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Grooming as an Agonistic Behavior in Garnett’s Small-Eared Bushbaby (*Otolemur garnettii*)

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GROOMING AS AN AGONISTIC BEHAVIOR IN GARNETT'S SMALL-EARED BUSHBABY (*OTOLEMUR GARNETTII*)

by

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ABSTRACT

GROOMING AS AN AGONISTIC BEHAVIOR IN GARNETT'S SMALL-EARED BUSHBABY (*OTOLEMUR GARNETTII*)

by Jennie L. Christopher

May2017

Social behaviors are a necessary component of group living and interactions between organisms. To correctly assess social interactions, researchers must be able to observe behaviors and interpret their function based on the behavior or the behavioral context. In primate species, grooming is often used to assess affiliations between group members and the consensus has been to always interpret grooming as an affiliative behavior. However, a number of avian, rodent and feline species have been shown to groom conspecifics aggressively. These instances of aggressive grooming appear most often when individuals are required to maintain close proximity to one another, such as in captivity. Rodents and felines share characteristics with Garnett's bushbaby (*Otolemur garnettii*). They are nocturnal, have a strong olfactory sense, and are semi-social. Additionally, Edens (2013), found a significant correlation between displacements and grooming when female *O. garnettii* were socially housed. If aggressive grooming were found in a primate species, researchers might need to re-assess their current model of behavioral interpretation for social interaction.

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I would like to acknowledge Dr. Heidi Lyn for her belief in this project when everyone else thought it wasn’t worthwhile and for providing an environment within which I could thrive. I would also like to thank Tiffany Baker; whose assistance was invaluable and who willingly went through the worst of it with me.

DEDICATION

This manuscript is dedicated to Jenny Reed for her unequivocal faith in me as well as her unwavering support. And to my brother, Jason Christopher, for his technical advice, unique insight, and for providing me with an eternal safety net.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

CHAPTER I - INTRODUCTION

To truly understand a species, one must understand the biology, ecology, and behaviors of that species. Behaviors that occur between conspecifics are dubbed social behaviors and among gregarious species can make up a large proportion of their behavioral repertoire, although social behaviors even occur in solitary species and can occur between species. Social behaviors function to manage group living and are vital to group cohesion. (Dunbar & Shultz, 2007) Social behavior can generally be divided into four categories: mating, care of offspring, group living, and fighting (Tinbergen, 1970).

Of the four categories, mating and care of offspring are more constrained by species-specific behavioral sets. Mating behaviors are biologically driven. Because they are clearly a requirement for the continuation of a species, they are therefore pretty ubiquitous across species, although forms vary greatly. Care of offspring is present, in various forms, in all mammalian species as well as some species in other taxa. The other two categories, group living, and fighting, are more general and the flexibility and breadth of these behaviors are influenced by the sociality of the species exhibiting the behaviors. Behaviors in the group living category allow aggregates of conspecifics to coexist, either temporarily or for an extended period of time. Fighting behaviors include all those relating to threat, fear, dominance, and defense. However, behavior can rarely be divided into such distinct categories. A single behavior may fit in multiple categories or change categories when the situational context is altered. Mating and fighting behaviors are a prime example, where the function of observable behavior may be indistinguishable until consequential behaviors are assessed. Therefore, we will classify behavior using two broader terms that speak to the function of a behavior, rather than the form: affiliative and agonistic.

Affiliative behaviors can include grooming, remaining in close proximity, infant care, and reconciliation. Most importantly, affiliative behaviors promote group cohesion and strengthen associations between conspecifics. Agonistic behaviors include all those relating to threat, fear, aggression, and defense. While some authors use the terms agonism and aggression interchangeably (e.g., Harrison, 1965; Henzi & Barrett, 1999; Seyfarth, 1977), we prefer to use agonism as an umbrella term for all behaviors that weaken social bonds, such as threat, defensive, submissive, and dominance behaviors, and to use the term aggression for behaviors that are overtly hostile, such as an attack. Many definitions of aggression are not inclusive enough for the types of behaviors described here, and a similar argument was made by Huntingford and Turner (1987). It is tempting to use intent to distinguish between these two categories, but there is no way to objectively operationalize intent in an animal species. Instead, it might be possible to determine the function of the behavior by observing the context in which it occurs. Affiliative behaviors are functionally distinct from agonistic behaviors and result in opposing consequences.

Many social behaviors are ambiguous or context dependent. In humans, dimorphous expression of emotion is where the behavioral expression does not seem consistent with the emotional state. For example, crying is generally an expression of sadness, yet some people cry when they are happy. Cute aggression is another example where the individual is compelled to act aggressively (i.e., squeeze or pinch) toward cute stimuli (i.e., puppies and human infants) (Aragón, Clark, Dyer, & Bargh, 2015). In nonhuman animals, play behavior may appear as an aggressive encounter but is integral to social bonding. Also, a variety of mating acts may resemble an attack, but there is no intent to harm, while other behaviors require the observation of a subsequent behavior to clarify purpose. For instance, approach behaviors could be either agonistic or affiliative. An approach could lead to a fight (agonistic) or may result in simple close proximity (affiliative). The function of the approach is difficult to extrapolate without taking into account context and behavioral response.

Context-Dependent Grooming

Much of the literature on social behavior, especially primate social behavior, has accepted that grooming - in any context - is affiliative (e.g., Cooper & Bernstein, 2000; Dunbar, 1991; Goodall 1986; Lehmann, Korstjens, & Dunbar, 2007; Yerkes, 1948). There is no doubt that, at least among the primates, grooming is integral to understanding the social structure of a population and is arguably the key factor and the best behavior to measure when assessing social networks among primates (Cooper & Bernstein, 2000; Sade, 1965). In fact, grooming interactions are the most widely used variable to determine affiliative relationships between primate individuals (Henzi & Barrett, 1999). Sade (1972) also stresses the importance of grooming interactions to establish associations between individuals and developed dyadic matrices based solely on grooming behavior. However, none of these studies record the sequences of behavioral observations. While not often explored, grooming may be an example of a context-dependent behavior.

A Brief History of Intraspecific Grooming

Early animal behaviorists describe grooming as an outgrowth of parental care and refer to it as mutual care or mutual aid (e.g., Jolly, 1985; Klopfer, 1974; Scott, 1958). However, few species extend this behavior beyond the caregiving stage. Though more commonly found among Aves, a few mammalian species continue to groom as adults. Most notably examined within the primate orders, it is also observed in ungulates, rodents, and some feline species (Sparks, 1965). There are also documented occurrences of grooming in vampire bats (*Desmodus rotundus*) (Wilkinson, 1986).

Within the primate orders, the absence of grooming is the exception (Sparks, 1969). Yerkes (1948) was among the first to suggest that grooming, at least within the primate taxa, served more than just a hygienic function. He observed that grooming was directed at difficult to reach areas, but the “eagerness” with which grooming was solicited and often expected led him to liken the behavior to a form of “social service.” Grooming occurred as frequently as autogrooming (self-grooming) and appeared to bring “great satisfaction” to both the actor and the recipient (Yerkes, 1948).

A Brief History of Primate Grooming

Seyfarth’s (1977) seminal model of primate grooming focused on female/female dyadic interactions to remove the confound of mating behaviors. The foundation of the model was built on the idea that grooming went beyond a biological function, and emphasized the importance in partner selection based on rank interactions and the potential for maximum benefit. The importance of this foundation was to stress that partner selection was integral to future social support. This model set the standard for grooming in exchange for later social support and the formation of a coalition between individuals. Therefore, grooming can either be reflective of a relationship outside of the grooming interaction or a more direct tit-for-tat trade (Dunbar, 1991). Reynolds (1981), expands this idea to suggests that grooming as a token exchange is the evolutionary precursor to material object exchange found in humans. In fact, chimpanzees (*Pan troglodytes*) were more likely to share food with individuals that had previously groomed them (de Waal, 1997).

