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Behavioral Thermoregulation and Urine-washing in White-faced Capuchins at Santa Rosa National Park, Costa Rica.

by

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for acceptance, a thesis entitled "Behavioral Thermoregulation and Urine-washing in White-

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ABSTRACT

White-faced capuchins in Santa Rosa National Park live in a seasonally variable environment. Heat stress and water scarcity significantly influence the capuchins' behavior. Capuchins travel shorter distances, rest more, and travel and forage less in hot conditions. They also expose their tongues to lower body temperature via evaporative heat loss. When water becomes scarce, capuchins remain closer to permanent water sources. Urine-washing (UW) is a highly seasonal behavior that occurs more frequently in the dry season. UW is not clearly related to any social context, and rates do not differ among different age/sex classes. The primary function of UW for these capuchins is non-social and probably related to improving grip for arboreal travel in dry conditions. Alpha males may also engage in UW during sexual contexts and when solicited for an olfactory signal by subordinates, and some capuchins appear to use UW to relieve ant stings.

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CHAPTER 1: A GENERAL INTRODUCTION

This thesis has two primary goals, whose relationship to each other will become clear in the synopsis below. The first goal is to understand how seasonal changes in climate affect the activity patterns and ranging behavior of wild white-faced capuchins, and to describe specific behaviors that the capuchins use to cope with their variable environment. The second goal is to test functional hypotheses for urine-washing, a curious behavior reminiscent of scent-marking, to understand why white-faced capuchins engage frequently in this behavior.

The Climate of Santa Rosa National Park

Climate and seasonality feature prominently throughout this thesis. This section is intended to provide a brief introduction to the climatic and vegetative peculiarities of the study site. This study was carried out in Santa Rosa National Park (SRNP), one of four nationally protected areas in northwestern Costa Rica that comprise the 147,000 hectare Area de Conservación Guanacaste (ACG). The boundaries of the ACG are contained by the rectangle defined by the coordinates 10°44' - 11°06' N and 85°15' - 86°00' W. While the ACG encompasses a multitude of life zones both marine and terrestrial, the Santa Rosa sector consists mostly of seasonal dry forest. SRNP was created in 1971 from a fragmented patchwork of disused pastures, gallery forest, regenerating forest in different stages of succession, and small patches of pristine evergreen forest (Janzen, 1988). Before being granted its protected status, the region was subjected to extensive anthropogenic disturbance in the form of ranching, fires, timber harvesting, and the introduction of invasive grasses. As a result, SRNP today is best characterized as a mosaic of recovering dry forest (Fedigan et al., 1996; Fedigan & Jack, 2001).

The SRNP region experiences a dry season from mid-December to mid-May, and a rainy season from late-May to early-December. The dry season in SRNP is not only drier, but hotter and sunnier as well. Janzen (1983) reports that SRNP receives on average 9.1 hours of sunshine daily in the dry season and only 5.7 hours in the wet season. As the dry season progresses, the forest canopy becomes more open as leaves fall from the majority of trees, with only small patches of primary and old-secondary forest remaining green. Although surface water remains naturally in some areas of the park throughout the year, the study area is particularly dry and nearly all natural water sources used by this study's subjects dry up completely before the end of the dry season. During the driest months, the capuchins may utilize artificial sources of water. These exist as results of the park's legacy as a former cattle ranch and its current infrastructure to accommodate tourists and researchers, and may include disused cattle troughs, leaky pipes, and runoff from sinks and hoses.

Urine-Washing: What Is It and Which Primates Do It?

Urine-washing (UW) is a stereotyped sequence of behaviors with at least three components: (1) one forelimb is drawn back underneath the posterior part of the abdomen; (2) the animal urinates onto the forelimb, often directly onto the palm of the hand; and (2) the animal repeatedly rubs together the palmar and plantar surfaces of the ipsilateral fore and hind limbs, spreading and splashing urine in the process. Urine can also be rubbed onto the fur of the limbs, abdomen, and/or tail. This sequence is sometimes repeated symmetrically with the opposite ipsilateral limbs (Robinson, 1979). Often after engaging in UW, the animal may sit down briefly

and rub the hands together, presumably to spread urine onto the hand which was not urinated upon.

UW has been documented in at least 24 primate species (Appendix 1), but it has a curious taxonomic distribution that suggests that its occurrence is determined in part by phylogeny. UW is wholly absent from several major primate radiations, including all catarrhines (old world monkeys and apes), tarsiiformes (tarsiers), and all but one genus of lemurifomes (lemurs). However, UW is taxonomically widespread among both platyrrhines (new world monkeys) and lorisiformes (galagos and lorises), and it also occurs in mouse lemurs of the genus *Microcebus*. The presence of UW behavior among these rather distantly related taxa suggests either that UW arose at least three times independently, or that it was present in the common ancestor to all extant primates and was subsequently lost in most lineages. UW has been observed in at least one species in all five extant platyrrhine subfamilies (Cebinae, Callitrichinae, Pitheciinae [including *Callicebus*], Atelinae, and Aotinae), but among platyrrhines it appears to be ubiquitous only among cebines, having been observed in all well-studied *Cebus* and *Saimiri* species. UW is poorly represented among callitrichines (1/43 species) and pitheciines (1/41 species). Undoubtedly, many of these species have not been well-studied, but regardless UW appears to be genuinely uncommon in these two platyrrhine subfamilies.

Urine-washing and Scent Marking in Platyrrhines

Is there reason to suspect that UW by platyrrhines might be an olfactory signal for communication? While the use of scent marking for communication by strepsirrhines is well known and widely acknowledged (Schilling, 1979), the notion that simians (monkeys and apes)

have a poor sense of smell is nearly universal. This belief, however, is changing. A rapidly

growing body of evidence demonstrates that some simians, particularly the platyrrhines, have

retained a surprisingly keen sense of smell and may not have suffered any significant reduction

in olfactory ability (Laska et al., 2000; Shepherd, 2004; Smith & Bhatnagar, 2004; Smith et al.,

2004). Captive experiments have demonstrated that both catarrhines and platyrrhines have

extremely sensitive olfactory discrimination thresholds for certain chemical odorants (e.g. Laska

et al., 2000). Platyrrhines have a repertoire of olfactory receptors that is comparable in size and

diversity to that of mice and significantly greater than that of catarrhines (Rouquier et al., 2000;

Gilad et al., 2004). Platyrrhines also possess intact and fully functional vomeronasal organs for

perceiving pheromones, structures which are absent or vestigial in catarrhines (Liman & Innan,

2003; Zhang & Webb, 2003). In short, there is a variety of evidence that the olfactory sense

remains important and highly developed in the platyrrhines.

Many platyrrhine species use specialized glands near the sternum, throat, and/or

anogenital region to deposit scent marks. Species with such glands include sakis (Brumloop et

al., 1994), titi monkeys (Fernandez-Duque et al., 2000), owl monkeys (Perkins, 1975), spider

monkeys (Perkins & Machida, 1967), squirrel monkeys (Boinski, 1992), and all callitrichines

(Perkins, 1975; Epple et al., 1982). In some platyrrhines, particularly those lacking scent glands,

urine might be used for olfactory communication (Candland et al., 1980), but most evidence

supporting the role of urine in communication is circumstantial. Olfactory signals have at least

one enormous advantage over other modes of communication: they persist in the absence of the

sender (Eisenberg & Kleiman, 1972). Epple (1974) posits that this property of olfactory signals

makes them especially well-suited to communicate information that is either constant or slowly

changing, such as individual identity, age, sex, and reproductive status. Furthermore, using

olfactory signals to mediate competitive interactions can minimize the risk of personal injury because the recipient can evaluate the signal without being in the physical presence of the signaler. Although scent-marking behavior is widespread among platyrrhines, there is a great deal of ambiguity regarding its functions (reviewed in Heymann, 2006).

Urine-washing may have the appearance of a scent-marking behavior, but it differs from glandular scent-marking in a number of important ways. First, urine is composed of water and water-soluble waste products whereas glandular scent marks may be composites of many different substances. For example, Smith (2006, p. 586) describes common marmoset (*Callithrix jacchus*) scent marks as "a complex mixture of scent from several sources, including secretions from the apocrine and sebaceous glands, secretions from nonspecialized circumanal skin glands, urine, genital tract secretions, fecal material, and old scent material adhering to the gland." The possible presence of proteins in glandular scent marks is one noteworthy difference, as proteins are not found in significant concentrations in the urine of healthy primates. Second, urination is a physiological necessity, used to remove wastes and maintain water balance, while the substances secreted from scent glands are produced specifically to be perceived by conspecifics. Thus, the information that could be encoded chemically in urine is under greater constraints because the chemical composition of urine is subject to physiological needs. In contrast, selection can act more freely on scent glands to favor the secretion of compounds that improve the fidelity of communication. Finally, during urine-washing the putative scent-containing substance (urine) is applied directly to a body part rather than to a substrate, whereas most scent glands are rubbed against substrates directly to deposit the scent. This difference is worth mentioning because it highlights the possibility that the ultimate goal of urine-washing might be to alter some physical or somatosensory property of the hands and feet rather than to deposit a scent.

Urine-Washing in Capuchins: What Do We Know Already?

At least six published studies have examined UW in capuchins, four of which had the explicit goal of testing functional hypotheses for this behavior. One major motivation for the present study is that, despite the attention that the subject has been given, we are still at a loss to explain why capuchins urine-wash. Each study seems to suggest something different, and little effort has been made to resolve the contradictions. In this section, I briefly describe the major findings of past studies of UW in capuchins, highlight methodological issues that may be muddling interpretation of their results, and discuss how I hope to overcome these problems.

Studies in the wild

Four published studies have examined patterns of UW in wild capuchins. Robinson (1979) was the first, carrying out an 11-month study of wedge-capped capuchins (*Cebus olivaceus*) inhabiting gallery forest in the llanos of Venezuela. His study is especially noteworthy in that it stressed the idea that UW is multifunctional; this has remained a central concept for understanding UW behavior to the present day. Robinson's major findings include: (1) UW frequency was markedly higher in the dry season; (2) no significant differences in UW rates existed between sexes and UW rates were not correlated with age; (3) UW by both males and females was associated with the close proximity of opposite-sex conspecifics; (4) the alpha male urine-washed more frequently than any other group member, but overall UW rates were not correlated with dominance rank; and (5) most urine-washes occurred with no evident stimulus. The major problem with Robinson's study is that most of his data were collected *ad libitum*, and

are therefore subject to biases in observation conditions. He states that UW rates were standardized for each individual's "visibility", but offers no description for how this was accomplished. Furthermore, with only one study group he was unable to generalize his results about the alpha male. Finally, he inferred a relationship between UW and both temperature and humidity based on seasonal averages; in other words, he did not measure these variables directly when UW occurred. He concludes that UW is probably a thermoregulatory behavior that may also be used for communication between sexes and possibly between groups.

Perry's (1998) study of male-male relationships in white-faced capuchins did not explicitly test functional hypotheses about UW, and the trends reported therein were derived from a very small sample consisting of only four adult males. Her results agree partially with those of Robinson in that UW was more frequent in the dry season and UW rates were higher in alpha males. However, Perry considered UW a display behavior. She writes on page 151:

> *"The alpha males… were very flamboyant in their urine-rubbing displays: they piloerected, splashed vigorously, and often vocalized while urine-rubbing, and they did so in full view of other monkeys, often splashing urine on others. In contrast, subordinate males were very discreet when they urine-rubbed. They surreptitiously placed a hand under the trickle of urine, after looking around (apparently to see whether they were being watched), and did not splash or assume the arched-back posture favored by alpha males who were urine-rubbing."*

The main problem with Perry's study is that her sample size was very small and limited only to adult males, despite the fact that all group members engage in UW. Furthermore, her conclusion

that UW is a display behavior was based on qualitative impressions that have not been reaffirmed by any other study of UW in capuchins.

Carnegie et al.'s (2005) study was also not designed to explicitly test functional hypotheses for UW, but she described the relationship between female UW rates and ovarian hormones. She found that UW rates among females were actually lower around the ovulatory period. Her investigation was limited to female UW, and the only hypothesis that was considered (and rejected) is that UW is used to communicate female reproductive status.

Finally, Campos et al. (2007) tested several functional hypotheses for UW in white-faced capuchins, improving on Robinson's (1979) methodology by drawing from a much larger data set of systematically collected focal data spanning several years. The major results include: (1) males urine-washed at significantly higher rates than females; (2) alpha males urine-washed at significantly higher rates than all other group members; (3) UW was not more frequent in areas where intergroup encounters occur frequently; (4) UW rates were higher during morning and evening hours than during midday; and (5) most UW occurred with no discernible context, although UW by alpha males was more likely to have an associated social context. The critical flaw in their study, however, is that their data collection procedures were not focused on UW events and olfactory behaviors, but rather were part of a broad study on social relationships. Consequently, and as in the case of Robinson's study, a number of variables potentially related to UW (e.g. temperature and relative humidity) were estimated rather than measured. Furthermore, they combined data from different seasons, overlooking any seasonal effects on UW rates. Their examination of UW in relation to intergroup encounter zones was flawed in that there was no correction for differential usage of areas. Finally, their contextual analysis is

descriptive, lacking any basis for separating UW statistically from a randomly occurring behavior.

Studies in captivity

Three captive studies of UW in capuchins have been published. The first, by Andrew & Klopman (1974), was a preliminary and descriptive interspecies comparison. The only noteworthy observation is that UW in captive white-fronted capuchins (*Cebus albifrons*) occurred occasionally in situations that the authors presumed were stressful, specifically the sudden appearance of a human observer. A more methodical examination of UW in tufted capuchins (*Cebus apella*) was carried out by Roeder & Anderson (1991). These authors designed a series of experiments to test various hypotheses for the function of UW. They found no significant differences in UW frequencies when (1) a mirror was placed in the enclosure; (2) the capuchins' hands were soiled with a sticky substance; and (3) the capuchins were transferred to a new cage or given new tree trunks to climb on. The first result was taken to mean that UW is unrelated to the presence of unfamiliar individuals (capuchins do not recognize themselves in mirrors); the second result that UW is not used to clean the hands; and the third that UW is not used to orient oneself in new surroundings or to improve grip (presumably, the capuchins would be unsure of their ability to grip unfamiliar trunks). As each of these tests involves highly unnatural conditions, their appropriateness for exploring the biological relevance of a naturally occurring behavior is questionable. Roeder & Anderson's strongest result is that UW rates were positively correlated with ambient temperature and were higher overall in sunny conditions. This is the strongest and most direct support for the hypothesis that UW is a thermoregulatory

behavior in capuchins, but it is also the *only* published study for capuchins that provides compelling evidence in favor of thermoregulation.

The most recent captive study of UW by Miller et al. (2007) paints an entirely different picture, one that has been seized upon by popular science writers for its provocative claims (e.g. Choi, 2007; Kaplan, 2007). Rather than designing experiments to test functional hypotheses, Miller et al. base their interpretation on behavioral, hormonal, and environmental data collected on one social group of captive tufted capuchins. They found that UW frequencies were not correlated with ambient temperature and that UW occurred more frequently in the outdoor portion of their enclosure than the indoor portion. Because the capuchins could make vocal contact with conspecifics of other social groups only from the indoor portion of their enclosure, the latter result was taken as evidence that UW is not a territorial behavior. This interpretation is dubious because it is unclear if the different areas of an enclosure are really meaningful to the monkeys in the same way as different parts of a vastly larger home-range in the wild. More interestingly, the authors found that the alpha male doubled his rate of UW during sexual solicitations by females, although it weakens the argument to learn that this male's increased rate is based on only 11 total urine-washes over 5 days. Finally, UW rates while receiving aggression were higher than UW rates while directing aggression, and individual UW rates were negatively correlated with individual levels of serum cortisol. The authors conclude that capuchins may use UW to appease attackers or relieve stress. Not explicitly stated is the fact that UW rates while receiving aggression were over 3 times *lower* that the overall individual mean rate of UW. UW rates while directing aggression were simply even lower.

Methodological differences in this study

I have designed this study to overcome many of the methodological problems discussed above. First, this is a non-invasive study of capuchins in their natural environment. As Robinson (1979, p. 138) articulated nearly 30 years ago in reference to UW, "understanding the adaptive significance of behaviors depends on observations of the natural contexts associated with the behavior." Second, I carry out a thorough examination of environmental effects on UW by measuring climatic variables directly in an attempt to gauge how the capuchins are affected by seasonal heat stress and water scarcity. This is important because previous studies have assumed overly-simplistic relationships between temperature, relative humidity, season, and the need to thermoregulate. Third, I use more precise and sophisticated methods to examine the spatial distribution of UW behavior. Fourth, I employ statistically rigorous randomization techniques to explore the relationship between UW and a variety of social contexts. Finally, my inclusion of several study groups allows me to examine between-group variation in UW, an aspect of UW behavior that has never before been examined in capuchins.

Synopsis

Chapter 2 describes how capuchins cope with the hot, dry conditions of SRNP during the dry season. I examine two strategies in particular: (1) avoidance of heat stress by minimizing physical exertion when it is hot, and (2) active lowering of body temperature by way of behavioral thermoregulation. I predict that temperature will exert considerable influence on activity, that water scarcity will have a major impact on ranging patterns, and that the capuchins'

general strategy during the hottest periods of the dry season will be to rest more and to stay closer to the few remaining sources of water.

Chapters 3 and 4 test functional hypotheses for UW, and my interpretation in these chapters draws heavily from the results of Chapter 2. Several of the hypotheses tested here make specific predictions that relate UW frequencies to environmental variables, including ambient temperature, relative humidity, and general aridity. Evaluating these predictions requires a detailed understanding of the environmental stresses that the capuchins experience. Non-social hypotheses and territorial scent marking are considered in Chapter 3. In particular, I evaluate evidence both for and against the hypotheses that UW is a mechanism for (1) lowering body temperature via evaporative heat loss; (2) relieving painful insect stings; (3) improving grip during arboreal travel; or (4) marking territory. Chapter 4 examines hypotheses that deal with individual variation and social context. Specifically, I examine whether or not UW is (5) a displacement behavior used in stressful situations; (6) a way of communicating social dominance or competitive ability to conspecifics; or (7) a mode of communication between sexes to convey reproductive status or express willingness to mate. I provide a theoretical introduction to these seven hypotheses in the introductions of Chapters 3 and 4.

Finally, Chapter 5 assimilates these results with the body of knowledge that I have reviewed above. I discuss how my results differ from those previously published, and I look for common ground in an effort to explain why the biological significance of UW remains a controversial issue. Finally, I attempt to synthesize what is currently known about UW behavior in capuchins to formulate a coherent set of ideas regarding its functions.

CHAPTER 2: BEHAVIORAL ADAPTATIONS TO HEAT STRESS AND WATER SCARCITY IN WHITE-FACED CAPUCHINS

Introduction

Like all homeothermic animals, primates can maintain an approximately constant body temperature with cardiovascular adjustments only within a particular range of ambient temperatures known as the thermoneutral zone (TNZ). At ambient temperatures above or below the TNZ, primates may regulate their body temperature with both physiological and behavioral adjustments (Elizondo, 1977). Physiological processes used by primates to regulate body temperature outside of the TNZ include sweating (e.g. common squirrel monkey: *Saimiri sciureus*: Nadel & Stitt, 1970; Stitt & Hardy, 1971; Japanese macaque, *Macaca fuscata*: Nakayama et al., 1971; rhesus macaque, *Macaca mulatta*: Elizondo, 1977) and panting (thick-tailed greater bush baby, *Otolemur crassicaudatus*, slow loris, *Nycticebus coucang*, potto, *Perodicticus potto*: Hiley, 1976) to lower the body temperature, and shivering (Elizondo, 1977) to raise the body temperature. Behavioral processes used to regulate body temperature vary widely across species and locations, and can include resting in shade (yellow baboon, *Papio cyanocephalus*: Stelzner, 1988), adopting certain body postures (yellow baboon: Stelzner & Hausfater, 1986; black-and-gold howler monkey, *Alouatta caraya*: Bicca-Marques & Calegaro-Marques, 1998), altering activity schedules (yellow baboon: Stelzner, 1988), adjusting inter-individual spacing (long-tailed macaque, *Macaca fascicularis*: Schino & Troisi, 1990; Japanese macaque: Wada et al., 2007), inhabiting caves (chacma baboon, *Papio ursinus*: Barrett et al., 2004), hibernating (fat-tailed dwarf lemur, *Cheirogaleus medius*: Dausmann et al., 2004), sand-bathing (chacma baboon: Brain & Mitchell, 1999), and orienting the ventrum away from the sun (yellow baboon: Pochron, 2000) or wind (yellow baboon: Stelzner & Hausfater, 1986).

There are two broad methods of dealing with heat stress, which I define as the external forces acting to move an organism away from thermal homeostasis *above* the TNZ. Following Stelzner & Hausfater (1986), I will refer to these methods as behavioral thermoregulation and heat stress avoidance. There are at least four non-exclusive strategies that an animal may use to moderate its body temperature when ambient temperature exceeds the TNZ: (1) selecting cooler microclimates; (2) avoiding physical exertion; (3) adopting body postures that facilitate convection or radiation of body heat; and (4) deliberately exposing moist body surfaces or respirating heavily to promote evaporative heat loss. Strategies 1 and 2 may be considered avoidance of heat stress while strategies 3 and 4 may be considered behavioral thermoregulation (Stelzner & Hausfater, 1986). This study investigates strategies 2 and 4 in wild white-faced capuchin monkeys (*Cebus capucinus*) inhabiting a seasonally hot and dry forest. I also examine the influence of water scarcity on capuchin behavior and ranging patters. Water balance is a critical factor to consider for interpreting responses to heat stress in dry environments. At temperatures above the TNZ, the maintenance of thermal balance in simians depends chiefly on the effectiveness of evaporative heat loss (Elizondo, 1977). Thus, increasing heat stress leads to increased water loss via evaporation and ultimately a loss of thermoregulatory ability if the animal becomes too dehydrated. It is a positive feedback cycle whose risk is exacerbated by the combination of high temperature, low relative humidity, and water scarcity. Brain & Mitchell (1999) found that drinking water can reduce body temperature in chacma baboons living in an extremely arid environment by as much as 3°C over the course of an hour. I expect both high temperature conditions and water scarcity to be important influences on the behavior patterns of capuchins. In particular, I expect capuchins to respond to heat stress by reducing physical

activity and increasing usage of areas that contain permanent water. This study seeks to answer the following specific questions:

1. Does the potential for heat stress vary seasonally?

2. Does the activity budget change with ambient temperature? If so, do the changes appear to minimize energetically costly activities at high temperatures?

3. Do capuchins use specific self-directed behaviors to regulate body temperature?

4. Is home-range usage affected by water scarcity?

Methods

Study site

This study was carried out in Santa Rosa National Park (SRNP), one of four nationally protected areas in northwestern Costa Rica that comprise the 147,000 hectare Area de Conservación Guanacaste. SRNP encompasses 49,515 hectares of mosaic habitat dominated by highly seasonal dry deciduous forest (Fedigan et al., 1996; Fedigan & Jack, 2001). The region experiences a dry season from mid-December to mid-May, and a rainy season from late-May to early-December. The dry season in SRNP is characterized by high ambient temperatures regularly exceeding 37°C, low relative humidity, and the near absence of precipitation. Large tracts of regenerating forest become completely devoid of leaves during the late dry season while small patches of primary and old-secondary forest remain green. Although surface water remains naturally in some areas of the park throughout the year, the study area is particularly dry and nearly all natural water sources used by this study's subjects dry up completely before the end of the dry season. During the driest months, the capuchins may utilize artificial sources of water.

These exist as results of the park's legacy as a former cattle ranch and its current infrastructure to accommodate tourists and researchers.

Study groups and subjects

I observed three social groups of well-habituated white-faced capuchins. Group characteristics are summarized in Table 2.1. Focal subjects included all sexually mature individuals in all three groups. Female white-faced capuchins typically begin reproducing at age 6, at which point they appear socially equivalent to older females. However, male white-faced capuchins reach sexual maturity before they attain the robust body size and high social status associated with complete physical maturity (Fedigan et al., 1996). Thus, my sample was comprised of individuals belonging to three distinct age/sex categories: subadult males (6-10 years), adult males (>10 years), and adult females (> 5 years) (Fedigan et al., 1996).

Data collection

Seasonal weather patterns and group movement data reported here are based on 940 total hours of observation from two separate field seasons. The first data collection period encompassed 2.5 early wet season months from mid-May 2006 until the end of July 2006. The second data collection period lasted from the beginning of January 2007 until the end of April 2007 and included the four hottest, driest months of the dry season. Most of my analyses focus on data collected during the dry season months of January – April because heat stress was most acute during this time (see results). A single group was followed from sunrise to sunset whenever

possible (approximately 5:00 to 18:00 hours), although collection days of shorter length occurred frequently. Two major data-collection procedures were utilized: half-hourly recording of temperature, humidity, and location; and focal animal samples. These methods are described in detail below.

Temperature, humidity, and location

Ambient temperature and relative humidity were recorded with a thermohygrometer (Fisher Scientific) every 30 minutes on the half-hour. The precision of the device was 0.1 °F (.056 °C) for temperature and 0.1% for relative humidity. Microclimate variation in the patchy regenerating forest of SRNP can significantly affect temperature (Chapman, 1988). To more accurately represent the conditions actually experienced by the capuchins, temperature and humidity readings were taken only when observers were standing beneath monkeys. Locations were recorded concurrently on the half-hour using Garmin GSP 12 and Garmin GPS 76 handheld GPS receivers.

Focal animal samples

This study uses focal animal samples (Altmann, 1974) from the dry season months only, drawing on 315 total follow hours on 25 individuals (Table 2.2). Focal animals included all adult males, subadult males, and adult females from CP, LV, and EX groups. A focal animal was followed for two hours continuously, during which all self-directed behaviors and social

interactions involving the focal animal were recorded. Instantaneous samples of the focal animal's state behavior were taken every 2.5 minutes throughout the entire focal sample.

Data analysis

Activity budgets

Activity budgets in the dry season were calculated from instantaneous samples of state behavior during focal samples. I examined proportion of time spent in five mutually-exclusive behavior states: Rest, Travel, Forage, Social, and Vigilant. Behavior states that did not fit into one of these five categories were relatively rare and have been excluded from this analysis. I calculated proportions separately for each focal animal (N=24) then averaged across subjects. One individual (NU) was excluded from this analysis because he had no follow-time in the "low" temperature category (see below). The temperature recorded at the half-hour nearest to the instantaneous sample was used to assign the observation into low, medium or high temperature category. Observations were not included if the nearest half-hour with a recorded temperature was more than 15 minutes away. Temperature category boundaries are defined as +1 and -1 standard deviation from the mean of all systematically-obtained temperature readings in the dry season (N=1073). This resulted in the following category limits: (1) low: $T \leq 26.834°C$; (2) medium: $26.834°C < T < 33.510°C$; (3) high: $T \geq 33.510°C$. The limits for the medium temperature category correspond approximately to the thermoneutral zone reported by Stitt & Hardy (1971) for squirrel monkeys (25°C- 35°C); similar data for capuchins were not available. I applied an arcsine transformation on all proportions to stabilize the variance for statistical tests. Differences among temperature categories were analyzed using Friedman's tests (the variance in

proportions for some behaviors still failed to meet equality assumption necessary for parametric tests). Post-hoc Wilcoxon tests were used to examine pairwise category differences where the Friedman's test was significant.

