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Effects of Food Dispersion on Dominance Related Behaviors in Garnett's Bushbaby (*Otolemur garnettii*)?

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The University of Southern Mississippi

EFFECTS OF FOOD DISPERSION ON DOMINANCE RELATED BEHAVIORS IN
GARNETT'S BUSHBABY (*OTOLEMUR GARNETTII*)?

by

Kyle Daniel Edens

Abstract of a Dissertation
Submitted to the Graduate School
of The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

May 2013

ABSTRACT

EFFECTS OF FOOD DISPERSION ON DOMINANCE RELATED BEHAVIORS IN GARNETT'S BUSHBABY (*OTOLEMUR GARNETTII*)?

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Socio-ecological theorists tie primate social structure diversity to variations in habitats within which primate species reside. This premise permits laboratory researchers to investigate specific factors that influence or relate to social structure formation and maintenance. The focus of the current investigation was three fold. We first aimed to determine the relationships between traditional and non-traditional behavioral measures of dominance, then evidence for dominance hierarchy formation was examined, and various hypotheses were tested to discern if adjustments in the foraging context altered social behaviors in Garnett's bushbaby (*Otolemur garnettii*). It was determined that animals likely to displace conspecifics were more apt to groom conspecifics. Animals likely to groom conspecifics did so for longer durations, and animals likely to arrive at the juice patch first were likely to feed more frequently and longer from the patch. There were no other consistent relationships between non-traditional and traditional measures of dominance. It was possible to construct dominance hierarchies from the directionality in displacement and grooming occurrences. Hierarchy construction using other agonistic interactions was not possible due to the inconsistent relationships with other behavioral measures, inconsistencies in the directionality of the occurrences, and extremely low rates of agonistic behavior. Similarly, the construction of hierarchies from feeding priority measures was not possible. The frequency of allo-grooming, duration of allo-

grooming, frequency of foraging on chow, and duration of foraging on chow decreased from the juice to the no juice conditions. Displacement interactions did not show a decrease in frequency. Although there was evidence that bushbabies are capable of constructing hierarchies, there was no conclusive evidence that dominance related measures were dictated by alterations in the foraging setting. This by no means invalidates socio-ecological theory. However, these findings suggest the dominance concept is more complex, warranting further investigations of social structure formation in Garnett's bushbaby and other prosimian primate species.

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CHAPTER I

INTRODUCTION

Investigations into the dominance concept among primates are quintessential to more thoroughly understanding the evolutionary significance of primate social behaviors. New insights (e.g., Isbell & Young, 2002) have hastened research efforts which are contributing a wealth of knowledge about the dominance concept in non-human primates. However, few researchers have studied the concept in prosimian primates; fewer yet have done so with regard to new theoretical positions and models. In order to fashion a more comprehensive understanding of the concept, as it relates to non-human primate behavior, it is necessary to include and reinforce investigations of prosimian primates. In doing so, researchers need be fastidious in their choice of behavioral measures, choosing those that historically are related to the original conceptualization of the dominance construct and appropriate for the target species' behavioral repertoire .

Conceptualization and Definitions of Dominance

Thorleif Schjelderup-Ebbe introduced the dominance concept to the animal behavior literature in the 1920's. He proposed domesticated hens (*Gallus domesticus*) formed dominance hierarchies to maintain peace within groups (Zuk, 2002). Since that time, however, the study of dominance has been plagued by inconsistency, circular definitions, and a host of other definitional and functional misconceptions (Drews, 1993). This has created confusion concerning the adaptive function of dominance hierarchies, as well as the adaptive functions of obtaining and maintaining high dominance ranks within social groups.

In an attempt to introduce consistency into the concept, Drews (1993) reviewed many commonly employed measures and definitions of dominance in the literature.

These definitions and measures ranged from measuring aggressiveness and attributing high social status to the most aggressive animals, to high social status being assigned to the animals that obtained preferential access to resources (e.g., food). Although these constructs are presumed to be good measures of dominance, in other literature (e.g., Dewsbury, 1982; Sterck, Watts, & Van Schaik, 1997), Drews (1993) challenged researchers to assign social status by observing repeated dyadic interactions between animals and investigating the outcomes of those interactions. Furthermore, he stated that if one animal consistently evoked submissive responses from another and the conspecific did not escalate the aggression social rank could be attributed to both animals. In this example, the animal that evoked the submissive responses could be considered the dominant animal, and the animal that did not escalate the aggression is classified as subdominant.