Seyfarth's model is not without criticism (e.g., Dunbar, 1991 & Schino, 2001). Henzi and Barrett (1999) state that there is little evidence to support Seyfarth's model of grooming and what little evidence there is remains mostly circumstantial. They suggest that rather than being traded for later agonistic support, grooming is used to decrease aggression between the dominant and submissive animals. This increased tolerance of subordinates by dominant individuals could potentially allow greater resource allocation to low-ranking individuals. To bolster their argument, they point out that similarly ranked individuals are more likely to have a reciprocal relationship, trading grooming for grooming, and more distantly ranked individuals are more likely to exchange grooming for other services (i.e., tolerance) (Henzi & Barrett, 1999).

Among primates, the stronger the structure of the dominance hierarchy, the greater the frequency of grooming (Sparks 1969). In addition, higher-ranking primate individuals overall receive a higher percentage of grooming whereas lower ranking individuals perform grooming at a higher rate (Schino, 2001). This, combined with the typical grooming postures (i.e. facing the back of the groomee, teeth/bill against skin, the often rigid posture of the groomee) supports the suggestion that grooming is an appeasement gesture (Sparks, 1969). Neither Seyfarth (1977) nor critics of his model consider grooming to be anything other than affiliative. In fact, of the three most prevalent hypotheses on the function of grooming, all studies characterize the benefits to the recipient (Russell & Phelps, 2013). However, grooming as an agonistic behavior is not a novel idea.

CHAPTER II – GROOMING AS AN AGONISTIC BEHAVIOR

Agonistic Grooming in Birds

Grooming in birds is called preening. Goodwin (1956) suggested that in socially bonded pigeons “caressing” (as he called allopreening) was a result of a “sublimation” of either sexual or aggressive drives. While head pecking (aggressive) and “caressing” are functionally distinct behaviors, they are structurally very similar, with one bird repeatedly shoving its bill between the dorsal feathers of the head and neck of another. Goodwin (1956) acknowledged the challenge this structural similarity presents to observers, with only the degree of “roughness” to differentiate between the two behaviors. This similarity in form also led him to later suggest that head pecking is an evolutionary precursor to [aggressive] allopreening (personal communication to Harrison, 1965). This is a challenge to observers of behavior due to the difficulty of identifying different levels of roughness. Whereas Goodwin (1956) focused his observations on pigeon behavior, the phenomenon of aggressive allopreening, and therefore the potential behavioral miscategorization, is characteristic of a host of avian species (Sparks, 1969).

The most vulnerable feature of avian physiology is the head. It is not surprising, then, that among most species of birds repeated head pecking is the most common form of attack. Allopreening appears rigidly stereotyped, is also targeted to the head and neck regions, and consistently resembles avian attack behavior (Harrison, 1965). From an observational standpoint, because behavioral markers of roughness are difficult to define, allopreening function must be deduced from the context of the event. This may include the response of the recipient and/or the intensity of the behavior (Harrison, 1965).

Close Proximity as a Context

Early researchers observed that mammals would exhibit changes in behavior patterns when the means of escape was removed (Chance, 1962). Often, when animal groups are kept in captivity, they are forced to remain in proximity to each other, and the means of escape is removed. Captivity, therefore, could be considered a context in which behavior is altered. Generally, rates of aggressive behaviors are higher after the initial introduction conspecifics and gradually decrease over time (Marler, 1976). For example, Goodwin (1965) noted that often captive birds would initially be observed engaging in aggressive allopreening. However, over time, a more reciprocal form of allopreening would begin to develop in these captive birds (personal communication to Harrison, 1965).

A wide range of stereotypic behaviors, displayed by all species of captive animals, represent behavioral alterations brought about within the context of captivity. However, research in primate grooming and social support show similar patterns between wild and captive populations (Schino, 2006). Furthermore, Henzi and Barrett (1999) suggested that because grooming and coalition formation both were recorded occurring in captive populations, captivity did not, necessarily, prevent behaviors from being present. They suggest that coalition formation, particularly, is more important in a captive setting because it allows for the mitigation of aggression (Henzi & Barrett, 1999).

The form and function of grooming are assumed to be commensurate with grooming behavior in the wild, however here is evidence to dispute this equivalence (Honess, Gimpel, Wolfensohn, & Mason, 2005; Reinhardt, Reinhardt, & Houser, 1986). Some captive primates show signs of overgrooming, where grooming and hair pulling are performed with such frequency and/or vigor that the hair of the recipient animal is removed. While very little research has explored this behavior, most overgrooming instances in socially housed primates occur during grooming sessions (Honess et al., 2005; Reinhardt et al., 1986). This behavior has also been demonstrated in captive rabbits (Bradbury, 2016). It should be noted, that overgrooming is not a result of captivity alone, but it has only been observed in captivity.

Aggressive Grooming in Rodents

An example of captivity as a context for aggressive grooming is found in rodents. Grant and Mackintosh (1963) were the first to document aggressive grooming in any species. Specifically, they looked at the social postures of four rodent species. Each species (rat, mouse, golden hamster, and guinea pig) demonstrated aggressive grooming. Social grooming in rodents involves one animal licking and running its mouth over the fur of a conspecific. This sometimes can include the use of the forepaws. Aggressive grooming, by contrast, includes the use of teeth, pulling of fur, and the act itself is more intense than affiliate allogrooming. Aggressive grooming is predominantly directed to the shoulder area of the groomee. Of the threat, attack, and aggressive postures recorded, over half were followed by aggressive grooming behavior (Grant & Mackintosh, 1963). In this case, the form differs slightly, yet the primary differentiator is still based on intensity level, but the antecedent behaviors predict the function of grooming.

Grant (1963) sequenced two separate behavior pathways in male laboratory rats (*Rattus norvegicus*). One pathway was reflective of the behaviors of the aggressive animal and started with an attend behavior and ending with an aggressive posture or an aggressive groom. The other pathway reflected the submissive animal and ended with either a submissive posture or a crouch behavior. He suggested that both the crouch and aggressive groom behaviors were a result of confinement and an inability to retreat. Fights in a confined context have the potential to be more dangerous, and therefore, it would be more prudent to express the aggressive drive in a way other than attacking (Grant, 1963).

Aggressive Grooming in the Domestic Cat

The domestic cat (*Felis catus*) has also been observed performing grooming as an aggressive behavior, but only when escape is prevented (Brown, 1993). Researchers concluded that grooming could be a redirection of aggression brought on by a confined space (Van den Bos, 1998). Outright aggression while in confinement could be costly and aggressive grooming would allow the individual to assert dominance over a lower rank without incurring the high cost of injury. When the density of a cat population is high, the grooming rates are also high, while when density is low, overt aggression is more likely to occur, but rates of agonism, overall, are less. Additionally, less grooming occurred overall in free-ranging groups where the density remained low (Brown, 1993). This is typically what happens with aggressive behaviors, the denser a population, the more pronounced the rates of aggression (Price & Stoinski, 2007). Also in line with typical aggressive behaviors was the decrease of agonism between unrelated feline individuals after being housed together for a period of time (Curtis, Knowles, &Crowell-Davis, 2003).

When Brown (1993) studied the social behaviors in domestic cats grooming was more closely related to agonistic behaviors than affiliative (see also: Van den Bos & de Vries, 1996). However, this was based on factor analysis, and none of the cat studies to date have attempted to assess grooming within a behavioral sequence. Patterns of behavior in sequence may be more informative to the function of aggressive grooming.