Distance traveled

Distance was calculated between location points taken at successive half-hours throughout the day in the dry season months. I assigned an average temperature to each 30-min interval by averaging the two temperatures that bound it. Thus, each 30-min interval contributed one distance and one temperature. Locations and temperatures for missed half-hour samples were excluded from the analysis rather than estimated. The three social groups were analyzed separately to avoid group-size or home-range quality effects that would confound any data pooling across groups. Distances were square-root transformed to satisfy the parametric assumption of equal variances. The relationship between temperature and distance traveled was examined using multiple regression analysis carried out in R, version 2.3.1(R Development Core Team, 2007). Square-root of distance traveled was the response variable, and three continuous explanatory variables were entered into the model: temperature, relative humidity, and distance traveled in the previous half-hour. Any data points missing any of these three variables were excluded from the analysis. I obtained the minimal adequate model for each group following Crawley (2002). I first fit the maximal model by including all three explanatory variables and their interaction terms. Non-significant terms were removed in a backward selection process until only significant terms remained.

Thermoregulation and self-directed behaviors

I examined the relationship between several self-directed behaviors and (1) ambient temperature and (2) relative humidity to determine if these behaviors occurred in weather conditions that were significantly different from systematically collected ("baseline") weather data. Baseline for this analysis is based all temperature and relative humidity measurements that were collected on a half-hour *during a focal sample* in the dry season ($N_{temperature} = 583$, $N_{humidity} = 581$). The self-directed behaviors tested include: self-groom, drink water, rub hand, scratch, sneeze, tongue-out, and yawn. Not all of these behaviors are hypothesized to play a role in thermoregulation, but to be thorough I included every self-directed behavior that occurred greater than 50 times. The hypothesized role of urine-washing in thermoregulation is the subject of chapter 3 of this thesis and is not dealt with here. The temperature or relative humidity recorded at the half-hour nearest to the behavior's occurrence was assigned to the behavior for this analysis. Observations were not included if the nearest half-hour with a recorded temperature or relative humidity was more than 15 minutes away.

The assigning procedure described above means that each temperature associated with a behavior is one of the 583 baseline temperatures. Thus, for a behavior occurring N times, the N assigned temperatures (one for each occurrence of the behavior) are in essence a single "draw" of N baseline temperatures sampled with replacement. I used bootstrapping to examine if the mean of this single observed draw was unusual by comparing it to the means of 10,000 simulated draws. Each simulated draw consisted of N baseline temperatures selected randomly with replacement from the entire set of baseline temperatures. The values occupying the highest and lowest 0.5% positions after sorting the 10,000 means were taken as the upper and lower bounds for 99% confidence intervals. A significant result is obtained if the observed mean temperature

or relative humidity at which a self-directed behavior occurred falls outside the confidence interval.

Home-range usage

I estimated home ranges using the "adaptive sphere of influence" Local Convex Hull method (*a*-LoCoH) (Getz & Wilmers, 2004; Getz et al., 2007). *a*-LoCoH is a recently developed approach to modeling home ranges and utilization distributions that performs better than standard kernel methods, particularly in cases where there are "hard boundaries" and substantial unused areas within the home range (see Getz et al., 2007 for details). These properties make *a*-LoCoH well-suited for dealing with the patchy distribution of forest at SRNP, which may include large clearings and grasslands that are not used by the monkeys. Home-ranges were calculated using only points taken systematically at half-hour intervals. I used the LoCoH R script and graphical user interface available at http://locoh.cnr.berkeley.edu. The script was executed in R, version 2.3.1 (R Development Core Team, 2007), and the results were exported to ArcGIS 9.2 for analysis. The software implementation of LoCoH for R makes use of the following packages: adehabitat (Calenge, 2006), gpclib (Peng, 2007), ade4 (Chessel et al., 2004), and shapefiles (Stabler, 2006).

The *a*-LoCoH method requires a user-specified parameter, *a*, that influences the shapes of the utilization distribution isopleths (UDIs). I followed Getz (2007) in choosing an initial value of *a* equal to the maximum distance between any two points in a given set, then adjusting until small lacunae were removed and large unused areas remained outside of the 100% UDI. Although this introduces a degree of arbitrariness, the *a*-LoCoH method is relatively robust

against suboptimal choices of *a* (Getz et al., 2007). By contrast, the shapes of the probability

contours generated by commonly-used parametric kernel methods depend heavily on the choice

of a smoothing factor (*h*); there is no universally accepted method for choosing a value of *h* that

is biologically relevant for a given data set of ranging points.

Results

Seasonal trends in temperature and relative humidity

Temperature was more variable over the course of a typical day in the dry season months

than in the wet season months (Figure 2.1). Temperature peaked between hours 1300-1330 and

was lowest between hours 0600-0630 (Figure 2.1). Mean daily minimum temperatures were

approximately equal across the seven study months, while mean daily maximum temperatures

were generally higher in the dry season months (Table 2.3, Figure 2.3). The hottest month, April,

occurred at the end of the dry season. Relative humidity was lower on average across all hours of

the day in the dry season months than in the wet season months (Figure 2.2). Whereas relative

humidity varied little throughout the day in the wet season months, during the dry season there

was a distinct trough in the early afternoon with minimum values occurring between hours 1200

and 1500. February and March were the two driest months (Table 2.3, Figure 2.4). Temperature

and humidity values in May were intermediate, presumably because the transition between dry

and wet seasons occurred in May.

Activity budget at low, medium, and high temperatures during the dry season

Table 2.4 summarizes the Friedman's tests for within-behavior differences under the three temperature conditions. Proportion of time resting increased consistently with increasing temperature (Table 2.4, Figure 2.5). Within the resting category, significant differences were found between medium and low conditions and between high and low conditions; the medium-high difference approached significance (Table 2.4, Figure 2.5). Resting was the most frequently observed behavior state in the high temperature condition. Proportion of time traveling and proportion of time foraging both decreased consistently with increasing temperature (Table 2.4, Figure 2.5). Significant differences were found between all temperature conditions for both traveling and foraging (Table 2.4). Foraging was the most frequent behavior overall, particularly in the low temperature condition where it accounted for nearly half of the activity budget. No differences were found among temperature conditions for proportion of time engaged in social behavior or vigilance.

Influences on distance traveled

The minimal adequate models of distance traveled are presented in Table 2.5. Distance traveled in the previous half-hour was retained as a significant explanatory variable for all three groups. Temperature was a significant explanatory variable for EX group and approached significance for LV group. Relative humidity was eliminated from all three models, as were all interaction terms. Although these variables produced statistically significant models for all three groups, the adjusted R^2 values were uniformly low (CP: 0.083, EX: 0.156, LV: 0.135). This indicates that the explanatory power of the models was relatively weak.

Other potential thermoregulatory behaviors during the dry season

Tongue-out and Yawn occurred in significantly hotter and drier conditions compared to baseline; that is, they occurred at mean temperatures above the 99% bootstrap confidence interval (BCI) for temperature and below the 99% BCI for humidity (Table 2.6). Scratch and Rub Hand occurred in significantly cooler and more humid conditions compared to baseline, below the 99% BCI for temperature and above the 99% BCI for humidity (Table 2.6). All other self-directed behaviors occurred in conditions that did not differ significantly from baseline.

Seasonal variation in ranging patterns

Home-range boundaries and ranging patterns changed considerably between wet and dry season months (Figure 2.6-8). Home-ranges were larger in all three groups during the dry season months, but this result could simply be an artifact of the greater number of location points that were used for constructing the UDIs in the dry season. This caveat applies to all home-range analyses presented here; nevertheless there were a few unambiguous seasonal trends with respect to permanent water sources.

More locations with permanent water fell within at least one group's home range during the dry season. The increased use of these locations was particularly striking. During wet season months, one permanent water source was located in CP group's 75% UDI and two were located in LV group's 100% UDI; none were located in EX group's home range. Thus, none of the six permanent water sources was located inside a zone of heavy use (<50% UDI) by any group during the wet season months. By contrast, in the dry season months all three groups had at least one water source in an area of heavy use. CP group's zone of heaviest use (25% UDI) was

centered on a permanent water source, one additional water source was located in the 75% UDI, and two more were in the 100% UDI (Figure 2.6). One permanent water source was located in EX group's 25% UDI (Figure 2.7). Finally, LV group had two permanent water sources in their 25% UDI, one in the 50% UDI, and one in the 100% UDI (Figure 2.8).

Discussion

Energy expenditure decreases at high temperatures

Capuchins at SRNP appear to follow a strategy of heat stress avoidance and behavioral thermoregulation in which energy expenditure is minimized at high temperatures and maximized at low temperatures. I base this assessment on differences in the proportion of time spent in three behavior states: Rest, Travel, and Forage. Resting is clearly the least energetically-costly behavior state. Capuchins have a variety of resting postures that tend to be used in specific contexts (Fragaszy et al., 2004); however, only one of these postures occurs commonly during daytime resting in warm, dry conditions. During the day, monkeys typically rest on their ventrum with all four limbs hanging down below the substrate. This posture is identical to the "stretched" posture described by Bicca-Marques & Calegaro-Marques (1998) as a heat-dissipating posture in Black-and-gold howler monkeys (*Alouatta caraya*). Proportion of time resting increased consistently with temperature. Resting was the most frequently observed behavior state in the high temperature condition, accounting for 33.5% of the activity budget. This represents a marked increase from the low temperature condition, at which resting accounts for only 7.6% of the activity budget.

Traveling and foraging are both high-cost activities. Foraging by capuchins is often

extractive and vigorous, with monkeys expending considerable effort to pry away bark, break twigs, and penetrate hard-husked fruits. Foraging monkeys make frequent use of small substrates that require precise body control, bracing, and powerful grip. Likewise, the mode of arboreal locomotion used by capuchins involves frequent running, leaping, and climbing. In the low temperature condition foraging and traveling together accounted for approximately 70% of the activity budget. Proportion of time traveling and foraging both decreased consistently with increasing temperature. Overall, there is a clear trade-off pattern in capuchins' activity budget for reduced energy expenditure at high temperatures and increased energy expenditure at low temperatures.

Temperature has a weak effect on distance traveled

I predicted that distance traveled would vary in inverse relation to temperature. While this prediction was supported in EX group and approached significance in LV group, the influence of temperature on distance traveled was weak overall. The model's poor fit could be due to any combination of the following issues. First, the two environmental variables included in the model, ambient temperature and relative humidity, can produce at best a very rough approximation of the thermal conditions actually perceived by the monkeys. Perceived temperature also depends on wind speed, solar radiation, and non-linear interactions between all of these variables. Although Hill et al. (2004) proposed an index for perceived environmental temperature that integrated these factors for chacma baboons (*Papio ursinus*), such an index cannot be considered relevant for different species with different thermal characteristics. For example, the effects of humidity on perceived temperature depend heavily on the degree to

which an animal relies on evaporative cooling for thermoregulation; the effects of wind speed

depend on insulating characteristics of the fur to resist thermal convection; the effects of solar

radiation depend on coat coloration and surface area-to-volume ratios. An accurate biophysical

model of capuchins' thermal characteristics with respect to these variables was beyond the scope

of this study, and so a greatly simplified model was utilized. A second limitation on the model is

that distance-traveled in any given half-hour probably depends on numerous other factors that

could not be included in this model. These may include the monkeys' current location relative to

food resources or favored resting spots. In addition there is probably a large semi-random

component to distance-traveled that may be affected by events occurring earlier in the day or the

location of neighboring social groups and predators. Finally, it is possible that environmental

stress has a genuinely weak effect on distance-traveled.

Despite the model's poor fit, a number of conclusions can be drawn. First, distance

traveled in the previous half-hour was retained as a significant predictor of distance traveled in

the subsequent half-hour for all three groups. The regression coefficients for distance traveled in

the previous half-hour were all positive, ranging from $0.287 - 0.335$. This indicates a

continuation of the previous state and suggests a pattern of long (relative to 30 minutes) bouts of

traveling and resting rather than frequent short bursts of traveling followed by short recuperation

periods. Second, the influence of temperature on distance traveled differed in strength among the

three groups. When temperature was retained in the model, the regression coefficients were

negative; this partially supports my prediction of an inverse relationship between temperature

and distance traveled.

Tongue-out is a thermoregulatory behavior

This study provides strong evidence that capuchins extend their tongues in hot, dry conditions to lower body temperature via evaporative heat loss. "Tongue-out" occurred at 0.6°C above the 99% BCI for mean temperature and 4.4 percentage points below the 99% BCI for mean relative humidity. Thus, "tongue-out" was non-random with respect to both of these environmental indices. Although wind speed data was not recorded, observers noted a strong tendency for "tongue-out" to occur contemporaneously with gusts of wind. Evaporative cooling would be most effective under hot, dry, windy conditions. Yawning also occurred in significantly hotter and drier conditions, but this is likely a byproduct of the association between yawning and resting. Because resting becomes increasingly common at higher temperatures, I cannot conclude that yawning has any thermoregulatory value. By contrast, there is no reason to expect "tongue-out" to occur more frequently in association with resting. Rubbing the hands together and scratching occurred in significantly cooler and more humid conditions compared to baseline. However, it is unlikely that these behaviors are related to thermoregulation. Monkeys appeared to rub their hands most often while foraging for insects, particularly in ant-defended *Acacia* trees. Foraging was significantly more frequent at lower temperatures than at higher temperatures. Scratching is a more puzzling case because it was not obviously associated with any particular behavioral context. However, with an absolute minimum temperature of 20.7°C during the dry season at SRNP and a mean daily minimum in the mid twenties (Table 2.3), it is doubtful that these capuchins ever experienced significant cold stress. I maintain that scratching is unlikely to have a thermoregulatory function because the mean temperature at which scratching occurred (30.1°C) is still well above the point at which capuchins would feel need to resort to behavioral mechanisms to raise body temperature.

Home-range usage in the dry season is heavily influenced by permanent water sources

Seasonal ranging differences appeared to be influenced by the locations of permanent water sources in the dry season. All three groups increased their use of areas that contained a permanent water source, including several locations that were never visited during wet season months. Furthermore, the "core" (<50% utilization distribution) of all three group's home ranges during the dry season included at least one permanent water source. As long as water was available, the capuchins visited at least one source daily to drink. Visits to water holes often had the appearance of goal-directed forays, with long periods of rapid, coordinated travel ending at the water source. These locations appear to dictate the movements of capuchins in SRNP during the dry season, and I suggest that water should be considered a vital resource for capuchins in very dry conditions.

Summary

This study provides evidence that (1) heat stress and water scarcity are significant influences on the behavior of capuchins in hot, dry conditions; (2) the capuchins use a number of behavioral adjustments to avoid overexertion and dehydration; and (3) at least one specific self-directed behavior has a thermoregulatory function. Capuchin monkeys travel shorter distances, rest more, and travel and forage less during the hottest and driest hours of the day. Capuchins expose their tongues during hot, dry, windy conditions to lower body temperature via evaporative heat loss. Finally, as water becomes scarce, home range areas of heavy use become increasingly centered on the remaining permanent water sources.

Table 2.1. Composition of the study groups.

	CP Group		EX Group		LV Group	
	Wet	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**
Adult Males	3	3	1 - 2	2	1	1
Adult Females	6	6	2	3	5	5
Subadult Males	2	2	0	0	3 - 4	3
Juveniles & Infants	7 - 9	9 - 10	3	4	5 - 6	6 - 8
Total	18 - 20	20 - 21	6 - 7	9	14 - 16	15 - 17
Contact Hours	**141.7**	**248.4**	**36.4**	**112.2**	**117.8**	**209.5**

Table 2.2. Data collected per individual.

Group	Focal	Age/Sex Class	# Instantaneous Samples	# Focal Samples	Follow Hours
CP	BH	Subadult Male	222	6	9.3
	ED	Adult Female	276	6	11.7
	LL	Adult Male	282	6	11.7
	MO	Subadult Male	268	6	11.4
	NN	Adult Male	275	6	11.3
	RR	Adult Male	283	6	11.8
	SA	Adult Female	280	6	11.6
	SI	Adult Female	277	6	11.7
	SS	Adult Female	290	6	12.0
	TT	Adult Female	270	6	11.2
	ZZ	Adult Female	272	6	11.4
			2995	**66**	**125.1**
EX	AN	Adult Female	330	7	13.8
	AR	Adult Male	335	7	14.0
	AT	Adult Male	327	7	13.5
	CL	Adult Female	337	8	14.0
	EL	Adult Female	329	7	13.7
			1658	**36**	**69.0**
LV	BB	Adult Female	315	7	13.3
	CH	Adult Female	335	9	13.9
	CY	Adult Male	310	7	13.0
	DL	Adult Female	297	7	12.5
	KL	Adult Female	306	7	13.0
	MZ	Subadult Male	327	7	13.6
	NU	Subadult Male	317	7	13.4
	SL	Adult Female	346	9	14.4
	WW	Subadult Male	332	7	13.9
			2885	**67**	**121.0**

Table 2.3. Temperature and humidity trends by month.

Month	Mean	Absolute Min	Avg Daily Min	Avg Daily Max	Absolute Max	Mean Daily Diff.
			Temperature (°C)			
May 06	29.7	24.7	25.7	32.8	37.1	7.2
Jun 06	27.2	23.4	24.7	29.2	32.3	4.6
Jul 06	27.0	23.1	25.0	28.9	31.7	3.9
Jan 07	29.1	22.6	24.6	32.4	34.7	7.8
Feb 07	30.2	20.7	23.6	34.5	37.8	10.9
Mar 07	30.8	21.6	25.2	34.8	37.8	9.6
Apr 07	31.3	22.6	25.4	34.9	38.9	9.4
			Relative Humidity (%)			
May 06	69.3	39.5	58.0	85.4	91.9	27.4
Jun 06	82.4	51.0	74.2	91.4	99.7	17.2
Jul 06	84.7	70.1	77.3	92.1	98.9	14.8
Jan 07	62.2	44.4	52.6	74.7	80.6	22.1
Feb 07	53.9	22.6	41.4	75.2	91.9	33.9
Mar 07	55.0	38.2	45.4	70.7	78.8	25.3
Apr 07	60.8	36.1	48.0	78.4	94.3	30.4

Table 2.4. Friedman's tests of activity budget differences at low, medium, and high temperatures.

	Temperature Category [a]			N	Chi-Square	df	p	Post-hoc Wilcoxon tests p-values		
	Low	Medium	High					Med - Low	High - Med	High - Low
Rest	0.076	0.227	0.335	24	25.2	2	< 0.001*	< 0.001*	0.074	< 0.001*
Travel	0.232	0.176	0.133	24	14.083	2	0.001*	0.021*	0.014*	0.001*
Forage	0.461	0.361	0.282	24	15.25	2	< 0.001*	0.002*	0.015*	< 0.001*
Social	0.060	0.077	0.080	24	4.442	2	0.115	-	-	-
Vigilant	0.139	0.125	0.127	24	0.083	2	0.989	-	-	-

[a] Values indicate proportion of samples in the following temperature categories: low: $T \leq 26.834°C$; medium: $26.834°C < T < 33.510°C$; high: $T \geq 33.510°C$
* indicates significant results using $\alpha = 0.05$

Table 2.5. Multiple regression analysis with square root of distance traveled as the response variable and temperature, relative humidity, and distance traveled in the previous half-hour entered as explanatory variables.

Group					
		Adj. R^2	**df**	**F**	**p**
CP	**Model**	0.083	1, 345	32.43	$< .001$
		Variables	**df**	**F**	**P**
		Previous distance	1	32.428	$< .001$
		Residuals	345		
		Coefficients	**Estimate**	**t**	**P**
		(Intercept)	5.752	11.862	$< .001$
		Previous distance	0.302	5.695	$< .001$
		Adj. R^2	**df**	**F**	**p**
EX	**Model**	0.1559	2, 164	16.33	$< .001$
		Variables	**df**	**F**	**P**
		Previous distance	1	24.641	$< .001$
		Temperature	1	8.023	0.005
		Residuals	164		
		Coefficients	**Estimate**	**t**	**P**
		(Intercept)	12.903	4.187	< 0.001
		Previous distance	0.287	3.712	< 0.001
		Temperature	-0.259	-2.832	0.005
LV		**Adj. R^2**	**df**	**F**	**p**
	Model	0.135	2, 308	25.1	< 0.001
		Variables	**df**	**F**	**P**
		Previous distance	1	46.701	< 0.001
		Temperature	1	3.491	0.063
		Residuals	308		
		Coefficients	**Estimate**	**t**	**P**
		(Intercept)	9.273	4.062	< 0.001
		Previous distance	0.335	6.17	< 0.001
		Temperature	-0.132	-1.868	0.063

Table 2.6. Mean temperature for self-directed behaviors compared to 99% bootstrap confidence intervals (BCI).

Behavior	N	Temperature			Relative Humidity		
		Mean (°C)	99% Lower BCI	99% Upper BCI	Mean (%)	99% Lower BCI	99% Upper BCI
Self-groom	544	30.55	30.35	31.09	57.21	55.48	57.99
Drink water	62	31.11	29.65	31.77	55.88	53.02	60.64
Rub hand	232	29.69**	30.17	31.29	59.08**	54.86	58.70
Scratch self	2003	30.06**	30.54	30.91	59.38**	56.07	57.40
Sneeze	100	30.86	29.87	31.55	55.42	53.85	59.77
Tongue out	253	31.94**	30.20	31.25	50.54**	54.94	58.58
Yawn	204	31.75**	30.14	31.29	53.44**	54.71	58.82

