitoring implants); like Shutt et al. (2007), however, the current study was done on a wild population and the physiological response to grooming behavior was measured via fecal (i.e., 'pooled') GC concentrations. Therefore, the short-term physiological benefits of the receipt of grooming do not appear to lower stress levels in the longer term (Shutt et al. 2007).

Why the link between the grooming of males (specifically) and lower female cortisol levels? Female rank may be a confounding factor if more dominant females, who have greater access to males, generally have lower stress levels. This was not the case, however, as there was no correlation between female social rank and baseline cortisol levels (Chapter 3), and after controlling for rank the dynamic remained between female GC concentration and the grooming of males. Alternatively, reduced HPA axis activity may have resulted from the expectation of a strengthened social relationship, supporting the notion that grooming serves to initiate, maintain and/or strengthen social bonds (Stammach and Kummer 1982; Dunbar 1996; Lehmann et al. 2007; Fedurek and Dunbar 2009). That the grooming of female troop-mates was not found to be

associated with a decrease in female cortisol levels indicates that grooming it itself is not an effective social outlet for reducing stress, but may be depending upon the partner involved and the potential benefits of strengthening that particular dyadic relationship. This finding further supports the conclusions that females in a female-philopatric species may not necessarily view other females as their most beneficial social partners, and that female brown capuchins in RV are generally more bonded to males than to females (Chapter 4). It is interesting to note, however, that despite the possible long-term physiological benefits of grooming males, females rarely (if ever) were observed to compete for grooming access to males.

Data also did not support the individual-level hypothesis that female cortisol levels vary with monthly variation in affiliative relationships. Such a short-term association, however, may have been lost due to variability in GC concentrations and in low rates of social behavior. When comparing the months in which females had strong bonds (the top 10% of dyadic interaction) against less sociable months, however, (non-significant) patterns began to emerge, especially in regard to the receipt of grooming: Female cortisol levels were higher in months in which they demonstrated at least one strong bond via the receipt of grooming as compared to months in which they had no strong bonds. This positive relationship may appear puzzling given the relaxing and stress-reducing benefits provided by the tactile stimulation of being groomed. As discussed above, however, such physiological benefits may be so temporary that longer-term fecal GC concentrations are unaffected. Although I cannot, with any degree of certainty, attribute a causal link between reduced cortisol levels and strong grooming bonds, it is possible that this relationship indirectly supports the idea that social support (i.e.,

specific or particularly strong bonds) is essential for mediating stress (Mendoza et al. 1991; Carter et al. 1995; Sachser et al. 1998; von Holtz 1998; Rukstalis and French 2005; Hennessey et al. 2006; Wittig et al. 2008), such that females may have received more grooming from specific bonding partners because they were more stressed. Each female's grooming network typically included one to three adult conspecifics (male and/or female) that categorically produced multiple monthly strong bonds, while Tinkerbell, the female with the highest mean GC concentration, did not have a single adult grooming partner that produced multiple monthly strong bonds. Thus, it may have been Tinkerbell's lack of adult social support that hindered effective stress management.

Alternatively, the positive association between female stress levels and their receipt of grooming may have been confounded by an outside variable, such as the presence of a young infant. The cortisol levels of lactating females were highest when their infants were less than three months of age, and this time span corresponds to the period of greatly intensified grooming effort directed towards mothers (Chapter 4). The increase in GC levels of lactating females may have resulted from the unsolicited attention they and their babies received and the lack of control they were able to exert over their grooming partners (Crockford et al. 2008), obscuring the HPA axis suppressive effect of lactation. Overall, however, lactating females had the lowest cortisol values (as compared to pregnant and cycling females) (see below), and although lactating females demonstrated multiple strong bonds via the receipt of grooming in the month of February (when they each had an infant that was less than three months old), the females without infants also demonstrated strong bonds via the

receipt of grooming during the month of February (Chapter 4). Therefore, infant presence alone does not account for the dynamic between the increased receipt of grooming and female cortisol levels. Aside from February, females most demonstrated strong bonds through the receipt of grooming in the months of (in descending order) May, September and April, an expanse of time that controls for the effect of season and reduces the impact of infant presence on the relationship between stress and social integration. Therefore, it is possible that a female was most groomed by her bonding partners in response to socioecological stress, providing short-term stress-relief to the groomed female (although uncaptured via measures of fecal cortisol) and longer-term stress relief to the groomer (i.e., bonding partner) via the expectation of the benefits provided by the strengthened relationship.

### **The Influence of Reproductive Condition on Cortisol Levels**

As expected, female cortisol levels varied with reproductive condition. In support of the consensus that late pregnancy results in the increased production of GCs (Ziegler et al. 1995; Lockwood et al. 1996; Smith and French 1997; Cavigelli 1999; Weingrill et al. 2004; Bales et al. 2005; Gesquiere et al. 2008), the pregnant females in my study had the highest baseline cortisol levels. Jane's high baseline cortisol value was most likely a sole repercussion of pregnancy, as the final month of her pregnancy (and of her disappearance) was an outlier, the primary cause of her elevated baseline value (Appendix E). Similarly, Tinkerbelle's pregnancy factored heavily into her elevated baseline cortisol value, but was not the only attributing factor. The GC levels of pregnant females are expected to rise only during late pregnancy (Ziegler et al. 1995; Lockwood et al. 1996; Smith and French 1997; Cavigelli 1999; Bales et al. 2005). Tinkerbelle's cortisol values, however, increased from mid-pregnancy, indicating the

presence of outside stressors. Further, prior to her pregnancy, she demonstrated two months of elevated cortisol levels (2 to 3 times baseline value) (Appendix E). I attribute Tinkerbell's high cortisol concentrations to a combination of factors, namely her pregnant condition, low status and non-existent adult social network. In fact, in a meta-analysis of both New and Old World primates, the lack of social support was found to be a primary predictor of high cortisol levels of subordinate individuals (Abbott et al. 2003). Tinkerbell was quantitatively most stressed from September to January, the time of year that, in part, corresponds to not only the transition season (characterized by a low and unpredictable food supply), the most stressful season for the females in general (Chapter 3), but also to her late pregnancy (Appendix E). Thus, during an ecologically stressful time span for a female of low rank (and thus with minimal access to high quality food resources) and with minimal social support, Tinkerbell had the additional physiological burden of energetically sustaining pregnancy.

As opposed to studies that found cycling females to have lower GC concentrations than pregnant or lactating females (Ziegler et al. 1995; Weingrill et al. 2004), the current study found estrus cycling to be the median condition in terms of cortisol concentration. As expected, however, females in estrus had (non-significantly) higher cortisol levels than did cycling females not in estrus. Given that lactation-induced hyporesponsiveness of the HPA axis acts as a protective physiological mechanism for both mother and infant (Slattery and Neumann 2008), it was not surprising that lactating females demonstrated the lowest cortisol values. With female stress response suppressed by some mechanistic action of lactation, however, I expected there to be a reduced effect as the infants aged (to year one) and nursing frequency decreased. This

was not the case, however. After controlling for season, maternal cortisol levels did not progressively increase as lactation demand decreased. I predict that the physical presence of the infants, as well as their continued (albeit decreased) suckling, was sufficient to maintain maternal HPA axis hyporesponsiveness, as high levels of circulating GCs in the mothers' milk would still be maladaptive to infant development. Alternatively, but not necessarily mutually exclusive from the previous prediction, it may be that decreased lactation demand does result in a decreased suppressive effect of maternal stress but that a new balance is achieved whereby cortisol levels are not significantly affected. As infants become more independent and nurse less, for example, the energetic and physiological demands of infant caretaking decrease, thereby reducing maternal stressors. Therefore, as infants age, lactation-induced suppression of stress responsivity may decrease, but so do potential stressors, thereby maintaining maternal GC concentrations at a low level.

### **The Influence of Reproductive Condition on Affiliative Behavior**

In terms of proximity and the rates at which females received grooming, data support the hypothesis that female reproductive condition affects affiliative behavior. Lactating females (i.e., those with dependent infants) were in close proximity to and received the most grooming from other females, reinforcing the strong attractivity effect of young infants (Chapter 4; Henzi and Barrett 2002); cycling females were the focus of male grooming effort. Interestingly, when in estrus, cycling females were observed to be groomed only by the alpha male; when these females became pregnant, however, the alpha male ceased all grooming interest. This finding provides empirical evidence supporting the conclusions in Chapter 4 that males demonstrated a clear preference for the females that were most likely to conceive and possibly use grooming to bias female

mate choice in their favor, and that the dominant male cannot rely solely on his status to acquire matings. There was no evidence linking the immediate exchange of grooming for sex, and so this dynamic might involve a longer-term tradeoff. The turnover rate of this trade-off, if one exists at all, would be of interest for future study.

Although there was no overall effect of reproductive state on the rates at which females groomed adult troop-mates, intriguing within-condition patterns emerged. For example, that estrus females dedicated nearly all of their grooming effort to the alpha male clearly depicts female mate choice (Janson 1984). Additionally, one of the pregnant females, Jane, demonstrated an interesting pattern to her grooming behavior, possibly as a means to expand her social network in preparation for her newborn's arrival. The rate at which Jane groomed females strongly correlated with her length of gestation, and in her final month of pregnancy, Jane's intensified grooming effort uncharacteristically focused on the alpha male and dominant female. I interpret this as a means to strengthen ties with the individuals that would soon become most involved and/or important in her and her baby's life. Not only does this indicate an ability to socially strategize, but also the ability to strategically plan ahead. Tinkerbell, the other pregnant female, did not demonstrate such effort, possibly because of her virtual lack of social interaction with adult troop-mates. A second possibility, however, evokes the importance of experience with pregnancy and post-natal care in being able to understand what to plan ahead for. As a multiparous female, Jane likely was able to call upon previous experience to comprehend her current and future situation, whereas Tinkerbell, a primiparous female, was unable to do so. While still conjecture at this

point, the possibility is supported by these initial data patterns and warrants further investigation.

Just as Jane's social investment was affected by gestation length, the social behavior of lactating females was associated with the length of their reproductive condition. Mothers steadily decreased grooming behavior towards females as their infants aged, suggesting a social and/or physiological significance to their grooming investment. Likely involved in this dynamic is the use of grooming as a commodity to be traded and/or the stress-reducing properties of the receipt of grooming, whereby the grooming of curious female neighbors by the infants' mothers promoted an immediately more relaxed/less potentially agonistic environment surrounding the infant. As the infants aged, becoming more independent and less vulnerable (and less attractive to female conspecifics), the mothers were able to decrease their grooming investment in females. Additionally, that female-female proximity scores decreased with infant age, while female-male proximity scores did not, further exemplifies that strong female-female relationships are temporary and situation-dependent, while female-male relationships are more beneficial and thus more stable.