Grooming in Bushbabies

Garnett's Bushbaby (*Otolemur garnettii*) is a nocturnal, African strepsirhine. They are primarily arboreal and omnivorous. The males have larger, overlapping territories that also overlap several female territories (Bearder, 1999). Bushbabies also share some behavioral characteristics with rats and domestic cats that make them a potential exemplar for aggressive grooming in a primate species. All three species are predominantly nocturnal. They rely heavily on their olfactory capabilities. In fact, strepsirhines retain the largest proportional vomeronasal organ among the primates (Garrett et al., 2013). They are semi-solitary with small, interrelated groups of females forming sleeping groups during the day. Communication in rats, cats, and bushbabies relies heavily on chemosensory ability. Like cats and rats, bushbabies have multiple scent glands and deposit urine, as well as other scents, on substrates within their territory. Therefore, we argue that they may potentially show evidence of aggressive grooming, even though it has never been shown in a primate species.

Previous studies of grooming in *Otolemur* species have shown two forms of grooming solicitation, head down and outstretched arm (Ehrlich, 1977). The majority of solicitation was head down. However, most grooming was not solicited. When grooming was solicited, it was often not successful. However, this study only looked at male/female dyads. Social grooming usually involved a face to face stance with the recipient sitting and the groomer either sitting or half-sitting. Often the groomer would grab the groomee while using tongue and toothcomb and the majority of grooming was to the face, head, and neck region (Ehrlich, 1977). It was not uncommon for roles to switch (groomer becoming the groomee) and many solicitors, when unsuccessful, groomed instead, which could lead to being groomed. One of the hallmarks of grooming among primates is the relaxed posture that the recipient assumes while being groomed. (Goodall, 1986; Yerkes, 1948). However, Ehrlich (1977) noted that when female bushbabies were being groomed, they held their ears back and had a visibly tense posture. They would even vocalize threat noises during the process.

In bushbabies, fights occur much less than other agonistic behaviors (Ehrlich, 1977). Most agonistic encounters are unidirectional, usually in the form of an attack or threat. Females are more aggressive than males and generally that aggression is focused toward the male. Overall, most agonistic encounters ended with the recipient leaving. Out of 469 agonistic encounters, 239 were brought about by typically affiliative behaviors. Although not reported, 58 of those encounters were instigated by grooming, which was more than double the number of post-conflict grooming encounters. It should be noted that almost all of these encounters were between male/female dyads and usually ended with an abrupt depart of one individual. However, more often, individuals just avoided interaction completely (Ehrlich, 1977).

Drews (1973) used grooming as one index for determining dominance in *O. crassicaudatus*, a closely related species of bushbaby. He recorded grooming rejections which included the recipient rearing in threat, slapping, pushing, or lunging, but this was coded separately from agonistic behaviors. He found that marking, displacement, and agonistic encounters won were correlated with each other but not grooming or grooming rejection. However, due to the small number of subjects (N=4), no correlation coefficients could be reported. He also found that when conspecifics were first introduced, grooming rates were higher, then dropped to a more stable rate, and within a few days, he observed only a low number of grooming rejections. Consistent with these results, Edens (2013) observed a decreasing number of grooming interactions across time when observing the social behavior of five female Garnett’s Bushbabies. This is important because if grooming was a constantly affiliative behavior, it should increase over time, instead of decrease. This decrease in grooming is more typical of an agonistic behavioral trend. This is also consistent with cats (Curtis et al., 2003). Edens (2013) also found a strong positive correlation between displacements and grooming frequencies that suggest grooming might be agonistic.

While avian and non-primate mammalian literature views grooming as a behavior where social function is determined by context, primate literature assumes function independent of context. Birds and non-primate mammals groom both as an agonistic and affiliative behavior. It may be that the function of primate grooming is also context dependent. This study investigated the function of grooming in female *Otolemur garnettii*, based on the context surrounding the behavior rather than in isolation. Sequences of behavior were used to infer that function. No other exploration of primate social behavior has examined the possibility of aggressive grooming.

CHAPTER III - METHODS

Subjects[1]

Five captive, female Garnett's Bushbabies resident at The University of Southern Mississippi's Primate Behavior Research Facility were used in the study. The subjects ranged in age from 5-15 years (M = 10). None of the females were pregnant, lactating, or recently pregnant at the time of data collection and had varying levels of relatedness. All five bushbabies were housed individually in 152.4 cm x 106.68 cm x 76.2 cm cages before the experiment, and none had previously shared a cage with another adult female. They were maintained on a diet of ad libitum monkey chow, supplemented with fresh fruit. Water was provided ad libitum. The bushbabies were kept under a 12:12 reverse light cycle which was not modified during the course of the experiment. The housing and procedures are in accordance with all state, federal, and institutional regulations.

Apparatus

All parts of this study took place in an open field apparatus. The open field was constructed of caging material (stainless steel frame and plastic coated wire mesh) measuring 239 cm x 147 cm x 239 cm. Plastic enrichment and wooden sticks were provided in the testing environment. The placement of enrichment and sticks was replicated as closely as possibly across the habituation phase (dyadic interaction) and the testing phase (group interaction). Behavior was then recorded on a digital video camera (Sony, Model #DCR-SR42) using the night mode.

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[1] Video data is taken from a previous study (see: Edens, 2013).

Procedure

All five bushbabies were introduced to the open field by allowing them to individually explore the area for 20 minutes. During the habituation phase, the females were placed in the open field in pairs for 20 minutes on two separate occasions. All behavior was recorded. In the group housing phase, all five females were placed in the open field where they remained 24 hours a day for seven days. All females were removed, kept separated for several weeks, and then returned for another seven days of group housing. During this phase, behavior was recorded in 20-minute intervals three times a day: morning, afternoon, and evening. There were 400 minutes of dyadic behavior recorded and 840 minutes of group interaction recorded, and this provided 1240 minutes of recorded behavior.

Code Definition

Behavior lists were developed using preexisting observational recording and ethograms of bushbaby behavior, in addition to personal, in situ observation. In particular, behaviors known to correlate with grooming (Edens, 2013) and behaviors that might correlate but have not been previously analyzed.

Behavioral interaction codes were established using the following format: $ARBxM_1M_2$, where A represents the actor of the during the behavior interaction, R represents the recipient of the interaction, Bx represents the behavior being coded, and M_1 and M_2 represent any modifiers that should be applied to that behavior. Some behaviors have no modifiers, some have one modifier, and some have two. No more than two modifiers were attached to any behavior. Animal identifier codes used the second letter of the name, as that is unique to the five individuals. For example, Piper sniffs

Brandine's tail while grasping her back. This is a behavior with two modifiers. The actor is Piper (I), and the recipient is Brandine (R). The behavior is sniffing (Sn). The first modifier is the body part sniffed, tail (T), and the second modifier is the grasping (G). So, the code for the interaction would be IRSnTG. Each behavior is tied to specific possible modifiers (see Appendix A for a list of all behaviors and corresponding codes and Appendix B for full descriptions of the behaviors).

Coding

Of the 400 minutes of dyadic interaction, there were 94 grooming occurrences. There were another 127 occurrences in group interactions. This gives a total of 221 grooming interactions across the 1240 minutes of recorded behavior. Each of these instances has been time stamped. Sequences of behavior were recorded using the time stamps as a reference, beginning at the initiating behavior of the grooming interaction. Often, this was the start of an approach behavior by either of the individuals involved. Behaviors were listed, in sequence, until five behaviors beyond the grooming interaction were recorded. In the event that another grooming instance happened during the five consequent behaviors, an additional five behaviors were recorded after that occurrence. This continued until five non-grooming behaviors concluded or the video ended.