** mean outside the 99% BCI.
Boxed cells indicate which confidence limit was exceeded.

Figure 2.1. Mean temperature by hour of the day.
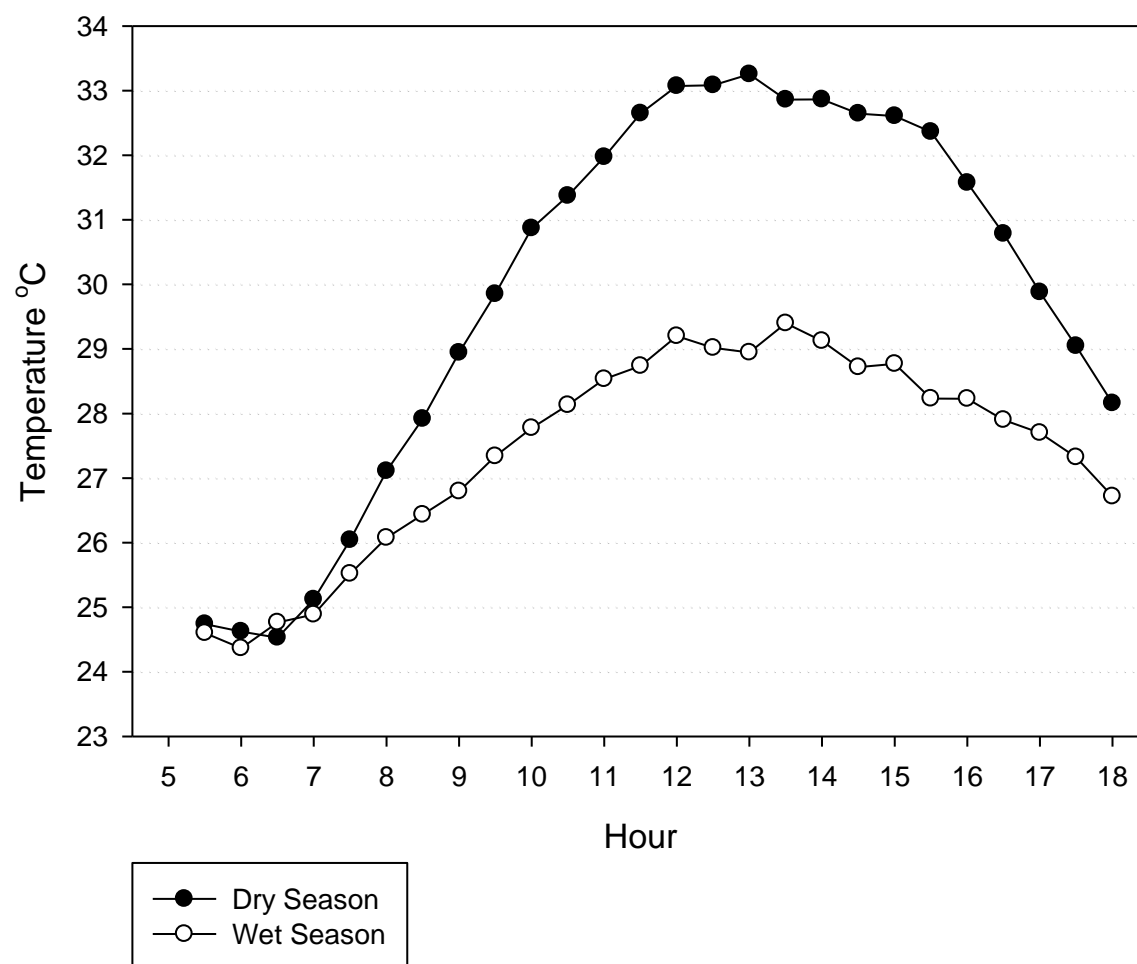
Figure 2.2. Mean relative humidity by hour of the day.
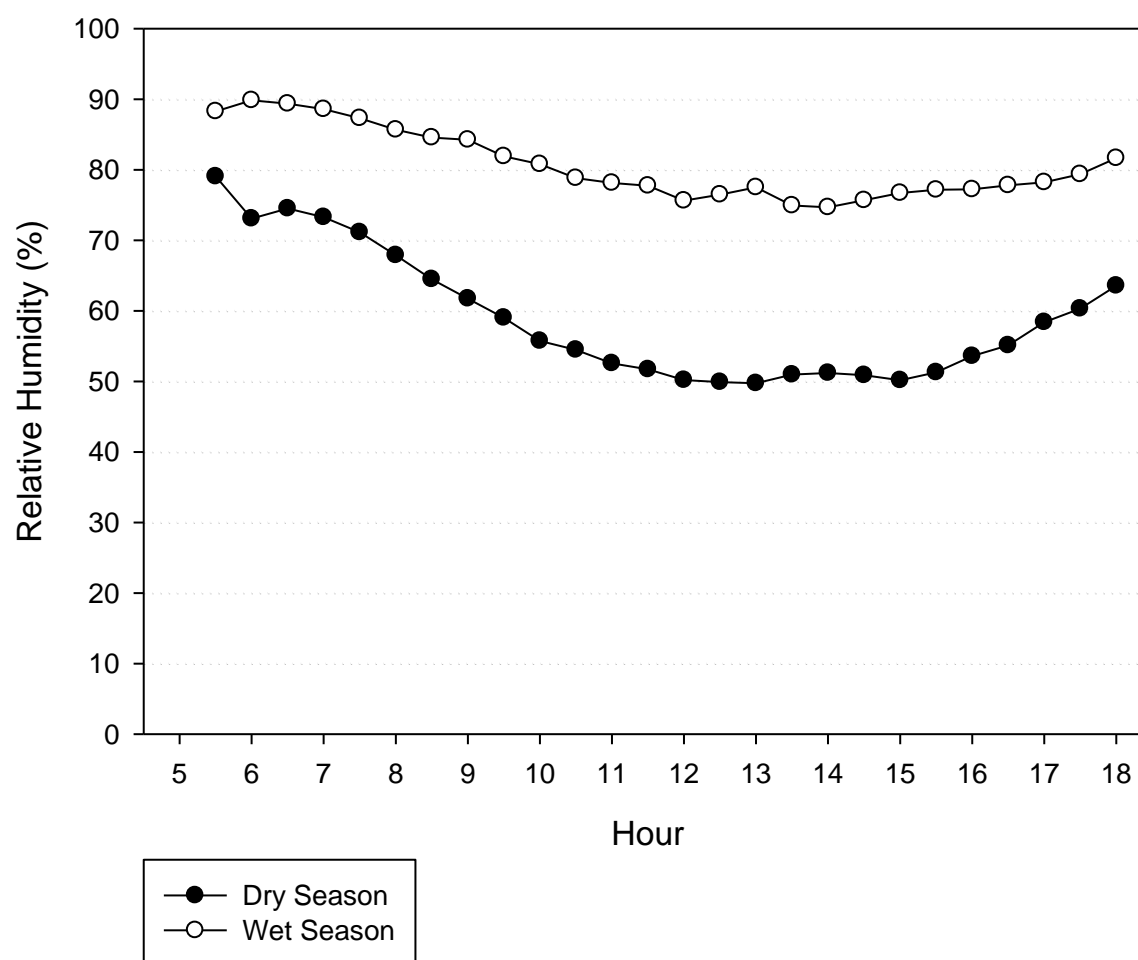
Figure 2.3. Monthly trends in temperature.
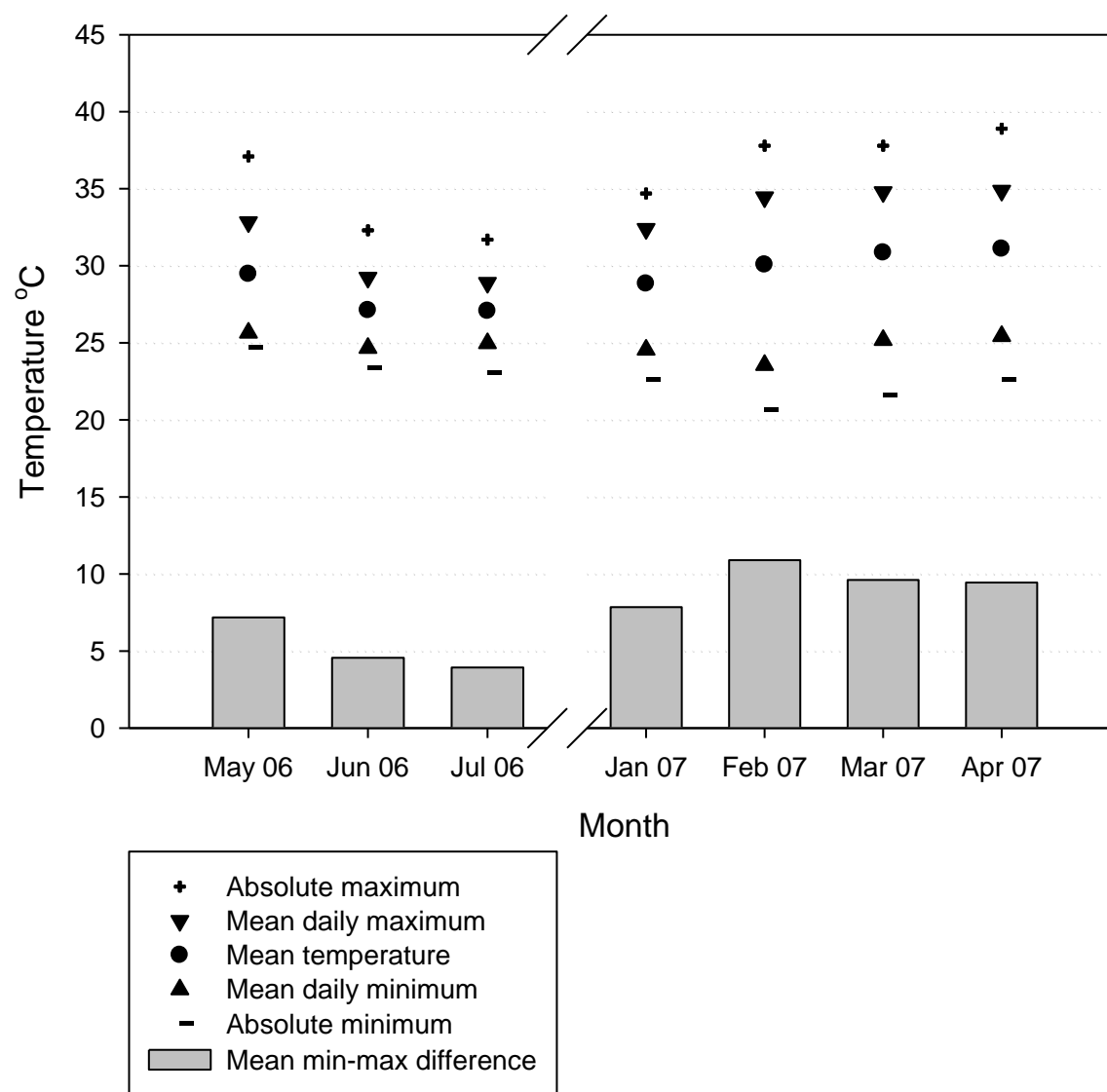
Figure 2.4. Monthly trends in relative humidity.
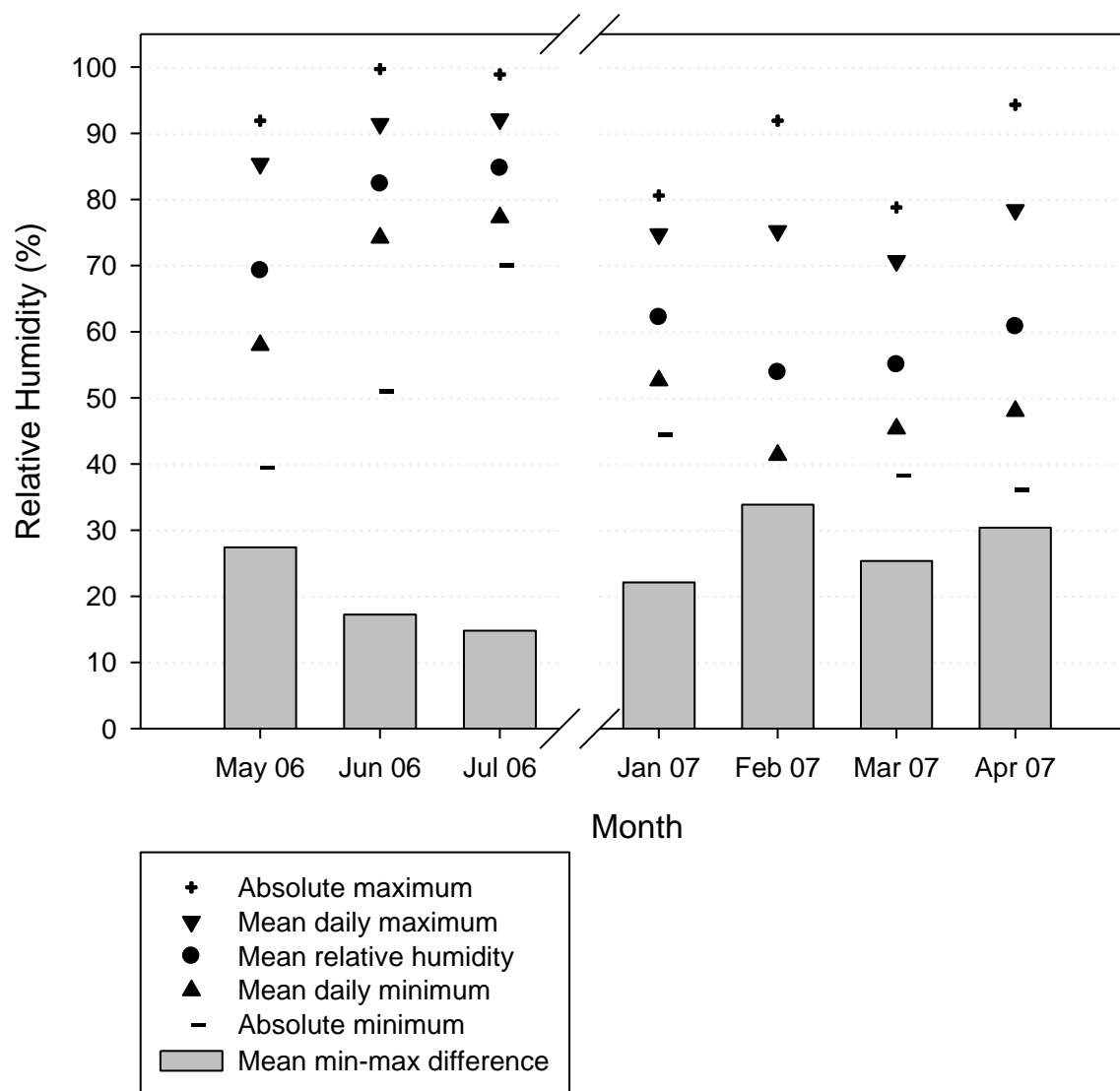
Figure 2.5. Activity budget by temperature category.
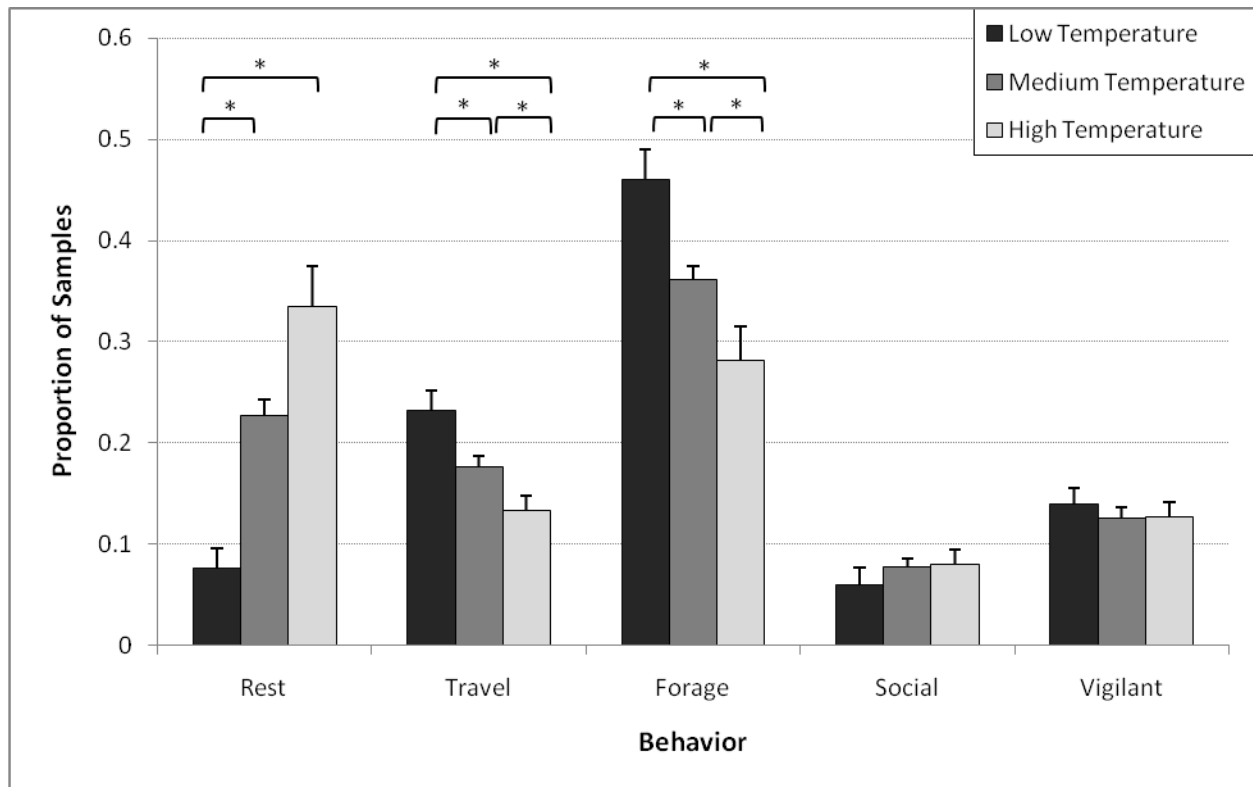
* indicates significant within-behavior differences between temperature conditions using α = 0.05

Figure 2.6. *a*-LoCoH home ranges in dry and wet season months for CP group.
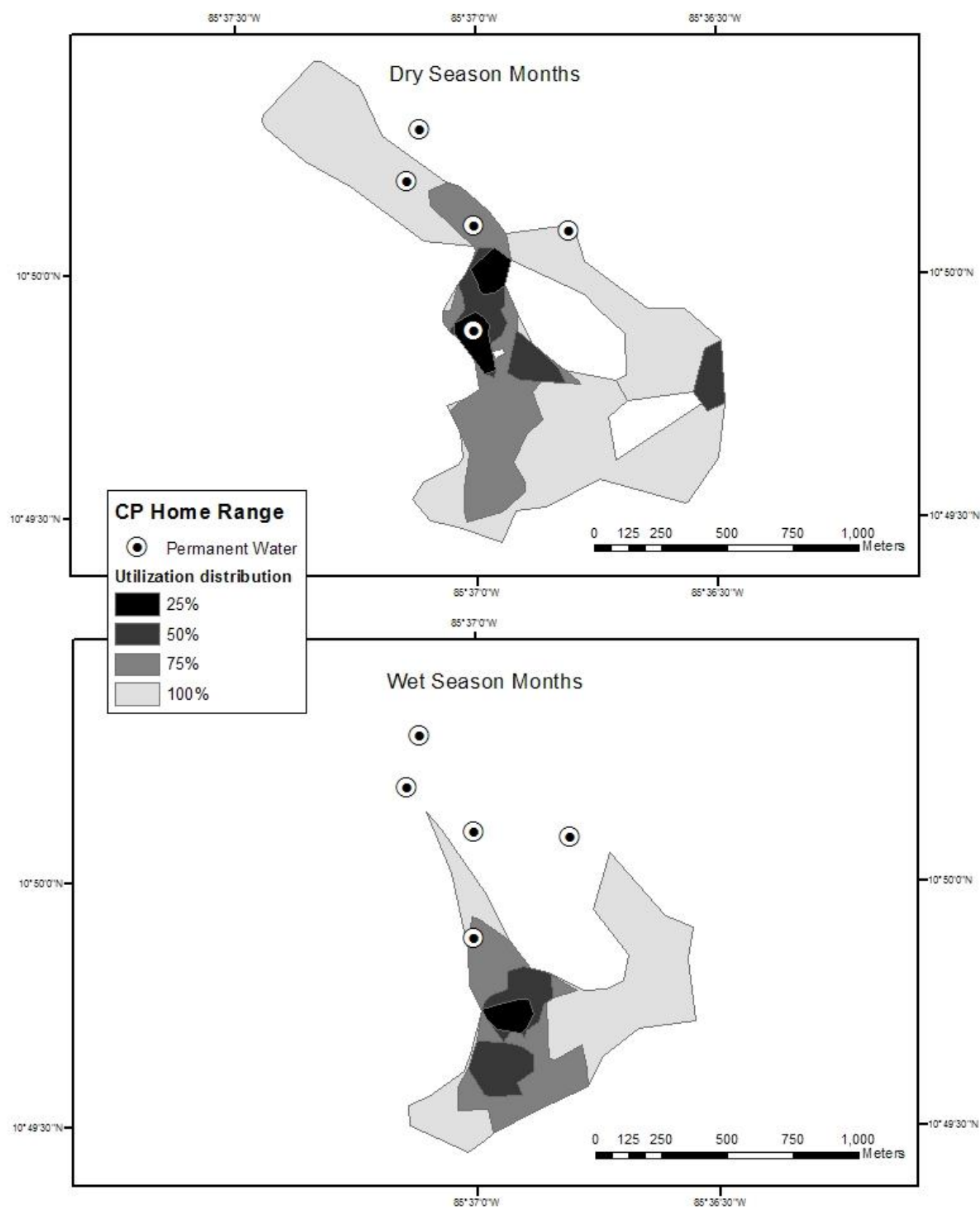
Figure 2.7. *a*-LoCoH home ranges in dry and wet season months for EX group.
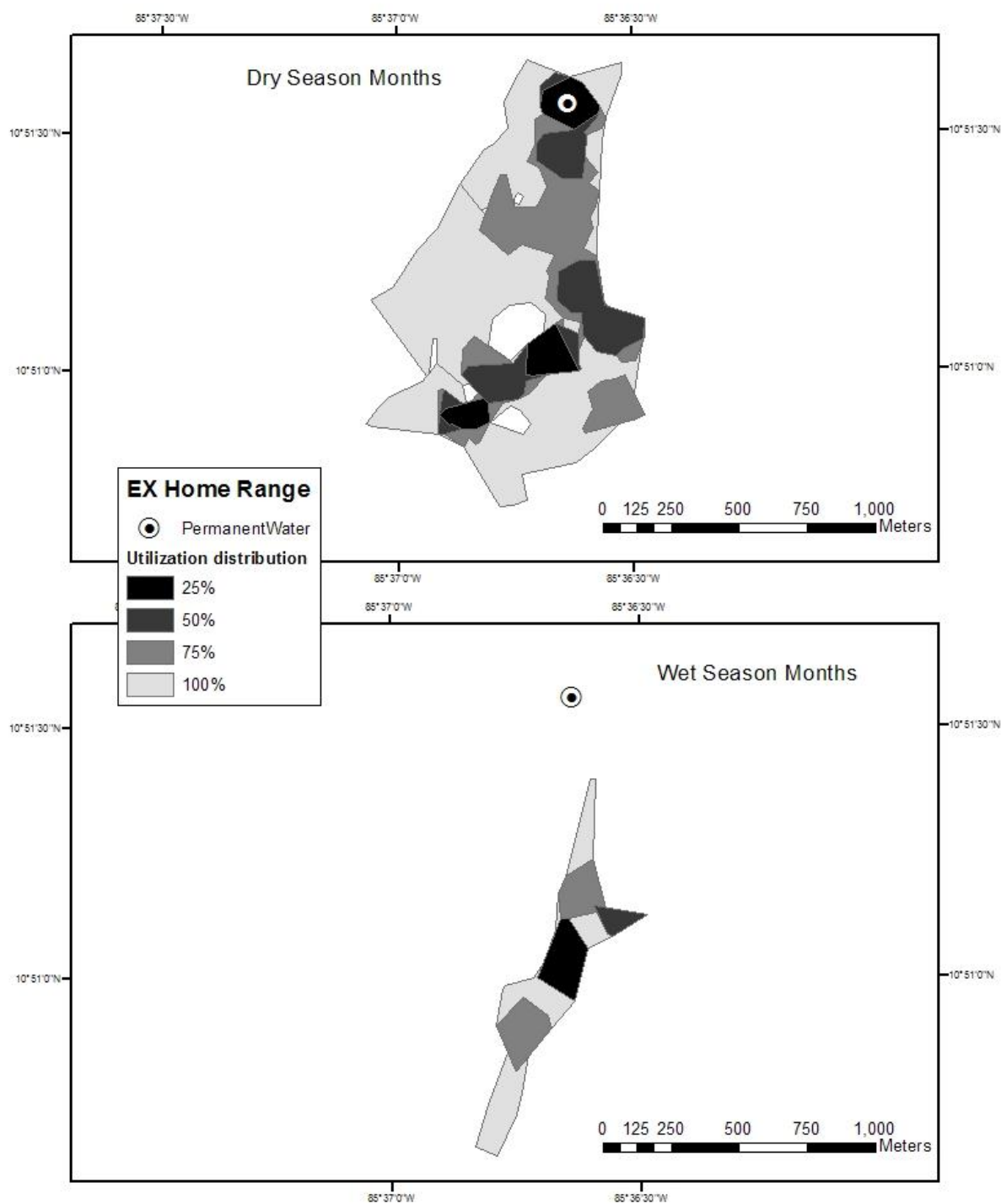
Figure 2.8. *a*-LoCoH home ranges in dry and wet season months for LV group.
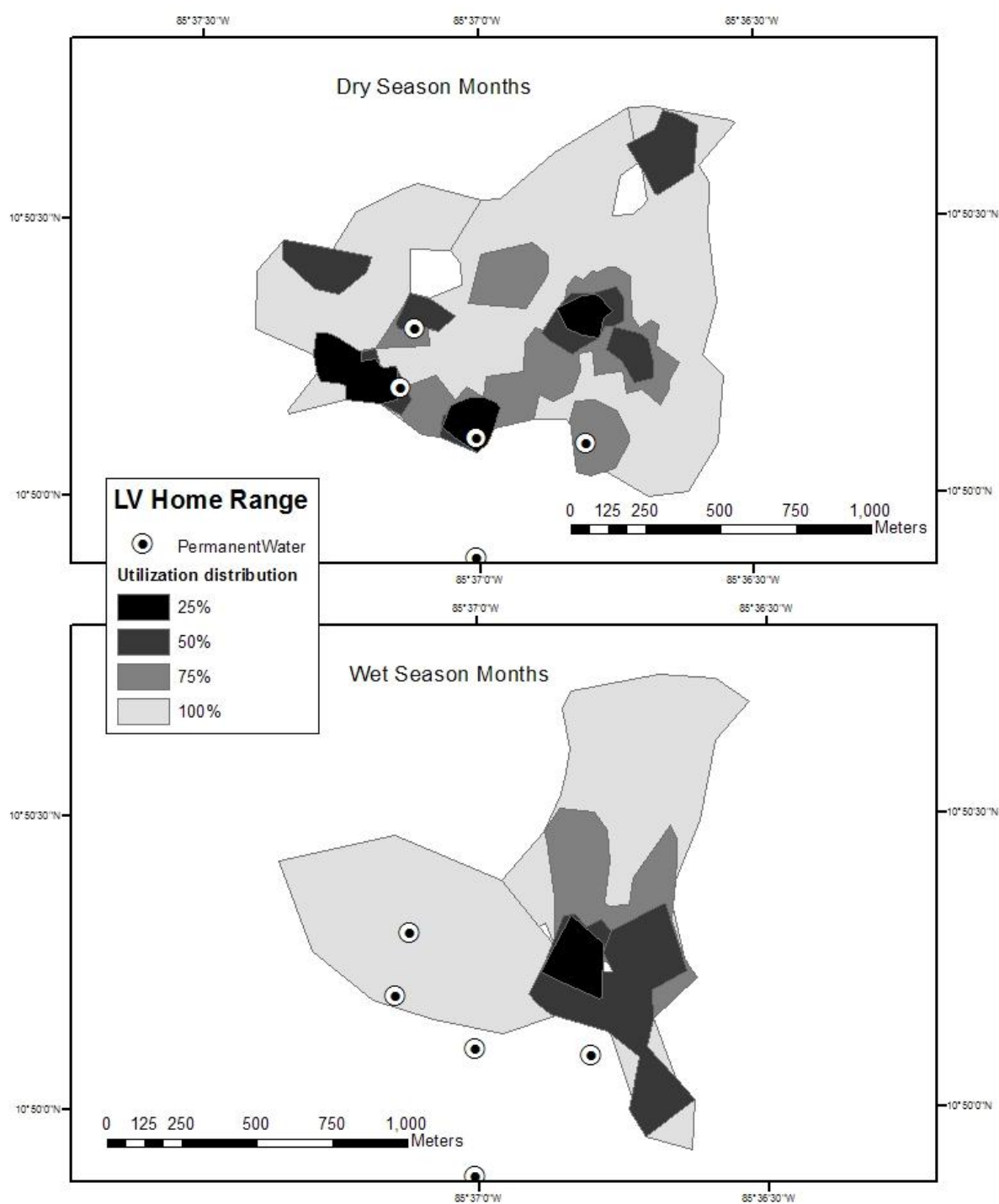
CHAPTER 3: FUNCTIONAL SIGNIFICANCE OF URINE-WASHING IN WHITE-FACED CAPUCHINS, PART 1: ENVIRONMENTAL FACTORS, BEHAVIORAL CONTEXT, AND LOCATION

Introduction

Capuchin monkeys (*Cebus* spp.) regularly engage in urine washing (UW), a behavioral sequence in which the animal urinates onto one forelimb and repeatedly rubs together the palmar and plantar surfaces of the ipsilateral fore and hind limbs (Oppenheimer, 1973). UW has been documented in at least 24 primate species representing 13 distinct genera, and a large number of hypotheses have been put forward to explain this behavior (Appendix 1). Previous studies of UW in wild capuchins (Robinson, 1979; Perry, 1998; Carnegie et al., 2005; Campos et al., 2007) have produced no conclusive answers regarding its function(s). Some research on captive capuchins suggests that UW may be used for thermoregulation (Roeder & Anderson, 1991)), but a recent captive study with tufted capuchins (*Cebus apella*) found that UW is associated with receiving aggression and that alpha males urine-wash in response to sexual solicitations from females (Miller et al., 2007). This chapter examines four hypotheses about the function of UW. These hypotheses relate UW to environmental factors, behavioral context, and location.

Thermoregulation hypothesis

First proposed by Schmidt & Seitz (1967, cited in Harcourt, 1981) for the common squirrel monkey (*Saimiri sciureus*), the thermoregulation hypothesis posits that UW is used by some primates to dissipate body heat via evaporative cooling. The literature regarding this hypothesis is highly contradictory. The most compelling evidence in support of the

thermoregulatory hypothesis comes from Schwartz & Rosenblum (1985), who found that UW

rates in captive common squirrel monkeys varied markedly in response to experimentally

manipulated ambient temperatures. Furthermore, group mean UW rates in captive brown

capuchins (*Cebus apella*) are higher on days with higher mean ambient temperature and more

sunlight versus rain or cloud cover (Roeder & Anderson, 1991). Robinson (1979) observed more

urine washes in wild wedge-capped capuchins (*Cebus olivaceus*) around midday (when ambient

temperatures are presumably hottest), and rates of UW were highest in the dry season (when

relative humidity is lowest). Similarly, Heymann (1995) observed more urine washes around

midday in wild mustached tamarins (*Saguinus mystax*), and Perry (1998) observed significantly

higher UW rates in the dry season among three wild adult male white-faced capuchins. However,

using an expanded data set from the same population of white-faced capuchins, Campos et al.

(2007) found no support for the thermoregulation hypothesis. Likewise, Miller et al. (2007)

found that UW rates were not positively related to temperatures in captive tufted capuchins.

Neutralization of noxious stimuli hypothesis

The neutralization of noxious stimuli hypothesis maintains that urine is applied to the

hands during UW to soothe painful stings or other irritating stimuli. Slender lorises (*Loris*

tardigradus) frequently urine wash while consuming stinging or toxic insects, and rates of UW

increase markedly in this species after being stung by ants (Nekaris, 2002; Nekaris &

Rasmussen, 2003). White-faced capuchins at SRNP feed heavily on the arils of Bull horn acacias

(*Acacia collinsii*) and on the larvae of ants (*Pseudomyrmex spp.*) that nest in the acacia's swollen

thorns (Young et al., 2007). Capuchins feeding on *Acacia* appear to be stung frequently by ants.

To my knowledge, the neutralization hypothesis has not been investigated previously in capuchins.

Moisten hands to improve grip / clean hands and feet hypotheses

These related hypotheses share the concept that UW occurs in response to factors affecting physical properties of the hands. In support of the hypothesis that UW moistens hands to improve grip (Boulenger 1936 for *Galago*, cited in Harcourt, 1981), Castell & Maurus (1967) found that captive common squirrel monkeys urine wash at considerably higher rates when the cage floor is covered in sand and lower rates when the cage floor is wet. Furthermore Welker (1973), introduced thick-tailed greater bush babies (*Otolemur crassicaudatus*) onto a variety of substrates under wet and dry conditions, and found that UW is more frequent on a given substrate when it is dry. Also, Harcourt (1981) noted a tendency for UW in southern lesser bush babies (*Galago moholi*) to accompany foraging bouts on resources that required precarious postures, and therefore good grip. Little direct support has been found for the cleaning hands hypothesis (Hill 1938 for *Nycticebus*, *Loris*, *Cebus*, and *Saimiri*, cited in Harcourt, 1981). Roeder & Anderson (1991) found that deliberately soiling the hands of captive tufted capuchin monkeys with a sticky substance did not significantly change UW rates.