Highlighting the potential benefits of female-male relationships, lactating females most groomed males when their infants were less than 3 months old and as the infants approached one year of age. I predict that the former primarily secures benefits for the newborns (e.g., socialization of the infants with the dominant male and increased tolerance and protection from predators and troop-mates) (Chapter 4), while the latter is an assertion of the females' relationships with males as they resume hormonal cycling. Alternatively, most infants were 9 to 12 months of age during the transition season, and

thus seasonality may be a confounding factor. As already discussed, the transition season was a stressful time characterized by an unpredictable food supply (Chapter 3), and lactating females may have increased grooming investment in males during this time as a means to strengthen their relationships and garner the benefit of increased protection from predators and tolerance around food resources (especially important when still producing energetically expensive milk) and/or, as previously discussed, physiologically mediate their incurred stress via grooming and the expectation of returned benefits.

### **Conclusion**

Do females use affiliative behavior to mediate stress? Overall, female GC concentrations were not associated with rates of affiliative behavior or with monthly shifts in social relationships; the lack of statistical association, however, may be due to the substantial inter- and intra-individual variation in cortisol levels. Emergent patterns provide indication of the social mediation of female stress and identify more focused research questions for future study. In primates, social bonds are not hormonally determined, but are physiologically rewarding (Curley and Keverne 2005; Dunbar 2009). If there is a causal basis to the inverse association between female cortisol levels and the grooming of adult males, then this underscores that female *C. apella* in RV, despite being female-philopatric, are more bonded to males than to females. That females received more grooming from strongly-bonded troop-mates during periods of increased GC concentration supports the notion that smaller, more concentrated grooming networks have a greater impact on stress reduction than do larger, more diverse ones (Wittig et al. 2008). Further evidence supporting the possible dynamic between affiliative relationships and stress management is the finding that the most subordinate

female demonstrated an obvious lack of adult social support and had the highest overall GC concentration.

Female cortisol levels did vary by reproductive condition, and female reproductive condition was found to affect female affiliative behavior. Elucidating a direct relationship between reproductive stress and social behavior, however, was beyond the scope of my study and requires a focused investigation in itself. The dynamic between stress hormones and pregnancy is particularly complicated, as the expected (and necessary) peripartum increase in GCs does not preclude pregnant females from experiencing actual stress, nor does it negate the internal stressor of being pregnant, especially when confounded by other exacerbating factors such as low rank, lack of social support, and/or ecological stress. My study, however, provided an initial foray into untangling such variables, and an intriguing possibility emerged: An experienced (i.e., multiparous) pregnant female may have understood her current and future reproductive situation and was able to plan ahead and socially strategize, focusing her grooming effort on the individuals that would become more important and/or involved in her and her infant's life, possibly as a means to circumvent some of the stress involved in pregnancy and infant-caretaking. Further, despite hyporesponsiveness of the maternal HPA axis, lactating females with young infants experienced increased cortisol levels, likely in response to unsolicited attention (namely from female troop-mates) that was beyond the mothers' control. The increased rate of grooming that mothers devoted to female neighbors during this time can be interpreted as an immediate means to promote a relaxed social setting, essentially protecting the infants from risk of escalated agonism.

Table 5-1. Summary of the dominance rank, approximate age, birthing history and reproductive classification (for purposes of my study) of the adult *C. apella* focal females.

Female	Rank	Est. age (years)	Birthing history (most recent birth, as of Dec 2006)	Reproductive Classification* (Jan-Dec 2006)	Notes of interest
Gina	1	> 10	Multiparous (Dec. 24, 2005)	Lactating	
Banana	2	6	Primiparous (Jan. 21, 2006)	Lactating	
Jane	3	8	Multiparous (Feb. 22, 2005), pregnant	Cycling, Pregnant	Disappeared in October '06. Suspected obstetric-related death (near full term)
Little Horns	4	> 15	Multiparous (Dec. 6, 2004)	Cycling	
Carol	5	> 10	Multiparous (Nov. 22, 2005)	Lactating	
Kate	6	> 10	Multiparous (Feb. 5, 2006)	Lactating	
Tinkerbelle	7	6	Nulliparous, pregnant	Cycling, Pregnant	Gave birth to 1 <sup>st</sup> infant after conclusion of study

\* Females typically spanned at least two different reproductive conditions during the study period; their dominant condition(s) (which they most represent in the data set) is/are listed.

Table 5-2. Females' mean monthly values ( $\pm$  SE) of cortisol (F), total proximity score (TPS), total female proximity score (TFPS) and male proximity score (MPS). Overall, there was no troop-wide association between females'  $\bar{x}$  proximity scores and cortisol levels (TPS:  $r_s = -0.43$ ,  $P = 0.34$ ; TFPS:  $r_s = -0.64$ ,  $P = 0.12$ ; MPS:  $r_s = -0.36$ ,  $P = 0.43$ ).

Female	F	TPS	TFPS	MPS
Gina	48.29 $\pm$ 15.36	214.9 $\pm$ 28.83	52.7 $\pm$ 15.47	41.1 $\pm$ 11.54
Banana	76.05 $\pm$ 16.06	215.6 $\pm$ 45.85	38.4 $\pm$ 13.10	39.3 $\pm$ 11.82
Jane	90.21 $\pm$ 22.89	69.1 $\pm$ 14.91	5.6 $\pm$ 2.37	21.5 $\pm$ 10.72
Little Horns	67.70 $\pm$ 12.63	63.2 $\pm$ 12.43	1.5 $\pm$ 0.79	14.3 $\pm$ 3.69
Carol	69.63 $\pm$ 19.26	105.7 $\pm$ 15.86	10.7 $\pm$ 4.91	12.4 $\pm$ 3.64
Kate	54.83 $\pm$ 21.83	79.5 $\pm$ 29.25	11.6 $\pm$ 5.83	12.2 $\pm$ 5.90
Tinkerbelle	100.65 $\pm$ 27.31	47.3 $\pm$ 10.88	0.7 $\pm$ 0.68	9.5 $\pm$ 4.96
Troop $\bar{x}$	72.15 $\pm$ 7.33	113.61 $\pm$ 27.08	17.31 $\pm$ 7.62	21.47 $\pm$ 5.04

Table 5-3. Range of values for each female's  $\bar{x}$  monthly cortisol levels and total monthly proximity to females (TFPS) and to males (MPS). There were no significant associations between cortisol and proximity for any focal female.

Female	Cortisol (ng/g)	TFPS	TFPS association	MPS	MPS association
Gina	10.9 - 214.1	2.4 - 155.5	$r_s=0.20$ , $P=0.61$	4.3 - 103.0	$r_s=0.38$ , $P=0.31$
Banana	16.4 - 188.3	0.0 - 133.0	$r_s=0.07$ , $P=0.85$	3.6 - 123.7	$r_s=0.30$ , $P=0.40$
Jane	26.4 - 321.6	0.0 - 21.5	$r_s=0.08$ , $P=0.83$	0.0 - 95.6	$r_s=0.58$ , $P=0.10$
Little Horns	18.5 - 127.8	0.0 - 7.8	$r_s=0.42$ , $P=0.22$	0.0 - 37.9	$r_s=0.39$ , $P=0.26$
Carol	19.5 - 238.3	0.6 - 31.7	$r_s=0.24$ , $P=0.51$	0.0 - 26.6	$r_s=0.14$ , $P=0.70$
Kate	8.7 - 274.1	0.0 - 58.3	$r_s=0.06$ , $P=0.88$	0.0 - 54.6	$r_s=0.13$ , $P=0.73$
Tinkerbelle	16.0 - 245.2	0.0 - 6.8	$r_s=-0.06$ , $P=0.87$	0.0 - 47.8	$r_s=-0.31$ , $P=0.38$

Table 5-4. Association between a female's frequency of occupying a central position in the troop and her social proximity to adult females (TFPS) and adult males (MPS). Most females showed a positive relationship between centrality and proximity scores, although only the two most subordinate females (Kate and Tinkerbelle) demonstrated significant relationships.

Female	TFPS	MPS
Gina	$r_s = 0.58$ , $P = 0.08$ *	$r_s = 0.44$ , $P = 0.21$
Banana	$r_s = 0.62$ , $P = 0.06$ *	$r_s = 0.16$ , $P = 0.66$
Jane	$r_s = -0.12$ , $P = 0.76$	$r_s = 0.41$ , $P = 0.27$
Little Horns	$r_s = -0.22$ , $P = 0.55$	$r_s = 0.12$ , $P = 0.73$
Carol	$r_s = 0.11$ , $P = 0.77$	$r_s = -0.33$ , $P = 0.34$
Kate	$r_s = 0.97$ , $P < 0.0001$ **	$r_s = 0.71$ , $P = 0.02$ **
Tinkerbelle	$r_s = 0.59$ , $P = 0.07$ *	$r_s = 0.77$ , $P = 0.01$ **

Notes: \*\*significant relationship ( $P < 0.05$ ); \* relationship approaching significance ( $0.05 < P \leq 0.08$ )

Table 5-5. Relationship between months with and without proximity strong bonds and  $\bar{x}$  monthly cortisol (F) levels (ng/g). No female had a significant association between the presence of proximity strong bonds and cortisol levels, nor was there a consistent pattern among the females in terms of whether their  $\bar{x}$  cortisol levels were higher in months with versus without strong proximity bonds.