Behavioral Sequence Analysis

Behavioral sequential analysis utilizes systematic observation using predetermined behavioral codes to quantify dynamic behavioral sequences. It encompasses the entirety of a social interaction within context. The sequence of events was scripted and entered into Sequential Data Interchange Standard (SDIS). This code was then entered into a Generalized Sequential Querier (GSEQ). Two independent coders were used. Interrater reliability coefficient was calculated using Cohen's Kappa on 20% of overlapping data, $\kappa = .89$.

Originally it was expected that the sequences of behavior would be analyzed using a log-linear analysis. However, a large number of possible behavior transitions resulted in zero frequencies. Therefore, the sequences of behavior were analyzed using conditional probability and adjusted residuals from contingency tables from each behavior transition (lag) (Bakeman & Quera, 1995).

Superordinate Codes

The main interest of this study rests on types of behaviors, and many of the variables are easily categorized, we recoded variables reflect the data of interest. First, codes were modified so that the actor and recipient placeholders in the codes were replaced with either a D for dominant or an S for submissive based on which was performing the behavior. All but two interactions recorded were pairings, and dominance and submissive status was based on the linear hierarchy Edens (2013) established for these individuals. Therefore, if the actor performing the behavior ranks higher than the other individual in the interaction, the code begins with a D. Two of the codes were a mutual behavior (Mg = mutual grooming and No = nosing) and did not have a dominant or submissive tag.

Additionally, superordinate codes were created that combined codes categorically. Two behavior codes (Am = grooming, and Sn = sniffing) had modifiers for the body part on which it took place. However, as these modifiers provide limited information beyond body part preference, all grooming and sniffing codes were combined under the dominate/submissive label. DomGroom encompassed all dominate grooming behaviors, and SubGroom encapsulated all submissive grooming behaviors. The same was repeated for sniffing behaviors as well as approach behaviors. All remaining submissive/dominant behavior codes, with the exception of the spatial relation and stand codes, were then divided between submissive/dominant agonist and affiliative codes. In this initial grouping of behavior codes, spatial relation codes were left separate based on type (stay, follow, leave), but the stand code was lumped with the stay code. The mutual groom and nose code remained the same.

CHAPTER IV – RESULTS

Over the course of this study, 193 behavior sequences were recorded resulting in 221 grooming instances. After the development of the superordinate codes, these 193 behavior sequences produced 1,647 individual behaviors. Overall grooming is a product of three grooming codes: mutual groom, dominant groom, and submissive groom. The frequencies of these behaviors differ significantly, $\chi^2(2, n=221) = 15.827, p.<.001$, with dominant groom representing 44% of grooming instances and submissive groom accounting for 25%. This suggests that bushbabies groom preferentially down the hierarchy. Rates of grooming also vary across the time frame of conditions (see Figure 1) with mutual grooming trending downward and dominant grooming trending upward across conditions. However, a Chi-squared did not show a significant difference, $\chi^2(6, n=221) = 9.4622$, p.=ns. Additionally, bushbabies do show preference for grooming, $\chi^2(4, n=142) =225.631, p.<.001$, and sniffing the head, $\chi^2(4, n=219) = 42.011, p.<.001$ (See Table 1).

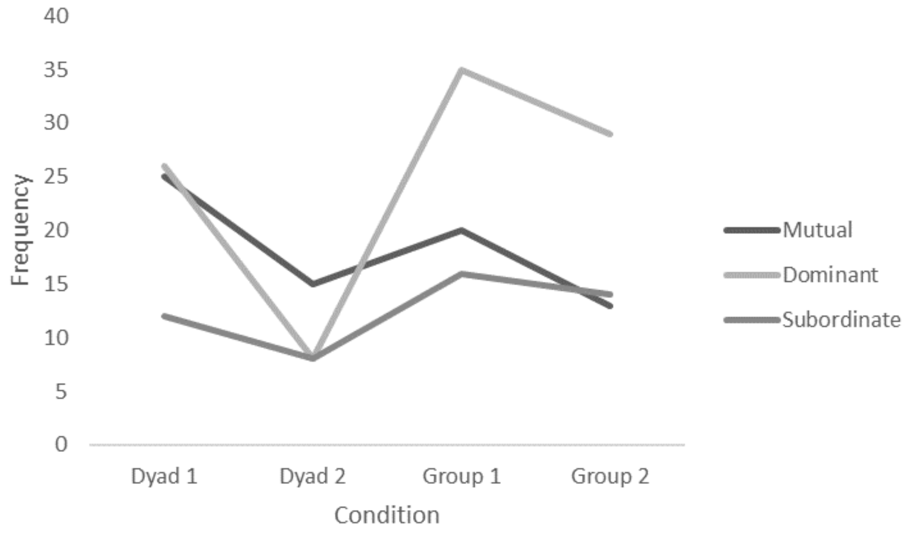

Figure 1. Grooming Frequencies Across Conditions

Table 1

Frequencies of Targeted Body Part for Sniffing and Grooming Behaviors

Behavior	Head	Neck	Torso	Anogenital	Limb	Tail
Grooming	97	29	8	3	4	1
Sniffing	70	21	30	26	34	3

To assess the sequences of behavior, contingency tables were calculated for Lag -2 Lag-1 Lag1, Lag2, and Lag3, where Lag 0 represented grooming behavior. There was not enough data for Lag -2 because many approaches initiated an immediate grooming occurrence, so it is not included. Lag 3 was not significant and was dropped, $\chi^2(48) = 59.97$, $p=.18$. Therefore, only associations between Lag -1, Lag 1, and Lag 2 were used. Lag -1 represents all behaviors that precede grooming behaviors. Frequencies were not large enough to examine the data across and between conditions, so all contingency tables were calculated with the total frequencies of behavior.

Mutual grooming was generally preceded (Lag -1) by one of four behaviors ($\chi^2(24) = 180.93$, $p=<.01$). The most likely preceding behavior was nosing (23%) with submissive approach (16%), and dominant sniffing a submissive (also 16%) the next most likely. Interestingly, a mutual grooming episode was also frequently preceded by a submissive performing an agonistic behavior (13%), suggesting that agonism is woven throughout grooming in these behavioral sequences. A dominant grooming a submissive was most likely initiated by dominant sniffing a submissive (24%), followed closely by dominant approach (21%). Once again likely was submissive agonism (17%), with a higher probability than when it preceded mutual grooming. Also, submissive stay (4%) was a probable initiator. When a submissive groomed a dominant, it was most likely proceeded by either the submissive approach (28%) or a dominant agonism (23%). All types of grooming have some form of agonism likely to precede the event. Additionally, when only the most likely preceding behavior is taken into account, it appears that the initiator of the previous behavior determines the type of grooming that occurs. Nosing, a mutual behavior precedes mutual grooming. A dominant approach most likely precedes dominant grooming behavior, and a submissive approach leads to a submissive groom behavior (See Table 2 & 3).

A dominant grooming a submissive and mutual grooming were both followed (Lag 1) by the same probable behaviors ($\chi^2(24) = 176.70$, $p = <.01$). Both were most likely followed by the submissive leaving (22% and 28% respectively), with the dominant leaving (13%, 22%) as the next likely behavior, suggesting that the most common response to grooming, is leaving the area. Dominant agonism is also a probable response to a dominant groom (13%) or a mutual groom (11%), suggesting that agonism is not just likely to precede grooming, but to follow it as well. Submissive groom had no significant associations with subsequent behaviors (see Tables 4 & 5). Taken overall, the most common response to grooming is to leave the occurrence. The second most common response is an agonistic behavior. This is counter to what one would expect if grooming were an affiliative behavior.