Drews (1993) claimed his definition more closely related to Schjelderup-Ebbe's original conceptualization because his definition encompasses agonistic interactions (e.g., displacements, threats, chases, bites, and aggressive gestures (see also Dewsbury, 1982; Hrdy & Hrdy, 1976) which parallel the pecking behavior reported by Schjelderup-Ebbe in domestic hens. Lastly, Drews' definition included a clause that stated escalation should not occur in dominance interactions. He maintained the idea that dominance behaviors reduced, rather than escalated, agonistic interactions was important because it was consistent with Schjelderup-Ebbe's initial supposition that dominance hierarchies in domestic hens maintained homeostasis within their group (Zuk, 2002). Drews essentially called for contemporary dominance research to revert to, and be standardized, around Schjelderup-Ebbe's original conceptualization.

Aggression, Grooming, and Hormone Levels as Related to Dominance

While Drews (1993) advocated for the use of displacement and outcome of other agonistic interactions to determine rank relationships, other variables have also been assessed with dominance rank. Among these are aggression (Ostner, Heistermann, & Schulke, 2008; Robbins, 2008), directionality of grooming occurrences (Payne, Lawes, & Henzi, 2003; Silk, 1982), hormone concentrations (e.g., glucocorticoids, cortisol, testosterone; Beehner, Phillips-Conroy, & Whitten, 2005; Muller & Wrangham, 2004b; Sapolsky, 2004), and neurotransmitter concentrations (e.g., Honess & Marin, 2006; Tse & Bond, 2002). These measures have been substituted for traditional measures of dominance (e.g., outcome and directionality of agonistic interactions and displacements) when traditional measures are not easily observable or the prevalence of such behaviors within a sample population low. However, these substitute measures must relate to traditional measures for their use to be validated (Dewsbury, 1982; Erhart & Overdorff, 2008).

Aggression has been utilized as an indicator of dominance status, although is inconsistently related to rank and may be species specific. For example, low-ranking Assemese macaques (*Macaca assamensis*) engage in more aggressive behaviors than high-ranking animals, especially during the mating season (Ostner et al., 2008). Conversely, high levels of aggressiveness have been linked with high dominance rank in other species (e.g., *Theropithecus gelada*, Dunbar, 1980; *Gorilla beringei beringei*, Robbins, 2008; *Pan troglodytes*, Muller & Wrangham, 2004a). Yet in some species (e.g., Bonobos, *Pan paniscus*), no relationship between dominance rank and aggressiveness has been reported (Sannen, Van Elsacker, Heistermann, & Eens, 2004). This inconsistency

raises concerns about levels of aggression being appropriate indicators of dominance relationships. One explanation for this inconsistency is that animals are aggressive to accomplish goals other than obtaining high dominance status. For example, animals may be forced to instrumentally implement aggressive behavior in order to defend themselves, their offspring, or resources from conspecifics (Ferrari, Palanza, Parmigiani, de Almeida, & Miczek, 2005; De Waal, 1986). This use of aggression for defensive purposes may be less related to dominance and more related to survival issues. Moreover, dominant and subordinate animals alike may avoid aggressive encounters to avoid the risk of injury or death (Koenig, 2002). Thus, for both dominant and subordinate animals the propensity to engage in or avoid aggressive behaviors may have a variety of underlying determinates that are complex and unrelated to the dominance concept. Base on these factors, aggression alone is an unreliable, or at least inconsistent, indicator of rank. Furthermore, relatively low rates of agonism in lemuroids, compared to old world monkeys, has been reported and may further complicate the relationship between aggression and dominance rank in prosimian primates (Erhart & Overdorff, 2008).

Grooming is a common behavior among primates. Clark (1985) identified allogrooming and mutual grooming as the two most prevalent social interactions in greater bushbabies (*Galago crassicaudatus*). These findings are particularly interesting because *Galago* species have historically been characterized as semi-solitary primates (Bearder, 1987; Clark, 1985). Grooming behavior is often linked with dominance rank. Grooming may be rank-related (i.e., animals groom adjacent ranks more frequently than distal ranks) and directed up the hierarchy (e.g., blue monkeys, *Cercopithecus mitis erythrchus*; Payne et al., 2003) such that subordinate animals groom dominant

animals in order to gain social support (Alexander, 1974; Stevens, Vervaecke, de Vries, & Van Elsacker, 2005). Grooming may also be directed down the hierarchy, such that dominant animals groom subordinate animals, though this is less likely and the adaptive mechanisms are not well understood (e.g., *Cebus apella*, Parr, Matheson, Bernstein, & De Waal, 1997). However, grooming behavior, like aggression, occurs for reasons unrelated to the social status. Animals groom to appease post-conflict tensions (Pereira & Kappeler, 1997; Rowell, Wilson, & Cords, 1991), to promote coalition formation (Silk, 1982), or to ease tensions in contexts where food is present (e.g., Barton, Byrne, & Whiten, 1996). Therefore, grooming is unreliable as a sole indicator of dominance rank.