Female	$n_{\text{with}}$	$\bar{X}_F \pm SE$	$n_{\text{without}}$	$\bar{X}_F \pm SE$	<i>P</i> -value	F levels higher
Gina	9	61.6 ± 22.9	0	--	--	--
Banana	9	77.5 ± 18.6	1	93.4 ± --	0.79	without bonds
Jane	5	103.3 ± 34.4	4	105.3 ± 75.1	0.98	same
Little Horns	4	58.4 ± 23.9	6	58.0 ± 13.3	0.99	same
Carol	5	98.6 ± 40.3	5	60.3 ± 23.3	0.44	with bonds
Kate	5	87.2 ± 49.1	4	44.7 ± 27.9	0.51	with bonds
Tinkerbelle	3	50.9 ± 31.6	7	114.7 ± 38.9	0.35	without bonds

Table 5-6. Relationship between months with and without grooming (given) strong bonds and  $\bar{x}$  monthly cortisol (F) levels (ng/g). One female, Banana, had significantly higher cortisol levels in months when she did not express any strong grooming bonds, while two females, Gina and Carol, had nearly significantly higher cortisol levels in months when they did express at least one strong dyadic grooming bond. Overall, there was no consistent pattern among female groomers in terms of whether their  $\bar{x}$  cortisol levels were higher in months with versus without strong grooming bonds.

Female	$n_{\text{with}}$	$\bar{X}_F \pm SE$	$n_{\text{without}}$	$\bar{X}_F \pm SE$	<i>P</i> -value	F levels higher
Gina	7	74.8 ± 27.7	2	15.5 ± 4.6	0.08	with bonds*
Banana	8	59.7 ± 11.9	2	156.8 ± 31.5	0.04	without bonds **
Jane	8	91.3 ± 36.4	1	207.2 ± --	0.25	without bonds
Little Horns	6	59.6 ± 12.7	4	55.9 ± 24.6	0.52	same
Carol	8	94.1 ± 26.2	2	20.7 ± 1.2	0.07	with bonds*
Kate	5	33.3 ± 16.6	4	111.9 ± 59.4	0.14	without bonds
Tinkerbelle	0	--	10	95.6 ± 29.5	--	--

Notes: \*\*significant relationship ( $P < 0.05$ ); \* relationship approaching significance ( $0.05 < P \leq 0.08$ )

Table 5-7. Relationship between months with and without grooming (received) strong bonds and  $\bar{x}$  monthly cortisol (F) levels (ng/g). Despite a lack of significant associations, a descriptive trend emerged: All females (with the exception of the most subordinate female, Tinkerbell) had higher cortisol levels in the months characterized by the presence of strong grooming bonds (grooming received).

Female	$n_{\text{with}}$	$\bar{X}_F \pm SE$	$n_{\text{without}}$	$\bar{X}_F \pm SE$	<i>P</i> -value	F levels higher
Gina	5	77.0 $\pm$ 38.0	4	42.4 $\pm$ 22.9	0.62	with bonds
Banana	5	105.2 $\pm$ 26.2	5	53.0 $\pm$ 15.0	0.08	with bonds *
Jane	3	167.7 $\pm$ 82.9	6	74.5 $\pm$ 29.9	0.12	with bonds
Little Horns	7	66.9 $\pm$ 14.9	3	37.8 $\pm$ 13.6	0.21	with bonds
Carol	4	114.1 $\pm$ 50.0	6	56.3 $\pm$ 17.2	0.40	with bonds
Kate	4	101.8 $\pm$ 60.6	5	41.5 $\pm$ 21.8	0.81	with bonds
Tinkerbell	2	19.3 $\pm$ 0.8	8	114.6 $\pm$ 33.7	0.30	without bonds

Note: \* relationship approaching significance ( $0.05 < P \leq 0.08$ )

Table 5-8. Effect of infant age on mothers' ( $n = 4$ ) monthly proximity to adult females (TFPS) ( $n = 6$ ) and adult males (MPS) ( $n = 3$ ). As the infants aged and became more independent, there was an associated decrease in the mothers' proximity to other females ( $r_s = -0.44$ ,  $P = 0.005$ ). No such association, however, resulted between infant age and mothers' proximity to males ( $r_s = -0.06$ ,  $P = 0.74$ ). There were no statistical differences between TFPS and MPS at any of the incremental infant age categories ( $P = 0.09$  to  $0.59$ ), but it is interesting to note that for mothers with dependent infants, TFPS remained higher than MPS for the first 6 months of their infants lives, after which MPS was higher than TFPS.

Infant age (months)	$n$	TFPS $\pm$ SE	MPS $\pm$ SE
0.0-3.0	11	47.15 $\pm$ 13.50	27.59 $\pm$ 9.15
3.1-6.0	11	35.61 $\pm$ 13.26	29.92 $\pm$ 11.99
6.1-9.0	9	17.24 $\pm$ 8.62	23.41 $\pm$ 8.81
9.1-12.0	8	8.30 $\pm$ 3.78	25.65 $\pm$ 9.67

Table 5-9. Monthly association between gestation length, proximity to females (TFPS) and proximity to males (MPS). Pregnant females ( $n = 2$ ) maintained a higher (non-significant) MPS than TFPS during each month of pregnancy. There was no relationship between gestation length and proximity to females ( $r_s = -0.09, P = 0.81$ ) or males ( $r_s = 0.24, P = 0.51$ ).

Month of pregnancy (approximated)	$n$	TFPS $\pm$ SE	MPS $\pm$ SE	$P$ -value
1	2	5.5 $\pm$ 5.5	17.9 $\pm$ 17.0	0.48
2	1	0.0	3.6 $\pm$ n.a.	--
3	1	0.0	6.8 $\pm$ n.a.	--
4	2	0.0	1.6 $\pm$ 0.75	0.29
5	2	10.8 $\pm$ 10.8	24.0 $\pm$ 20.6	0.41
6	2	4.3 $\pm$ 4.3	5.6 $\pm$ 0.7	0.77

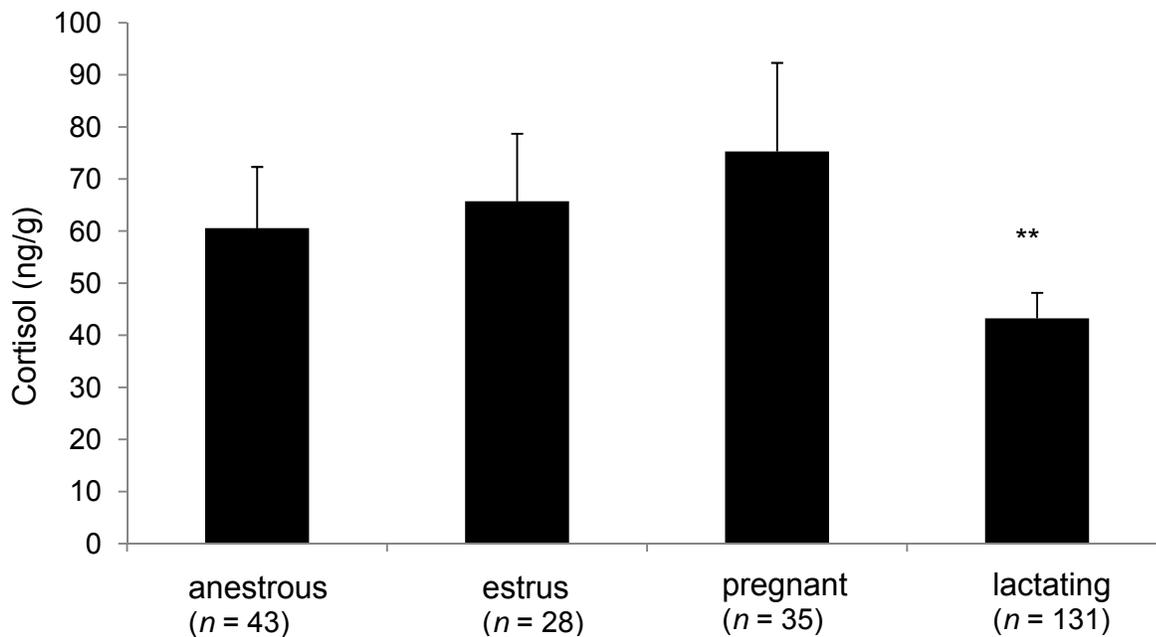


Figure 5-1. Troop-level comparison of female reproductive state and  $\bar{x}$  baseline cortisol level  $\pm$  SE (ng/g). Overall, pregnant females had the highest cortisol levels ( $\bar{x} = 75.29 \pm 17.01$ ), while lactating females had the lowest cortisol levels ( $\bar{x} = 43.26 \pm 4.90$ ). Posthoc analysis revealed that lactating females had significantly lower cortisol levels than anestrus ( $P = 0.027$ ), estrus ( $P = 0.018$ ) and pregnant ( $P = 0.033$ ) females.

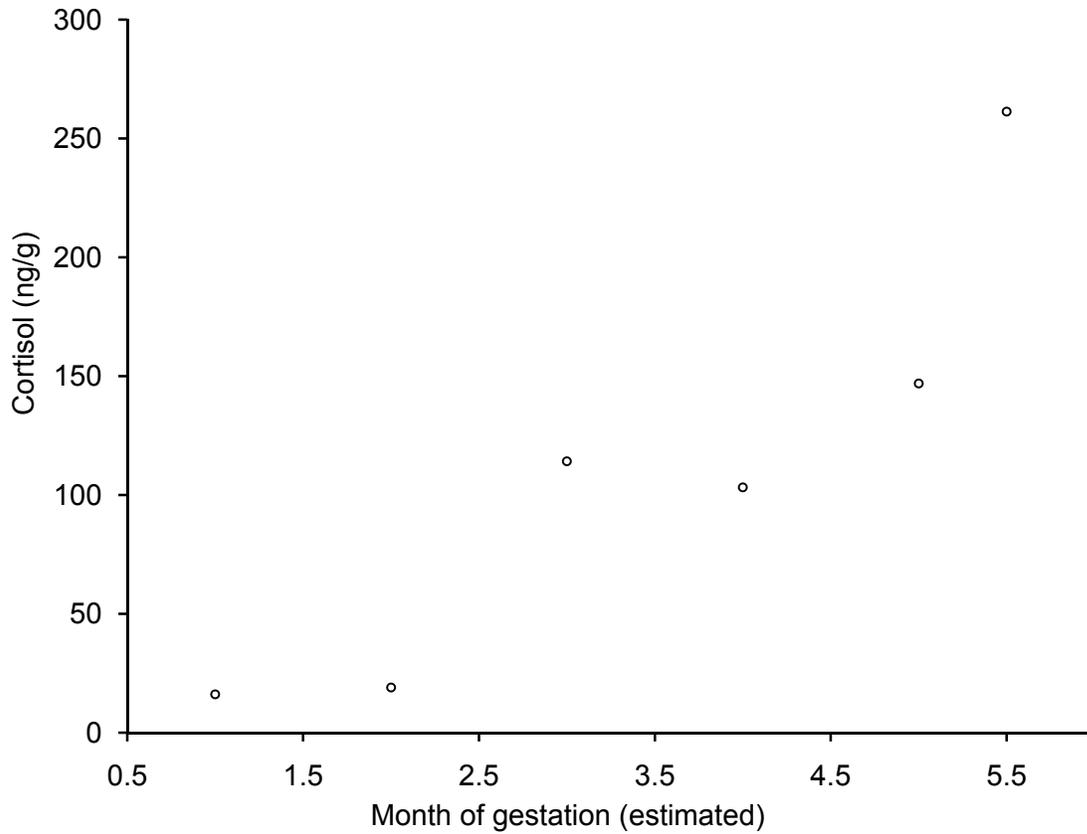


Figure 5-2. Correlation between Tinkerbell's cortisol levels (ng/g) and month of pregnancy. Her cortisol levels increased steadily throughout her pregnancy and were strongly and positively correlated with gestation length ( $r_s = 0.94$ ,  $P = 0.005$ ).