The most likely behavior to follow the subsequent behavior (Lag 2) was consistent across all types of grooming ($\chi^2(24) = 154.91$, $p = <.01$). Dominant stay/stand was the most likely behavior to occur across all grooming types with conditional probabilities of 46% for mutual groom, 21% for dominant groom, and 24% for submissive groom. The only other significant positive association is submissive stay/stand (24%) after dominant groom. However, these statistics are difficult to interpret because they include both stay and stand. In Lag 1, submissive leave was the most likely behavior, and dominant leave was also significantly likely to happen. These leaves often ended in standing behavior removed from the proximity of the grooming occurrence (see Tables 6 & 7).

Contingency tables were also calculated looking at the dominant and submissive behaviors overall. One table used dominant behaviors as Lag 0 and submissive behaviors as Lag 2. This configuration gives the likelihood of a submissive behavior given any dominant behavior. All behaviors are given in Tables 8 and 9, but only two behaviors of interest are presented here. Dominant agonism is associated with two subsequent behaviors: submissive agonism (20%) and submissive groom (18%), suggesting an equivalence between grooming and agonism. Dominant affiliative behaviors are also only associated with two behaviors: submissive stay (31%) and submissive affiliative (28%). Additionally, when the initiating behavior is affiliative, the submissive is most likely to stay or return an affiliative behavior. Recall that the most common response to grooming was leaving. If grooming were affiliative, it would be expected that the recipient would stay and/or return affiliative behavior, as we see here with other affiliative behaviors.

A second contingency table was generated to look at submissive behaviors (Lag 0) and the subsequent dominant response (Lag 1). All behaviors are listed in Tables 10 and 11, but we only present the two behaviors of interest. Submissive agonism is associated with dominant grooming (18%) and dominant agonism (13%). This is similar to what we see in response to dominant agonism, but with submissive agonism, the more likely response is grooming rather than agonism. Submissive affiliative behaviors are only positively associated with dominant stay (36%). Again, we see that affiliative behaviors are followed by a stay behavior.

Table 2

Joint Frequencies and Conditional Probabilities for Grooming Types and Lag -1 Behavior

	Target									
Given	No	SubSniff	SubStay/Sd	SubAgon	DomAgon	DomSniff	DomApp	SubApp	All Other	Totals
MutGroom	16(.23)	2(.03)	4(.06)	9(.13)	3(.04)	11(.16)	7(.10)	11(.16)	7(.10)	70
DomGroom	5(.05)	6(.06)	4(.04)	16(.17)	2(.02)	23(.24)	20(.21)	5(.05)	13(.14)	94
SubGroom	5(.11)	4(.09)	2(.04)	0(.00)	11(.23)	2(.04)	5(.11)	13(.28)	5(.14)	47
All Other	20(.02)	58(.12)	146(.12)	62(.05)	45(.04)	77(.06)	94(.08)	33(.03)	670(.56)	1205
Totals	46	70	156	87	61	113	126	62	695	1416

Note: Joint frequencies are listed outside parentheses, while conditional probabilities are listed within. Target behaviors that had less than five frequencies were placed in the all other variable. MutGroom = mutual groom; DomGroom = dominant groom; SubGroom = submissive groom; SubSniff = submissive sniff; SubStay/Sd = submissive stay or stand; SubAgon = submissive agonism; DomAgon = dominant agonism; DomSniff = dominant sniff; DomApp = dominant approach; SubApp = submissive approach.

Table 3

Adjusted Residuals for Grooming Types and Lag -1 Behavior

	Target								
Given	No	SubSniff	SubStay/Sd	SubAgon	DomAgon	DomSniff	DomApp	SubApp	All Other
MutGroom	9.49**	-.83	-1.45	2.40*	-.01	2.45*	.33	4.75**	-6.71**
DomGroom	1.17	.67	-2.14*	4.55**	-1.08	6.11**	4.36**	.46	-7.08**
SubGroom	2.91	1.15	-1.51	-1.78	6.56**	-.96	.43	7.93**	-5.36**
All Other	-8.06**	-.54	3.16**	-3.74**	-2.54**	-5.28**	-3.47**	-7.21**	11.73**

Note. Positive number indicate a behavior is more likely to occur, negative numbers indicate a behavior is less likely to occur. MutGroom = mutual groom; DomGroom = dominant groom; SubGroom = submissive groom; SubSniff = submissive sniff; SubStay/Sd = submissive stay or stand; SubAgon = submissive agonism; DomAgon = dominant agonism; DomSniff = dominant sniff; DomApp = dominant approach; SubApp = submissive approach.

*p<.05. **p<.01.

Table 4

Joint Frequencies and Conditional Probabilities for Grooming Types and Lag 1 Behavior

	Target									
Given	DomSniff	DomStay/Sd	DomLea	DomAgon	SubSniff	SubStay/Sd	SubAgon	SubLea	All Other	Totals
MutGroom	3(.04)	1(.01)	16(.22)	8(.11)	1(.01)	15(.21)	7(.10)	20(.28)	1(.01)	72
DomGroom	9(.09)	7(.07)	14(.13)	12(.13)	9(.09)	8(.08)	8(.08)	21(.22)	7(.07)	95
SubGroom	8(.16)	6(.12)	3(.06)	4(.08)	4(.08)	8(.16)	6(.12)	8(.16)	3(.06)	50
All Other	107(.09)	134(.11)	78(.06)	44(.04)	72(.06)	156(.13)	74(.06)	95(.08)	439(.37)	1199
Totals	127	148	111	68	86	187	95	144	450	1416

Note. Joint frequencies are listed outside parentheses, while conditional probabilities are listed within. Target behaviors that had less than five frequencies were placed in the all other variable. MutGroom = mutual groom; DomGroom = dominant groom; SubGroom = submissive groom; DomSniff = dominant sniff; DomStay/Sd = dominant stay or stand; DomLea = dominant leave; DomAgon = dominant agonism; SubSniff = submissive sniff; SubStay/Sd = submissive stay or stand; SubAgon = submissive agonism; SubLea = submissive leave.

Table 5

Adjusted Residuals for Grooming Types and Lag 1 Behavior

	Target								
Given	DomSniff	DomStay/Sd	DomLea	DomAgon	SubSniff	SubStay/Sd	SubAgon	SubLea	All Other
MutGroom	-1.46	-2.58*	4.66**	2.57*	-1.71	1.96	1.05	5.07**	-5.68**
DomGroom	.18	-1.02	2.59*	3.70**	1.44	-1.43	.69	3.99**	-5.29**
SubGroom	1.77	.36	-.49	1.08	0.58	.59	1.52	1.39	-3.99**
All Other	-.14	2.09	-4.09**	-4.69**	-.25	-.51	-1.90	-6.57**	9.18**

Note. Positive numbers indicate a behavior is more likely to occur, negative numbers indicate a behavior is less likely to occur. MutGroom = mutual groom; DomGroom = dominant groom; SubGroom = submissive groom; DomSniff = dominant sniff; DomStay/Sd = dominant stay or stand; DomLea = dominant leave; DomAgon = dominant agonism; SubSniff = submissive sniff; SubStay/Sd = submissive stay or stand; SubAgon = submissive agonism; SubLea = submissive leave.

*p<.05. **p<.01.