Recently there has been a great deal of interest in physiological indicators of dominance rank. Glucocorticoids, cortisol and testosterone each relate to aggression and rank. Glucocorticoid secretions tend to increase as aggression received increases, and high-ranking male Assamese macaques (*Macaca assamensis*) tend to have lower glucocorticoid levels than subordinate males (Ostner et al., 2008). Cortisol levels tend to be higher in dominant animals, and lower levels of cortisol are typically reported when dominance hierarchies are stable (reviewed in Honess & Marin, 2006). However, mixed results have been reported (e.g., no relationship between dominance and rank in *Macaca fascicularis*, Stavisky, Adams, Watson, & Kaplan, 2001), thus the relationship between cortisol and rank may be mediated by species or cultural differences. For example, stress hormones are typically higher for dominant animals in groups where dominant animals must continually reinforce their position within the group with aggressive displays, but cortisol is higher for subordinates in groups where dominant animals use formal gestures rather than overt aggression to reinforce their status (Sapolsky, 2005).

High testosterone levels tend to correspond with high dominance rank (Bernhardt, 1997; Muehlenbein & Watts, 2010), but there are also inconsistent findings within and across species (e.g., *Lemur catta*; Von Engelhardt, Kappeler, & Heistermann, 2000; *Pan paniscus*; Sannen et al., 2004). High testosterone levels have been reported to relate with high rank in female hybrid baboons (*Papio hamadryas hamadryas* and *Papio hamadryas anubis*; Beehner et al., 2005). However, testosterone levels did not explain female social dominance (i.e., females consistently evoking submissive signals from males) in *Lemur catta* (Von Engelhardt et al., 2000), nor did it explain dominance ranks in the bonobo (*Pan paniscus*) in either stable or unstable social contexts (Sannen et al., 2004).

Feeding Success and Reproductive Success as Related to Dominance

As female animals gain feeding priority (i.e., preferential access to food resources) they increase their access to higher quality nutrients, thus correspondingly increasing their reproductive fitness (Eisenberg, Muckenhirn, & Rudran, 1972; Ellis, 1995; Kappeler & van Schaik, 2002; Whitten, 1983). Furthermore, feeding priority, food intake, energy intake rate, net energy gain, and reproductive success are related to dominance status (e.g., Dubuc & Chapais, 2007; Gerald, 2002; Hemingway, 1999; Janson, 1988; Pusey, Williams, & Goodall, 1997; Vogel, 2005).

Feeding priority is often assumed to directly reflect dominance rank in that high-ranking animals are presumed to have preferential access to food resources (Isbell, 1991; Wrangham, 1980). However, high rank does not lead to feeding priority in all species (Jolly, 1984). For example, feeding priority was inversely related to dominance rank in male vervet monkeys (*Cercopithecus aethiops sabaues*; Gerald, 2002). Similarly, Roeder and Fornasieri (1995) did not find a relationship between feeding priority and dominance,

but White, Overdorff, Keith-Lucas, Rasmussen, Kallam, and Forward (2007) reported that feeding priority was related to dominance rank in *Lemur catta*. Therefore, the relationship between feeding priority and dominance rank may be species dependent.

Dominance rank has been linked to foraging success (e.g., preferential access to food resources, or relatively high levels of net energy intake) in capuchins (Janson, 1988), baboons (Barton et al., 1996), macaques (Dubuc & Chapais, 2007; Saito, 1996), and chimpanzee (Wittig & Boesch, 2003). A basic unit of foraging is the food patch, an “aggregation of food items” (Leighton & Leighton, 1982, p. 82). They vary in size, distribution, density, quality, and number of feeding sites (Leighton & Leighton, 1982; Isbell, Pruett, & Young, 1998). Because rank has been linked to feeding success in some studies, Dubuc and Chapais (2007) examined behaviors exhibited by subordinate macaques (*Macaca fascicularis*) to compensate for foraging losses to their dominant counterparts. Among possible strategies employed by subordinates were feeding on remaining items in a patch after dominants stopped foraging, feeding on other lower quality food patches while dominants foraged on high quality patches, departing from the group to find similar high quality food patches, attempting to increase the dominants tolerance of their presence while foraging, and fleeing with stolen food to feed on the high quality items elsewhere. In particular, they examined whether subordinates arrived at high quality food patches prior to dominants (i.e., the early arrival tactic) and/or left food patches before dominants arrived in order to avoid attack. They reported that feeding time and gains positively correlated with dominance ranks, and, contrary to their original hypothesis, dominants were more likely than subordinates to implement the early arrival tactic in small food patches.