Marking home-range or resources hypothesis

Some primates use scent marks to demarcate territories, and UW could be a mechanism for depositing such signals. In some species, the spatial distribution of scent marking behavior differs in relation to home range boundaries or valuable resources, although this relationship is

widely variable across species. For example, some species scent mark more at home range borders (slow loris, *Nycticebus coucang*, Demidoff's bush baby, *Galagoides demidoff*, and gray mouse lemur, *Microcebus murinus*: Schilling, 1979), others scent mark more in core areas of the home range (saddleback tamarin, *Saguinus fuscicollis*: Yoneda, 1984), others scent mark most in areas of home range overlap (Allen's bush baby, *Galago alleni*: Charles-Dominique, 1977), and others scent mark near valuable food resources regardless of the location in the home range (common marmoset, *Callithrix jacchus*: Coimbra-Filho & Mittermeier, 1976; Lazaro-Perea et al., 1999; Hershkovitz's tassle-eared marmoset, *Callithrix humeralifer intermedius*: Rylands, 1981). Finally, a number of studies explicitly examining the spatial distribution of scent marking behavior have found an essentially random distribution of scent marks throughout the home range (southern lesser bush baby: Harcourt, 1981; common marmoset: Lazaro-Perea et al., 1999; mustached tamarin: Heymann, 2000; but see Gosling & Roberts, 2001 for an alternate interpretation). Captive studies of UW in capuchins have not found any clear pattern in the spatial distribution (Roeder & Anderson, 1991; Miller et al., 2007). However, it is questionable whether or not captive animals can be used to test the role of UW in territory defense. Different areas of a relatively small enclosure are probably not meaningful to monkeys in the same way as different parts of a much larger home range in the wild, and captive animals may not feel the need to defend their enclosure if animals from different social groups can never intrude or come into physical contact. Wild capuchin studies have also failed to find a pattern in the spatial distribution of UW (Robinson, 1979; Campos et al., 2007), but the methods used previously have been either descriptive or preliminary.

Differences in the defensibility of a group's home range might account for the high degree of variability across species in the spatial distribution of territorial scent marking behavior.

Gosling (1982) argued that the optimal strategy for territorial animals should be to concentrate scent marks in areas where they are likely to be detected: territorial boundaries and areas with a high likelihood of intrusion. In a study of brown hyenas (*Hyaena brunnea*), Gorman & Mills (1984) modified this model to account for species with relatively large home ranges: when home ranges are not economically defensible, the most efficient strategy changes such that scent marking behavior should be concentrated in core areas or near valuable resources. The defensibility of a home range is a function of day-journey length, home range boundary length, the number of independently-moving subgroups, and visibility for intruder detection (Mitani & Rodman, 1979; Lowen & Dunbar, 1994). Based on Lowen & Dunbar's (1994) analysis, white-faced capuchins' home ranges are too large to defend. This has been confirmed observationally: capuchins at SRNP do not defend strict territories, and the degree of home range overlap varies for different social groups (Rose & Fedigan, 1995). Hence, I predict that if UW is a form of marking territory, its spatial distribution will be clustered in core areas and/or near important resources.

The objective of this study is to test predictions generated by each of the four hypotheses described above. Table 3.1 lists the hypotheses and summarizes the specific predictions that were examined.

Methods

Study site

This study was carried out in Santa Rosa National Park (SRNP), one of four nationally protected areas in northwestern Costa Rica that comprise the 147,000 hectare Area de Conservación Guanacaste. SRNP encompasses 49,515 hectares of mosaic habitat dominated by highly seasonal dry deciduous forest (Fedigan et al., 1996; Fedigan & Jack, 2001). The region experiences a dry season from mid-December to mid-May, and a rainy season from late-May to early-December.

Study groups and subjects

I observed four social groups of well-habituated white-faced capuchins (BH, CP, EX, and LV). Focal subjects included all sexually mature individuals. Female white-faced capuchins typically begin reproducing at age 6, at which point they appear socially equivalent to older females. However, male white-faced capuchins reach sexual maturity before they attain the robust body size and high social status associated with complete physical maturity (Fedigan et al., 1996). Thus, my sample was comprised of individuals belonging to three distinct age/sex categories: subadult males (6-10 years), adult males (>10 years), and adult females (> 5 years) (Fedigan et al., 1996).

Data collection

Data reported here are based on 940 total hours of observation from two separate field seasons. The first data collection period encompassed 2.5 early wet season months from mid-May 2006 until the end of July 2006. The second data collection period lasted from the

beginning of January 2007 until the end of April 2007 and included the four hottest, driest months of the dry season. BH group was not observed in the dry season months. Typically, a single group was followed from sunrise to sunset whenever possible (approximately 5:00 to 18:00 hours), although collection days of shorter length occurred frequently. Most of the analyses presented here pertain to the dry season months of January – April because of the enormous disparity in UW frequency between wet and dry seasons (see results). Three major data-collection procedures were utilized: half-hourly recording of temperature, humidity, and location; focal animal samples (Altmann, 1974), and urine-wash scans. These methods are described in detail below.

Temperature, humidity, and location

Ambient temperature and relative humidity were recorded with a thermohygrometer (Fisher Scientific) every 30 minutes on the half-hour. The precision of the device was 0.1 °F (.056 °C) for temperature and 0.1% for relative humidity. Microclimate variation in the patchy regenerating forest of SRNP can significantly affect temperature (Chapman, 1988). To represent the conditions actually experienced by the capuchins more accurately, temperature and humidity readings were taken only when observers were standing beneath monkeys. Locations were recorded concurrently on the half-hour using Garmin GSP 12 and Garmin GPS 76 handheld GPS receivers.

Focal animal samples

During focal animal samples (Altmann, 1974), a single individual was followed by two trained observers for two hours (dry season) or four hours (wet season) continuously. I chose to carry out lengthy follows to ensure that the complete social and environmental context would be captured for the majority of observed urine-washes. Adult females were not followed in the wet season because UW by females during this time was extremely rare (see Chapter 4 of this thesis). Observers recorded all self-directed behaviors and social interactions involving the focal animal. Instantaneous samples were recorded every 2.5 minutes throughout the entire focal sample, at which time the focal animal's state behavior and proximity to all conspecifics within contact, 1-m, and 5-m were recorded. I collected a total of 395.5-hr of focal animal samples (Table 3.2).

Urine-wash scans

Whenever UW was observed, the following information was recorded immediately: identity of urine-washer, location, ambient temperature, relative humidity, last state behavior immediately before UW, first state behavior immediately after UW, and the identities of all individuals in contact, 1-m, and 5-m proximity categories.

Data analysis

Environmental factors

I examined the relationship between UW and environmental variables by determining if UW occurred in weather conditions that were significantly different from systematically collected ("baseline") weather data. Baseline for this analysis is based on all temperature and

relative humidity recordings that were collected on a half-hour *during a focal sample* in the dry season ($N_{temperature} = 583$, $N_{humidity} = 581$). I used only measurements collected during focal samples to control for observation conditions, as poor light in the very early morning and late evening impaired my ability to observe UW but not to collect baseline weather data. In the dry season, temperature and relative humidity were recorded for 734 urine-washes during focal samples. I used bootstrapping to determine if the two means of these 734 measurements were unusual by comparing each one to the means of 10,000 simulated draws. Each simulated draw consisted of 734 baseline temperature or relative humidity measurements selected randomly with replacement from the entire set of baseline weather data. The values occupying the highest and lowest 2.5% and 0.5% positions after sorting the 10,000 means were taken as the upper and lower bounds for 95% and 99% confidence intervals, respectively. A significant result is obtained if the actual mean temperature or relative humidity at which UW occurred falls outside the confidence interval.

Acacia *foraging*

I examined the association between UW and foraging in *Acacia* trees by posing the question: did UW occur significantly more frequently within 2.5 minutes of *Acacia* foraging than expected for a randomly distributed behavior? Using focal data from the dry season only, I first defined 5 minute intervals centered on the beginning of each foraging bout on *Acacia* arils or ant larvae. I considered two acts of foraging as different bouts if they were separated by at least 2.5 minutes with no *Acacia* foraging behavior. Bouts were discarded if the focal animal was ever out of sight during the 5 minutes. I used bootstrapping techniques to compare the frequency of

Acacia-related UW with simulated randomly occurring events. For an individual X with N total urine-washes during X's focal samples, N events were placed at random in X's follows; I then counted the number or randomly placed events that happened to fall within one of X's *Acacia* foraging bouts. Each second during which X was being followed had an equal probability of being selected as a random event. I repeated this simulation 10,000 times for each individual and took the counts occupying the highest and lowest 2.5% and 0.5% positions after sorting as limits to 95% and 99% confidence intervals, respectively.

Behavioral context

I compared the proportion of samples in six state behaviors among three different conditions: (1) immediately before UW, (2) immediately after UW, and (3) baseline. The state behaviors were rest, travel, forage (including visual forage), social, vigilant (scanning long-range, not for food), self-groom, and defecate. Behavior states that did not fit into one of these six categories were rare and have been excluded from this analysis. This analysis was carried out for dry season only because there were too few urine-washes in the wet season for statistical testing. Baseline for each behavior category was calculated from instantaneous samples of state behavior taken every 2.5 minutes during focal samples in the dry season. I used only urine-washes that had been observed during a focal animal sample (no *ad libitum* urine-washes). All proportions were calculated separately for each focal animal (N=25) then averaged across subjects. Friedman's tests were used to examine mean proportion of time in each behavior state among the three conditions, with post-hoc Wilcoxon signed-rank tests for pair-wise comparisons.

Spatial distribution of UW

Four different methods were used to analyze the spatial distribution of UW, each addressing a specific question. The first two methods test the hypothesis that UW is used to mark important resources, while the latter two methods test the hypothesis that UW is used to mark home-range boundaries and zones of overlap with neighboring social groups. I combined my ranging data with that of other researchers studying the same groups to maximize the number of location points. For each method described below, I used the Hawth's Tools extension (Beyer, 2004) for ArcGIS 9.2 to compare the number of observed urine-washes in each zone of interest to an expected value. Expected values were based on the proportion of systematic ranging points from my data that fell within that home-range zone. I multiplied these proportions by the total number of urine-washes observed in that group for which location data were available (*ad libitum* urine-washes included) to get an expected number of urine-washes in each zone. I used chi-square goodness-of-fit tests for the comparisons. Low UW frequencies did not allow for statistical testing of any group in the wet season with the second, third, and fourth methods.

The first method examined whether the spatial distribution of UW could be explained by differential use of areas in the home-range. I estimated usage of home-range areas using the adaptive sphere of influence Local Convex Hull (*a*-LoCoH) method (Getz & Wilmers, 2004; Getz et al., 2007; see chapter 2 for details). Utilization distribution isopleths (UDIs) in each home-range were calculated using only points taken systematically at half-hour intervals. I define four home-range zones for each group/season based on frequency of use: (1) intense use, the 25% UDI; (2) heavy use, outside the 25% UDI and inside the 50% UDI; (3) moderate use, outside the 50% UDI and inside the 75% UDI; and (4) light use, outside the 75% UDI but inside

the 100% UDI. Statistical tests were not performed for three groups in the wet season because >10 % of zones had expected UW frequencies of less than 5.

The second method examined whether UW was clustered around important resources. I selected permanent water sources as the foci of this analysis because home-range usage by capuchins in the dry season at SRNP is heavily influenced by water (see chapter 2 of this thesis). I examined frequency of UW within circles of radius 100-m around each permanent water source.

The third method examined whether UW was more frequent around the spatial periphery of each group's home range. The periphery does not correspond to the zone of light use described above because the a-LoCoH UDIs reflect time spent in an area without regard for proximity to borders. Some groups spent a great deal of time near their home-range boundaries, resulting in some heavy or intense usage zones along the edges of the home-range. Therefore, I used the buffer tool in ArcGIS 9.2 to create a 100-m wide "periphery zone" extending for 50-m on either side of the 100% UDI (UW locations could be outside the 100% UDI if the monkey came back inside before the next 30-min systematic location sample). The a-LoCoH method is adept at recognizing unused lacunae in a home-range, resulting in "holes" in the 100% UDI. Because the edges around such holes probably do not represent a meaningful periphery in the way that outer edges of the 100% UDI might, I excluded edges around holes from the periphery zone.

The fourth method compared UW frequencies in areas where intergroup encounters occurred to frequencies in non-intergroup zones. For each intergroup encounter, I placed a 100-m buffer around the location where the encounter began. These locations tended to be spatially

clustered and many of the circular buffers overlapped. Therefore, I dissolved overlapping buffers together to form distinct "intergroup zones", thus removing overlap wherever it occurred.

Results

Seasonal differences in UW frequency

The overall frequency of UW per observation hour was over 21 times greater in the dry season than the wet season (Table 3.2). In fact, there were some individual *days* in the dry season in which more urine-washes were observed than in the entire 2.5-month wet season data collection period. The difference was due in part to the large disparity in *ad libitum* urine-washes. Only 25 urine-washes by non-focal animals were observed in the wet season, compared to 687 in the dry season. One major reason for this difference is that in the dry season individuals of all age and sex classes urine-washed relatively frequently, whereas in the wet season the behavior was performed almost exclusively by alpha males, who were frequent focal subjects. If we narrow the scope by ignoring *ad libitum* data, the overall frequency per pooled focal hour is still 10.0 times greater in the dry season. The precision of these comparisons is clearly subject to data-pooling biases, but the overall pattern is clear: UW is more frequent in the dry season by at least an order of magnitude.

Environmental influences on UW

The mean temperature for UW during focal samples was within the 95% BCI in both seasons (Table 3.3). The mean relative humidity for UW during focal samples was within the

95% BCI in the wet season months, while in the dry season months the mean was below the 95% BCI but still within the 99% BCI (Table 3.3). Thus, there was only one significant difference from baseline: in the dry season, UW occurred in significantly less humid conditions.

Acacia *foraging*

Although Young et al. (2007) found that capuchins at SRNP spend more time foraging on *Acacia* arils than on any other fruit, only 16 of 25 individuals were observed to forage on or in *Acacia* trees during focal samples in this study. Approximately 40% (23/58) of *Acacia* foraging bouts were accompanied by a urine-wash within 2.5 minutes, but the majority (70%) of these urine-washes were performed by only three individuals (Table 3.4). The number of urine-washes within 2.5 minutes of *Acacia* foraging was above the 95% BCI for these three individuals, which indicates that the association was non-random. However, the upper BCI limit was not exceeded (i.e. there was no significant association) for the other 13 individuals who were observed to feed on *Acacia*.

Behavioral context

Travel, vigilance, and self-grooming were more likely to occur both before and after urine-washing compared to baseline activity rates while resting, foraging, and social behavior were all less likely (Table 3.5, Figure 3.1). Travel was the most frequent state behavior both immediately before and immediately after urine-washing (36.0% and 37.4% of samples, respectively). The proportion of samples was similar for each behavior in the before-UW and

after-UW conditions. There was only one significant difference between before-UW and after-UW conditions: the proportion of samples defecating was significantly greater before UW than after (Table 3.5).This suggests that UW may sometimes occur simply because urine is being produced during waste elimination. However, in absolute terms, defecation was a relatively rare context for UW, with only 3.4% of observed urine-washes preceded by defecation.

Spatial distribution of UW

UW frequencies were significantly different than expected based on usage of home-range zones for all four conditions tested (Table 3.6). The differences were generally consistent among groups but varied in degree: more UW than expected occurred in light use zones while less UW than expected occurred in zones of heavy or intense use (Table 3.6; Figure 3.2a, 3.3a, 3.4a). UW was too infrequent in the wet season for within-group comparisons among home-range zones for BH, LV, and EX groups. UW was significantly less frequent within 100-m of permanent water sources in the dry season for all three groups (Table 3.6; Figure 3.2a, 3.3a, 3.4a). CP and EX groups urine-washed significantly more than expected in the spatial periphery of their home-range during the dry season, while UW frequency in the periphery was not significantly different for LV group (Table 3.6; Figure 3.2b, 3.3b, 3.4b). Finally, CP group urine-washed significantly less frequently than expected in intergroup zones; LV group exhibited a similar pattern that approached significance. However, UW frequencies for EX group were not significantly different in intergroup and non-intergroup zones (Table 3.6; Figure 3.2b, 3.3b, 3.4b).

Discussion

UW is a highly seasonal behavior, but is probably not involved in thermoregulation

Urine-washing was observed much more frequently in the dry season than the wet season. These results echo those of Robinson (1979) for wedge-capped capuchins. Because heat stress is greater in the dry season, it is tempting to conclude, as did Robinson, that the seasonal difference supports a thermoregulatory explanation for UW. However, I submit that the seasonal difference is not sufficient to support this explanation for the following reasons. First, the difference between UW temperatures and baseline temperatures was not significant in either season. The lack of a significant difference in the dry season is particularly damaging to the thermoregulatory explanation, as this should be the most direct means of assessing any link between UW and thermal stress. Second, the large seasonal difference is not inconsistent with several other proposed functions for UW. For example, the simplest explanation for UW is that moistening the hands and feet with urine cleans off dust and debris and improves grip for arboreal travel. Clearly, this action would be less useful in a wet environment. Alternatively, it has been suggested that UW lays down an olfactory signal that communicates social information to conspecifics. The great advantage of olfactory signals over other modes of communication is that scent marks can persist for a relatively long time in the absence of the sender. In the rainy season the signals would be washed away by near-daily rain showers and would therefore be of little use to signalers or their intended recipients.

Some hypothesized functions for UW are not consistent with a large seasonal difference in UW frequency. The displacement behavior hypothesis, which maintains that UW occurs during motivational conflict or stressful situations, should not vary under wet or dry conditions. Similarly, seasonal differences are inconsistent with Miller et al.'s (2007) suggestion that UW in captive tufted capuchins occurs to appease attackers or relieve stress when receiving aggression.

If the act of washing with urine relieves stress or diffuses aggression, there is no reason why this function should be any less useful in the wet season. Chapter 4 of this thesis will examine these and other social hypotheses in closer detail.

UW may be used by some monkeys to relieve ant stings

This study provides suggestive evidence that some capuchin monkeys may use UW in association with foraging on ant-defended *Acacia* trees. As with the slender loris, which urine-washes in response to ant stings (Nekaris & Rasmussen, 2003), urine might be used by capuchins to soothe the painful stings of *Acacia* ants. It is also possible that capuchins apply urine to their hands to *deter* the ants from stinging. It was impossible to determine with confidence when a monkey had been stung. Capuchins would occasionally rub their hands against a tree branch after foraging in *Acacia* trees, but otherwise ant stings did not appear to bother the monkeys greatly. The timing of the urine-washes relative to the start of *Acacia* foraging could potentially indicate whether the urine was used as a deterrent or a response to stinging. Among the three individuals who urine-washed in significant association with *Acacia* foraging, the number of urine-washes that occurred just before the start of the foraging bout (n=9) was approximately equal to the number that occurred during or after the foraging bout (n=7). Thus, the data in this study do not favor or refute either explanation. An alternative possibility is that urine-washes are stochastic with respect to the *Acacia* foraging bouts themselves, but some confounding variable(s) whose effects are magnified during *Acacia* foraging increase the probability of UW during these times. For example, *Acacia* foraging often involves an increased reliance on grasping the thin terminal branches of neighboring trees to access *Acacia* resources while

avoiding the ants. Capuchins at SRNP usually access *Acacia* trees by "swinging into them" from neighboring trees that lack stinging ants (Young et al., 2007). UW could be used in this situation to improve grip on slender branches. Another possible confounding factor is the relatively open, savanna-like microclimate that characterizes *Acacia* patches. These areas tend to be particularly dry, and may therefore intensify the factors that make UW much more frequent in the dry season. If in fact UW is used to relieve or deter insect stings, then it is a relatively minor function. The vast majority (97.1%) of urine-washes occurred outside of *Acacia* foraging contexts. I suggest that the primary function of UW is not coping with stinging insects, but that at least some individuals may occasionally use UW for this purpose.

UW occurs with increased frequency in traveling and vigilant contexts

This study partially supports the hypothesis that capuchins urine-wash to moisten their hands for improved grip, but some results were inconsistent with this interpretation. The fundamental predictions of this hypothesis are that UW should be more frequent (1) in drier conditions, and (2) in behavioral contexts that require secure grip on tree branches. The first prediction was fully supported – UW was much more common in the dry season, and within the dry season UW occurred at a mean relative humidity that was significantly below the baseline. The second prediction was partially supported by my finding that traveling is the most common behavioral context for UW. Traveling is arguably the context in which precise grip would be most important for capuchins. Compared to baseline activity rates, traveling is approximately twice as common immediately before and after UW. However, vigilance was the second most common behavioral context, accounting for approximately 25% samples both before and after

urine-washes. This represents a significant increase in vigilance over baseline activity rates, suggesting that vigilance and UW are non-randomly associated. There is no reason why improved grip should be important while animals are engaged in long-range scanning. Furthermore, UW appeared to be negatively associated with foraging. Improved grip should be useful for foraging animals because capuchins frequently utilize thin terminal branches while feeding on fruits or insects. A more detailed study of positional behavior and substrate use in UW contexts would help to clarify this issue.

UW frequency varies by home-range zone

My analysis of the spatial distribution of UW indicates that (1) the proportion of UW in different home-range zones does not match the proportion of time spent in each zone, (2) capuchins do not use UW to mark permanent water resources, (3) capuchins might urine-wash more around the periphery of their home-range, and (4) capuchins do not urine-wash more frequently than expected in areas where intergroup encounters occur.

The first point suggests that UW does not occur randomly throughout the day but rather is disproportionately frequent in zones of light use and infrequent in zones of heavy use. Activity is probably a confounding variable: some behavior states might be more common in different areas and UW frequencies could reflect these differences. I have demonstrated that UW is most frequent in traveling contexts and less frequent in resting and foraging contexts (Table 3.5). The heavy and intense use zones probably contain a disproportionate number of favored resting spots and important food resources. Activity in these zones is therefore likely to be biased toward resting and foraging. The light use zone probably contains more areas through which the

capuchins travel quickly; thus behavior in the light use zone may be biased toward traveling. The spatial distribution of UW appears to reflect these differences in activity rather than the locations of important resources or resting locations. This interpretation is strengthened by the second point, which is that UW is infrequent around important permanent water sources in the dry season. In summary, there is no evidence from this study that UW is used by capuchins to mark important resources.

The third point – that UW is more frequent in the spatial periphery for 2 of 3 groups – is more difficult to interpret. I predicted based on models of scent-marking in hyenas (Gorman & Mills, 1984) that if UW were a form of marking territory, more UW would be observed in the central areas of heavy use. This prediction was not supported by my data. It is possible that my assumptions were faulty because capuchins are not territorial. Capuchins do not defend precise boundaries, and home-ranges of adjacent groups may overlap considerably. However, capuchins are highly intolerant of other social groups, and they are an anomaly among most primates in that females are philopatric, but males are the primary participants in intergroup encounters. Capuchin intergroup encounters typically involve intense aggression between males that may occasionally escalate to lethal coalitionary attacks (Gros-Louis et al., 2003). Thus, it might be advantageous for capuchins to avoid such encounters by advertising their use of an area to neighboring social groups. Urine is an extremely low-cost signal that could persist on branches for extend periods when there is no rain in the dry season. The fact that capuchins do not pass through their entire home-range each day may be irrelevant for predicting the spatial distribution of UW if the scent remains for long periods of time and can be produced virtually without cost. Thus, the periphery rather than the core might be the best place to deposit scent marks if their

function is to avert intergroup aggression by discouraging neighboring groups from entering an area.

It is therefore surprising, and seriously damaging to this line of reasoning, that capuchins do not urine-wash more – and may in fact urine-wash less – in areas where intergroup encounters occur. It is likely that the circles of 100-m radius that I designated as intergroup zones do not adequately represent the locations that the monkeys themselves might perceive as having a high risk of intrusion. Regardless, the results of this study are not strong enough to conclude that capuchins use UW to communicate usage of an area to conspecifics of neighboring groups. The question is far from resolved. Further study is needed to determine why large differences were observed in the spatial distribution of UW among groups in the dry season.

Summary

Urine-washing in wild white-faced capuchins is a highly seasonal behavior that occurs much more frequently in the dry season. I found no support for the thermoregulation hypothesis and cautious support for the neutralization of noxious stimuli hypothesis. Some individuals urine-washed at higher frequencies in association with foraging bouts on ant-defended *Acacia* trees, but the great majority of urine-washes occurred outside of these contexts. The behavior states immediately before and after UW differed significantly from baseline activity rates, although UW was not performed exclusively in any particular behavioral context. Compared to baseline, UW was more frequent in travel, vigilance, and self-grooming contexts and less frequent in resting, foraging, and social contexts. Because secure grip would be important for both traveling and foraging, this study neither supports nor refutes the moistening / cleaning hands hypotheses.

The hypothesis that UW is used for between-group signaling was not strongly supported. Although UW was more frequent in spatially peripheral areas and less frequent in heavily-used areas, UW was not more common in areas where intergroup encounters occur.

Table 3.1. Hypotheses for urine-washing and predictions tested in this study.

Hypothesis		Predictions
Thermoregulation	1	UW frequency will be greater at low relative humidity.
	2	UW frequency will be greater at high temperature.
	3	Overall UW frequency will be greater in the dry season because heat stress is greater in the dry season.
Neutralization of noxious stimuli	1	UW will be more likely to occur during and immediately after the manipulation of insects that sting or have other chemical defenses.
Moisten hands to improve grip / clean hands and feet	1	UW frequency will be greater in less humid conditions.
	2	UW will be more frequent in traveling and foraging contexts because there is a greater need for secure grip.
	3	Overall UW frequency will be greater in the dry season.
Mark home-range or resources	1	UW will be more likely to occur in core areas of the home range.
	2	UW will be more likely to occur in areas with frequent inter-group encounters.
	3	UW will be more likely to occur near valuable resources such as water holes.
	4	Overall UW frequency will be greater in the dry season because rainy conditions would make scent-marks short-lived and less effective.

Table 3.2. Number of urine-washes and total amount of data collected per group in wet and dry seasons.

Season	Group	Contact hours	Total # UW	Focal hours	# UW by focal animals
Wet	**BH**	74.3	3	14.7	1
	CP	141.7	24	30.5	9
	EX	36.4	1	14.4	1
	LV	117.8	17	20.8	9
		370.1	**45**	**80.4**	**20**
Dry	**CP**	248.4	815	125.2	407
	EX	112.2	228	69	157
	LV	209.5	431	120.9	223
		570.1	**1474**	**315**	**787**

Table 3.3. Mean temperature and relative humidity for urine-washing compared to 95% and 99% bootstrap confidence intervals (BCI).

			Temperature (°C)			
			95% Confidence Interval		99% Confidence Interval	
Season	N	Mean	Lower	Upper	Lower	Upper
Wet	41	28.26	27.18	28.43	26.99	28.66
Dry	1264	30.62	30.55	30.90	30.50	30.96

			Relative Humidity (%)			
			95% Confidence Interval		99% Confidence Interval	
Season	N	Mean	Lower	Upper	Lower	Upper
Wet	41	78.98	77.36	83.63	76.35	84.55
Dry	1264	55.97*	56.12	57.36	55.93	57.58

* mean outside the 95% BCI.
Boxed cells indicate which confidence limit was exceeded.