Table 6

Joint Frequencies and Conditional Probabilities for Grooming Types and Lag 2 Behavior

	Target									
Given	DomSniff	DomStay/Sd	DomLea	DomAgon	SubSniff	SubStay/Sd	SubAgon	SubLea	All Other	Totals
MutGroom	0(.00)	33(.46)	1(.01)	3(.04)	2(.03)	13(.18)	6(.08)	5(.07)	9(.13)	72
DomGroom	3(.03)	20(.21)	9(.10)	5(.05)	5(.05)	23(.24)	5(.05)	10(.11)	14(.15)	94
SubGroom	3(.06)	12(.24)	5(.10)	2(.04)	1(.02)	11(.22)	1(.02)	8(.16)	7(.14)	50
All Other	86(.09)	78(.24)	96(.10)	53(.05)	64(.06)	122(.12)	65(.06)	118(.12)	325(.32)	1007
Totals	92	143	111	63	72	169	77	141	355	1223

Note. Joint frequencies are listed outside parentheses, while conditional probabilities are listed within. Target behaviors that had less than five frequencies were placed in the all other variable. MutGroom = mutual groom; DomGroom = dominant groom; SubGroom = submissive groom; DomSniff = dominant sniff; DomStay/Sd = dominant stay or stand; DomLea = dominant leave; DomAgon = dominant agonism; SubSniff = submissive sniff; SubStay/Sd = submissive stay or stand; SubAgon = submissive agonism; SubLea = submissive leave.

Table 7

Adjusted Residuals for Grooming Types and Lag 2 Behavior

	Target								
Given	DomSniff	DomStay/Sd	DomLea	DomAgon	SubSniff	SubStay/Sd	SubAgon	SubLea	All Other
MutGroom	-2.49*	9.29**	-2.34*	-.39	-1.16	1.07	.73	-1.26	-3.18**
DomGroom	-1.66	3.01**	.18	.08	-.24	3.11**	-.41	-.28	-3.14**
SubGroom	-.42	2.77*	.23	-.38	1.19	1.71	-1.28	1.01	-2.39*
All Other	2.91	-9.27**	1.20	38	1.50	-3.73**	0.49	.45	5.40**

Note. Positive numbers indicate a behavior is more likely to occur, negative numbers indicate a behavior is less likely to occur. MutGroom = mutual groom; DomGroom = dominant groom; SubGroom = submissive groom; DomSniff = dominant sniff; DomStay/Sd = dominant stay or stand; DomLea = dominant leave; DomAgon = dominant agonism; SubSniff = submissive sniff; SubStay/Sd = submissive stay or stand; SubAgon = submissive agonism; SubLea = submissive leave.

*p<.05. **p<.01.

Table 8

Joint Frequencies and Conditional Probabilities for Dominant and Subsequent Submissive Behaviors

	Target									
Given	SubApp	SubSniff	SubFoll	SubStay/Sd	SubLea	SubAgon	SubAff	SubGroom	All Other	Totals
DomApp	0(.00)	2(.02)	0(.00)	17(.13)	2(.02)	17(.13)	0(.00)	5(.04)	83(.66)	126
DomSniff	0(.00)	11(.10)	0(.00)	3(.03)	23(.20)	15(.13)	2(.02)	2(.02)	57(.50)	113
DomFoll	0(.00)	2(.04)	0(.00)	15(.33)	2(.04)	2(.04)	0(.00)	0(.00)	25(.54)	46
DomStay/Sd	4(.03)	7(.06)	1(.01)	40(.33)	17(.14)	4(.04)	10(.08)	0(.00)	40(.33)	123
DomLea	2(.02)	5(.05)	16(.17)	37(.40)	10(.11)	2(.03)	4(.04)	0(.00)	16(.17)	92
DomAgon	0(.00)	6(.10)	0(.00)	7(.11)	5(.08)	12(.20)	2(.03)	11(.18)	18(.30)	61
DomAff	1(.03)	2(.07)	0(.00)	9(.31)	2(.07)	0(.00)	8(.28)	0(.00)	7(.24)	29
DomGroom	0(.00)	9(.09)	0(.00)	8(.08)	21(.22)	8(.08)	0(.00)	1(.01)	48(.51)	95
All Other	6(.01)	42(.06)	3(.00)	51(.07)	62(.08)	35(.05)	12(.02)	28(.04)	492(.67)	731
Totals	13	86	20	187	144	95	38	47	786	1416

Note. Joint frequencies are listed outside parentheses, while conditional probabilities are listed within. Target behaviors that had less than five frequencies or did not have a dominant/submissive designation were placed in the all other variable. DomApp = dominant approach; DomSniff = dominant sniff; DomFoll = dominant follow; DomStay/Sd = dominant stay or stand; DomLea = dominant leave; DomAgon = dominant agonism; DomAff = dominant affiliative; DomGroom = dominant groom. Base codes are repeated for submissive behaviors.

Table 9

Adjusted Residuals for Dominant and Subsequent Submissive Behaviors

	Target								
Given	SubApp	SubSniff	SubFoll	SubStay/Sd	SubLea	SubAgon	SubAff	SubGroom	All Other
DomApp	-1.13	-2.21*	-1.41	.10	-3.34**	3.19**	-1.95	.43	2.45*
DomSniff	-1.07	1.70	-1.33	-3.45**	3.73**	2.91**	-.63	-.96	-1.13
DomFoll	-.66	-.50	-.83	3.95**	-1.33	-.65	-1.15	-1.28	-.16
DomStay/Sd	2.84**	-.19	-.59	6.62**	1.40	-1.60	3.91**	-2.15*	-5.37**
DomLea	1.31	-.27	13.43**	7.91**	.23	-1.80	1.02	-1.84	-7.61**
DomAgon	-.77	1.26	-.96	-.41	-.52	4.14**	.29	6.56**	-4.18**
DomAff	1.44	.19	-.65	2.87**	-.59	-1.46	8.38**	-1.01	-3.43**
DomGroom	-.97	1.44	-1.21	-1.43	3.99**	.69	-1.68	-1.28	-1.01
All Other	-.40	-.53	-3.30	-7.15**	-2.17*	-2.98**	-2.51*	1.11	9.23**

Note. Positive number indicate a behavior is more likely to occur; negative numbers indicate a behavior is less likely to occur. DomApp = dominant approach; DomSniff = dominant sniff; DomFoll = dominant follow; DomStay/Sd = dominant stay or stand; DomLea = dominant leave; DomAgon = dominant agonism; DomAff = dominant affiliative; DomGroom = dominant groom. Base codes are repeated for submissive behaviors.

*p<.05. **p<.01.

Table 10

Joint Frequencies and Conditional Probabilities for Submissive and Subsequent Dominant Behaviors

	Target									
Given	DomApp	Dom Sniff	DomStay /Sd	DomFoll	Dom Agon	DomLea	DomAff	Dom Groom	All Other	Totals
SubApp	0(.00)	1(.02)	4(.06)	0(.00)	0(.00)	1(.02)	0(.00)	5(.08)	51(.82)	62
SubSniff	0(.00)	10(.14)	9(.13)	1(.01)	7(.10)	5(.07)	2(.03)	6(.09)	30(.43)	70
SubStay/Sd	4(.03)	17(.11)	49(.31)	1(.01)	5(.03)	14(.09)	14(.09)	4(.03)	48(.31)	156
SubFoll	1(.06)	0(.00)	1(.06)	0(.00)	0(.00)	1(.06)	0(.00)	2(.12)	12(.71)	17
SubAgon	1(.01)	11(.13)	9(.10)	1(.01)	11(.13)	10(.11)	0(.00)	16(.18)	28(.32)	87
SubLea	1(.01)	5(.04)	33(.27)	41(.34)	2(.02)	10(.08)	2(.02)	1(.01)	26(.21)	121
SubAff	1(.04)	1(.04)	9(.36)	0(.00)	0(.00)	4(.16)	1(.04)	0(.00)	9(.36)	25
SubGroom	0(.00)	8(.16)	6(.12)	0(.00)	4(.08)	3(.06)	0(.00)	1(.02)	28(.56)	50
All Other	8(.01)	74(.09)	28(.03)	6(.01)	39(.05)	63(.08)	17(.02)	59(.07)	534(.64)	828
Totals	16	127	148	50	68	111	36	94	766	1416

Note. Joint frequencies are listed outside parentheses, while conditional probabilities are listed within. Target behaviors that had less than five frequencies were placed in the all other variable. DomApp = dominant approach; DomSniff = dominant sniff; DomFoll = dominant follow; DomStay/Sd = dominant stay or stand; DomLea = dominant leave; DomAgon = dominant agonism; DomAff = dominant affiliative; DomGroom = dominant groom. Base codes are repeated for submissive behaviors.