Direct relationships between reproductive success and rank have been documented. Dunbar (1980) reported high-ranking female gelada baboons (*Theropithecus gelada*) birthed offspring in fewer estrous cycles than low-ranking females. The sons of high-ranking macaque (*Macaca mulatta*) mothers are more likely to achieve higher dominance ranks and greater reproductive success post emigration than the sons of low-ranking mothers (Vessey, 1984). High-ranking female vervet monkeys (*Cercopithecus aethiops*) mate earlier and produced more offspring than low-ranking females even though there is no difference in offspring survival rates between high and low-ranking mothers (Whitten, 1983). High reproductive rates are related to high dominance status in chimpanzee (*Pan troglodytes*, Pusey et al., 1997). However, dominance ranks were not related to higher reproductive success in Barbary macaques (*Macaca sylvanus*, Kummerli & Martin, 2005). Therefore, the relationship between reproductive success and dominance rank also appears species specific.

Dominance ranks among male macaques are directly related to their mother's social status (Eisenberg et al., 1972). It has been documented in rhesus monkeys (*Macaca mulatta*) that the sons of high-ranking females have a competitive advantage over the sons of low-ranking females in that they live longer, and are more likely to join and obtain favorable social statuses in non-natal groups (Meikle & Vessey, 1988; Meikle, Tilford, & Vessey, 1984).

Socio-Ecological Models as Related to Dominance

Wrangham (1980) was the first to formally establish a model that included the necessary assumptions for dominance hierarchy formation. He posited that studies of dominance should focus on female relationships rather than male relationships because

food competition is directly related with female reproductive fitness but not male reproductive fitness due to females having a greater reproductive need for higher quality food resources in order to support their physiologically expensive gametes. He also suggested that the distribution of food resources (e.g., uniformly distributed versus clumped) determined whether females would form bonded relationships.

Although Wrangham (1980) acknowledged predation as a possible selection pressure he did not give it much credence. Van Schaik (1989) disagreed with Wrangham and suggested predation pressure was the main factor that influenced the evolution of group living. He maintained that predation pressure established group size's lower limit, whereas feeding competition established its upper limit. Furthermore, he predicted if predation pressure was high and food competition low, then group size would be high in order to increase predator avoidance via detection, as well as reconcile other negative effects of predation (e.g., injury). Conversely, if predation pressure was low and food competition high, then group size would be low to prevent the negative effects of feeding competition.

Van Schaik (1989) differentiated between four types of food competition, as well as theorized about the potential ecological pressures that determine each type. Elaborating on Nicholson's (1954) initial differentiation between scramble competition and contest competition, Van Schaik (1989) identified within group scramble competition (WGS), within group contest competition (WGC), between group scramble competition (BGS), and between group contest competition (BGC) as the four primary types of competitive regimens within animal societies. The defining characteristics of WGS are depletion of resources leading to equal fitness reductions across all group members and

female reproductive success is dependent on group size. Secondary characteristics of WGS include a low displacement rate, weak grooming bonds, bi-directional outcomes in agonistic interactions, and multiple reversals in dominance interactions. The primary ecological conditions that promote WGS are extremes in food distribution, be it a small food patches with short handling times (e.g., single insects) or relatively large and uniformly distributed food patches (e.g., grasslands), neither of which can be monopolized.

WGC is characterized as a point when fitness differs between individuals within the group, and female reproductive success is dependent on net energy intake. Correspondingly, displacements are common, grooming bonds are strong, and dominance interactions are unidirectional. This leads to low reversal rates and dominance hierarchies that are classified as linear, despotic, and nepotistic (Van Schaik, 1989).

BGS occurs when group ranges overlap extensively. It is characterized by mutual avoidance between groups and all members from all groups suffer the same reduction in feeding success and subsequent fitness reductions as food intake increases. Furthermore, high population densities promote intense BGS.

BGC, the final primary food competition type, is promoted when food patches are large enough for all members of a group to forage but small enough for the group to monopolize and defend from other groups. The primary identifying characteristic of BGC is dominant groups have greater feeding success than subordinate groups (Van Schaik, 1989).

To more thoroughly categorize the social systems of species rather than simply document the bounding competitive regimens, Sterck et al. (1997) proposed all species be

categorized according to variations in social behavior along three different identifying dimensions. The first dimension is egalitarian versus despotic. In egalitarian social systems animals have poorly defined relationships. Conversely, in a despotic social system animals have clearly defined and linear relationships. The second dimension is individualistic versus nepotistic relationships. In an individualistic social system the dominance ranks of individual animals do not reflect the degree of relatedness between individuals. However, in nepotistic social systems dominance ranks are directly related to the degree of relatedness between the animals. The final dimension is degree of tolerance. That is, in some groups high-ranking animals tolerate members of lower status whereas in other groups they do not. In tolerant groups aggression rates decrease, but threats towards dominants from low-ranking members may increase.

Sterck et al. (1997) further elaborated on their three dimensions by combining them to form different categories that are used to more relevantly label the various social structures observed in wild populations of nonhuman primates. The category that most likely characterizes *O. garnettii* is resident-nepotistic (RN). In resident-nepotistic (RN) societies there is relatively intense WGC, low levels of BGC, a general lack of female dispersal, and a discernible hierarchy among related females. Three other defining categories are dispersal-egalitarian (DE), resident-egalitarian (RE), and resident-nepotistic-tolerant (RNT). Furthermore, they suggested most species should meet the categorization requirements for either RN or DE since WGC is more important for social structure formation than BGC.