Table 3.4. Frequency of urine-washing associated with foraging bouts on *Acacia*.

Monkey	*Acacia* foraging bouts	# UW within 30 sec.	95% BCI Upper Limit	99% BCI Upper Limit
AN	1	0	1	1
AR	0	0	0	0
AT	0	0	0	0
BB	0	0	0	0
BH	1	0	2	2
CH	6	0	2	2
CL	4	3**	1	2
CY	5	0	4	5
DL	1	0	1	1
ED	7	1	4	5
EL	0	0	0	0
KL	0	0	0	0
LL	3	0	3	3
MO	1	1	2	3
MZ	0	0	0	0
NN	0	0	0	0
NU	8	6*	5	7
RR	0	0	0	0
SA	2	1	3	3
SI	4	0	4	5
SL	0	0	0	0
SS	8	7**	5	6
TT	1	1	2	2
WW	3	0	2	3
ZZ	3	3	3	4

* mean outside the 95% BCI.
** mean outside the 99% BCI.
Boxed cells indicate which confidence limit was exceeded.
Monkeys who were not observed to forage on *Acacia* fruit or ant larvae are shaded in gray.

Table 3.5. Friedman's tests of differences among behavior states in baseline, before-UW, and after-UW conditions.

| | Condition (proportion of samples) | | | N | Chi-square | df | p | Post-hoc Wilcoxon tests p-values | | |
	Baseline	Before UW	After UW					Baseline vs. Before UW	Baseline vs. After UW	Before UW vs. After UW
Rest	0.231	0.056	0.058	25	39.811	2	< 0.001**	< 0.001**	< 0.001**	0.869
Travel	0.177	0.360	0.374	25	36.571	2	< 0.001**	< 0.001**	< 0.001**	0.501
Forage	0.365	0.213	0.185	25	33.388	2	< 0.001**	< 0.001**	< 0.001**	0.070
Social	0.076	0.023	0.025	25	26.756	2	< 0.001**	< 0.001**	< 0.001**	0.815
Vigilant	0.124	0.247	0.267	25	26.808	2	< 0.001**	< 0.001**	< 0.001**	0.390
Self-groom	0.024	0.067	0.088	25	15.979	2	< 0.001**	0.001**	< 0.001**	0.100
Defacate	0.002	0.034	0.004	25	8.690	2	0.013*	0.030*	0.233	0.002*

* significant at $\alpha = 0.05$
** significant at $\alpha = 0.01$

Table 3.6. Urine-washing frequencies in home-range zones compared to expected values.

Season	Group	Zone	Prop. of Locations	Expected UW	Observed UW	Residual	df	χ^2	p
Wet	CP	Light use	0.257	10	16	6	3	9.63	0.022*
		Moderate use	0.243	10	11	1			
		Heavy use	0.265	11	3	-8			
		Intense use	0.235	9	10	1			
Dry	CP	Light use	0.253	177	286	109	3	121.61	< 0.001**
		Moderate use	0.281	196	189	-7			
		Heavy use	0.218	152	147	-5			
		Intense use	0.248	174	77	-97			
		Near water	0.203	142	50	-92	1	74.80	< 0.001**
		Not near water	0.797	557	649	92			
		Periphery	0.313	219	263	44	1	12.87	< 0.001**
		Non-periphery	0.687	480	436	-44			
		Intergroup Zone	0.123	86	55	-31	1	12.74	< 0.001**
		Non Intergroup	0.877	613	644	31			
	EX	Light use	0.222	48	57	9	3	8.79	0.032*
		Moderate use	0.226	49	61	12			
		Heavy use	0.308	66	58	-8			
		Intense use	0.244	53	40	-13			
		Near water	0.041	9	3	-6	1	4.17	0.041*
		Not near water	0.959	207	213	6			
		Periphery	0.195	42	61	19	1	10.67	0.001**
		Non-periphery	0.805	174	155	-19			
		Intergroup Zone	0.421	91	102	11	1	2.30	0.130
		Non Intergroup	0.579	125	114	-11			
	LV	Light use	0.276	109	144	35	3	26.62	< 0.001**
		Moderate use	0.266	105	114	9			
		Heavy use	0.207	82	74	-8			
		Intense use	0.251	99	62	-37			
		Near water	0.187	74	50	-24	1	9.58	.002**
		Not near water	0.813	320	344	24			
		Periphery	0.190	75	78	3	1	0.15	0.700
		Non-periphery	0.810	319	316	-3			
		Intergroup Zone	0.234	92	76	-16	1	3.63	0.057
		Non Intergroup	0.766	302	318	16			

 * significant at α = 0.05
** significant at α = 0.01.

Figure 3.1. Activity immediately before and immediately after UW compared to baseline activity.
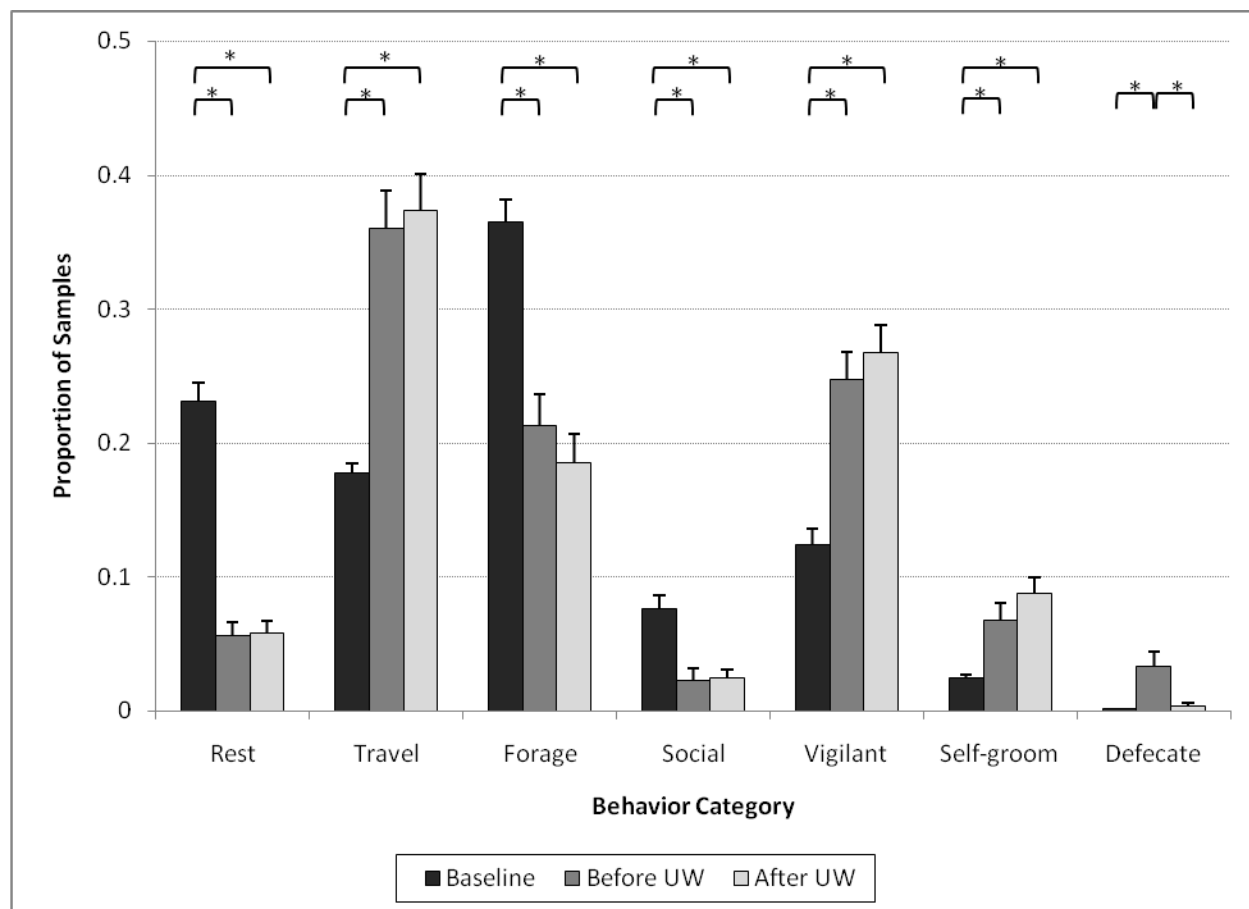
* indicates significant within-behavior differences between UW conditions using α = 0.05

Figure 3.2. Spatial distribution of UW for CP group in the dry season in relation to (A) zone usage and permanent water, and (B) home-range periphery and intergroup encounters.
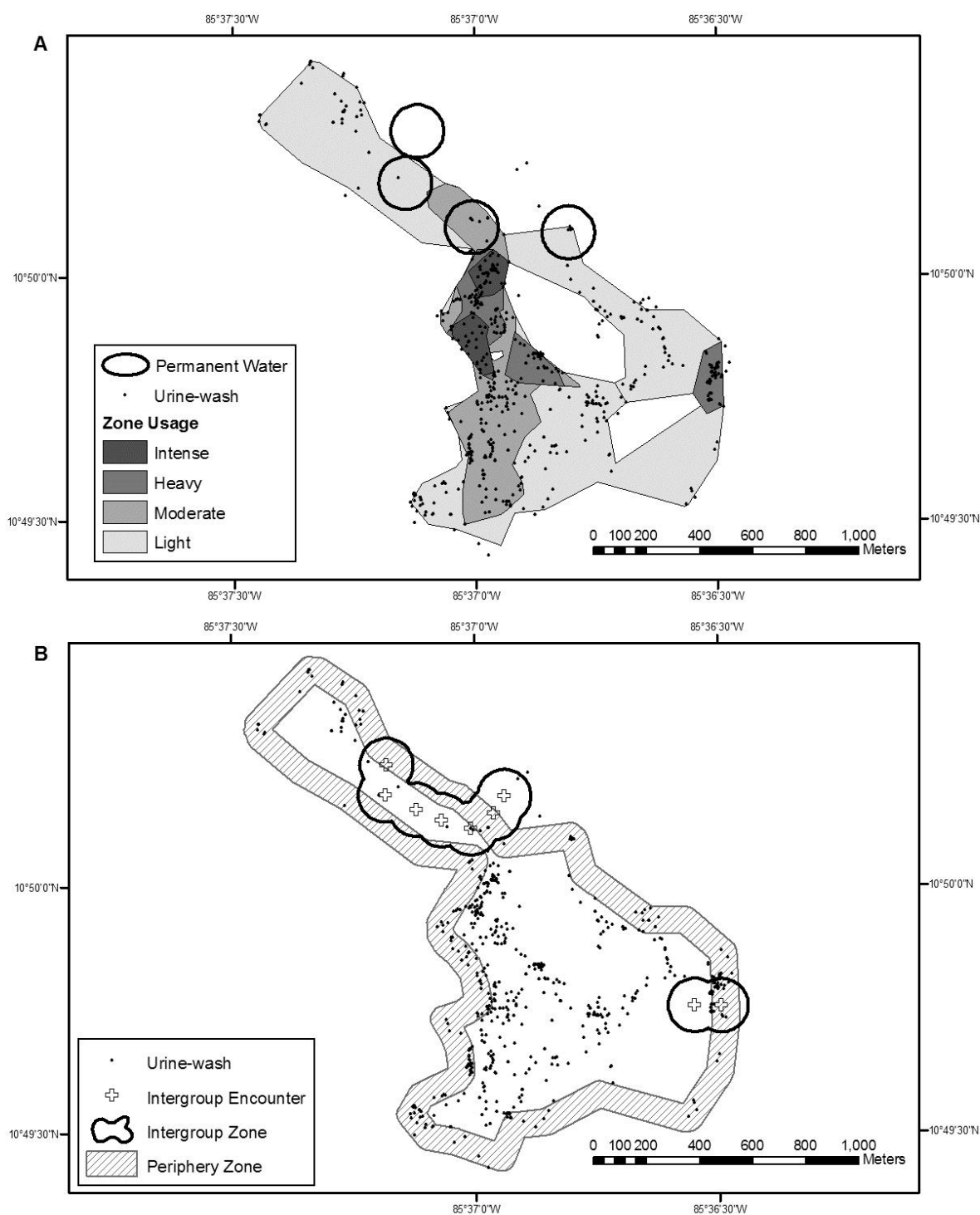
Figure 3.3. Spatial distribution of UW for EX group in the dry season in relation to (A) zone usage and permanent water, and (B) home-range periphery and intergroup encounters.
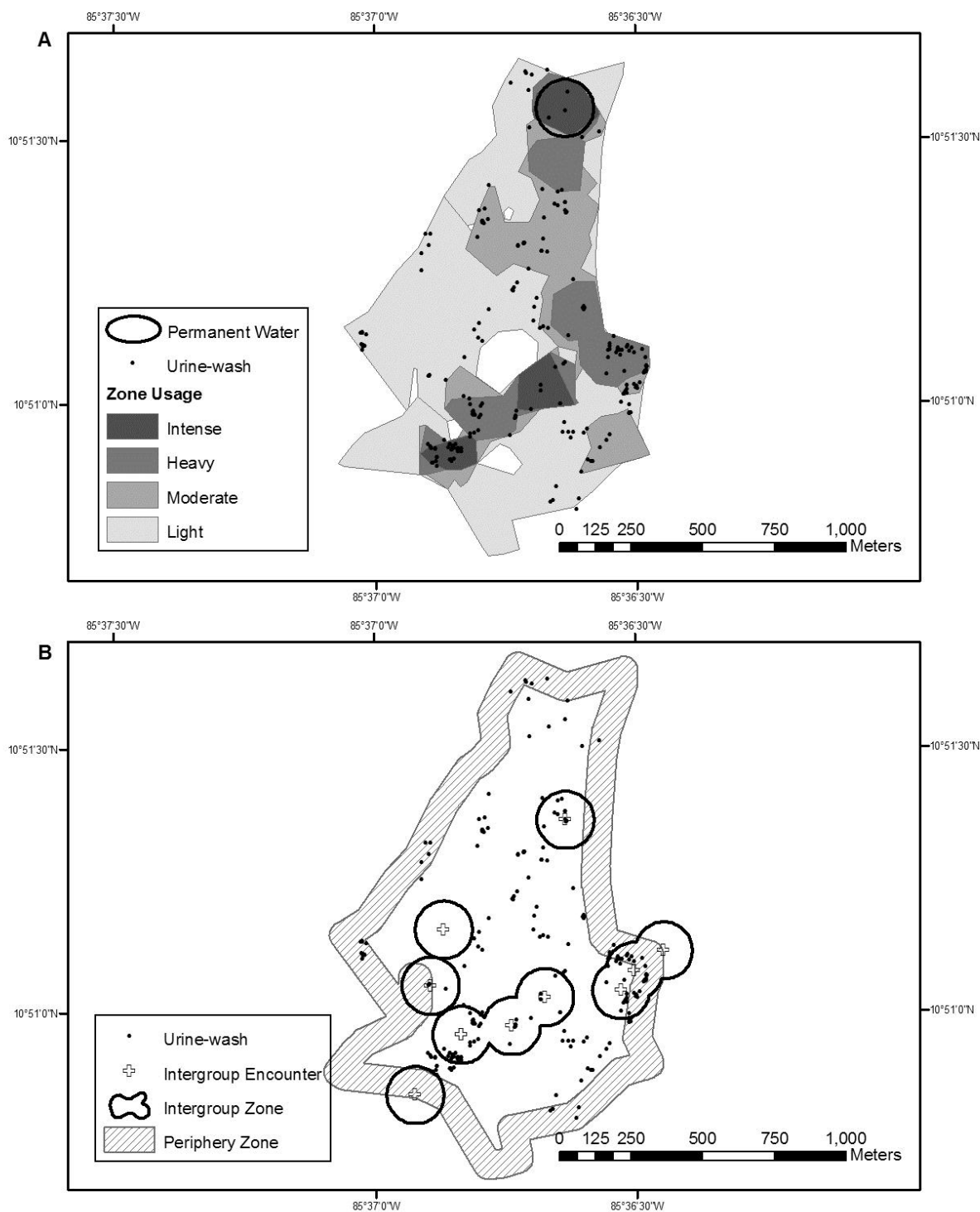
Figure 3.4. Spatial distribution of UW for LV group in the dry season in relation to (A) zone usage and permanent water, and (B) home-range periphery and intergroup encounters.
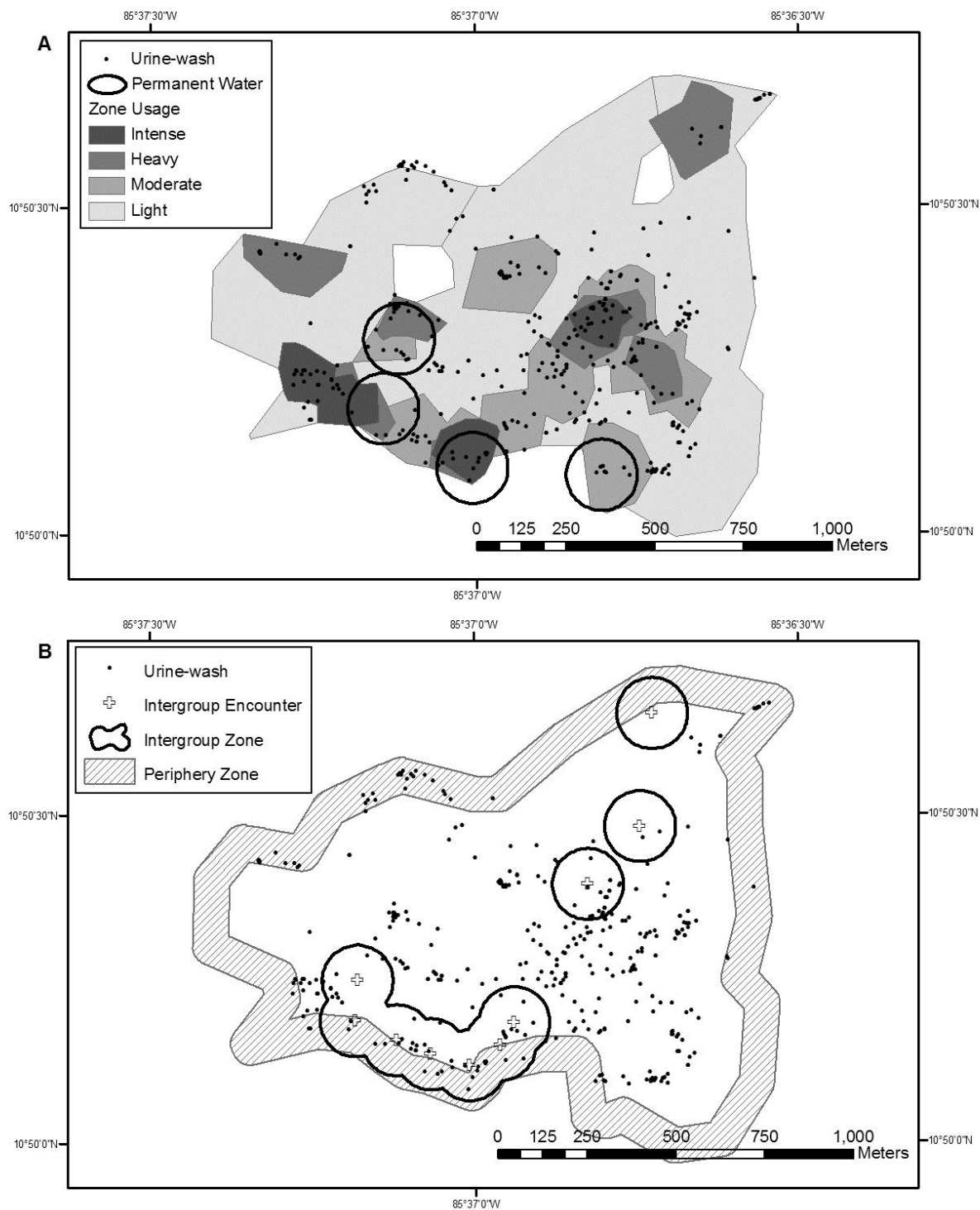
CHAPTER 4: FUNCTIONAL SIGNIFICANCE OF URINE-WASHING IN WHITE-FACED CAPUCHINS, PART 2: INDIVIDUAL VARIATION AND SOCIAL CONTEXT

Introduction

This study examines individual differences in the urine-washing (UW) behavior of wild white-faced capuchins (*Cebus capucinus*), and tests some functional hypotheses related to the social context for this behavior. UW is a behavioral sequence in which the animal urinates onto one forelimb and repeatedly rubs together the palmar and plantar surfaces of the ipsilateral fore and hind limbs (Oppenheimer, 1973). UW is common among platyrrhines (New World monkeys) and lorisiforms (lorises and galagos), and a large number of hypotheses, both social and non-social, have been put forward to explain this behavior (Appendix 1). Previous studies of UW in wild capuchins (Robinson, 1979; Perry, 1998; Carnegie et al., 2005; Campos et al., 2007) have produced no conclusive answers regarding its function(s), but there is general agreement that UW is most likely multifunctional and that one of its functions may be communication. Past research on captive capuchins suggested that UW may be used for thermoregulation (Roeder & Anderson, 1991), but a recent captive study with tufted capuchins (*Cebus apella*) found that UW is associated with receiving aggression and that alpha males urine-wash in response to sexual solicitations from females (Miller et al., 2007). This chapter examines the following three hypotheses about the function of UW that relate to individual variation and social context.

Displacement behavior hypothesis

Displacement activity consists of behavior patterns that are performed in abnormal contexts, possibly as a result of motivational conflict. The most common displacement behaviors

in nonhuman primates are associated with body care: scratching, self-grooming, shaking, stretching, and yawning (Troisi, 2002). Displacement behaviors often accompany stressful events, particularly those in which there is uncertainty about the risk of future harm to one's self or to a valuable relationship (Aureli, 1997; Troisi, 2002). For example, rates of scratching or other self-directed behaviors increase in unfamiliar pairs of long-tailed macaques (*Macaca fascicularis*) when the establishment of a clear dominance relationship is protracted (Schino et al., 1990). Furthermore, subordinate long-tailed macaques self-groom at higher rates when in close proximity to dominant individuals (Troisi & Schino, 1987). Rates of displacement behaviors also increase after both receiving (long-tailed macaque: Aureli et al., 1989; olive baboon, *Papio anubis*: Castles & Whiten, 1998) and directing aggression (Barbary macaque, *Macaca sylvanus*: Aureli, 1997; olive baboon: Castles & Whiten, 1998), and the relative amount of this increase depends on the relationship quality of the participants (Aureli, 1997).

The displacement behavior hypothesis for UW maintains that animals urine-wash either to relieve stress or simply as a nonfunctional "byproduct" during intense, stressful situations (common squirrel monkey, *Saimiri sciureus*: DuMond, 1968). Several studies have found a tendency for UW to occur often in conjunction with potentially stressful social contexts such as inter-group encounters (mantled howler monkey, *Alouatta palliata*: Milton, 1975; wedge-capped capuchin, *Cebus olivaceus*: Robinson, 1979), copulation or sexual excitement (common squirrel monkey: Latta et al., 1967; muriqui, *Brachyteles arachnoides*: Milton, 1985), and the presence of unfamiliar males (common squirrel monkey: Epple & Manson unpublished data, cited in Epple, 1974). Stressful nonsocial contexts may also elicit UW in some species. Wild Allen's bush babies (*Galago alleni*) may urine wash following a large tree fall or the arrival of a storm (Charles-Dominique, 1977) and Nekaris (2003) found that shining a white light at wild slender

lorises (*Loris tardigradus*) provoked UW accompanied by either freezing or fleeing. Finally, UW can be associated with agitation resulting from the sudden appearance of a human observer (common squirrel monkey: Latta et al., 1967; wedge-capped capuchin: Oppenheimer & Oppenheimer, 1973; white-fronted capuchin monkey, *Cebus albifrons*: Andrew & Klopman, 1974; mantled howler monkey: Milton, 1975).

Assertion of dominance hypothesis

Many mammals use olfactory signals to mediate competitive interactions. Mammalian scent marking behaviors are performed especially frequently by dominant animals that are intolerant of conspecifics, and in such situations scent marking may indicate a high likelihood of attack (Ralls, 1971). For example, saddleback tamarins (*Saguinus fuscicollis*) of both sexes use olfactory signals to assert dominance and demonstrate aggressive motivation. Aggressive interactions in this species are usually associated with increased rates of scent marking in dominant animals and decreased rates in subordinate animals; aggressive inter-group encounters are also accompanied by striking increases in marking rates (Epple et al., 1982). In some primate species, both urine and circumgenital secretions can encode information that individuals can use to discriminate between conspecifics on the basis of individual identity, sex, and social status (reviewed in Epple et al., 1982; Smith, 2006). For example, callitrichines express more olfactory interest in the scents of individuals who are dominant (saddleback tamarin: Epple, 1974), unfamiliar (common marmoset, *Callithrix jacchus*: Smith et al., 1997), or recent agonistic opponents (saddleback tamarin: Epple, 1974). Although such data are scant for capuchins, tufted

capuchins have the ability to distinguish familiar from unfamiliar individuals based only on chemical signatures present in urine (Ueno, 1994).

The assertion of dominance hypothesis posits that urine-washing is a way of communicating social dominance to conspecifics, and that it is functionally similar to scent marking behaviors used by many strepsirrhines (e.g. Pochron et al., 2005; Palagi et al., 2005) and callitrichines (e.g. Epple et al., 1982), as well as numerous carnivores, ungulates, and rodents (e.g. Ralls, 1971). Supporting evidence comes from studies of mantled howler monkeys (Milton, 1975) and wedge-capped capuchins (Robinson, 1979). In these species, UW rates may increase during inter-group encounters, but only among adult males. Several studies report that adult males urine wash at higher rates overall than other age or sex classes (mantled howler monkey: Milton, 1975; white-faced capuchin: Campos et al., 2007), and in particular the alpha male of a social group urine washes at a higher rate than any other group member (wedge-capped capuchin: Robinson, 1979; tufted capuchin: Roeder & Anderson, 1991; white-faced capuchin: Perry, 1998; Campos et al., 2007). The strongest evidence in favor of this hypothesis comes from Campos et al. (2007), who found that the trend for alpha males to urine-wash more than subordinates persisted across numerous rank reversals: formerly subordinate males increased their rates of UW upon achieving the alpha rank, and former alpha males decreased their rates of UW after falling in rank.

Sexual attraction

Olfactory communication of female reproductive status appears to be especially important for platyrrhines (Epple, 1974), which lack the conspicuous sexual swellings and

brightly colored sexual skins of many apes and Old World monkeys that serve as visual cues of

female reproductive status (Rowell, 1972). Male platyrrhines of many species frequently sniff or

lick the perineal regions, secretions, and urine of female conspecifics (common squirrel monkey:

Latta et al., 1967; Hennessy et al., 1978; red-backed squirrel monkey, *Saimiri oerstedii*: Boinski,

1992; common marmoset: Epple, 1974; black-handed spider monkey, *Ateles geoffroyi*, and

white-bellied spider monkey, *Ateles belzebuth*: Klein, 1971; muriqui: Milton, 1985; white-faced

capuchin: Manson et al., 1997), a practice which may increase during mating periods (Hennessy

et al., 1978; Boinski, 1992) and precede copulation (Epple, 1974). These behavioral patterns

suggest that male platyrrhines use olfactory cues to monitor the reproductive status of females.

Less is known about the role that olfaction might play in inter-sexual communication in the

opposite direction; that is, if female primates can use olfactory cues to judge male quality.