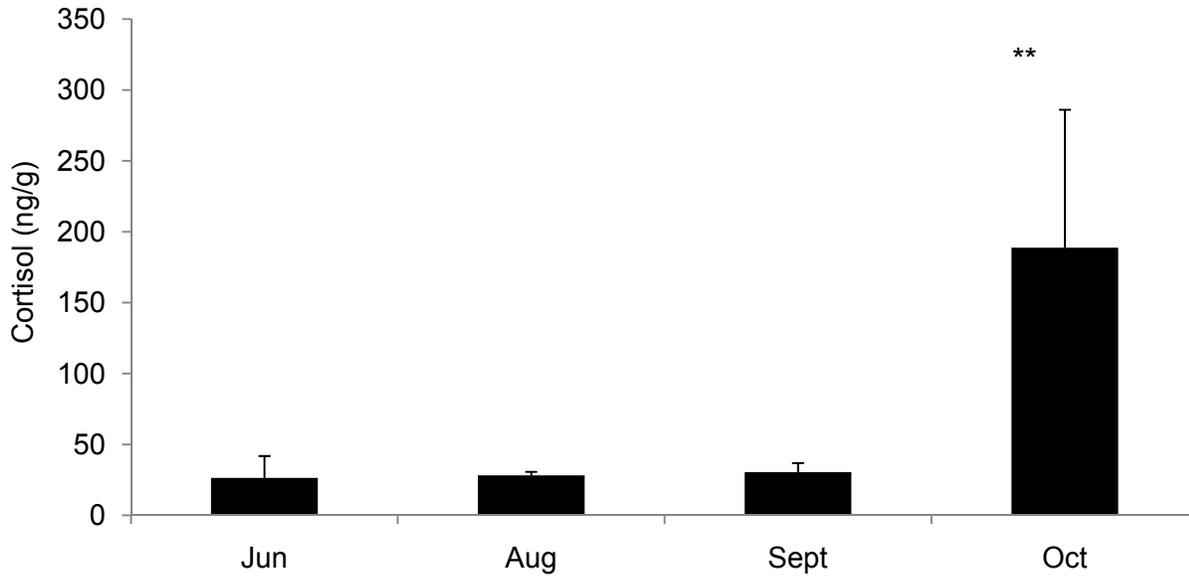


Figure 5-3. Comparison of Jane's mean cortisol levels  $\pm$  SE (ng/g) during months of her pregnancy. In October, her final month of pregnancy (also the month of her presumed death), Jane's mean cortisol level was significantly higher than in all other months in which she was pregnant (and baseline cortisol data available).

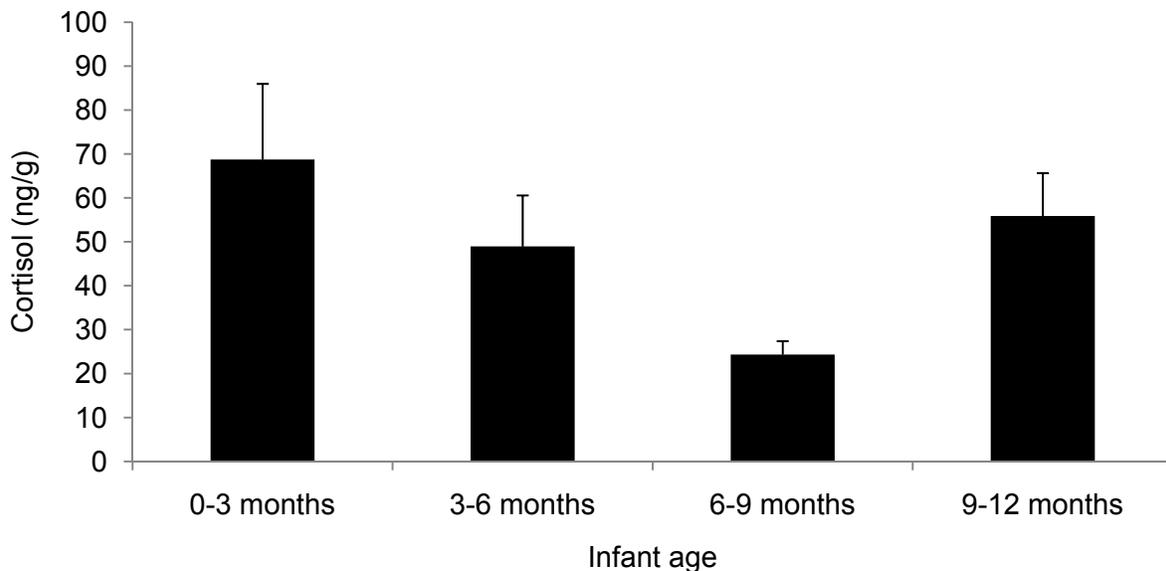


Figure 5-4. Cortisol levels of lactating females ( $n = 4$ ) at incremental stages of infant age. Cortisol levels were highest for lactating females when their infants were  $\leq 3$  months of age and lowest when their infants were 6 to 9 months of age. The cortisol levels of lactating females were significantly higher when their infants were 9 to 12 months old as compared to 3 to 6 months ( $P = 0.050$ ) and 6 to 9 months ( $P < 0.0001$ ), and when the infants were 0 to 3 months as compared to 6 to 9 months ( $P = 0.028$ ).

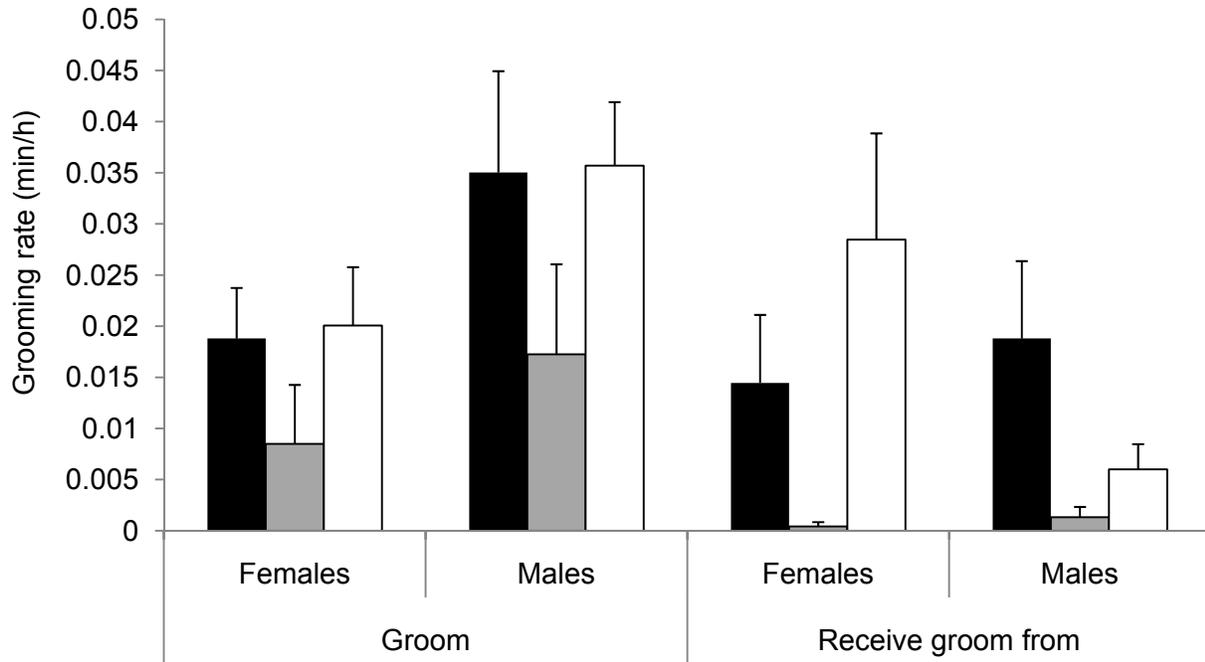


Figure 5-5. Rates ( $\pm$  SE) at which cycling (black bars), pregnant (grey bars), and lactating (white bars) females groomed and received grooming from adult female and male troop-mates. Reproductive condition did not have a significant effect on the rates at which females groomed females ( $P = 0.293$ ) or groomed males ( $P = 0.196$ ). There was, however, a significant effect on the rates at which females of different reproductive condition were groomed by females ( $P = 0.010$ ), and a nearly significant effect on the rates at which such females were groomed by males ( $P = 0.056$ ). In each reproductive condition, females groomed males ( $n = 3$ ) at a higher (non-significant) rate than they groomed females ( $n = 7$ ). In turn, lactating females received a significantly higher rate of grooming from females than males ( $P = 0.012$ ), while cycling females received a higher (non-significant) rate of grooming from males than females.