Phylogenetic Inertia

An additional factor may influence the social structure formation among non-human primates. Phylogenetic inertia is the concept researchers employ to suggest modern species' characteristics were derived from those of similar ancestral species (Berger, 1988). The concept provides an alternative explanation for the observed social systems of nonhuman primate species (Di Fiore & Rendall, 1994; Kappeler & van Schaik, 2002; Thierry, Iwaniuk, & Pellis, 2000). Furthermore, phylogenetic inertia may be a tool to determine the limits of behavioral plasticity within species (Di Fiore & Rendall, 1994; Kappeler & van Schaik, 2002).

Di Fiore and Rendall (1994) conducted an extensive review of the nonhuman primate social literature and credited phylogenetic inertia with strong explanatory power in describing female social behaviors. For example, they differentiated between 34 social traits, those most likely to be maintained after their initial evolutions were female social traits (e.g., female-female grooming, female dominance relationships, and female-female agonism), along with reproductive care and allogrooming. Male traits, however, were determined to be more plastic and were not easily explained by phylogenetic inertia. Much like Di Fiore and Rendall (1994), Thierry et al. (2000) concluded macaque social behavior was more likely a product of phylogeny than ecology pressures (e.g., resource distribution). Therefore, it is possible that in some species' phylogeny is more of an influence on social behaviors than ecology.

Phylogenetic Deliberation

Although phylogenetic inertia may explain the social behaviors of some species, there are many variables and considerations that must be acknowledged as contributing to

social behavior acquisition. One important consideration is animals must be given appropriate time to learn and alter their social behavior (Berger, 1988; Sterck et al., 1997). Another is when systematic investigations have been conducted to determine the explanatory power of phylogenetic inertia there often is an alternative explanation. Kappeler and Heymann (1996), operating under the assumptions of convergence theory, tested whether phylogenetic inertia hindered convergence. They concluded there was too much trait variability (e.g., body size, activity levels, and group size) amongst the prosimians and haplorhines for phylogenetic inertia to hinder convergence; thus ecological mechanisms were most likely responsible for the lack of convergence. Isbell and Pruettz (1998) suggested that ecological pressures (e.g., usurpability of food resources) overrode phylogeny as a selective pressure on social behavior in vervets. Therefore, socio-ecological models often have more explanatory power than phylogeny.

Support for Socio-ecological Models

Several studies on hominoids (Riedel, Franz, & Boesch, 2010; Robbins, Robbins, Gerald-Steklis, Steklis, 2005; Utami, Wich, Sterck, & van Hooff, 1997), cercopithecoids (Cooper & Bernstein, 2008; Henzi, Lusseau, Weingrill, Van Schaik, & Barrett, 2009; Isbell, Pruettz, Lewis, & Young, 1999), ceboidea (Boinski, Sughrue, Selvaggi, Quatrone, Henry, & Cropp, 2002; Mitchell, Boinski, & van Schaik, 1991), lemuroidea (Fornasieri, Caubere, & Roeder, 1993; Pereira & Kappeler, 1997), and lorisoidea (Dammhahn & Kappeler, 2009; Kappeler, Wimmer, Zinner, & Tautz, 2002) have provided supporting evidence for socio-ecological models. The importance of food resource distribution in contributing to dominance hierarchy formation and stability is demonstrated by studies on vervets (*Chlorocebus aethiops*) and patas (*Erythrocebus patas*) monkeys. Vervets and

patas are closely related phylogenetically but form radically different social structures (Isbell & Pruettz, 1998; Pruettz & Isbell, 2000). Vervets generally form stable and linear dominance hierarchies, whereas patas have more egalitarian societies. This difference has been attributed to the distribution of resources throughout their respective environments. *Acacia xanthophloea* (*A. xanthophloea*) trees are distributed in clumps within the vervets' habitat, thus promoting WGC. However, in the habitat of the patas, *Acacia drepanolobium* (*A. drepanolobium*) trees are uniformly distributed, thus promoting WGS. Moreover, vervets forage in *A. drepanolobium* trees, as well. When this occurs, they exhibit a lack of organization in their social structure that resembles that of the patas. A similar effect cannot be measured in patas because *A. xanthophloea* trees are not distributed within the habitat of the patas (Isbell et al., 1998; Isbell et al., 1999).