Data relating patterns of sexual activity to UW are inconsistent. Although Robinson

(wedge-capped capuchin: 1979) and Latta (common squirrel monkey: 1967) report that females

increase their UW rates when "receptive", Carnegie (2005) found that female white-faced

capuchin monkeys exhibit lower UW rates when periovulatory. Similarly, female southern lesser

bush babies urine wash at significantly lower rates during "behavioral estrus" (Lipschitz et al.,

2001). Furthermore, Milton (1985) reports that while 67% of male urine washes in a wild group

of muriquis occurred during sexual excitement, female UW did not seem related to sexual

contexts. Hennessey (1978) found no significant difference in UW rates in male or female

captive common squirrel monkeys in relation to the mating season. Finally, the alpha male in a

captive group of tufted capuchins doubled his rate of UW during sexual solicitations by females

(Miller et al., 2007). These apparent discrepancies might be due to inter-species differences,

imprecise measures of reproductive status, small sample sizes, different or unsystematic sampling regimes, or a genuine lack of correspondence between UW and sexual contexts.

The objective of this study is to test predictions generated by each of the three hypotheses described above. Table 4.1 lists the hypotheses and summarizes the specific predictions that were examined.

Methods

Study site

Santa Rosa National Park (SRNP) is located on the Pacific coast of northwestern Costa Rica and lies adjacent to three other nationally protected areas that, collectively, form the 147,000 hectare Area de Conservación Guanacaste. SRNP encompasses 49,515 hectares of mosaic habitat dominated by highly seasonal dry deciduous forest (Fedigan et al., 1996; Fedigan & Jack, 2001). This region of Costa Rica experiences a dry season from mid-December to mid-May, and a rainy season from late-May to early-December.

Study groups and subjects

My sample consisted of four social groups of white-faced capuchins (BH, CP, EX, and LV). The groups were well-habituated to human observers, and all individuals were individually recognized on the basis of distinctive facial and body features. Focal subjects included all

sexually mature individuals. Female white-faced capuchins typically begin reproducing at age 6, at which point they appear socially equivalent to older females. However, male white-faced capuchins reach sexual maturity before they attain the robust body size and high social status associated with complete physical maturity (Fedigan et al., 1996). Thus, my sample was comprised of individuals belonging to three distinct age/sex categories: subadult males (6-10 years), adult males (>10 years), and adult females (> 5 years) (Fedigan et al., 1996).

Data collection

This study is based on 940 total observation hours collected in two separate field seasons. The first data collection period (370 hours) included 2.5 early wet season months from mid-May 2006 until the end of July 2006. The second data collection period (570 hours) lasted from the beginning of January 2007 until the end of April 2007 and included the four hottest, driest months of the dry season. BH group was not observed in the dry season months. Typically, a single group was followed from sunrise to sunset whenever possible (approximately 5:00 to 18:00 hours), although collection days of shorter length occurred frequently. Most of the analyses presented here pertain to the dry season months of January – April because of the enormous disparity in UW frequency between wet and dry seasons (see Chapter 3 of this thesis). Two major data-collection procedures were utilized: focal animal samples (Altmann, 1974), and urine-wash scans. These methods are described in detail below.

Focal animal samples

During focal animal samples (Altmann, 1974), a single individual was followed by two trained observers for two hours (dry season) or four hours (wet season) continuously. I chose to carry out lengthy follows to ensure that the complete social and environmental context would be captured for the majority of observed urine-washes. Adult females were not followed in the wet season because UW by females during this time was extremely rare (see results). Observers recorded all self-directed behaviors and social interactions involving the focal animal. Instantaneous samples were recorded every 2.5 minutes throughout the entire focal sample, at which time the focal animal's state behavior and proximity to all conspecifics within contact, 1-m, and 5-m were recorded. I collected a total of 395.5-hr of focal animal samples.

Urine-wash scans

Whenever UW was observed, the following information was recorded immediately: identity of urine-washer, location, ambient temperature, relative humidity, last state behavior immediately before UW, first state behavior immediately after UW, and the identities of all individuals in contact, 1-m, and 5-m proximity categories.

Data analysis

Individual differences

I calculated individual UW rates from focal data only, dividing the number of urine washes performed by the number of hours during which that individual was a focal subject.

Rates were calculated separately for wet and dry seasons because of the major difference in UW frequencies between seasons (see Chapter 3 of this thesis).

Dominance

Dominance scores were calculated from avoid, cower, flee, and supplant interactions between dyads. I used only interactions between adult and subadult animals for whom a dominance score was calculated (i.e. dominance interactions with juveniles were ignored). Dominance rank order among male white-faced capuchin monkeys can be difficult to determine below the alpha position (Perry 1998; Fragaszy et al. 2004). Although Fedigan (1993) was able to determine a linear dominance hierarchy among the males of one group at Santa Rosa, undecided bouts of agonism were relatively common and several decided bouts represented dominance reversals. In light of these issues, I used the method of probabilistic dominance ranks that Jameson et al. (1999) developed from the Batchelder-Bershad-Simpson model of dynamic paired-comparison scaling (Batchelder et al. 1992). This method takes into account the number of agonistic encounters won and lost, and the scaled values of each opponent encountered. Thus, a score can be calculated for every individual even if some dyads do not interact directly. The relationship between dry season UW rates and dominance was evaluated using Spearman's coefficient of rank correlation.

Proximity

I used instantaneous samples during focal follows to calculate, for each individual, the proportion of time in which at least one conspecific of a given age/sex category was within 5 meters. These values are referred to as "baseline proximity." The age/sex categories examined in this analysis were adult male, adult female, subadult male, juvenile, and infant. The first three categories are defined above; infants are less than two years old while juveniles are 2-5 years old. An additional category included alpha males to address Miller et al.'s (2007, p. 9) suggestion that "the alpha male may stimulate a UW reaction" in captive tufted capuchins. I compared baseline proximity to proximity scores drawn from urine-wash scans using the same age/sex categories. Within-subject differences between the two conditions (baseline and urine-wash) were compared with Wilcoxon tests. This analysis was carried out using dry-season data only, as there were too few urine-washes in the wet season for statistically valid proximity comparisons.

Social context of UW

I examined the association between UW and various social contexts by posing the question: did UW occur significantly more frequently within 2.5 minutes of a particular type of social interaction than expected for a randomly distributed behavior? The following categories of social interaction were considered: affiliation, conspecific aggression, display, fear, observer-directed aggression, olfactory behavior, and sexual behavior. For each of these categories (except observer-directed aggression), I examined focal-directed behavior separately from focal-received behavior. These thirteen conditions are referred to hereafter as "social contexts." Time intervals ("bouts") were the units of analysis for each social context. Bouts were centered on the

beginning of any behavior grouped within the given social context (Appendix 2). I considered

two within-context interactions as different bouts if they were separated by at least 2.5 minutes

with no within-context behavior. Thus, bouts were typically exactly 5 minutes long,

encompassing 2.5 minutes before and after the interaction, but were occasionally longer if the

behavior continued for longer than 2.5 minutes. Bouts were discarded if the focal animal was

ever out of sight. I used bootstrapping techniques to compare, for each focal subject and each

social context, the frequency of UW during bouts with simulated randomly occurring events. For

an individual X with N total urine-washes during X's focal samples, N events were placed at

random in X's follows during each simulation; I then counted the number of randomly placed

events that happened to fall within one of X's bouts. Each second during which X was being

followed had an equal probability of being selected as a random event. I repeated this simulation

10,000 times for each individual / social context combination and took the counts occupying the

highest and lowest 2.5% and 0.5% positions after sorting as limits to 95% and 99% confidence

intervals, respectively. If the actual number of urine-washes that an individual performed during

bouts of a particular social context exceeds the upper limit of his or her 95% bootstrap

confidence interval, then the context and UW can be considered significantly positively

associated at $\alpha=0.05$ for that individual. This analysis was carried out for both wet and dry

season months.

I performed these simulations to bring rigor to the contextual analysis for UW. Previous

studies that have attempted to examine the social context of UW in capuchins (e.g. Robinson,

1979; Roeder & Anderson, 1991; Campos et al., 2007; Miller et al., 2007) have reported raw

counts or proportions of urine-washes that occurred within a given time interval of specific kinds

of interactions. This kind of analysis is interesting but qualitative; it lacks any basis for

separating UW from a randomly occurring behavior statistically. One drawback to the bootstrapping analysis is that it produces a multiple-comparisons problem; the probability of committing a Type I error (false significant result) increases as the number of significant results increases. Thus I have also included confidence limits based on a more stringent significance level ($\alpha=0.01$), and I interpret significant results based on few urine-washes with caution.

Results

Qualitative differences in UW behavior

The appearance of UW was clearly different in some cases. The great majority of urine-washes by all individuals in the dry season had the following characteristics: (1) small volume of urine released; (2) few languid, unfocused washing motions; and (3) no clear social or environmental context. By contrast, almost all urine-washes in the wet season and a few urine-washes in the dry season were characterized by (1) greater volume of urine splashed onto the body and tail; (2) vigorous, exaggerated washing motions repeated several times; and (3) the presence of juveniles or subordinate individuals following the urine-washing animal while emitting the "gargle" vocalization (Gros-Louis et al., in press; synonym: "guttural chatter" Oppenheimer, 1973) and often sniffing the deposited urine. Urine-washes of the latter type were performed almost exclusively by alpha males.

Individual differences and dominance

Dominance scores were not significantly correlated with individual UW rates for any of the three social groups in the dry season (Table 4.2). In the dry season months, there was no difference in UW rates among the three age/sex classes (Kruskal-Wallis test, df = 2, χ^2 = 1.382, p = 0.501) or between sexes, ignoring the age distinction between adult and subadult males (Mann-Whitney U test, N_{male} = 11, N_{female} = 14, U = 60, p = 0. 352). There were significant between-group differences in UW rates, and post-hoc testing revealed that the sole significant difference existed between CP and LV groups (Table 4.3). Overall, individual UW rates were greater in CP group than in LV group. The alpha male exhibited the highest rate of UW in LV group, but not in CP or EX groups (Table 4.2).

In the wet season months, the extremely low frequency of UW (see Chapter 3 of this thesis) and my focus on adult males made statistical testing of age and sex differences impossible. However, there were obvious differences between individuals. The majority of urine-washes in the wet season were performed by alpha males (29/42 total urine-washes, *ad libitum* included; 16/18 urine-washes during focal samples). It was rare to observe UW by females (4/42 urine-washes) or juveniles of either sex (2/42 urine-washes) in the wet season.

Proximity

Compared to baseline proximity, individuals of every age/sex category were less likely to be within 5 meters of an animal engaging in UW (Table 4.4, figure 4.1). Correspondingly, an animal washing with urine was more likely to be alone, with no conspecific animals within 5 meters (Table 4.4, figure 4.1). This pattern held true whether the animal engaging in UW was an adult male, an adult female, or a subadult male (Table 4.4).

Social context

The results of the social context analysis are presented in complete form in Appendices 4.1 (dry season) and 4.2 (wet season). Overall, there were very few significant associations between UW and any social context. In the dry season, one adult female (TT) engaged in UW in significant association with directing affiliation, receiving conspecific aggression, and directing aggression at the observer. The latter two associations are highly suspect because they are based on a single urine-wash in each case. In the dry season, the alpha male of LV group (CY) urine-washed in significant association with receiving olfactory behavior and directing sexual behavior, and the alpha male of CP group (NN) urine-washed in significant association with both receiving and directing sexual behavior. No other associations were significant for any individual in the dry season. In the wet season, the alpha male of LV group (CC, before his replacement by CY) urine-washed in significant association with receiving olfactory behavior and directing aggression at the observer. No other social contexts were significantly associated with UW for any individual in the wet season.

UW and the "gargle" vocalization

As noted above, UW by alpha males occasionally appeared to be solicited. Typically, a subordinate individual—often an infant, but sometimes an adult female—would approach while making "gargle" vocalizations. The alpha male would then urine-wash, and the approaching individual sometimes sniffed the deposited urine or continued gargling. Gargles are produced by infants, juveniles, and adult females and are directed primarily at alpha males, although infants

frequently gargle at subordinate adult males as well (Gros-Louis et al., in press). Oppenheimer (1973, p. 256) describes the social context for gargling as "tense encounter[s]" and proposes that gargles express the subordinate's recognition of another animal's dominance. Gros-Louis et al. (in press, p. 10) suggest that gargles are given in affiliative contexts, but also note that "garglers often exhibit signs of emotional arousal, such as penile/clitoral erection, piloerection, head-shaking, scratching, squirming, and grimacing". Recipients of gargles may ignore the gargling animal or respond with mild annoyance (e.g. swatting), but neither study mentions urine-washing as a possible response to gargles.

I explored the relationship between UW and gargling in more detail using a post-hoc bootstrapping analysis identical to that described for social contexts, with "gargle bouts" centered on the first received gargle of a bout. I suggest that such time intervals are an appropriate unit of analysis for gargles because unlike many vocalizations, gargles tend to be given in bouts that can last for several minutes (personal observation; Gros-Louis et al., in press). The bootstrapping techniques revealed a highly significant ($p < 0.01$) positive association between UW and bouts of received gargles for alpha males NN and CC in the wet season (Appendix 4.2). The association was not significant for any alpha male in the dry season.

Discussion

UW during the dry season seems unrelated to any social context for most individuals

The broad conclusion that can be drawn from this study is that individual differences and social context had very little or no consistent effect on the frequency of UW for most individuals during the dry season. Alpha males may be an exception however (see below), and the remainder

of this section pertains only to subordinates. None of the three hypotheses for UW listed in Table 4.1 was supported by my results from the dry season, and in fact not a single prediction for any hypothesis was born out. I therefore conclude that—in the dry season at least—UW is not a displacement behavior, nor is it used to communicate dominance or sexual attraction to conspecifics.

The displacement behavior hypothesis can be rejected because UW did not occur more frequently in situations of high emotional arousal or when high-ranking individuals were in close proximity. Moreover, the displacement behavior hypothesis is incompatible with the remarkable seasonal difference in UW frequencies. There is no reason why a displacement behavior should be any less useful in the wet season. A recent related hypothesis, supported by the work of Miller et al. (2007) with captive tufted capuchins, proposes that UW among subordinates is a response to received aggression which functions either to relieve stress or to appease the attacker. I found no support for this hypothesis. Only 3 of 787 (0.38%) urine-washes by focal animals in the dry season occurred within 2.5 minutes of a bout of received aggression (n = 44) in over 315 focal follow hours (Appendix 4.1). This discrepancy suggests either that (1) UW has different functions in tufted and white-faced capuchins; and/or (2) captivity eliminates the primary functional value of UW for capuchins, who may then co-opt the behavior for different purposes. The latter suggestion is supported by the fact that no other study of UW in capuchins—wild or captive—has found unequivocal support for the appeasement or stress-relief hypotheses.

Individual frequencies of UW (Table 4.2, Appendix 3) should be enough to dispense with the dominance hypothesis outright. If juveniles and low-ranking individuals engage regularly in UW—and at frequencies that are not statistically distinguishable from those of high ranking adults—it seems very unlikely that UW by capuchins is a scent-marking behavior analogous to

those observed in many strepsirrhines, callitrichines, and various other mammals. One of the hallmarks of scent-marking throughout the mammalian class is that the individuals who mark most frequently are usually the most dominant. My focus on sexually mature individuals surely biases UW frequencies against immature capuchins, but even a cursory glance at Appendix 3 makes it clear that juvenile capuchins urine-wash regularly in the dry season. It was, in fact, exceedingly rare to see any capuchin urinate in the dry season *without* washing. The ubiquity of UW behavior across age and sex classes, the lack of any association between UW and aggressive contexts, and the lack of a correlation between dominance scores and UW rates all argue strongly against the dominance hypothesis for UW. The sexual attraction hypothesis can be rejected on similar grounds for subordinate animals but not for alpha males (see below). Very little can be said about UW by subordinate capuchins at SRNP in the wet season because they simply do not urine-wash with any regularity during this period.

Is a separate, social signaling function for UW for alpha males "revealed" in the wet season?

If a lesser social function for UW exists for wild white-faced capuchins, it might be masked in the dry season by a non-social function that becomes overwhelmingly primary in very dry conditions. It appears that something about the wet season—perhaps some combination of higher relative humidity, lower temperatures, frequent rain showers, more dense foliage, and cloudier conditions on average—eliminates the need or usefulness of UW for most capuchins. It is therefore extremely interesting that two of three alpha males continued to urine-wash in the wet season at rates that were relatively high, albeit greatly reduced from the dry season (Appendix 3; subordinate male SM is also listed with a relatively high rate in the wet season, but

this is misleading because he was followed very infrequently and his "rate" is based on a single urine-wash). It is therefore worth examining alpha males separately to see if there are any consistencies among the social contexts in which they were observed to engage in UW. In addition to their social dominance, alpha male white-faced capuchins differ from the other adult males in the group in a number of important ways. First, they father the majority of infants (Jack & Fedigan, 2006), especially those born to females who are not the alpha male's daughter (Muniz et al., 2006). Second, a preliminary study suggests that alpha male capuchins at SRNP have significantly higher testosterone levels than subordinate males (Jacks & Schoof, unpublished data). Third, alpha males tend to be the most spatially central adult male in the social group; subordinate males often wander around the group periphery and leave periodically (personal observation). Finally, adult females direct gargle vocalizations at the alpha male exclusively (Gros-Louis et al., in press).

For alpha males NN and CY (but no other individuals), the positive association between UW and sexual contexts was non-random with 95% confidence in the dry season but not the wet season. This result agrees somewhat with Miller et al. (2007, p. 6), who report that in their captive colony of tufted capuchins, "the alpha male urine-washed 11 times on the 5 days in which he was solicited by females," more than doubling his UW rate "during solicitations." The precise temporal span to which their term "during solicitations" refers is unclear, but it seems considerably different from the 2.5 minute limit that I have used. The methodological difference does not invalidate the comparison, however; a longer time span for tufted capuchins may be appropriate. Female tufted capuchins are extraordinarily proceptive and their sexual solicitations to adult males may persist for days (reviewed in Fragaszy et al., 2004). By contrast, proceptive behavior in white-faced capuchins consists of brief but bizarre "courtship dances" that include

wheezing, reciprocal pacing, and pirouettes, all given with "duck-face" expressions in which the face is wrinkled with pursed lips (Manson et al., 1997; Fragaszy et al., 2004). In sum, the evidence is suggestive but not conclusive that alpha male white-faced and tufted capuchins may use UW during sexual behavior.

Alpha males CC in the wet season and CY in the dry season both engaged in UW significantly more frequently in association with receiving olfactory behavior, mostly in the form of subordinates sniffing the deposited urine. This observation does not inform our understanding of the conditions that led to UW by the male, but does corroborate other research showing that capuchins express olfactory interest in the urine of conspecifics (Robinson, 1979; Ueno, 1994; Lynch 2001, cited in Fragaszy et al., 2004; Carnegie et al., 2005; Campos et al., 2007).

Perhaps most intriguing is the suggestion that subordinate animals may solicit UW from alpha males by gargling at them. My analysis revealed that there was a highly significant positive association between UW and received gargles during the wet season for two alpha males. After several of these urine-washes, the gargling animal sniffed the deposited urine. Alpha males were the most frequent recipients of urine sniffs in all groups in all seasons (Table 4.5). What might a subordinate capuchin gain from sniffing the alpha male's urine? This study is inadequate for answering this question, but perhaps the contexts in which gargles are given might offer some direction for future research. Gargles are among the very first vocalizations that capuchins produce; Gros-Louis et al. (in press) report that capuchins as young as 15 days old may gargle at adult males. Infant capuchins typically appear strongly affected by nervous excitement when they gargle. Females gargle less frequently, but in the weeks immediately after the birth of a new infant, the mother's rate of gargling often increases dramatically (personal observation). Finally, rates of gargling appear to spike immediately after periodic aggressive take-overs in which

resident males are evicted and replaced by one or more immigrant males (personal observation).

The common thread among these contexts is the formation of a new relationship between an

infant and an alpha male. Therefore, one possibility is that subordinates solicit UW from alpha

males to gain access to an olfactory signal that can be used to familiarize themselves and/or their

infants with the current alpha male. A number of platyrrhines can distinguish between

individuals from their odors (reviewed in Epple et al., 1982; Smith, 2006), and capuchins can

discriminate at least between familiar and unfamiliar individuals based on urine scents alone

(Ueno, 1994). Individual olfactory signatures may be more salient to infants and/or more

invariant over long time scales compared to visual characteristics (e.g. facial features). Perhaps

the males urine-wash to reassure subordinates, or simply to satisfy the soliciting animal and thus

put an end to the irritation of being subjected to repeated gargles. The relationship between UW

and gargles that I have proposed remains highly speculative, and there is a clear need for further

study. I suggest playback experiments in which gargle vocalizations are broadcast to alpha males

to explore this possibility further.

Summary

Urine-washing by capuchins at SRNP is not clearly related to any social context. Among

subordinate animals I found no support for the hypotheses that UW is a displacement behavior,

an assertion of dominance, or a sexual attractant. UW rates in the dry season were not

significantly different among animals of different age or sex, nor were UW rates correlated with

dominance. No particular age/sex classes elicited increased frequencies of UW; on the contrary

UW was more frequent when no conspecifics were within 5 meters of the washing animal. Thus,

the results of this study argue strongly against a social function for most instances of UW during the dry season. I found some support for the idea that alpha males may use UW in social contexts, albeit infrequently. Two of three alpha males in the dry season urine-washed in significant positive association with sexual contexts, while two of three alpha males in the wet season urine-washed in significant positive association with receiving "gargle" vocalizations by conspecifics. Further study is needed to verify the validity and generality of these associations.

Table 4.1. Hypotheses for urine-washing and predictions tested in this study.

Hypothesis	Predictions
Displacement behavior	1 UW will be more likely to occur during and immediately after stressful situations, especially directing and receiving aggression.
	2 UW will be more likely to occur in proximity of dominant individuals.
	3 There will be no seasonal difference in UW frequency.
Assertion of dominance	1 Individual mean UW rates will be positively correlated with dominance rank.
	2 UW will be more likely to occur in proximity of subordinate individuals.
	3 UW will be more likely to occur during and immediately after directing, but not receiving, aggression.
	4 Seasonal differences in UW frequency, if present, will be slight.
Sexual attraction	1 UW will be more likely to occur in sexual contexts.
	2 UW will be more likely to occur in proximity of opposite-sex individuals.
	3 Seasonal differences in UW frequency, if present, will be slight.

Table 4.2. Spearman coefficient of rank correlation of dry season UW rates vs. dominance score.

Group	r_s	p (two-tailed)	Monkey	Age / Sex	Dominance Score	UW Rate (UW/hr)
CP	0.118	0.729	NN	AM	2.108	3.374
			LL	AM	0.907	2.560
			RR	AM	0.580	2.791
			SI	AF	0.359	3.666
			MO	SAM	0.023	4.553
			SA	AF	-0.767	3.952
			ED	AF	-1.040	2.224
			TT	AF	-1.063	3.299
			SS	AF	-1.482	3.168
			ZZ	AF	-1.593	3.157
			BH	SAM	-2.167	2.915
EX	0.500	0.391	AT	AM	1.527	3.042
			EL	AF	0.609	1.534
			AR	AM	0.230	3.082
			CL	AF	-0.675	2.990
			AN	AF	-1.411	0.724
LV	0.617	0.077	CY	AM	1.509	3.011
			WW	SAM	1.287	1.875
			KL	AF	1.066	2.389
			MZ	SAM	0.851	1.470
			DL	AF	0.623	0.960
			SL	AF	-0.133	2.228
			NU	SAM	-0.379	2.984
			CH	AF	-1.388	0.719
			BB	AF	-1.509	0.527

Boxed cells indicate alpha males.

Table 4.3. Tests of between-group differences in mean individual UW rates in the dry season.

		Kruskal-Wallis test				Post-hoc Mann-Whitney U tests		
Group	N	Median UW rate	df	χ^2	p (two-tailed)	Comparison	U	p (two-tailed)
CP	11	3.168	2	10.135	0.006 **	CP-EX	12	0.079
EX	5	2.990				CP-LV	10	0.003 **
LV	9	1.875				LV-EX	13	0.205

** significant at $\alpha = 0.01$.

Table 4.4. Comparison of baseline proximity to proximity during UW.

| UW animal | N | Condition | # Samples | Individual in proximity (mean proportion of samples) | | | | | | |
				None	AF	AM	SAM	JUV	INF	α-male
All	25	Urine-wash	1157	0.563	0.194	0.122	0.133	0.124	0.254	0.084
		Baseline	7540	0.421	0.308	0.193	0.181	0.255	0.370	0.138
		Difference		0.142	-0.114	-0.072	-0.048	-0.131	-0.116	-0.054
AF	14	Urine-wash	497	0.576	0.137	0.119	0.118	0.126	0.280	0.076
		Baseline	4261	0.383	0.280	0.203	0.163	0.274	0.448	0.143
		Difference		0.193	-0.144	-0.084	-0.045	-0.148	-0.169	-0.067
AM	6	Urine-wash	373	0.592	0.222	0.106	0.133	0.112	0.169	0.057
		Baseline	1813	0.525	0.324	0.206	0.207	0.199	0.242	0.099
		Difference		0.068	-0.102	-0.100	-0.074	-0.087	-0.073	-0.041
SAM	5	Urine-wash	287	0.491	0.319	0.147	0.167	0.135	0.284	0.088
		Baseline	1466	0.401	0.364	0.154	0.199	0.270	0.307	0.089
		Difference		0.089	-0.045	-0.007	-0.032	-0.135	-0.022	-0.001

Table 4.5. Received urine sniffs in wet and dry seasons. Individuals not listed in this table were not observed to receive any urine sniffs.

Season	Group	Recipient [a]	Received Urine Sniffs
Dry	CP	NN	10
	CP	LL	2
	CP	SS	2
	CP	TT	2
	CP	BH	1
	CP	ED	1
	EX	AT	2
	EX	AN	1
	EX	EL	1
	LV	CY	5
	LV	CH	3
	LV	KL	2
	LV	DL	1
	LV	NU	1
Wet	BH	GO	1
	CP	NN	3
	CP	BH	1
	CP	LL	1
	CP	SI	1
	LV	CC	7
	LV	BB	2

[a] Boxed cells indicate alpha males.