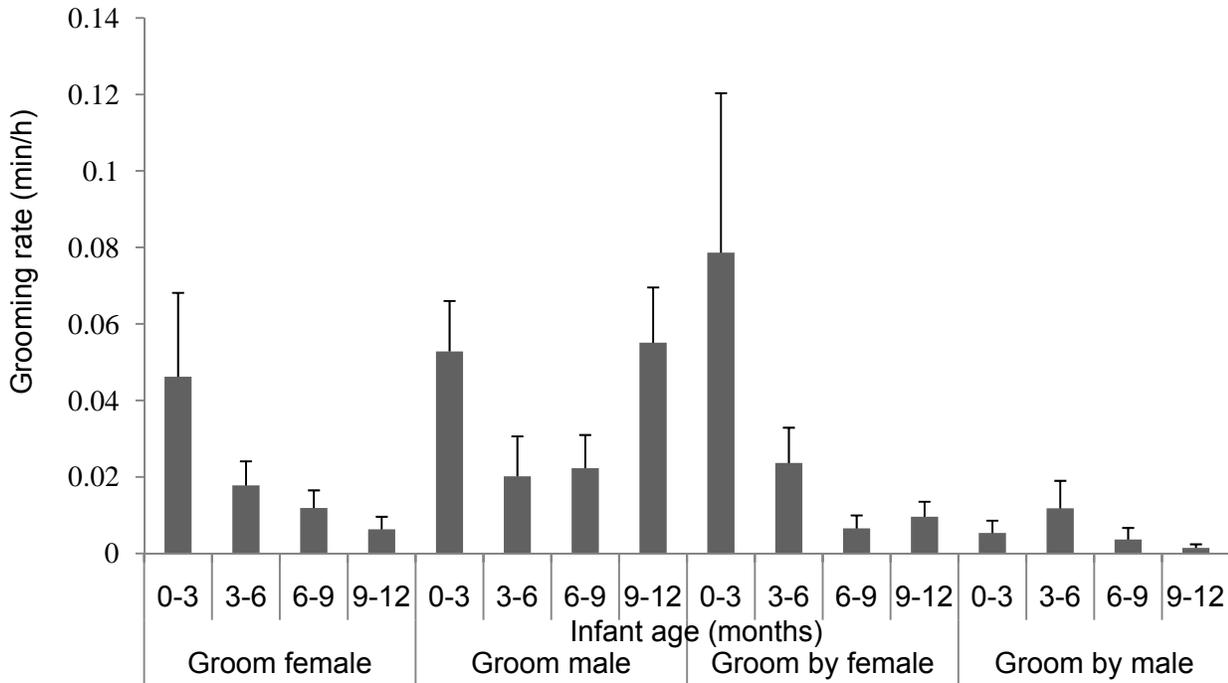


Figure 5-6. Effect of infant age (3-month increments) on the rate ( $\pm$  SE) at which mothers (i.e., lactating females) groomed and received grooming from adult females and males. Although there was no significant effect of infant age on the rate at which mothers groomed females ( $P = 0.249$ ), grooming decreased steadily as infants became more dependent, and the two variables were moderately correlated ( $r_s = -0.37$ ,  $P = 0.021$ ). Mothers most groomed males when their infants were 0 to 3 and 9 to 12 months old as compared to the other infant age increments, and this difference approached significance ( $P = 0.061$ ). Although infant age did not significantly affect the rate at which mothers received grooming from females ( $P = 0.107$ ) or males ( $P = 0.420$ ), mothers received most grooming from females when their infants were 0 to 3 months old.

## CHAPTER 6 CONCLUSION

The central premise of my research addressed the intrinsic effects of affiliation and the social, reproductive and ecological circumstances that may prompt shifts in female relationships. Laboratory studies indicate a reciprocal relationship between stress (as measured by glucocorticoid levels) and social support, but typically do so in an environment that controls for the natural range of social and ecological variables that characterize an animal's evolutionary history. Female brown capuchins at Raleighvallen (RV), Suriname are faced with the complex challenges of residing in an unpredictable environment, one in which the cost/benefit tradeoffs of sociality can quickly shift. The purpose of my study was to determine how females adapt to such challenges, both behaviorally and physiologically.

In order to evaluate female response to stress, I first had to identify the socioecological variables that act as primary stressors to females. For group-living species, it is generally accepted that the main cost of sociality is increased within-group competition, while the main benefit is improved predator protection (Isbell 1994; Sterck et al. 1997). The cost/benefit regime is much more complicated, however, and adjusts in response to changes in local and temporal circumstances. The dynamics of group living are further exacerbated by group size, as the costs and benefits of sociality are differently balanced for large versus small groups.

I studied two capuchin troops of disparate size (representing opposite ends on the group size continuum scale) and found that females in the larger group (Troop A) incurred more of the costs of sociality (i.e., increased agonism and greater ecological demands) but did not receive the benefits of a large social group. In fact, Troop A

females received less grooming than did females in the small group (Troop B), despite a three-fold difference in the possible number of social partners. Further, the large social setting did not appear to alleviate perceived predation risk, but did affect the source (aerial versus terrestrial) of their greatest perceived risk (Chapter 2). Fecal cortisol levels supported these findings; overall, females in Troop A had higher cortisol levels than did the females in Troop B, mostly in response to aerial predators and an unpredictable food supply (Chapter 3).

With the intense ecological variation, both within and between years, and the strong presence of both aerial and terrestrial predators that characterizes the RV forest, the expectation of shifts in the cost/benefit regime for a group of any given size must be enough to maintain disparate group size. Despite the prolonged consequences felt by Troop A females during the study period, the risks of emigrating must have been greater and/or they expected the scale to soon tip in their favor. In such a dynamic ecological landscape, the ability to adapt is most adaptive. As any natural environment of wild living social mammals is more dynamic than stable, the theoretical notion of an 'optimal' group size (Silk 2007a) is rather unrealistic and may only apply to captive populations.

After establishing the foundation for intergroup variation in the socioecological lives of female brown capuchins in RV, I shifted my focus to studying more fine-scaled within-group social behavior (Chapter 4) and the potential physiological benefits of affiliation (Chapter 5). Because most group-living non-human primates are female-philopatric, it is often assumed that relationships among females are strong and adaptive. In fact, the concept of female bonds is at the core of primate social evolution theory (Wrangham 1980). Although capuchins are supposedly a female-bonded genus,

with females demonstrating stronger relationships with females than with males (Perry 1996; Di Bitetti 1997), the results of my study indicated that, overall, the females in RV are not female-bonded but are better characterized as cross-bonded with adult males. The term 'cross-bonded' is commonly used to describe baboon females (Byrne et al. 1990; Barton et al. 1992; Swedell 2002) but has not been previously used to describe any capuchin group or population. Despite being linked to their female troop-mates through kinship and a long history of familiarity, proximity and grooming relationships between females were transient and most predictably occurred in response to an infant. Female relationships with males were more stable and appeared to be related to the acquisition of increased tolerance and protection-commodities that are especially important in the high risk, low energy environment of RV. Female-female and female-male relationships are strategic responses to ecological and reproductive demands and thus cannot be generalized at the genus, or even species level (Chapter 4).

Regardless of whether a female's primary social partners are male or female, the proximate mechanism underlying the relationship remains: Primate social bonds are said to be physiologically rewarding (Dunbar 2009) based, in part, on the potentially stress-reducing properties of grooming (Boccia et al. 1989; Keverne et al. 1989; Gust et al. 1993; Aureli et al. 1999; Shutt et al. 2007). Thus, the elevated cortisol levels of Troop A females (Chapter 3) likely resulted from an interplay of the direct and indirect consequences of larger group size. Since their intensified foraging demands reduced the time available to rest and groom, the females in Troop A had less opportunity to benefit from grooming than did the Troop B females.

As prolonged stress deleteriously affects the health and fitness of females and their developing offspring (Sachser et al. 1998; Bardi et al. 2005; Sapolsky 2005; Shively et al. 2005; Wadhwa 2005), females should take an active role in managing their stress through the strategic use of grooming. Although the physiological benefits of the receipt of grooming occur immediately upon tactical contact and thus are difficult to capture using measures of longer-term fecal cortisol (Shutt et al. 2007), my study presents anecdotal evidence and empirical patterns that implicate an association between affiliation and stress mediation. For example, females with young infants ( $\leq 3$  months old) may have intensified their grooming of curious conspecifics in order to promote an immediately more relaxed social environment surrounding their vulnerable infants. Females also tended to be groomed more intensely by specific adult troop-mates during periods of increased stress, a system of social support similar to that found in humans (Kirschbaum et al. 1995; Taylor et al. 2000; Heinrichs et al. 2003; Rosal et al. 2004) and some captive mammals (Mendoza et al. 1991; Carter et al. 1995; Sachser et al. 1998; von Holtz 1998; Rukstalis and French 2005; Hennessey et al. 2006).

Further, the results of my study support the novel finding that the giving of grooming is associated with a decrease in cortisol levels (Shutt et al. 2007). Shutt et al. (2007), however, found such an association within female-female grooming dyads, whereas in my study, it was the female grooming of males that was specifically linked to lower cortisol concentrations. Not only does this finding support the notion that female brown capuchins in RV are more strongly bonded to males than to females, but it identifies a possible motivating factor for the maintenance of social bonds (Chapter 5).

The present research (1) expands the breadth of known intraspecific variation in behavioral responses to ecological diversity of a social mammal; (2) provides an operationalized approach to the study of social bonds and identifies issues that limit the comparative application of current published studies; and (3) contributes the first investigation into the behavioral endocrinology of wild female brown capuchin monkeys, strengthening the known evidence linking social bonds to fitness consequences. The incidence of stress-related disease is increasing in both human (Tamashiro et al. 2005) and captive animal populations. By providing an improved understanding of natural stressors and the adaptive implications of social evolution, my study has direct ramifications for the health and well-being of humans and nonhumans alike.

APPENDIX A  
CHAPTER 2 RESULTS SUMMARY

Variable	Troop A	Troop B	Statistical result	Association between group size and variable
Troop size	27	9		
Density (# individuals/m) (based on $\bar{X}$ troop dispersion)	0.4	0.2		
# of ♀	7	3		
# of contact hours	2284	495		
Home range size	700 m <sup>2</sup>	500 m <sup>2</sup>		
Home range composition (%)				
• Bamboo	13	10		
• High forest	54	44		
• Liana/low forest	28	43		
• Swamp forest	5	3		
Habitat preference (time %)	Bamboo (37%)	Liana/low forest (49%)		
$\bar{X}$ daily travel rate (m/h)	171	159		
Most traveled season	Transition	Transition		
Least traveled season	Wet	Wet	A > B ( <i>P</i> = 0.037)*	(+)
$\bar{X}$ canopy cover (0-3 incremental scale; 0=fully exposed; 3=full cover)	2.41	2.34	A = B	none

Appendix A. Continued.