Squirrel monkeys, much like vervets and patas, have been observed to form different social structures between closely related species. These differences are due to differences in resource distribution throughout their habitats. For example, the intensity of WGC and subsequent dominance hierarchy formation differs between *Saimiri oerstedii* (*S. oerstedii*), *Saimiri sciureus* (*S. sciureus*), and *Saimiri boliviensis* (*S. boliviensis*) due to resource distribution. *S. oerstedii* forage on uniformly distributed patches and do not establish hierarchies, whereas *S. sciureus* and *S. boliviensis* forage on clumped patches and form dominance hierarchies (Boinski, 1999; Boinski et al., 2002; Mitchell et al. 1991).

Studies on prosimians have also produced supporting evidence for socio-ecological models. For example, when the social structures and habitats of Madame Berthe's mouse lemur (*Microcebus berthae*) and the grey mouse lemur (*Microcebus*

murinus) were compared, differences were consistent with the tenets of socio-ecological models. Madame Berthe's mouse lemur forage in small, uniformly distributed, food patches. They are not philopatric and are characterized by high WGS and no WGC. On the other hand, the grey mouse lemur forages on medium size, higher quality, and clumped food resources (e.g., fruits). They are philopatric, and, although still are characterized by high WGS, exhibit signs of weak, yet noticeable, WGC (Dammhahn & Kappeler, 2009).

It has also been reported that fork-marked lemurs (*Phaner furcifer*) forage primarily on gums, saps, and animal matter. Furthermore, individuals often avoided each other at feeding sites, and low-ranking animals left feeding sites once high-ranking animals entered (Schulke, 2003). These findings are consistent with the basic tenets of socio-ecological models in that foraging on gums, saps, animal matter, and small amounts of fruit (i.e., uniformly distributed food resources mixed with clumped food resources) typically promotes both WGS and WGC at varying degrees.

Prosimians and *O. Garnettii*

Scientists have called for more research to be conducted with unusual species in order to determine the generalizability of socio-ecological models (e.g., Isbell & Young, 2002). It has been proposed that the first primates were similar to *O. garnettii* in that they were nocturnal, arboreal, and fed regularly on insects and fruit (Eisenberg et al., 1972; Harcourt & Nash, 1986; Kappeler & Heymann, 1996). Present day prosimian primates reside in similar ecological niches as their ancestral predecessors (Charles-Dominique, 1978). They have social structures that vary in complexity, and are more variable than those observed in simians (Eisenberg et al., 1972; Charles-Dominique,

1978; Kappeler, 1997). Furthermore, due to the inherent difficulty of recording nocturnal nonhuman primate behavior in the wild, little is known about the nuances in the social structures and organizations of many nocturnal prosimians (Kappeler & Heymann, 1996).

O. garnettii are nocturnal and arboreal prosimian primates. They forage on insects, seeds, and fruit (Harcourt & Nash, 1986; Masters, Lumsden, & Young, 1988; Nash, Bearder, & Olsen, 1989). Females rarely disperse, live in small groups, and maintain relationships with their female offspring. Males, however, are the dispersing sex, and their home ranges overlap the ranges of several female groups (Charles-Dominique, 1978; Nash & Harcourt, 1986).

Group formation has been studied in *Galago crassicaudatus*, a closely related species to *O. garnettii*. Rosenson (1973) tested the stability of agonistic interactions, as well as affiliative behaviors with four bushbabies (3 F, 1 M). A dominant female initiated and won the majority of agonistic interactions. The same female was successful at hoarding access to the male by herding the other females to the opposite side of the enclosure. A linear dominance hierarchy was not observed. However, at the time their social structure was classified similarly to vervets which now are characterized by linear and stable dominance hierarchies (Isbell, & Pruett, 1998; Isbell et al., 1999; Rosenson, 1973).

Others have studied group formation in captive groups of greater galagos, and all were reluctant to classify them as capable of forming linear dominance hierarchies (*Galago agisymbanus*, Welker & Witt, 1982; *Galago crassicaudatus*, Drews, 1973; Roberts, 1971). It should be noted that most of these reports precede Wrangham's (1980) formalization of the socio-ecological model, and all precede Van Schaik's (1989) version

of the socio-ecological model. Likewise, these reports precede Appleby's (1983) original test for linearity in dominance hierarchies, as well as modern statistical techniques for determining the probability of individual rank orderings (e.g., Adams, 2005). Therefore, a new investigation is warranted to determine if female *O. garnettii* form dominance hierarchies. Dominance related behaviors and the influence of food resource distribution will be measured to determine their appropriateness in defining dominance as well as hierarchy formation in *O. garnettii*.

It is expected that *O. garnettii* will exhibit a combination of WGS and WGC as a desired, and clumped, resource becomes available or disappears. For example, it is expected that when the desired resource is available, WGC will be exhibited as measured by unidirectionality of displacement, grooming, and agonistic interactions with lowering aggression rates over time, as well as a definitive order of access to the desired resource. When the desired resource is not available, WGS will be exhibited as measured by bidirectionality of displacement, grooming, and agonistic interactions with stable aggression rates.