Figure 4.1. Comparison of proximity patterns (averaged across all individuals) under baseline and urine-wash conditions.
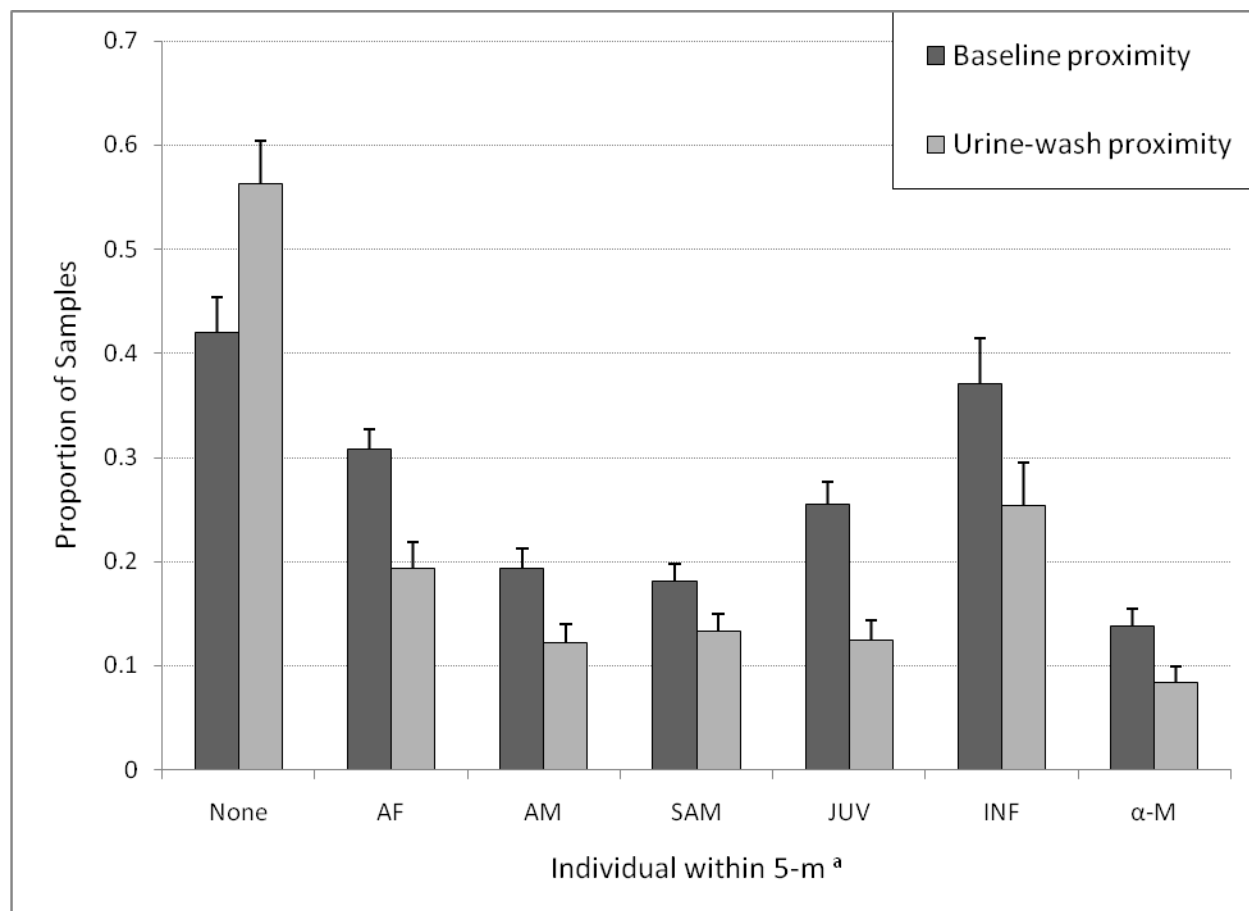
[a] AF = adult female; AM = adult male; SAM = subadult male; JUV = juvenile; INF = infant; α-M = alpha male

CHAPTER 5: GENERAL DISCUSSION AND SYNTHESIS

Behavioral Thermoregulation and Heat-Stress Avoidance in Wild Capuchins

White-faced capuchins at Santa Rosa National Park (SRNP) employ a variety of strategies—both active and passive—to cope with hot, dry conditions. In Chapter 2 of this thesis, I investigated whether capuchins at SRNP (1) avoid physical exertion in the heat, (2) engage in behaviors to lower body temperature via evaporative heat loss, and (3) shift their ranging patterns when water becomes scarce. I found that capuchins travel shorter distances, rest more, and travel and forage less during the hottest and driest hours of the day. These tendencies reveal a pattern in which energetically costly activities are minimized when there is a high potential of overheating, and I propose that water conservation is an important underlying principle. At high temperatures, evaporative heat loss becomes the primary mechanism upon which capuchins rely to maintain a stable body temperature (Elizondo, 1977). Because evaporative heat loss requires the loss of moisture, by avoiding overexertion at high ambient temperatures capuchins are also minimizing water loss. Well-known physiological mechanisms for evaporative heat loss include sweating and panting, but these processes were impossible for me to monitor in wild animals. However, the capuchins at SRNP regularly engaged in a behavior that was probably functionally similar—extending the tongue. The tongue-out behavior occurred in significantly hotter and drier conditions than one would expect if its occurrence were randomly distributed. Ranging patterns provide further evidence that water conservation is a major concern to capuchins in the dry season. As water becomes scarce, home range areas of heavy use become centered on remaining permanent water sources, and some peripheral areas expand to include additional water sources.

Overall, it was clear that during the dry season, both temperature and the location of water were major influences on the capuchins' behavior.

Urine-Washing by Capuchins at SRNP

Why is there such a large seasonal difference in urine-washing frequency?

The most important factor affecting urine-washing (UW) behavior among the capuchins of SRNP appears to be season. My research makes obvious that *something* about the dry season at SRNP promotes UW to such an extent that its frequency increases by approximately an order of magnitude from wet to dry seasons. What could be causing this difference? The weather trends that I report in Chapter 2 lay down an important foundation for interpreting the hypotheses tested in Chapters 3 and 4. Temperatures in the dry season were not uniformly hotter than in the wet season across all hours of the day; in fact, mean daily minimum temperatures were approximately equal in the two seasons. However, mean daily maximum temperatures were higher in the dry season. Thus, temperature was more *variable* in dry season, with equal lows and greater highs than the more moderate wet season. If the increase in heat stress that the capuchins experienced during the hot hours of a typical dry season day were enough to cause the large seasonal difference, then one would expect UW frequency to track temperature closely, with more urine-washes occurring at relatively high temperatures. This was not the case in my study—UW did not occur at temperatures that were significantly different from baseline. Interestingly, UW in the dry season did occur at significantly lower relative humidity compared to baseline. This suggests that the dryness (low humidity and lack of rain) rather than the heat of

the dry season may have been primarily responsible for the seasonal difference in UW

frequency.

Evaluating the hypotheses

Table 5.1 summarizes the hypotheses, predictions, and results of Chapters 3 and 4

regarding the functional significance of UW. Not a single prediction was supported for two of

the hypotheses: displacement behavior and assertion of dominance. Therefore, I reject these

hypotheses and will not discuss them further. Although 2 of 3 predictions associated with the

thermoregulation hypothesis were met, the fundamental prediction was not. For this reason and

others discussed in the previous paragraph, I reject this hypothesis as well. The sexual attraction

hypothesis was supported for 2 of 3 alpha males in the dry season, but not for any other

individuals. Sexual behavior among male white-faced capuchins is not restricted to alphas nor to

the dry season (Manson et al., 1997), and most urine-washes—even by alpha males—occurred

outside of sexual contexts. Therefore, sexual attraction may be a valid minor function for UW by

alpha males, but it cannot explain the high frequency of UW among subordinate capuchins.

There was weak evidence in favor of the marking home range hypothesis, but overall I conclude

that these results were probably due to confounding variables for which I was unable to control.

Cautious support was also found for the neutralization hypothesis. A very small proportion of

urine-washes occurred in *Acacia* foraging contexts; nevertheless, a significant positive

association was found between *Acacia* foraging and UW for three individuals. Therefore,

neutralizing ant stings may be another minor function for UW, practiced by only a few

individuals. Strongest support was found for the hypothesis that capuchins urine-wash to moisten

their hands for better grip. UW was most frequent in traveling contexts and when relative humidity was low. Two of my results provide additional indirect evidence that UW is used primarily during travel. First, UW was disproportionately frequent in home-range zones of light use, which are likely to be areas through which the capuchins travel quickly. Second, 56.3% of UW in the dry season (mean percentage across individuals) occurred with no conspecifics within 5 meters; this is a significant increase from baseline, as capuchins spent on average only 42.1% of their time alone. Traveling animals are probably less likely to be in close proximity to conspecifics than animals engaged in other kinds of behavior (with the possible exception of foraging). In sum, there is a variety of indirect evidence that the primary function of UW in wild capuchins at SRNP is nonsocial and possibly related to improving grip during travel. Additional studies of positional behavior and substrate use are needed to investigate this possibility further.

Urine-Washing in Capuchins: A Synthesis of Available Evidence

Almost every study of UW in capuchins (and primates in general) concludes with the same ambiguity. Often a particular hypothesis is favored, but overall the significance of the behavior remains controversial. This has led to a very confusing and contradictory body of knowledge. In this section, I intend to synthesize what is currently known about UW in capuchins by relating the results of this study to those previously published.

Comparison with previous studies

The results of chapters 3 and 4 differ from previous studies in a number of important ways. Dry season rates of UW reported here (2.5/h) are considerably higher than rates reported elsewhere, especially for a study of wild animals (Robinson, 1979 [wild]: overall 0.16/h, dry season 0.94/h; Campos et al., 2007 [wild]: males 0.38/h, females 0.05/h; Roeder & Anderson, 1991 [captive]: 2.2/h; Miller et al., 2007 [captive]: 0.5/h). In addition, the capuchins at SRNP are anomalous in that they exhibit no consistent differences in UW rates between individuals of different age or sex classes. Other studies of UW in capuchins, both wild and captive, have found that males urine-wash at significantly higher rates than females (Campos et al., 2007; Miller et al., 2007; but see Robinson, 1979; Roeder & Anderson, 1991), and alpha males in particular urine-wash at higher rates than every other group member (Robinson, 1979; Roeder & Anderson, 1991; Perry, 1998; Campos et al., 2007; Miller et al., 2007). Qualitative observations support this pattern among the capuchins of SRNP during the wet season, but during the dry season UW rates were not significantly different among individuals of different age, sex, or dominance status.

Because the "primary" function of UW in the dry season at SRNP appears to be a response to the dry environment, the discrepancies that have plagued studies of UW might be due to the different conditions in which the studies were carried out. Under moderate conditions (e.g. captivity), the functions that were "minor" or less-frequent at SRNP may become primary. I suggest that the key difference that distinguishes the capuchins at SRNP from those in the studies listed above is the severity of the dry season at this study site. The studies by Roeder & Anderson (1991) and Miller et al. (2007) used captive capuchins, for whom water was available *ad libitum* and environmental conditions were both mild and carefully regulated. Although there are pronounced wet and dry seasons in the llanos region of Venezuela in which Robinson (1979) carried out his study, the capuchins there utilized gallery forest bordering a large river and were

therefore probably not as strongly affected by water scarcity. The studies by Perry (1998) and Campos et al. (2007) were carried out in Lomas Barbudal, Costa Rica, which is a biological reserve relatively close to SRNP with a very similar climate. However, an extensive network of spring-fed streams run throughout Lomas Barbudal, fostering mature gallery forest and providing cool, fresh water for the capuchins to drink and bathe in throughout the year. SRNP appears to be a much drier environment, and none of the capuchin groups in this study ranged in primary or gallery forest.

Converging on an answer?

Despite the differences, there are a number of commonalities among the various studies discussed above. First, every study of UW in wild capuchins that has compared UW across seasons has found markedly higher frequencies in the dry season. Second, there is a consensus that UW behavior among alpha males appears to be qualitatively different from all other group members. Third, no study has found direct support for the marking territory hypothesis. Beyond those broad points of agreement, there are a few other shared conclusions. The results of this study agree with those of Campos et al. (2007) and Miller et al. (2007) in rejecting the thermoregulation hypothesis. Robinson's (1979) and Perry's (1998) cautious support for this hypothesis cannot be considered strong because in both studies, the relationship between UW and temperature was inferred rather than measured. Roeder & Anderson (1991) offer more convincing support for the thermoregulation hypothesis, and their study is somewhat of an anomaly in that regard. The results of this study also agree to some extent with Miller et al.'s (2007) suggestion that UW by alpha males is related to sexual contexts. Miller et al.'s other

suggestion linking UW to receiving aggression is difficult to interpret because the authors

compare UW rates for directing vs. receiving aggression, but the rates are not standardized by

comparing them to baseline activity. The numerical value that they report—a mean rate of 0.14

urine-washes per hour of aggression received—is still 10-20 times lower than typical UW rates

in the dry season that I have reported for capuchins at SRNP. Two of my suggestions have not

been previously considered: (1) some capuchins may use UW to soothe ant stings, and (2) alpha

males may urine-wash in response to "gargle" vocalizations. To summarize, the primary function

of UW for wild capuchins, especially those at SRNP, is probably non-social and related to body

care in especially dry conditions, but alpha males may also engage in UW during sexual contexts

and when solicited for an olfactory signal by subordinates.

Table 5.1. Summary of results regarding the seven hypotheses for UW tested in this study. Supported predictions are shaded dark gray; partially supported predictions are shaded in light gray. Fundamental predictions for each hypothesis are shown in bold italics.

Hypothesis		Predictions	Supported?
1. Thermoregulation	1	↑ *UW at high temperature*	No
	2	↑ UW at low relative humidity	**Yes**
	3	↑ UW in dry season	**Yes**
2. Neutralization of noxious stimuli	1	↑ *UW during* **Acacia** *foraging*	**Some individuals**
3. Moisten hands to improve grip / clean hands and feet	1	↑ *UW at low relative humidity*	**Yes**
	2	↑ *UW during traveling*	**Yes**
	3	↑ UW during foraging	No
	4	↑ UW in dry season	**Yes**
4. Mark home-range or resources	1	*UW concentrated either in core or peripheral areas*	**Partially**
	2	↑ UW in areas with intergroup encounters	No
	3	↑ UW near valuable resources such as water holes	No
	4	↑ UW in dry season	**Yes**
5. Displacement behavior	1	↑ *UW in stressful situations (e.g. aggression)*	No
	2	↑ UW in proximity of dominant individuals	No
	3	No seasonal difference in UW frequency	No
6. Assertion of dominance	1	*UW rates positively correlated with dominance*	No
	2	↑ UW when directing aggression	No
	3	↑ UW in proximity of subordinate individuals	No
	4	Seasonal difference in UW frequency slight or absent	No
7. Sexual attraction	1	↑ *UW in sexual contexts*	**α-males**
	2	↑ UW in proximity of opposite-sex individuals	No
	3	Seasonal difference in UW frequency slight or absent	No

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Appendix 1. Primate species known to urine wash and proposed functions.

Scientific name (common name)	Wild (W) / Captive (C)	Proposed function
Alouatta palliata (mantled howler monkey)		
Milton 1975	W	troop cohesion, displacement behavior?
Aotus azarae boliviensis (Azara's owl monkey)		
Chambers 2004	C	-
Aotus lemurinus griseimembra (grey-legged night monkey)		
Hunter 1981, cited in Zito et al. 2003	?	?
Aotus trivirgatus (northern gray-necked night monkey)		
Andrew & Klopman 1974	C	-
Brachyteles arachnoides (muriqui)		
Milton 1985	W	communicate reproductive status
Cebus albifrons (white-fronted capuchin)		
Andrew & Klopman 1974	C	response to observer
Cebus apella (tufted capuchin)		
Nolte 1958, cited in Oppenheimer 1973	?	?
Roeder & Anderson 1991	C	thermoregulation; social signaling between groups
Carosi et al. unpublished ms.	C	thermoregulation
Miller et al. 2007	C	sexual signal and response to receiving aggression
Cebus capucinus (white-faced capuchin)		
Oppenheimer 1973	W	-
Perry 1998	W	display; assertion of dominance; thermoregulation?
Carnegie 2005	W	-
Campos et al. 2007	W	assertion of dominance?
Cebus olivaceus (wedge-capped capuchin)		
Oppenheimer & Oppenheimer 1973	W	display; response to observer
Robinson 1979	W	thermoregulation; social signaling between groups
Galago alleni (Allen's bush baby)		
Charles-Dominique 1977	W	marking home range; excitement (displacement?)
Galago senegalensis (northern lesser bush baby)		
Boulenger 1936, cited in Harcourt 1981	?	improve grip
Andrew & Klopman 1974	C	mobbing
Galago moholi (southern lesser bush baby)		
Harcourt 1981	W	improve grip

Galagoides demidoff (Demidoff's bush baby)

Andrew & Klopman 1974	C	mobbing

Loris tardigradus (slender loris)

Ilse 1955, cited in Harcourt 1981	C	marking home range
Nekaris 2002	W	neutralize insect stings
Nekaris & Rasmussen 2003	W	neutralize insect stings

Microcebus murinus (gray mouse lemur)

Petter 1962, cited in Charles-Dominique 1977	?	?

Microcebus ravelobensis (golden brown mouse lemur)

Braune et al. 2005	W	regulate inter-group spacing

Nycticebus coucang (slow loris)

Hill 1938, cited in Harcourt 1981	?	cleaning hands

Otolemur crassicaudatus (thick-tailed greater bush baby)

Welker 1973	C	moistening hands to improve grip
Eibl-Eibesfeldt 1953, cited in Harcourt 1981	?	laying down scent trails for orientation
Andrew & Klopman 1974	C	mobbing; aggression

Otolemur garnettii (Garnett's greater bush baby)

Watson et al. 1999	C	social signaling; possible displacement behavior

Pithecia pithecia (white-faced saki)

Dugmore 1986	C	-

Saguinus mystax (mustached tamarin)

Heymann 1995	W	thermoregulation

Saimiri boliviensus (Bolivian squirrel monkey)

Ruiz 2005	C	thermoregulation

Saimiri oerstedii (red-backed squirrel monkey)

Boinski 1992	W	communicate reproductive status

Saimiri sciureus (common squirrel monkey)

Andrew 1964, cited in Oppenheimer & Oppenheimer 1973	?	?
Castell & Maurus 1967	C	cleaning hands
Latta et al. 1967	C	moistening hands, displacement behavior (?)
DuMond 1968	C	displacement behavior
Epple & Manson unpublished data, cited in Epple 1974	?	presence of unfamiliar male
Hennessey 1978	C	communicate reproductive status
Schmidt & Seitz 1967, cited in Harcourt 1981	?	thermoregulation
Schwartz & Rosenblum 1985	C	thermoregulation

Appendix 2. Behavioral definitions for social contexts.

Affiliation

Groom: Using the fingers and/or mouth to pick methodically through another individual's fur

Groom solicit: Lying down in a stretched position immediately in front of another individual in an obvious attempt to invite grooming

Climb: Clambering on the body of a resting individual; usually practiced by infants

Inspect: Drawing the face close to another individual's body and peering intently, often while touching or pulling softly; usually directed toward infants

Touch: Using one or more hands to make gentle physical contact with another individual

Hug / cuddle: Embracing another individual in a relaxed context

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Conspecific aggression

Open-mouth threat: Staring with a tense, open-mouthed expression exposing the canines

Vocal threat: Variable vocalization ranging in character and intensity from mild peeps to intense roars, noisy pulses, shrieks, and brays

Lunge: Short, rapid jumping or rushing toward another individual

Chase: Running rapidly in pursuit of another individual

Hit: Striking forcefully with the hand

Wrestle: Grappling intensely with another individual

Bite: Using the teeth to seize or slash at another individual

Supplant: Taking the place of another individual, who withdraws at the approach of the supplanting individual

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Display

Bounce: Bobbing quickly up and down while standing quadrupedally; usually remains standing firmly on all four limbs, but the front limbs may be lifted quickly to slap the substrate

Branch shake: Moving a tree limb quickly and forcefully while staring at an individual

Branch break: Intentionally snapping a tree limb

Tail branch drag: Holding a branch with the tail while running on the ground

Stiff walk: Walking with rigid limbs and exaggerated steps

Piloerect: Body hair raised and standing on end

Leaf-litter display: Jumping into and scattering dry leaves

Fear

Avoid: Actively moving out of the way of another individual who does not approach or supplant the avoiding individual

Cower: Cringing, crouching, or shrinking back from another individual

Grimace: Facial expression in which the corners of the mouth are retracted, exposing the teeth, but the teeth remain together

Flee: Running away rapidly from another individual

Yelp: A sharp, shrill, brief cry

Scream: Loud, high-pitched cry of distress varying from staccato pulses to undulating roars

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Observer-directed aggression

Open-mouth threat at observer: Staring at human observer with a tense, open-mouthed expression exposing the canines

Vocal threat at observer: Variable vocalization ranging in character and intensity from mild peeps to intense roars, noisy pulses, shrieks, and brays

Olfactory behavior

Sniff: Smelling or softly nuzzling urine, a conspecific's body, or a substrate

Rub nose on branch: Vigorous wiping of the nose against a substrate, often preceding sneezes or lying down

Lick: Drawing the tongue over urine, a conspecific's body, or a substrate

Social hand-sniff: Inserting fingers into the nostrils or eyes of another monkey or cupping the hand over the face of another monkey; often mutual, and accompanied by trance-like facial expressions among participants

Sexual behavior

Duck face: Face wrinkled with the lips protruded; part of the white-faced capuchin "courtship dance"

Pace: Moving back and forth over the same substrate, often accompanied by duck face, pirouettes, and sex grunt; part of the white-faced capuchin "courtship dance"

Pirouette: Spinning around and looking at another individual over the shoulder or under the arm; part of the white-faced capuchin "courtship dance"

Sex grunt: Harsh, noisy, low-pitched notes, usually given while pulling back the corners of the mouth

Sex squeak: Series of staccato notes ascending in pitch

Mount: Assuming superior dorsal-ventral position for copulation

Mount and thrust: Mount with pelvic thrusting and no intromission

Copulate: Mount with pelvic thrusting, intromission, and possibly ejaculation

Appendix 3. Individual urine-washing behavior for all individuals in the four study groups. "Total # UW" includes all *ad libitum* data. A dash ("-") indicates that no data were collected for the individual in that study period. Age abbreviations include A = adult (>10 y.o.); SA = subadult (6-10 y.o.); JUV = juvenile (2-5 y.o.); INF = infant (<2 y.o.). Individual UW rates are calculated per focal follow hour. Alpha males are boxed.

| | | | | Wet Season | | | | Dry Season | | | |
Group	Monkey	Age	Sex	Total # UW	# UW as focal	Follow hrs	UW rate	Total # UW	# UW as focal	Follow hrs	UW rate
BH	AS	JUV	F	0	-	-	-	-	-	-	-
	BD	A	M	0	0	1.53	0	-	-	-	-
	BE	JUV	M	2	-	-	-	-	-	-	-
	CA	A	F	0	-	-	-	-	-	-	-
	DQ	A	F	0	-	-	-	-	-	-	-
	GO	A	M	0	0	4.01	0	-	-	-	-
	GU	SA	M	0	-	-	-	-	-	-	-
	HE	JUV	M	0	-	-	-	-	-	-	-
	HU	SA	M	0	-	-	-	-	-	-	-
	JA	A	F	0	-	-	-	-	-	-	-
	JD	A	M	0	0	3.83	0	-	-	-	-
	KA	SA	M	0	-	-	-	-	-	-	-
	MA	A	F	0	-	-	-	-	-	-	-
	MJ	SA	M	0	0	2.97	0	-	-	-	-
	RO	SA	M	0	-	-	-	-	-	-	-
	SB	INF	U	0	-	-	-	-	-	-	-
	SG	A	F	0	-	-	-	-	-	-	-
	SK	A	F	0	-	-	-	-	-	-	-
	SM	SA	M	1	1	2.38	0.42	-	-	-	-
	SR	JUV	F	0	-	-	-	-	-	-	-
CP	AB	JUV	F	0	-	-	-	22	-	-	-
	AL	INF	F	0	-	-	-	8	-	-	-
	BH	SA	M	3	-	-	-	83	27	9.26	2.915
	BL	JUV	F	0	-	-	-	20	-	-	-
	BT	INF	F	0	-	-	-	4	-	-	-
	ED	A	F	0	-	-	-	36	26	11.69	2.224
	KI	JUV	F	0	-	-	-	16	-	-	-
	LL	A	M	0	0	8.32	0	57	30	11.72	2.56
	MO	SA	M	0	-	-	-	91	52	11.42	4.553
	NM	JUV	F	0	-	-	-	25	-	-	-
	NN	A	M	15	6	8.52	0.704	98	38	11.26	3.374
	RJ	JUV	M	0	-	-	-	-	-	-	-
	RR	A	M	1	1	13.68	0.073	52	33	11.83	2.791
	SA	A	F	1	-	-	-	66	46	11.64	3.952
	SH	JUV	F	0	-	-	-	13	-	-	-

	ID										
	SI	A	F	0	-	-	-	52	43	11.73	3.666
	SS	A	F	1	-	-	-	48	38	11.99	3.168
	ST	INF	U	0	-	-	-	-	-	-	-
	TT	A	F	2	-	-	-	54	38	11.21	3.299
	ZZ	A	F	0	-	-	-	45	36	11.4	3.157
EX	AN	A	F	0	-	-	-	12	10	13.8	0.724
	AR	A	M	0	0	2.65	0	51	43	13.95	3.082
	AT	A	M	1	1	11.74	0.085	74	41	13.48	3.042
	CB	INF	M	-	-	-	-	2	-	-	-
	CL	A	F	0	-	-	-	51	42	14.05	2.99
	EL	A	F	0	-	-	-	28	21	13.69	1.534
	HL	JUV	F	0	-	-	-	8	-	-	-
	HR	INF	M	0	-	-	-	1	-	-	-
	OP	INF	M	-	-	-	-	0	-	-	-
LV	AF	SA	M	0	-	-	-	-	-	-	-
	BB	A	F	0	-	-	-	8	7	13.29	0.527
	CC	A	M	13	9	16.65	0.541	-	-	-	-
	CE	JUV	F	0	-	-	-	20	-	-	-
	CH	A	F	0	-	-	-	16	10	13.92	0.719
	CY	A	M	-	-	-	-	73	39	12.95	3.011
	DL	A	F	0	-	-	-	16	12	12.5	0.96
	KL	A	F	0	-	-	-	44	32	12.98	2.389
	MS	INF	M	-	-	-	-	0	-	-	-
	MZ	SA	M	0	-	-	-	26	20	13.61	1.47
	NT	INF	M	0	-	-	-	0	-	-	-
	NU	SA	M	0	-	-	-	81	45	13.41	2.984
	OR	JUV	F	0	-	-	-	5	-	-	-
	PK	JUV	F	0	-	-	-	8	-	-	-
	SL	A	F	0	-	-	-	46	32	14.36	2.228
	TY	JUV	M	2	-	-	-	21	-	-	-
	VV	JUV	F	0	-	-	-	12	-	-	-
	WW	SA	M	0	0	3.95	0	40	26	13.86	1.875

Appendix 4.1. Bootstrapping analysis of the social context for urine-washing in the dry season. Gray shading indicates individuals for whom no bouts of a given social context were observed. Significant associations are denoted by asterisks; * = significant a α=0.05, ** = significant at α=0.01. Boxed cells indicate which confidence limit was exceeded.