Table 11

Adjusted Residuals for Submissive and Subsequent Dominant Behaviors

	Target								
Given	DomApp	DomSniff	DomStay /Sd	DomFoll	DomAgon	DomLea	DomAff	DomGroom	All Other
SubApp	-.86	-2.07*	-1.05	-1.54	-1.81	-1.87	-1.30	.46	4.55**
SubSniff	-.92	1.60	.67	-.98	2.09*	-.22	.17	.67	-1.94
SubStay/Sd	1.80	.89	9.07**	2.07*	-.99	.56	5.41**	-2.17*	-6.20**
SubFoll	1.87	-1.30	-0.62	-.79	-.93	-.30	-.67	.85	1.37
SubAgon	.02	1.24	-.03	-1.24	3.53**	1.31	-1.56	4.55**	-4.23**
SubLea	-.33	-1.95	6.32**	18.92**	-1.69	.18	-.65	-2.69*	-7.53**
SubAff	1.37	-.88	4.21**	-.97	-1.13	1.53	.47	-1.35	-1.83
SubGroom	-.77	1.77	.36	-1.38	1.08	-.49	-1.16	-1.34	.28
All Other	-.69	-.05	-10.32**	-6.79**	-.19	-.38	-1.39	.87	9.32**

Note. Positive number indicate a behavior is more likely to occur; negative numbers indicate a behavior is less likely to occur. DomApp = dominant approach; DomSniff = dominant sniff; DomFoll = dominant follow; DomStay/Sd = dominant stay or stand; DomLea = dominant leave; DomAgon = dominant agonism; DomAff = dominant affiliative; DomGroom = dominant groom. Base codes are repeated for submissive behaviors.

*p<.05. **p<.01.

CHAPTER V – DISCUSSION

Results support the hypothesis that grooming between same-sex conspecifics in captive Garnett's bushbabies is apparently an agonistic behavior. It is evident that spatial proximity proved an important variable for assessing context in bushbaby behavior. The most common subsequent behavior following a grooming bout was to leave, regardless of type. While a corresponding leave behavior may not intuitively imply that the previous behavior was agonistic, the results strongly suggest that affiliative behaviors are more likely to be followed by a stay behavior. Beyond mere proximity, the association between agonism and grooming has become apparent, and they seem almost interchangeable in response to agonism. There has never been a documented example of agonistic grooming in a primate species.

There has been no consensus of the functional significance of primate grooming with three predominant hypotheses ranging from fulfilling a simple hygienic function to grooming being a traded commodity. In all cases, it is assumed that grooming is beneficial to the recipient and that it is affiliative in nature (Russell & Phelps, 2013). However, grooming in Garnett's Bushbaby functions as an agonistic behavior and therefore grooming may be even more complicated than has been previously thought. My results illustrate the importance of using situational context and proximity when evaluating primate grooming behavior.

Grooming is part of the establishment of dominance hierarchies in primates, and these results align with that assumption. Usually, grooming is used to assess affiliative relationships between dominance ranks, whereas in this colony of bushbabies it appears that grooming merely represents a way of establishing and possibly maintaining dominance. While not significant, the trend in types of grooming across conditions is important. Mutual grooming may represent two bushbabies trying to assert dominance over each other as a reduction in this behavior occurred across time. The incidences of dominant grooming behavior started low, increased sharply, and then remained more prevalent than either submissive grooming or mutual grooming. To lend clarity, future research should investigate after the establishment of dominance, to see if dominant grooming remains consistent over time.

This study in no way assumes to explain why bushbabies groom agonistically. Nevertheless, I would like to suggest possible influencing mechanisms. As previously stated, agonistic grooming has been found in rodents (Grant & Mackintosh, 1963) and cats (Brown, 1998). These instances, as well as the current instances of agonistic grooming, were of animals within captivity. It is possible that the inability to escape from other conspecifics leads to a modification of behaviors to allow for agonism that is not outright aggression, avoiding possible injury or death. Other common characteristics of these species are a high reliance on olfaction and scent marking. Grooming could serve to remove the scent from a submissive conspecific, or some other mechanism of olfaction may lead to this behavior. Sociality might also be a factor. Bushbabies are not known for having strong social bonds typical of upper primates. It might be possible that grooming served an early evolutionary function that became repurposed as primate sociality advanced. The directionality of grooming might also play a factor in functionality. Grooming down the hierarchy may be functionally different than grooming up the hierarchy. Captive capuchins (*Cebus apella*) were shown to groom down the hierarchy (Parr et al., 1997) but are much more gregarious than bushbabies. Capuchins may be a good model for the expansion of knowledge in primate agonistic grooming. Lastly, nocturnality may play a factor.

The biggest drawback of this study was the low number of frequencies across behavior. This precluded log-linear analysis and the ability to examine the data across and between conditions. A much larger sample size would allow behaviors to be investigated individually and uncover the effects of modifiers. Yet, this is an important first step. The first observation of agonistic grooming in a primate species refutes the assumption that grooming in primates is always affiliative. Functional assessment of primate grooming behavior has always been challenging at best. The results of this study do not help clarify the matter, but rather add another potential dimension to an already convoluted task.

APPENDIX A – Ethogram and Codes

Table A1.

Ethogram and Codes

Coding Ethogram

Bushbaby	**Codes:**	**ID Shave Marks**
Brandine -	R	Shoulders
Pebbles -	E	Hips & Sides
Piper -	I	Sides
Sam -	A	Hips
Sybil -	Y	Hips & Shoulders

*** In the following behavior codes the first code "A" represents the "actor" of the behavior. As behavior is being coded, this "A" should be replaced with the appropriate Bushbaby code. (ex. If Pebbles is doing something the "A" should be replaced with "E".)

*** In the following behavior codes the second code "R" represents the "recipient" of the behavior. As behavior is being coded, this "R" should be replaced with the appropriate Bushbaby code. (ex. If Piper is receiving a behavior the "R" should be replaced with "I".) If the behavior does not a have a recipient, leave the "0" in the code.

Approach Behaviors

Codes	**Behaviors**
ARApSS	Slow Approach with Stare: a bushbaby locomotes at a normal walking pace, from a previous location towards a conspecific, coming at least within a body length, and has a fixed gaze on the conspecific being approached

ARApSN	Slow Approach without Stare:	a bushbaby locomotes at a normal walking pace, from a previous location towards a conspecific, coming at least within a body length, and **does not** have a fixed gaze on the conspecific being approached
ARApFS	Fast Approach with Stare:	a bushbaby locomotes at an accelerated pace beyond normal walking (could include long leaps), from a previous location towards a conspecific, coming at least within a body length, and has a fixed gaze on the conspecific being approached
ARApFN	Fast Approach without Stare:	a bushbaby locomotes at an accelerated pace beyond normal walking (could include long leaps), from a previous location towards a conspecific, coming at least within a body length, and **does not** fixed gaze on the conspecific being approached
MaS	Mutual Approach with Stare	Bushbabies approach each other at the same time while maintaining eye contact.
Ma	Mutual Approach without Stare	Bushbabies approach each other at the same time.