Variable	Troop A	Troop B	Statistical result	Association between group size and variable
$\bar{X}$ height in canopy				
• Lower limit (m)	4.95	6.50	B > A ( $P < 0.0001$ )	
• Upper limit (m)	10.97	12.23	B > A ( $P < 0.0001$ )	(-)
$\bar{X}$ monthly rate of <i>M. maripa</i> feeding (min/h)				
• Troop rate	4.36	5.70	A = B	
• Individual rate	0.37	1.26	B > A ( $P = 0.020$ )	(-)
$\bar{X}$ monthly rate of AAs (alarms/h)				
• Troop rate	0.62	0.66	A = B	
• Individual rate	0.03	0.09	B > A ( $P < 0.0001$ )	(-)
$\bar{X}$ monthly rate of TPAs (alarms/h)				
• Troop rate	0.17	0.07	A > B ( $P = 0.010$ )	
• Individual rate	0.008	0.010	A = B	(+)
$\bar{X}$ monthly individual rate of agonism (bouts/h)				
• ♀ as aggressor	0.009	0.004	A > B ( $P = 0.004$ )	
• ♀ as victim	0.009	0.002	A > B ( $P = 0.001$ )	(+)
♀-♀ agonism (% of intragroup agonism)	11.8	0.0%		
♀-♀ hierarchy	Present, weakly linear	Absent		(+)
$\bar{X}$ monthly individual rate of grooming (min/h)				
• ♀ as groomer	0.14	0.19	A = B	
• ♀ as recipient	0.06	0.13	A = B	(-)

APPENDIX B  
ADDITIONAL RESULTS PERTAINING TO TABLES 4-5 AND 4-6: DYADIC PATTERNS  
OF FEMALE AFFILIATION (TROOP A)

**Proximity**

Gina's proximity scores significantly differed by adult dyadic partner ( $F = 8.489$ ,  $P < 0.0001$ ,  $df = 8$ ), and this difference was due to her proximity to Boris, the alpha male (mean  $\pm$  SE =  $27.25 \pm 8.27$ ), and Banana, the 2<sup>nd</sup> ranking female (mean  $\pm$  SE =  $23.37 \pm 4.63$ ). Gina's scores were significantly higher with Boris ( $P = 0.000$  to  $0.001$ ) and with Banana ( $P = 0.000$  to  $0.013$ ) than with all other adults (mean  $\pm$  SE =  $0.15$  to  $5.31$ ). There was no significant difference between Gina's proximity scores with Boris and Banana ( $P = 0.997$ ).

Banana's proximity scores significantly differed by adult dyadic partner ( $H = 46.50$ ,  $P < 0.0001$ ,  $df = 8$ ), and this difference was due to her proximity to Gina (mean  $\pm$  SE =  $23.33 \pm 4.65$ ) and Boris (mean  $\pm$  SE =  $15.17 \pm 3.70$ ). Banana's scores were significantly higher with Gina ( $P = 0.000$  to  $0.003$ ) and with Boris ( $P = 0.000$  to  $0.015$ ) than with all other adults (mean  $\pm$  SE =  $0.02$  to  $5.44$ ). There was no significant difference between Banana's proximity scores with Gina and Boris ( $Z = -1.209$ ,  $P = 0.247$ ).

Jane's proximity scores significantly differed by adult dyadic partner ( $H = 22.364$ ,  $P = 0.004$ ,  $df = 8$ ), and this difference was due to her proximity with the alpha male. Jane's proximity to Boris (mean  $\pm$  SE =  $12.67 \pm 6.39$ ) was significantly higher than with most adult social partners: Tinkerbell (mean  $\pm$  SE =  $0.0 \pm 0.0$ ,  $P = 0.004$ ), Little Horns (mean  $\pm$  SE =  $0.29 \pm 0.19$ ,  $P = 0.008$ ), Kate (mean  $\pm$  SE =  $0.47 \pm 0.27$ ,  $P = 0.008$ ), Andycap (mean  $\pm$  SE =  $0.48 \pm 0.36$ ,  $P = 0.011$ ), Carol (mean  $\pm$  SE =  $0.49 \pm 0.28$ ,

$P = 0.011$ ), and Banana (mean  $\pm$  SE =  $0.77 \pm 0.27$ ,  $P = 0.024$ ), except for Gina (mean  $\pm$  SE =  $4.88 \pm 2.81$ ,  $P = 0.190$ ) and Darwin (mean  $\pm$  SE =  $9.17 \pm 5.81$ ,  $P = 0.222$ ).

Little Horn's proximity scores significantly differed by adult dyadic partner ( $H = 31.508$ ,  $P < 0.0001$ ,  $df = 8$ ), and this difference was due to her proximity to the males. Little Horns dyadic proximity scores were significantly higher ( $P < 0.0001$ ) with adult males (mean  $\pm$  SE =  $3.84 \pm 0.98$ ) than with adult females (mean  $\pm$  SE =  $0.32 \pm 0.13$ ). There was no significant difference in her dyadic proximity scores among the males (means = 2.30 to 5.06,  $P = 0.839$ ) or among females (means = 0.07 to 0.68,  $P = 0.238$ ).

Carol's proximity scores did not significantly differ by adult dyadic partner (means = 0.14 to 4.98) ( $H = 12.033$ ,  $P = 0.150$ ,  $df = 8$ ); the individuals with whom she scored the highest average proximity scores were both males: Andycap (mean  $\pm$  SE =  $4.98 \pm 2.88$ ) and Darwin (mean  $\pm$  SE =  $4.85 \pm 3.40$ ).

Kate's proximity scores significantly differed by adult dyadic partner ( $H = 19.445$ ,  $P = 0.013$ ,  $df = 8$ ), but there was no discernable pattern to the differences. Although her highest average proximity score was with Boris (mean  $\pm$  SE =  $8.39 \pm 3.99$ ), only the mean rank of Kate's proximity scores with Carol (mean  $\pm$  SE =  $4.61 \pm 2.31$ ) and with Banana (mean  $\pm$  SE =  $5.44 \pm 3.18$ ) were significantly higher than with Tinkerbell (mean  $\pm$  SE =  $0.07 \pm 0.05$ ,  $P_{\text{both}} = 0.005$ ), Little Horns (mean  $\pm$  SE =  $0.18 \pm 0.13$ ,  $P_{\text{both}} = 0.015$ ), and Andycap (mean  $\pm$  SE =  $0.38 \pm 0.26$ ,  $P_{\text{Carol}} = 0.029$ ,  $P_{\text{Banana}} = 0.043$ ).

Tinkerbell's proximity scores significantly differed by adult dyadic partner ( $H = 18.367$ ,  $P = 0.019$ ,  $df = 8$ ), and this difference was due to her proximity to Andycap (mean  $\pm$  SE =  $1.43 \pm 0.69$ ). Although Tinkerbell's highest average dyadic score was

with Boris (mean  $\pm$  SE = 11.0  $\pm$  5.47), monthly measures of her proximity to the alpha male varied drastically (SD = 17.31) and thus the mean value is an unreliable predictor. Only the mean rank of Tinkerbell's proximity score with Andycap was significantly higher than with Jane (mean  $\pm$  SE = 0.00  $\pm$  0.0,  $P$  = 0.028) and with Carol (mean  $\pm$  SE = 0.05  $\pm$  0.05,  $P$  = 0.043).

### **Grooming**

Gina was observed to groom all of the adult females except Tinkerbell, although 86.5% of the bouts were devoted to Banana. Of the three adult males, Gina was observed to only groom the alpha male. Overall, Gina dedicated the most grooming to Boris (48.6% of bouts and 48.7% of total duration) and Banana received the remaining majority of her attention (44.4% of grooming bouts and 47.1% of total duration).

Banana was observed to groom all of the adult females except Jane and Carol, although 56.9% of the bouts were devoted to Gina. Of the three adult males, Banana was observed to groom Boris almost exclusively. Overall, Banana groomed Gina most frequently (37.7% of bouts), but she groomed Boris for the longest duration (50.8% of total grooming time).

Jane was observed to groom all of the adult females except Kate and Tinkerbell, with Little Horns receiving 45% of the bouts. Of the three adult males, Jane was observed to groom only Boris. Overall, Jane dedicated the most grooming to Boris (45.9% of bouts and 45.0% of total duration).

Little Horns was observed to groom all of the adult females except Tinkerbell, with no single female receiving a distinct majority, and she groomed all three adult males. Little Horns groomed a male during 54.5% of her grooming bouts, and males received

58.6% of her grooming time. Overall, Little Horns dedicated the most grooming to Darwin (39.4% of bouts and 49.4% of total duration).

Carol was observed to groom all of the adult females and males of the group; the group's six females received 54.5% of her grooming bouts, but the three males received 65.2% of Carol's grooming time. Overall, Carol dedicated the most grooming to Boris (30.3% of bouts and 29.1% of total duration).

Kate was observed to groom all of the adult females except Gina and Jane, with Banana receiving 75% of the bouts. Of the three adult males, Kate was observed to groom only Boris and Andycap. Overall, Kate dedicated the most grooming to Boris (41.7% of bouts and 64.6% of total duration).

Tinkerbelle rarely participated in grooming with other adults. She was observed to groom only Banana, Carol and Darwin, and only for a total of 3.8 min (4 bouts) throughout the study period. In fact, Tinkerbelle was never observed to groom or be groomed by five of the nine adult troop members.

Boris was observed to groom all of the adult females except Tinkerbelle. He devoted the most grooming attention to Jane (29% of bouts and 32.6% of total duration). Andycap groomed only Little Horns and Carol, with Carol receiving 92.5% of his total grooming duration. Darwin, on the other hand, groomed all of the females except Banana, with the vast majority devoted to Little Horns (54.5% of bouts and 59.2% of total duration).

APPENDIX C  
TOTAL PROXIMITY SCORES (PS) FOR ALL FEMALE-FEMALE AND FEMALE-MALE  
DYADS (TROOP A) (JANUARY-DECEMBER, 2006)

Focal ♀	Dyad partner	Total PS
Gina	Boris	272.492
Gina	Banana	233.69
Banana	Gina	233.27
Banana	Boris	151.674
Jane	Boris	114.048
Tinkerbelle	Boris	110.026
Kate	Boris	83.929
Jane	Darwin	82.56
Banana	Kate	54.399
Kate	Banana	54.399
Gina	Darwin	53.135
Banana	Darwin	51.857
Little Horns	Darwin	50.604
Carol	Andycap	49.843
Carol	Darwin	48.461
Banana	Andycap	46.414
Carol	Kate	46.103
Kate	Carol	46.103
Jane	Gina	43.932
Little Horns	Boris	41.648
Gina	Kate	31.773
Kate	Gina	31.773
Banana	Jane	28.163
Gina	Jane	25.551
Carol	Boris	23.847
Gina	Carol	23.409
Little Horns	Andycap	23.013
Carol	Gina	21.349
Kate	Darwin	19.972
Gina	Little Horns	18.615
Tinkerbelle	Andycap	14.299
Gina	Andycap	14.1
Tinkerbelle	Banana	11.151
Banana	Carol	10.105
Carol	Banana	10.105

} Strong bonds (top 10% of scores)

Appendix C. Continued.