Monkey	Social Context	# Bouts	# UW within 2.5 minutes	95% BCI Lower	95% BCI Upper	99% BCI Lower	99% BCI Upper
AN	Affiliative Directed	5	0	0	1	0	2
AR	Affiliative Directed	2	0	0	2	0	3
AT	Affiliative Directed	5	3	0	3	0	4
BB	Affiliative Directed	13	0	0	2	0	3
BH	Affiliative Directed	4	1	0	3	0	4
CH	Affiliative Directed	12	0	0	3	0	4
CL	Affiliative Directed	12	1	0	7	0	8
CY	Affiliative Directed	3	0	0	3	0	4
DL	Affiliative Directed	14	1	0	4	0	5
ED	Affiliative Directed	13	1	1	7	0	9
EL	Affiliative Directed	19	2	0	6	0	7
KL	Affiliative Directed	13	2	0	6	0	8
LL	Affiliative Directed	5	2	0	4	0	5
MO	Affiliative Directed	13	3	1	10	1	11
MZ	Affiliative Directed	11	0	0	4	0	5
NN	Affiliative Directed	0	0	0	0	0	0
NU	Affiliative Directed	11	1	0	7	0	8
RR	Affiliative Directed	3	0	0	3	0	3
SA	Affiliative Directed	15	7	1	9	0	11
SI	Affiliative Directed	18	6	3	13	2	15
SL	Affiliative Directed	19	0	0	6	0	7
SS	Affiliative Directed	10	0	0	6	0	7
TT	Affiliative Directed	19	11 **	1	9	0	10
WW	Affiliative Directed	15	1	0	6	0	7
ZZ	Affiliative Directed	8	2	0	3	0	4
AN	Affiliative Received	8	0	0	1	0	2
AR	Affiliative Received	6	0	0	3	0	4
AT	Affiliative Received	6	1	0	4	0	5
BB	Affiliative Received	10	0	0	2	0	2
BH	Affiliative Received	5	0	0	4	0	5
CH	Affiliative Received	12	0	0	3	0	3
CL	Affiliative Received	8	0	0	6	0	8
CY	Affiliative Received	8	1	0	6	0	7
DL	Affiliative Received	12	1	0	3	0	4
ED	Affiliative Received	13	1	0	7	0	8
EL	Affiliative Received	16	2	0	6	0	7

KL	Affiliative Received	15	4	0	6	0	7
LL	Affiliative Received	10	0	0	5	0	7
MO	Affiliative Received	10	5	0	7	0	8
MZ	Affiliative Received	6	0	0	3	0	4
NN	Affiliative Received	4	2	0	4	0	4
NU	Affiliative Received	12	0	1	8	0	9
RR	Affiliative Received	13	0	0	6	0	8
SA	Affiliative Received	18	6	2	11	1	13
SI	Affiliative Received	21	1	2	11	1	13
SL	Affiliative Received	25	1	1	8	0	10
SS	Affiliative Received	6	0	0	4	0	5
TT	Affiliative Received	21	5	0	7	0	8
WW	Affiliative Received	6	0	0	3	0	4
ZZ	Affiliative Received	5	0	0	2	0	3
AN	Aggressive Directed	2	1	0	1	0	2
AR	Aggressive Directed	7	1	0	4	0	5
AT	Aggressive Directed	12	3	0	7	0	8
BB	Aggressive Directed	3	0	0	1	0	1
BH	Aggressive Directed	1	0	0	1	0	2
CH	Aggressive Directed	2	0	0	1	0	1
CL	Aggressive Directed	2	0	0	2	0	3
CY	Aggressive Directed	9	0	0	5	0	7
DL	Aggressive Directed	5	0	0	2	0	3
ED	Aggressive Directed	6	1	0	3	0	5
EL	Aggressive Directed	7	0	0	3	0	4
KL	Aggressive Directed	9	0	0	5	0	6
LL	Aggressive Directed	11	1	0	5	0	6
MO	Aggressive Directed	3	2	0	5	0	6
MZ	Aggressive Directed	6	0	0	3	0	4
NN	Aggressive Directed	4	0	0	4	0	4
NU	Aggressive Directed	3	0	0	4	0	5
RR	Aggressive Directed	4	0	0	3	0	4
SA	Aggressive Directed	6	1	0	5	0	6
SI	Aggressive Directed	10	1	0	6	0	8
SL	Aggressive Directed	5	1	0	3	0	4
SS	Aggressive Directed	2	0	0	2	0	3
TT	Aggressive Directed	5	2	0	3	0	4
WW	Aggressive Directed	7	0	0	3	0	5
ZZ	Aggressive Directed	1	0	0	2	0	2
AN	Aggressive Received	4	0	0	1	0	2
AR	Aggressive Received	1	0	0	2	0	2
AT	Aggressive Received	3	1	0	3	0	4
BB	Aggressive Received	1	0	0	1	0	1
BH	Aggressive Received	0	0	0	0	0	0

CH	Aggressive Received	5	0	0	2	0	2
CL	Aggressive Received	0	0	0	0	0	0
CY	Aggressive Received	2	0	0	2	0	3
DL	Aggressive Received	2	0	0	1	0	2
ED	Aggressive Received	3	0	0	3	0	3
EL	Aggressive Received	1	0	0	1	0	2
KL	Aggressive Received	0	0	0	0	0	0
LL	Aggressive Received	3	0	0	3	0	3
MO	Aggressive Received	2	0	0	3	0	4
MZ	Aggressive Received	0	0	0	0	0	0
NN	Aggressive Received	0	0	0	0	0	0
NU	Aggressive Received	0	0	0	0	0	0
RR	Aggressive Received	2	0	0	2	0	3
SA	Aggressive Received	1	1	0	2	0	2
SI	Aggressive Received	2	0	0	2	0	3
SL	Aggressive Received	1	0	0	0	0	0
SS	Aggressive Received	5	0	0	4	0	5
TT	Aggressive Received	1	1 **	0	0	0	0
WW	Aggressive Received	2	0	0	2	0	2
ZZ	Aggressive Received	3	0	0	3	0	4
AN	Display Directed	0	0	0	0	0	0
AR	Display Directed	0	0	0	0	0	0
AT	Display Directed	11	5	0	6	0	7
BB	Display Directed	0	0	0	0	0	0
BH	Display Directed	1	0	0	1	0	2
CH	Display Directed	0	0	0	0	0	0
CL	Display Directed	0	0	0	0	0	0
CY	Display Directed	3	3	0	3	0	4
DL	Display Directed	0	0	0	0	0	0
ED	Display Directed	0	0	0	0	0	0
EL	Display Directed	1	0	0	1	0	2
KL	Display Directed	0	0	0	0	0	0
LL	Display Directed	8	2	0	5	0	6
MO	Display Directed	3	1	0	4	0	5
MZ	Display Directed	3	0	0	2	0	2
NN	Display Directed	4	2	0	3	0	4
NU	Display Directed	1	0	0	2	0	2
RR	Display Directed	3	0	0	3	0	4
SA	Display Directed	0	0	0	0	0	0
SI	Display Directed	0	0	0	0	0	0
SL	Display Directed	0	0	0	0	0	0
SS	Display Directed	0	0	0	0	0	0
TT	Display Directed	0	0	0	0	0	0
WW	Display Directed	3	0	0	2	0	3

ZZ	Display Directed	0	0	0	0	0	0
AN	Display Received	0	0	0	0	0	0
AR	Display Received	0	0	0	0	0	0
AT	Display Received	0	0	0	0	0	0
BB	Display Received	0	0	0	0	0	0
BH	Display Received	0	0	0	0	0	0
CH	Display Received	0	0	0	0	0	0
CL	Display Received	0	0	0	0	0	0
CY	Display Received	0	0	0	0	0	0
DL	Display Received	1	0	0	1	0	1
ED	Display Received	0	0	0	0	0	0
EL	Display Received	0	0	0	0	0	0
KL	Display Received	0	0	0	0	0	0
LL	Display Received	0	0	0	0	0	0
MO	Display Received	0	0	0	0	0	0
MZ	Display Received	0	0	0	0	0	0
NN	Display Received	0	0	0	0	0	0
NU	Display Received	0	0	0	0	0	0
RR	Display Received	0	0	0	0	0	0
SA	Display Received	0	0	0	0	0	0
SI	Display Received	0	0	0	0	0	0
SL	Display Received	0	0	0	0	0	0
SS	Display Received	0	0	0	0	0	0
TT	Display Received	0	0	0	0	0	0
WW	Display Received	0	0	0	0	0	0
ZZ	Display Received	0	0	0	0	0	0
AN	Fear Directed	3	0	0	1	0	2
AR	Fear Directed	2	0	0	2	0	3
AT	Fear Directed	2	1	0	2	0	3
BB	Fear Directed	4	0	0	1	0	2
BH	Fear Directed	1	0	0	2	0	2
CH	Fear Directed	6	1	0	2	0	3
CL	Fear Directed	0	0	0	0	0	0
CY	Fear Directed	0	0	0	0	0	0
DL	Fear Directed	2	0	0	1	0	2
ED	Fear Directed	3	0	0	3	0	4
EL	Fear Directed	2	0	0	2	0	3
KL	Fear Directed	1	0	0	1	0	2
LL	Fear Directed	1	0	0	1	0	2
MO	Fear Directed	1	0	0	2	0	3
MZ	Fear Directed	0	0	0	0	0	0
NN	Fear Directed	0	0	0	0	0	0
NU	Fear Directed	1	1	0	2	0	2
RR	Fear Directed	0	0	0	0	0	0

SA	Fear Directed	2	1	0	3	0	3
SI	Fear Directed	1	0	0	2	0	2
SL	Fear Directed	0	0	0	0	0	0
SS	Fear Directed	7	1	0	5	0	6
TT	Fear Directed	3	0	0	2	0	3
WW	Fear Directed	4	0	0	2	0	3
ZZ	Fear Directed	1	0	0	2	0	2
AN	Fear Received	2	0	0	1	0	2
AR	Fear Received	4	0	0	3	0	4
AT	Fear Received	1	0	0	2	0	2
BB	Fear Received	2	0	0	1	0	1
BH	Fear Received	0	0	0	0	0	0
CH	Fear Received	0	0	0	0	0	0
CL	Fear Received	2	1	0	2	0	3
CY	Fear Received	6	2	0	4	0	5
DL	Fear Received	2	0	0	1	0	2
ED	Fear Received	4	1	0	3	0	4
EL	Fear Received	4	0	0	2	0	3
KL	Fear Received	1	0	0	1	0	2
LL	Fear Received	9	1	0	5	0	6
MO	Fear Received	1	1	0	2	0	3
MZ	Fear Received	8	0	0	3	0	4
NN	Fear Received	4	2	0	3	0	5
NU	Fear Received	2	0	0	3	0	4
RR	Fear Received	4	1	0	3	0	4
SA	Fear Received	4	1	0	3	0	4
SI	Fear Received	9	1	0	6	0	7
SL	Fear Received	3	0	0	2	0	3
SS	Fear Received	0	0	0	0	0	0
TT	Fear Received	1	0	0	0	0	0
WW	Fear Received	6	1	0	3	0	4
ZZ	Fear Received	4	0	0	3	0	4
AN	Observer Directed	4	1	0	1	0	2
AR	Observer Directed	3	0	0	3	0	4
AT	Observer Directed	12	4	0	7	0	8
BB	Observer Directed	4	0	0	1	0	2
BH	Observer Directed	3	1	0	3	0	4
CH	Observer Directed	5	0	0	1	0	2
CL	Observer Directed	1	0	0	2	0	2
CY	Observer Directed	8	2	0	5	0	6
DL	Observer Directed	2	0	0	1	0	2
ED	Observer Directed	0	0	0	0	0	0
EL	Observer Directed	4	1	0	2	0	3
KL	Observer Directed	3	2	0	3	0	4

LL	Observer Directed	5	0	0	3	0	4
MO	Observer Directed	1	0	0	2	0	3
MZ	Observer Directed	4	0	0	2	0	3
NN	Observer Directed	15	7	0	7	0	8
NU	Observer Directed	3	3	0	3	0	4
RR	Observer Directed	6	1	0	4	0	5
SA	Observer Directed	2	1	0	3	0	3
SI	Observer Directed	7	0	0	5	0	6
SL	Observer Directed	0	0	0	0	0	0
SS	Observer Directed	2	1	0	2	0	3
TT	Observer Directed	1	1 **	0	0	0	0
WW	Observer Directed	4	0	0	2	0	3
ZZ	Observer Directed	3	1	0	2	0	3
AN	Olfactory Directed	3	0	0	1	0	2
AR	Olfactory Directed	8	3	0	5	0	6
AT	Olfactory Directed	17	3	1	8	0	9
BB	Olfactory Directed	8	0	0	2	0	2
BH	Olfactory Directed	4	1	0	3	0	4
CH	Olfactory Directed	4	0	0	1	0	2
CL	Olfactory Directed	6	1	0	4	0	5
CY	Olfactory Directed	15	5	1	8	0	10
DL	Olfactory Directed	10	3	0	3	0	4
ED	Olfactory Directed	8	1	0	4	0	5
EL	Olfactory Directed	7	0	0	3	0	4
KL	Olfactory Directed	12	4	0	5	0	6
LL	Olfactory Directed	9	3	0	3	0	4
MO	Olfactory Directed	7	4	0	6	0	7
MZ	Olfactory Directed	9	2	0	3	0	4
NN	Olfactory Directed	18	7	1	8	0	10
NU	Olfactory Directed	15	7	1	9	0	10
RR	Olfactory Directed	11	5	0	6	0	7
SA	Olfactory Directed	4	0	0	4	0	5
SI	Olfactory Directed	8	3	0	6	0	8
SL	Olfactory Directed	7	2	0	4	0	5
SS	Olfactory Directed	9	1	0	5	0	7
TT	Olfactory Directed	9	4	0	4	0	6
WW	Olfactory Directed	12	2	0	5	0	6
ZZ	Olfactory Directed	8	0	0	5	0	6
AN	Olfactory Received		0	0	0	0	0
AR	Olfactory Received	1	0	0	2	0	2
AT	Olfactory Received	1	1	0	2	0	2
BB	Olfactory Received		0	0	0	0	0
BH	Olfactory Received	3	1	0	3	0	4
CH	Olfactory Received	2	1	0	1	0	2

CL	Olfactory Received		0	0	0	0	0
CY	Olfactory Received	4	4 *	0	3	0	4
DL	Olfactory Received	1	1	0	1	0	1
ED	Olfactory Received	2	2	0	2	0	2
EL	Olfactory Received	1	1	0	1	0	2
KL	Olfactory Received	1	1	0	1	0	2
LL	Olfactory Received	2	1	0	2	0	3
MO	Olfactory Received		0	0	0	0	0
MZ	Olfactory Received	1	0	0	1	0	2
NN	Olfactory Received	3	3	0	3	0	4
NU	Olfactory Received	1	0	0	2	0	2
RR	Olfactory Received	4	1	0	3	0	4
SA	Olfactory Received		0	0	0	0	0
SI	Olfactory Received	2	0	0	2	0	3
SL	Olfactory Received		0	0	0	0	0
SS	Olfactory Received	3	1	0	3	0	4
TT	Olfactory Received	1	0	0	2	0	2
WW	Olfactory Received	1	0	0	1	0	2
ZZ	Olfactory Received		0	0	0	0	0
AN	Sexual Directed	1	0	0	1	0	1
AR	Sexual Directed	0	0	0	0	0	0
AT	Sexual Directed	5	1	0	4	0	5
BB	Sexual Directed	1	0	0	1	0	1
BH	Sexual Directed	2	0	0	2	0	3
CH	Sexual Directed	0	0	0	0	0	0
CL	Sexual Directed	1	0	0	1	0	2
CY	Sexual Directed	1	3 **	0	2	0	2
DL	Sexual Directed	0	0	0	0	0	0
ED	Sexual Directed	3	0	0	2	0	3
EL	Sexual Directed	0	0	0	0	0	0
KL	Sexual Directed	1	0	0	1	0	2
LL	Sexual Directed	3	0	0	3	0	3
MO	Sexual Directed	3	1	0	4	0	5
MZ	Sexual Directed	3	0	0	2	0	2
NN	Sexual Directed	6	5 *	0	4	0	5
NU	Sexual Directed	2	0	0	2	0	3
RR	Sexual Directed	5	1	0	4	0	5
SA	Sexual Directed	1	0	0	2	0	3
SI	Sexual Directed	1	0	0	2	0	2
SL	Sexual Directed	0	0	0	0	0	0
SS	Sexual Directed	0	0	0	0	0	0
TT	Sexual Directed	0	0	0	0	0	0
WW	Sexual Directed	2	0	0	2	0	3
ZZ	Sexual Directed	0	0	0	0	0	0

AN	Sexual Received	0	0	0	0	0	0
AR	Sexual Received	0	0	0	0	0	0
AT	Sexual Received	1	0	0	2	0	2
BB	Sexual Received	4	0	0	1	0	2
BH	Sexual Received	0	0	0	0	0	0
CH	Sexual Received	0	0	0	0	0	0
CL	Sexual Received	0	0	0	0	0	0
CY	Sexual Received	0	0	0	0	0	0
DL	Sexual Received	3	0	0	1	0	2
ED	Sexual Received	1	0	0	1	0	2
EL	Sexual Received	0	0	0	0	0	0
KL	Sexual Received	2	0	0	2	0	3
LL	Sexual Received	1	0	0	1	0	2
MO	Sexual Received	1	0	0	2	0	3
MZ	Sexual Received	0	0	0	0	0	0
NN	Sexual Received	5	5 *	0	4	0	5
NU	Sexual Received	3	2	0	3	0	4
RR	Sexual Received	1	0	0	1	0	2
SA	Sexual Received	0	0	0	0	0	0
SI	Sexual Received	2	0	0	2	0	3
SL	Sexual Received	0	0	0	0	0	0
SS	Sexual Received	1	0	0	2	0	2
TT	Sexual Received	0	0	0	0	0	0
WW	Sexual Received	1	0	0	1	0	2
ZZ	Sexual Received	0	0	0	0	0	0
AN	Gargle Received	0	0	0	0	0	0
AR	Gargle Received	4	1	0	3	0	4
AT	Gargle Received	4	1	0	3	0	4
BB	Gargle Received	0	0	0	0	0	0
BH	Gargle Received	0	0	0	0	0	0
CH	Gargle Received	0	0	0	0	0	0
CL	Gargle Received	0	0	0	0	0	0
CY	Gargle Received	16	7	1	9	0	11
DL	Gargle Received	0	0	0	0	0	0
ED	Gargle Received	1	0	0	1	0	2
EL	Gargle Received	0	0	0	0	0	0
KL	Gargle Received	0	0	0	0	0	0
LL	Gargle Received	6	0	0	3	0	4
MO	Gargle Received	0	0	0	0	0	0
MZ	Gargle Received	0	0	0	0	0	0
NN	Gargle Received	10	5	0	5	0	7
NU	Gargle Received	0	0	0	0	0	0
RR	Gargle Received	14	0	0	7	0	8
SA	Gargle Received	1	0	0	2	0	2

SI	Gargle Received	0	0	0	0	0	0
SL	Gargle Received	0	0	0	0	0	0
SS	Gargle Received	0	0	0	0	0	0
TT	Gargle Received	0	0	0	0	0	0
WW	Gargle Received	0	0	0	0	0	0
ZZ	Gargle Received	0	0	0	0	0	0

Appendix 4.2. Bootstrapping analysis of the social context for urine-washing in the wet season. Gray shading indicates individuals for whom no bouts of a given social context were observed. Significant associations are denoted by asterisks; * = significant a α=0.05, ** = significant at α=0.01. Boxed cells indicate which confidence limit was exceeded.

Monkey	Social Context	# Bouts	# UW within 2.5 minutes	95% BCI		99% BCI	
				Lower	Upper	Lower	Upper
AR	Affiliative Directed	1	0	0	0	0	0
AT	Affiliative Directed	6	0	0	1	0	1
BD	Affiliative Directed	0	0	0	0	0	0
CC	Affiliative Directed	5	0	0	1	0	2
GO	Affiliative Directed	3	0	0	0	0	0
JD	Affiliative Directed	4	0	0	0	0	0
LL	Affiliative Directed	2	0	0	0	0	0
MJ	Affiliative Directed	3	0	0	0	0	0
NN	Affiliative Directed	1	0	0	1	0	1
RR	Affiliative Directed	4	0	0	0	0	1
SM	Affiliative Directed	1	0	0	1	0	1
WW	Affiliative Directed	1	0	0	0	0	0
AR	Affiliative Received	0	0	0	0	0	0
AT	Affiliative Received	7	1	0	1	0	1
BD	Affiliative Received	0	0	0	0	0	0
CC	Affiliative Received	9	0	0	2	0	3
GO	Affiliative Received	6	0	0	0	0	0
JD	Affiliative Received	4	0	0	0	0	0
LL	Affiliative Received	4	0	0	0	0	0
MJ	Affiliative Received	1	0	0	0	0	0
NN	Affiliative Received	7	1	0	2	0	3
RR	Affiliative Received	8	0	0	1	0	1
SM	Affiliative Received	1	0	0	1	0	1
WW	Affiliative Received	0	0	0	0	0	0
AR	Aggressive Directed	1	0	0	0	0	0
AT	Aggressive Directed	2	0	0	0	0	1
BD	Aggressive Directed	1	0	0	0	0	0
CC	Aggressive Directed	4	0	0	1	0	2
GO	Aggressive Directed	2	0	0	0	0	0
JD	Aggressive Directed	0	0	0	0	0	0
LL	Aggressive Directed	3	0	0	0	0	0
MJ	Aggressive Directed	0	0	0	0	0	0
NN	Aggressive Directed	7	1	0	2	0	3
RR	Aggressive Directed	2	0	0	0	0	1
SM	Aggressive Directed	2	0	0	1	0	1
WW	Aggressive Directed	2	0	0	0	0	0

AR	Aggressive Received	0	0	0	0	0	0
AT	Aggressive Received	0	0	0	0	0	0
BD	Aggressive Received	0	0	0	0	0	0
CC	Aggressive Received	0	0	0	0	0	0
GO	Aggressive Received	0	0	0	0	0	0
JD	Aggressive Received	0	0	0	0	0	0
LL	Aggressive Received	3	0	0	0	0	0
MJ	Aggressive Received	0	0	0	0	0	0
NN	Aggressive Received	2	0	0	1	0	2
RR	Aggressive Received	1	0	0	0	0	1
SM	Aggressive Received	0	0	0	0	0	0
WW	Aggressive Received	0	0	0	0	0	0
AR	Display Directed	0	0	0	0	0	0
AT	Display Directed	1	0	0	0	0	1
BD	Display Directed	0	0	0	0	0	0
CC	Display Directed	2	0	0	1	0	1
GO	Display Directed	2	0	0	0	0	0
JD	Display Directed	2	0	0	0	0	0
LL	Display Directed	1	0	0	0	0	0
MJ	Display Directed	2	0	0	0	0	0
NN	Display Directed	4	0	0	2	0	2
RR	Display Directed	1	0	0	0	0	1
SM	Display Directed	1	0	0	1	0	1
WW	Display Directed	2	0	0	0	0	0
AR	Display Received	0	0	0	0	0	0
AT	Display Received	0	0	0	0	0	0
BD	Display Received	0	0	0	0	0	0
CC	Display Received	0	0	0	0	0	0
GO	Display Received	0	0	0	0	0	0
JD	Display Received	0	0	0	0	0	0
LL	Display Received	0	0	0	0	0	0
MJ	Display Received	0	0	0	0	0	0
NN	Display Received	0	0	0	0	0	0
RR	Display Received	0	0	0	0	0	0
SM	Display Received	0	0	0	0	0	0
WW	Display Received	0	0	0	0	0	0
AR	Fear Directed	0	0	0	0	0	0
AT	Fear Directed	0	0	0	0	0	0
BD	Fear Directed	0	0	0	0	0	0
CC	Fear Directed	0	0	0	0	0	0
GO	Fear Directed	0	0	0	0	0	0
JD	Fear Directed	0	0	0	0	0	0
LL	Fear Directed	2	0	0	0	0	0
MJ	Fear Directed	1	0	0	0	0	0

NN	Fear Directed	0	0	0	0	0	0
RR	Fear Directed	0	0	0	0	0	0
SM	Fear Directed	0	0	0	0	0	0
WW	Fear Directed	0	0	0	0	0	0
AR	Fear Received	0	0	0	0	0	0
AT	Fear Received	1	0	0	0	0	1
BD	Fear Received	1	0	0	0	0	0
CC	Fear Received	3	0	0	1	0	2
GO	Fear Received	1	0	0	0	0	0
JD	Fear Received	1	0	0	0	0	0
LL	Fear Received	3	0	0	0	0	0
MJ	Fear Received	1	0	0	0	0	0
NN	Fear Received	5	1	0	2	0	2
RR	Fear Received	2	0	0	0	0	1
SM	Fear Received	2	0	0	1	0	1
WW	Fear Received	0	0	0	0	0	0
AR	Observer Directed	0	0	0	0	0	0
AT	Observer Directed	3	0	0	0	0	1
BD	Observer Directed	0	0	0	0	0	0
CC	Observer Directed	7	3 **	0	2	0	2
GO	Observer Directed	2	0	0	0	0	0
JD	Observer Directed	4	0	0	0	0	0
LL	Observer Directed	6	0	0	0	0	0
MJ	Observer Directed	1	0	0	0	0	0
NN	Observer Directed	23	1	0	4	0	5
RR	Observer Directed	2	0	0	0	0	1
SM	Observer Directed	0	0	0	0	0	0
WW	Observer Directed	0	0	0	0	0	0
AR	Olfactory Directed	3	0	0	0	0	0
AT	Olfactory Directed	7	0	0	1	0	1
BD	Olfactory Directed	0	0	0	0	0	0
CC	Olfactory Directed	19	2	0	3	0	4
GO	Olfactory Directed	2	0	0	0	0	0
JD	Olfactory Directed	4	0	0	0	0	0
LL	Olfactory Directed	7	0	0	0	0	0
MJ	Olfactory Directed	1	0	0	0	0	0
NN	Olfactory Directed	14	2	0	3	0	4
RR	Olfactory Directed	13	0	0	1	0	1
SM	Olfactory Directed	2	0	0	1	0	1
WW	Olfactory Directed	7	0	0	0	0	0
AR	Olfactory Received	0	0	0	0	0	0
AT	Olfactory Received	0	0	0	0	0	0
BD	Olfactory Received	0	0	0	0	0	0
CC	Olfactory Received	4	3 **	0	1	0	2

GO	Olfactory Received	1	0	0	0	0	0
JD	Olfactory Received	0	0	0	0	0	0
LL	Olfactory Received	1	0	0	0	0	0
MJ	Olfactory Received	0	0	0	0	0	0
NN	Olfactory Received	1	1	0	1	0	1
RR	Olfactory Received	0	0	0	0	0	0
SM	Olfactory Received	0	0	0	0	0	0
WW	Olfactory Received	0	0	0	0	0	0
AR	Sexual Directed	0	0	0	0	0	0
AT	Sexual Directed	0	0	0	0	0	0
BD	Sexual Directed	0	0	0	0	0	0
CC	Sexual Directed	5	0	0	2	0	3
GO	Sexual Directed	0	0	0	0	0	0
JD	Sexual Directed	2	0	0	0	0	0
LL	Sexual Directed	0	0	0	0	0	0
MJ	Sexual Directed	0	0	0	0	0	0
NN	Sexual Directed	1	0	0	1	0	1
RR	Sexual Directed	3	0	0	0	0	1
SM	Sexual Directed	0	0	0	0	0	0
WW	Sexual Directed	1	0	0	0	0	0
AR	Sexual Received	0	0	0	0	0	0
AT	Sexual Received	0	0	0	0	0	0
BD	Sexual Received	0	0	0	0	0	0
CC	Sexual Received	6	0	0	2	0	2
GO	Sexual Received	0	0	0	0	0	0
JD	Sexual Received	1	0	0	0	0	0
LL	Sexual Received	1	0	0	0	0	0
MJ	Sexual Received	0	0	0	0	0	0
NN	Sexual Received	1	0	0	1	0	1
RR	Sexual Received	2	0	0	0	0	1
SM	Sexual Received	0	0	0	0	0	0
WW	Sexual Received	1	0	0	0	0	0
AR	Gargle Received	0	0	0	0	0	0
AT	Gargle Received	8	0	0	1	0	1
BD	Gargle Received	0	0	0	0	0	0
CC	Gargle Received	28	6 **	0	4	0	5
GO	Gargle Received	9	0	0	0	0	0
JD	Gargle Received	0	0	0	0	0	0
LL	Gargle Received	8	0	0	0	0	0
MJ	Gargle Received	1	0	0	0	0	0
NN	Gargle Received	17	6 **	0	4	0	5
RR	Gargle Received	6	0	0	1	0	1
SM	Gargle Received	2	0	0	1	0	1
WW	Gargle Received	1	0	0	0	0	0