Sniffing Behaviors

Codes	**Behaviors**	
ARSnHG	Sniffing Head with Grasping	nose of the bushbaby comes into contact or close contact with the **head** of another bushbaby and the

		actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARSnHN	Sniffing Head with No Grasping	nose of the bushbaby comes into contact or close contact with the **head** of another bushbaby and the forelimbs are not engaged
ARSnNG	Sniffing Neck with Grasping	nose of the bushbaby comes into contact or close contact with the **neck** of another bushbaby and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARSnNN	Sniffing Head with No Grasping	nose of the bushbaby comes into contact or close contact with the **neck** of another bushbaby and the forelimbs are not engaged
ARSnOG	Sniffing Torso with Grasping	nose of the bushbaby comes into contact or close contact with the **torso** of another bushbaby and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARSnON	Sniffing Torso with No Grasping	nose of the bushbaby comes into contact or close contact with the **torso** of another bushbaby and the forelimbs are not engaged
ARSnFG	Sniffing Flank with Grasping	nose of the bushbaby comes into contact or close contact with the **flank** of another bushbaby and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs

ARSnFN	Sniffing Flank with No Grasping	nose of the bushbaby comes into contact or close contact with the **flank** of another bushbaby and the forelimbs are not engaged
ARSnLG	Sniffing Limb with Grasping	nose of the bushbaby comes into contact or close contact with any of the four **limbs** of another bushbaby and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARSnLN	Sniffing Limb with No Grasping	nose of the bushbaby comes into contact or close contact with any of the four **limbs** of another bushbaby and the forelimbs are not engaged
ARSnTG	Sniffing Tail with Grasping	nose of the bushbaby comes into contact or close contact with the **tail** of another bushbaby and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARSnTN	Sniffing Tail with No Grasping	nose of the bushbaby comes into contact or close contact with the **tail** of another bushbaby and the forelimbs are not engaged
ARSnAG	Sniffing Anogenital region with Grasping	nose of the bushbaby comes into contact or close contact with the **anogenital region** of another bushbaby and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs

ARSnAN	Sniffing Tail with No Grasping	nose of the bushbaby comes into contact or close contact with the **anogenital region** of another bushbaby and the forelimbs are not engaged

Allogrooming Behaviors

Codes	**Behaviors**	
ARAmHG	Allogrooming Head with Grasping	the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **head** of another bushbaby without reciprocation and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARAmHN	Allogrooming Head with No Grasping	the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **head** of another bushbaby without reciprocation and the forelimbs are not engaged
ARAmNG	Allogrooming Neck with Grasping	the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **neck** of another bushbaby without reciprocation and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARAmNN	Allogrooming Head with No Grasping	the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **neck** of another bushbaby without reciprocation and the forelimbs are not engaged
ARAmOG	Allogrooming Torso with Grasping	the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of

		the **torso** of another bushbaby without reciprocation and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARAmON	Allogrooming Torso with No Grasping	the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **torso** of another bushbaby without reciprocation and the forelimbs are not engaged
ARAmFG	Allogrooming Flank with Grasping	the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **flank** of another bushbaby without reciprocation and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARAmFN	Allogrooming Flank with No Grasping	the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **flank** of another bushbaby without reciprocation and the forelimbs are not engaged
ARAmLG	Allogrooming Limb with Grasping	the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of **any of the four limbs** of another bushbaby without reciprocation and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARAmLN	Allogrooming Limb with No Grasping	the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of **any of the four limbs** of another bushbaby

	without reciprocation and the forelimbs are not engaged
ARAmTG	Allogrooming Tail with Grasping the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **tail** of another bushbaby without reciprocation and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARAmTN	Allogrooming Tail with No Grasping the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **tail** of another bushbaby without reciprocation and the forelimbs are not engaged
ARAmAG	Allogrooming Anogenital region with Grasping the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **anogenital region** of another bushbaby without reciprocation and the actor grabs and maintains a hold of the fur or a body part of the recipient with at least one their forelimbs
ARAmAN	Allogrooming Anogenital region with No Grasping the mouth, including teeth, tongue, and/or dental comb comes into contact with the hair or skin of the **anogenital region** of another bushbaby without reciprocation and the forelimbs are not engaged

Presentation of Body Part

Codes	**Behaviors**
ARPbH	Presentation of Head One animal presents its head to the other animal for grooming. Grooming does not necessarily follow.

ARPbN	Presentation of Neck	One animal presents its neck to the other animal for grooming. Grooming does not necessarily follow.
ARPbO	Presentation of Torso	One animal presents its torso to the other animal for grooming. Grooming does not necessarily follow.
ARPbF	Presentation of Flank	One animal presents its flank to the other animal for grooming. Grooming does not necessarily follow.
ARPbL	Presentation of Limb	One animal presents its limb to the other animal for grooming. Grooming does not necessarily follow.
ARPbT	Presentation of Tail	One animal presents its tail to the other animal for grooming. Grooming does not necessarily follow.
ARPbA	Presentation of Anogenital region	One animal presents its anogenital region to the other animal for grooming. Grooming does not necessarily follow.

Agonistic Behaviors

Codes	**Behaviors**	
ARAgA	Attack	Bite, manual attack (slap, strike, pull, push, etc…)
ARAgT	Threat	

		attack with no contact, arched-back with front limbs rigid, bipedal standing with outstretched arms and/or bared teeth
ARAgF	Fight	mutual attack, in this instance, the actor is the initiator
ARAgD	Defensive Stance	rearing up with or without arms out (usually occurs after an aggressive act by the other)
ARAgS	Subordinance	head down (lower head and turn body away), flight (rapid, undirected withdrawal)

Ear Positions

Codes	**Behaviors**	
AREpU	Ears up	Ears erect and pointed forward
AREpB	Ears Back	Ears erect and swiveled to point back on the head
AREpF	Ears Flat	Ears flat against the head and neck, flush against body
AREpR	Ears Rolled/Folded	Ear skin rolled/folded down so that only the edges of ears are visible

Spatial Relation

Code	**Behaviors ***only coded after a grooming bout has ended**

ARSrLS	Leave w/ stare	One bushbaby deliberate moves out of the 12in range while staring at the other bushbaby, ending the bout.
ARSrL	Leave	One bushbaby deliberate moves out of the 12in range ending the bout.
ARSrF	Follow	One bushbaby moves deliberately after the other bushbaby and maintaining visual orientation to it, In this instance, the "actor" is the follower.
ARSrSS	Stay w/ stare	Bushbabies stay within a 12in proximity for at least 5 seconds after the bout ends and no contact occurs
ARSrS	Stay	Bushbabies stay within a 12in proximity for at least 5 seconds after the bout ends and no contact occurs

Other

Code	**Behavior**	
ARTL	Tail Lashing	Tail is swished quickly from side to side
ARMg	Mutual or Reciprocal Grooming	Both bushbabies groom each other
ARAu	Autogrooming	using tongue and toothcomb on self
ARSt	Stereotypy	generalized, repetitive, non-goal directed movement
ARSm	Scent Marking	

		the transfer of a scent from the bushbaby to another object or conspecific (can be Chest, Face, or Foot)
ARFt	Foot Rubbing	scraping the foot vigorously across a surface
ARNo	Nosing	both bushbabies touch their nose to the others nose
ARYa	Yawn	wide, open mouth that is often accompanied by the outstretching of tongue
ARRe	Rest	a period of inactivity
AREx	Explore	Bushbaby is wandering around the cage, with or without sniffing. No other behavior is included in this action.
ARSa	Startled	Bushbaby is interrupted from another behavior by another bushbaby. An abrupt change in body posture or a jump must be included.
OoC	Out of Camera	One or more bushbaby involved in the interaction is out of view from the camera.
ARSdS	Stand w/ stare	Bushbaby remains in one location while staring at an approaching bushbaby
ARSd	Stand w/o stare	Bushbaby remains in one place without performing a different behavior

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