CHAPTER II

METHOD

Subjects

Five female bushbabies (*O. garnettii*) from the colony at the University of Southern Mississippi were used in the study. They ranged from five to eighteen years of age ($M = 11.4$ years). The females were not pregnant or lactating during the study, and were maintained on a 12:12 reverse light cycle which began at 0900. Purina High Protein monkey chow and fruit juice were provided consistent with the procedures of the experiment. Water was available to the subjects *ad libitum*. This study was approved by the University of Southern Mississippi's Institutional Animal Care and Use Committee (IACUC) and conformed to all state and federal laws.

Materials and Apparatus

O. garnettii were individually housed in cages measuring 152.4 cm x 91.4 cm x 91.4 cm, or group housed in an indoor enclosure (239 cm x 147 cm x 239 cm). Both were constructed of stainless steel framing and plastic coated wire mesh.

Purina High Protein monkey chow and apple or grape juice (Great Value Model # 35228, and Model # 22979) were available to the animals in a manner consistent with the experimental conditions. The juice was made from concentrate and diluted as per label instructions to produce 48 fluid ounces of 100% fruit juice.

An Acculab scale (ALC – 1100.2) was used to weigh chow, and a veterinary scale (Shor-Line, model number HEINE) was used to weigh the animals. All behavior was recorded with a digital hard-drive video camera (Sony, model #DCR-SR42), and all target behaviors were coded using a DVD player/TV combo (Sylvania Model #

LD155SL8). SPSS 17.0, WinBUGS 14, Microsoft Excel, and Coda Reader (Adams, 2005) were used to analyze data.

Methodological Considerations

Fruit

Fruit is typically distributed in distinct patches that are relatively easy to define and measure (Leighton & Leighton, 1982). Fruit is also present in the diets of many species that establish dominance hierarchies and past literature has implicated fruit as promoting WGC (e.g., *Cercopithecus mitis erythrorhynchus*, Payne et al., 2003; *Gorilla beringei beringei*, Robbins, 2008; *Macaca mulatta*, Van Schaik & Van Noordwijk, 1988; *Cebus capucinus*, Vogel, Munch, & Janson, 2007). The potential link between fruit and dominance hierarchy formation is not well understood, but some suggest this may be related to the energy potential in fruit, or an inherent desire in the animals to obtain high quality resources (e.g., Vogel, 2005).

Patch Size Determination

In the current research, a clumped food patch was established in a manner that maintains the integrity of behavioral observations, as well as simulates the characteristics of naturally occurring food patches. To achieve this effect, fruit juice was selected and presented in a clump by attaching three adjacent water bottles to the side of the open field.

Physical Evaluations

Animals were administered to routine physical evaluations. The physical evaluations consisted of documenting physical injuries, dental health, signs of estrus, behavioral changes, and animals' weights.

Procedure

Animals were progressively habituated to each other and the open field for thirty days. Once habituated, they were housed inside the open field for 14 days. During the 14 day testing period there were two seven day testing phases. During the first phase, animals were exposed to a clumped juice patch. Apple juice and 250 (\pm 0.5) g of Purina High Protein monkey chow were presented daily at 0900. Juice bottles were attached adjacently to the side of the open field, and chow was distributed throughout the bottom of the enclosure.

Apple juice was not presented to the animals in the second phase, but 250 (\pm 0.5) g of Purina High Protein monkey chow was available to provide them with adequate nutrition. The chow was presented daily at 0900 and distributed along the bottom of the open field as before.

Behavioral Observations and Coding

Behaviors were video recorded randomly and three times daily (i.e., 0900-1300, 1300-1700, 1700-2100) in 20 minute time intervals. Direction of displacement interactions, as well as other agonistic interactions, was the primary determinates of dominance status. Displacements were determined when a subject approached within a body length of a conspecific followed by the conspecific moving more than a body length away without escalating the aggression (i.e., no threatening, attacking, fighting, or other aggressive posturing directed toward the approaching subject). The approaching animal(s) were documented as the “winner” and the displaced conspecific(s) as the “loser” of the interaction.

Aggressive behaviors (i.e., overt agonistic interactions) consisted of threats, attacks, fights, or pursuits (see ethogram, adopted from Ehrlich, 1977). The frequency of aggressive behaviors was documented. If a fight was observed, the instigator(s) (i.e., the one that initiated the fight), winner(s) (i.e., the subject that did not first move a body length or more from the origin of a fight), and loser(s) (i.e., the subject that first moved a body length or more away from the origin of a fight) of the interaction were documented.