Focal ♀	Dyad partner	Total PS
Banana	Tinkerbelle	8.536
Jane	Banana	6.893
Little Horns	Gina	6.801
Little Horns	Carol	5.775
Carol	Little Horns	5.775
Jane	Carol	4.367
Carol	Jane	4.367
Jane	Andycap	4.295
Jane	Kate	4.273
Kate	Jane	4.273
Kate	Andycap	3.789
Jane	Little Horns	2.615
Tinkerbelle	Darwin	2.564
Little Horns	Jane	1.874
Little Horns	Kate	1.835
Kate	Little Horns	1.835
Little Horns	Tinkerbelle	1.7
Tinkerbelle	Little Horns	1.7
Gina	Tinkerbelle	1.545
Tinkerbelle	Gina	1.545
Carol	Tinkerbelle	1.36
Kate	Tinkerbelle	0.732
Tinkerbelle	Boris	0.732
Little Horns	Banana	0.695
Tinkerbelle	Carol	0.504
Banana	Little Horns	0.21
Jane	Tinkerbelle	0
Tinkerbelle	Jane	0

Lowest 10% of scores

Females (in order of decreasing rank): Gina, Banana, Jane, Little Horns, Carol, Kate, and Tinkerbelle; Males: Boris (alpha), Andycap, and Darwin

APPENDIX D  
TOTAL GROOMING DURATIONS FOR ALL FEMALE-FEMALE AND FEMALE-MALE  
DYADS (TROOP A) (JANUARY-DECEMBER, 2006)

Groomer	Recipient	Total Grooming duration (min)
Gina	Boris	86.5
Gina	Banana	83.8
Banana	Boris	82.5
Kate	Boris	51.2
Banana	Gina	49.8
Little Horns	Darwin	40.6
Jane	Boris	36.25
Darwin	Little Horns	30.2
Carol	Boris	24.2
Carol	Darwin	20
Banana	Kate	18.8
Boris	Jane	18.2
Jane	Little Horns	17.8
Kate	Banana	17.5
Boris	Little Horns	16.2
Andycap	Carol	16
Jane	Banana	12.2
Jane	Gina	12
Little Horns	Gina	12
Carol	Andycap	10
Carol	Little Horns	9.2
Carol	Banana	9
Little Horns	Carol	8.5
Little Horns	Boris	7.1
Darwin	Tinkerbelle	7
Boris	Banana	6.7
Boris	Kate	6.1
Little Horns	Kate	6
Kate	Andycap	5.3
Darwin	Gina	5.3
Boris	Carol	5
Darwin	Kate	5
Banana	Tinkerbelle	4.7
Carol	Gina	4.5

Strong bonds (top 10% of total durations)

Appendix D. Continued.

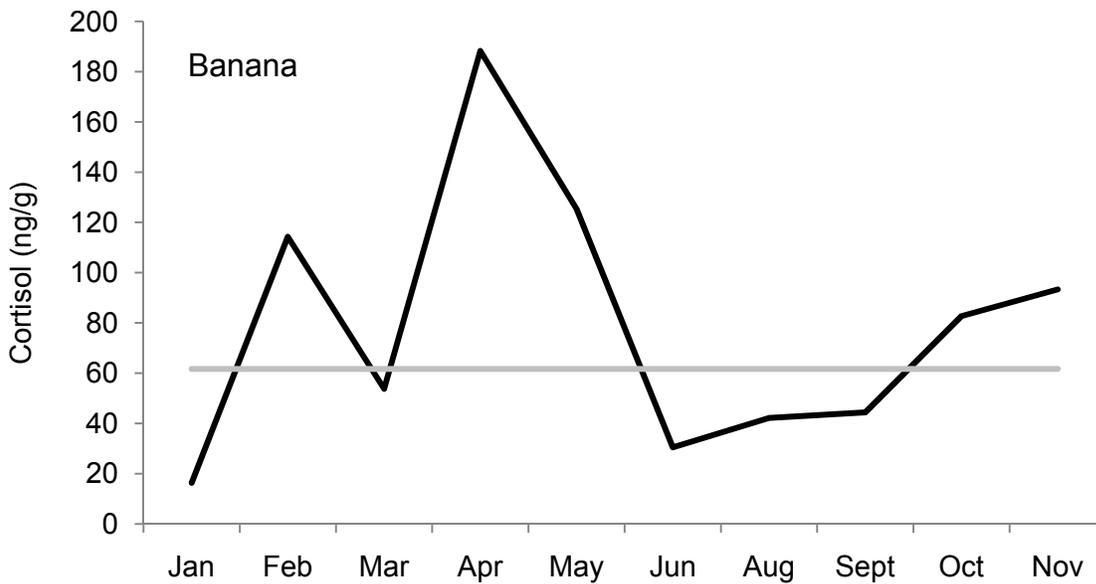
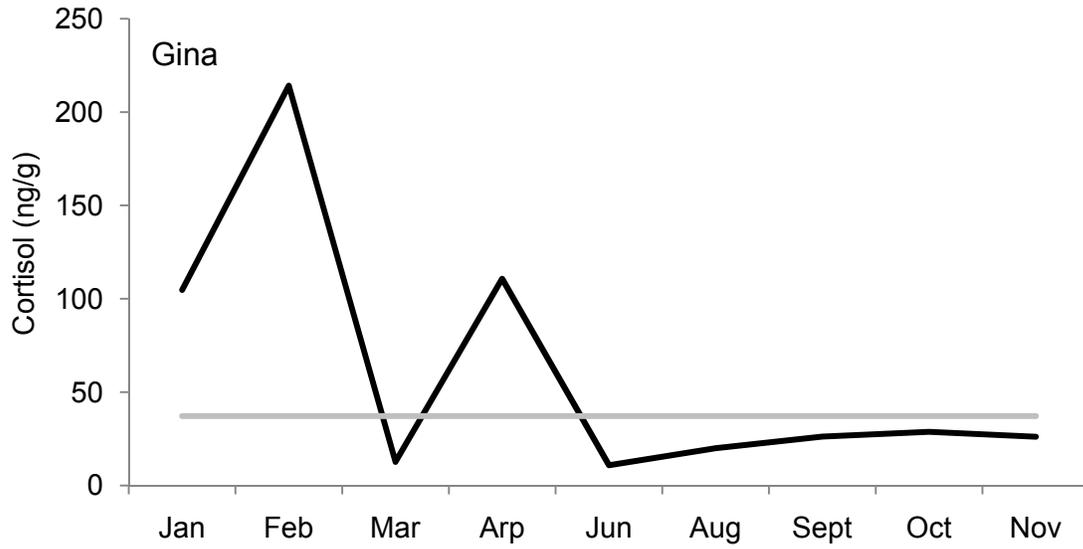
Groomer	Recipient	Total Grooming duration (min)
Little Horns	Banana	4
Boris	Gina	3.7
Gina	Carol	3.5
Banana	Little Horns	3.5
Little Horns	Jane	3.5
Carol	Jane	3.2
Banana	Darwin	3
Kate	Tinkerbelle	3
Tinkerbelle	Banana	2.5
Jane	Carol	2.3
Gina	Little Horns	2
Carol	Kate	2
Kate	Little Horns	2
Darwin	Jane	2
Darwin	Carol	1.5
AndyCap	Little Horns	1.3
Gina	Jane	1
Gina	Kate	1
Carol	Tinkerbelle	1
Tinkerbelle	Carol	1
Little Horns	AndyCap	0.5
Tinkerbelle	Darwin	0.3
Kate	Carol	0.2
Gina	Tinkerbelle	0
Gina	AndyCap	0
Gina	Darwin	0
Banana	Jane	0
Banana	Carol	0
Banana	AndyCap	0
Jane	Kate	0
Jane	Tinkerbelle	0
Jane	AndyCap	0
Jane	Darwin	0
Little Horns	Tinkerbelle	0
Kate	Gina	0
Kate	Jane	0
Kate	Darwin	0

Appendix D. Continued.

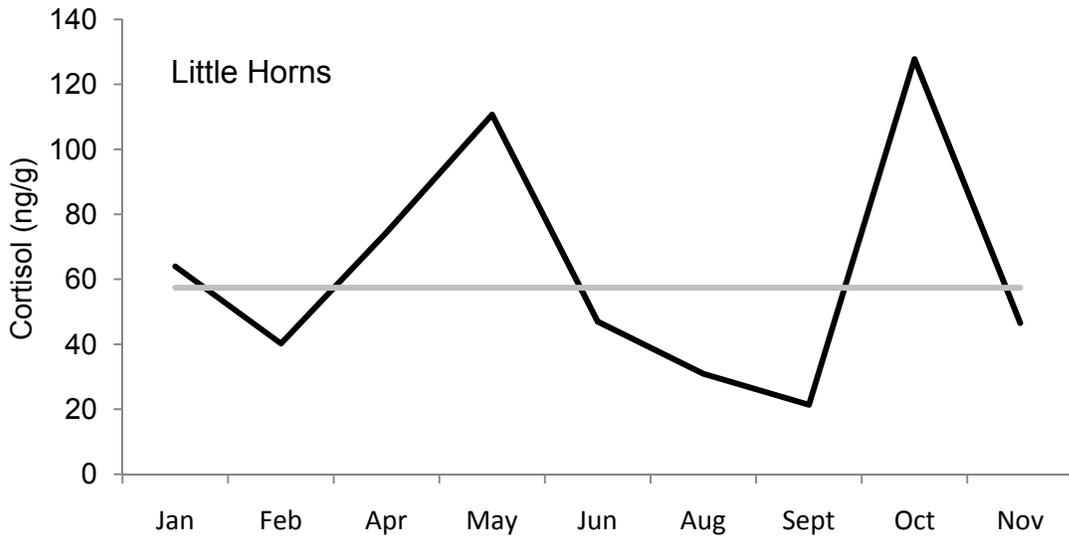
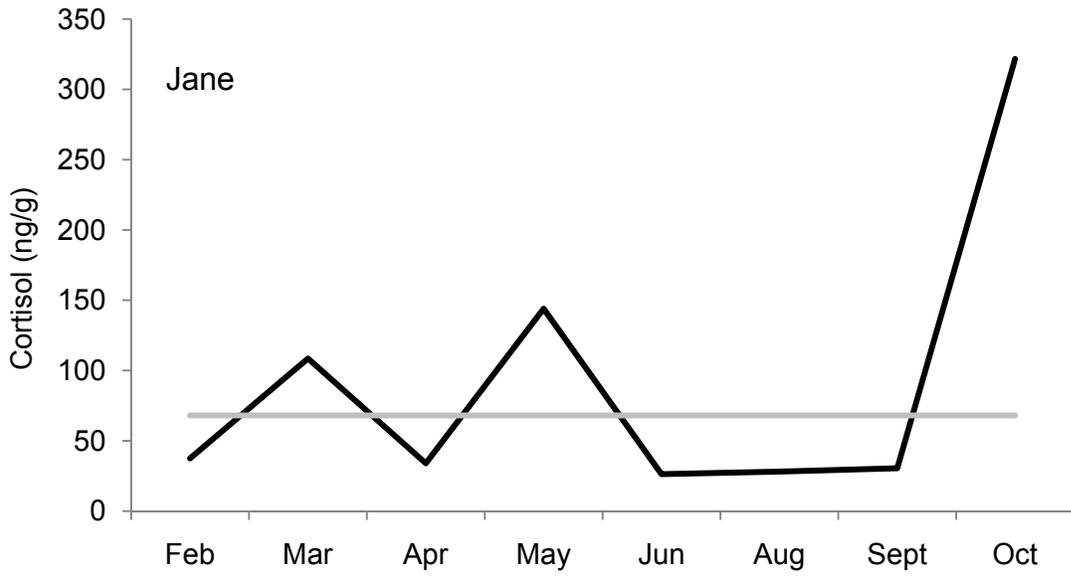
Groomer	Recipient	Total Grooming duration (min)
Tinkerbelle	Gina	0
Tinkerbelle	Jane	0
Tinkerbelle	Little Horns	0
Tinkerbelle	Kate	0
Tinkerbelle	Boris	0
Tinkerbelle	AndyCap	0
Boris	Tinkerbelle	0
AndyCap	Gina	0
AndyCap	Banana	0
AndyCap	Jane	0
AndyCap	Kate	0
AndyCap	Tinkerbelle	0
Darwin	Banana	0

Females (in order of decreasing rank): Gina, Banana, Jane, Little Horns, Carol, Kate, and Tinkerbelle; Males: Boris (alpha), AndyCap, and Darwin

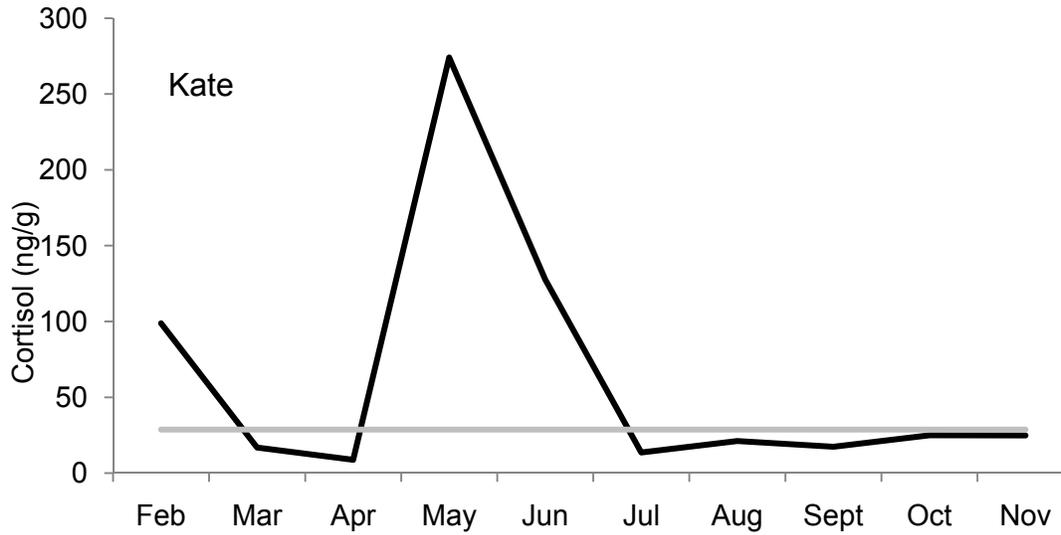
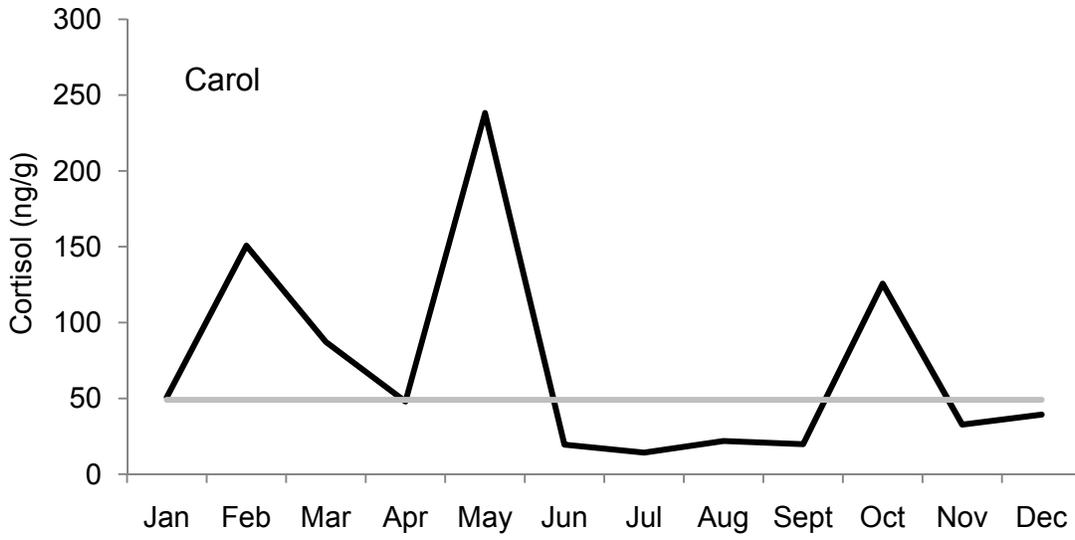
APPENDIX E  
GRAPHICAL REPRESENTATION OF EACH FEMALE'S BASELINE CORTISOL  
VALUE AND MONTHLY VARIATION ABOUT THAT MEAN (JANUARY-NOVEMBER,  
2006)



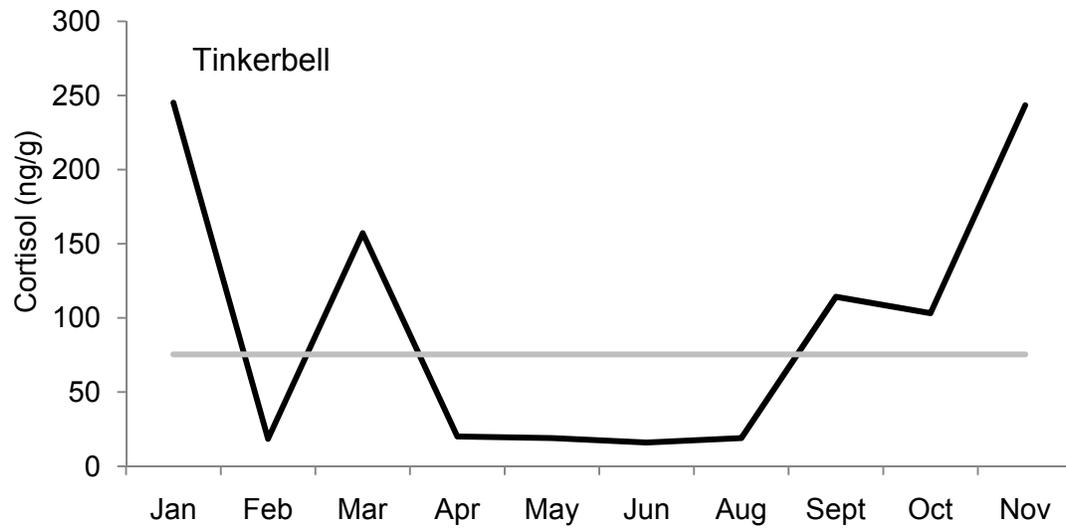
Appendix E. Continued.



Appendix E. Continued.



Appendix E. Continued.



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## BIOGRAPHICAL SKETCH

Erin Elizabeth Ehmke graduated from The University of Florida in 1999 with a Bachelor of Science in wildlife ecology and conservation, a specialization in conservation and minors in zoology and environmental science. As director of Jungle Friends Primate Sanctuary in Gainesville, Florida from 1999 to 2001, Erin's dream of working with primates became a reality and set in motion her future educational and career goals. Her experience studying wild primates began in Panama with The Institute for Tropical Ecology and Conservation and continued with a year-long field assistantship studying brown capuchin monkeys in Raleighvallen, Suriname. Erin began her graduate education in Biological Anthropology at The University of Florida in 2002 and earned her Master of Arts in 2004 with the thesis study "Social Interactions of Alpha, Natal and Immigrant Males with Juveniles among Brown Capuchins in Suriname". Erin then continued her education in the Department of Anthropology's doctoral program at UF and returned to Suriname to conduct her dissertation research. Her Ph.D. dissertation, "Stress and Affiliation among Wild Female Primates: Effects of Group Size, Risk, and Reproductive Condition in a Dynamic Forest Community", provides a direction of study that Erin plans to expand upon, including the comparative effects of captive and natural environments on the behavioral endocrinology and socioecology of social mammals. The teaching experience Erin acquired during her graduate career, through assistantships in the Departments of Zoology and Anthropology and as an instructor with the Duke Talent Identification Program (TIP), inspired a future in academia subsequent to the completion of her doctorate in 2010.