Mutual grooming was defined as two or more animals licking each other simultaneously. This occurred when a conspecific began grooming within five seconds of the initiator ceasing to groom, and ended once all animals involved ceased grooming for five or more seconds. Allo-grooming was defined as one animal licking a conspecific without reciprocation. A bout of allo-grooming began when an animal licked a conspecific, and ended when the animal stopped grooming for five or more seconds. Both types of grooming will be coded as frequency and duration measures.

Coders determined feeding priority (i.e., preferential access to a food resource) three ways. They documented the order in which animals began feeding on food items, tabulated the total time spent feeding on food items (i.e., licking or chewing on chow or juice bottle spigot), and recorded the frequency of visits to food items. A visit began when an animal licked the juice bottle spigot or a chow pellet, and concluded once an animal stopped licking the food item for five or more seconds.

Rank Analysis

Adams (2005) reviewed the various available statistical methods to analyze dominance rank and determined the Bayesian version of the method of paired comparisons offers several strategic advantages not inherent to nonparametric techniques.

For example, the Bayesian version does not assume all animals are equally as likely to win interactions with conspecifics, and provides probabilities for rank orderings other than the most likely rank ordering. These advantages do not compromise accuracy of identifying the most likely rank ordering. In fact, the Bayesian version has been shown to be more accurate at identifying the most probable rank ordering than nonparametric techniques (e.g., Adams, 2005; Chancellor & Isbell, 2009).

WinBUGS14 will be employed to determine the probability of the most likely dominance hierarchies (as specified in Adams, 2005). Since initial values generated in Markov chains are usually atypical, the first 10,000 iterations were discarded and only the next 50,000 iterations were used to determine posterior ranks.

Two Markov chains were initially simulated to test for convergence. Multiple techniques were used to determine whether convergence between the chains occurred. One of the most prominent techniques to determine convergence between the chains is to compute the Gelman-Rubin statistic in order to determine if the pooled variance for the chains is similar to the average within chain variance. The two variances are considered similar when the Gelman-Rubin values are less than 1.2. Another prominent technique is to test if the two chains are mixing well within the same vertical range. Additional techniques were used to determine if the Markov chains converging during the sample of 50,000 iterations (percom Eldridge Adams).

Rank orderings were predicted from the posterior distribution only after convergence had been determined. Standard distance from a middle ranked focal animal and the 95% confidence interval for the ranks were reported for each animal. Coda Reader was employed to determine the probability of various rank orderings within the

95% confidence interval of all possible rank orderings. Fewer rank orderings and higher probabilities indicated greater certainty that those ordering(s) were the true ordering(s) of the animals (Adams, 2005; Chancellor & Isbell, 2009).

Other Analyses and Inter-rater Reliability

Repeated-Measures Analysis of Variance (RMANOVA) was utilized to test for changes in dominance related behaviors across conditions. The statistical hypotheses were one-tailed to correspond with the assumptions of the socio-ecological model being tested. Statistically significant results were determined at a p-value < 0.05 .

Spearman correlations between all measures were produced and tested for statistical significance ($p < 0.05$). Feeding priority measures were computed as totals. All other measures were reported as proportion of wins to total interactions (i.e., actor/total interactions) in each of the ten unique dyads.

At least 20% of the observational time was coded by a separate rater to determine inter-rater reliability. All inter-rater reliability coefficients were above 0.85. If any measure was not at least this consistent the operational definition and tape were revisited by both raters to spot inconsistencies. Once inconsistencies were determined the tapes were re-coded and inter-rater reliability re-evaluated as before.

CHAPTER III

RESULTS

Social Behavior

A total of 726 agonistic interactions were observed in 14 hours of observation. Displacement was the most frequently occurring agonistic behavior (90.22%) followed by attacks (4.96%), fights (3.44%), and threats (1.38%). Frequencies of these measures and total observation times are reported in the cross-tabular table in Appendix C.

Winners were determined for 15 of the 25 observed fights (60%). Three pursuits were also observed, but this behavioral measure was not included to compute the percentages of agonistic behaviors since pursuits were partially determined from other agonistic measures (refer to ethogram in Appendix B).

Allo-grooming was observed for 1329 seconds across 114 occurrences while mutual grooming was observed for 873 seconds across 36 occurrences. RM-ANOVA revealed a significant decrease in time spent allo-grooming from the juice present to the no juice condition ($F_{(1, 8)} = 12.224, p = 0.025$). This effect is illustrated in Figure 1. Similar decreases in the frequency of allo-grooming ($F_{(1, 8)} = 1.306, p = 0.317$), frequency of mutual grooming ($F_{(1, 8)} = 0.478, p = 0.528$), duration of mutual grooming ($F_{(1, 8)} = 4.765, p = 0.094$), displacements ($F_{(1, 8)} = 1.645, p = 0.269$), and other agonistic interactions ($F_{(1, 8)} = 0.000, p = 1.000$) were not observed. Frequencies and durations of allo-grooming are reported in cross-tabular tables in Appendixes C and D.

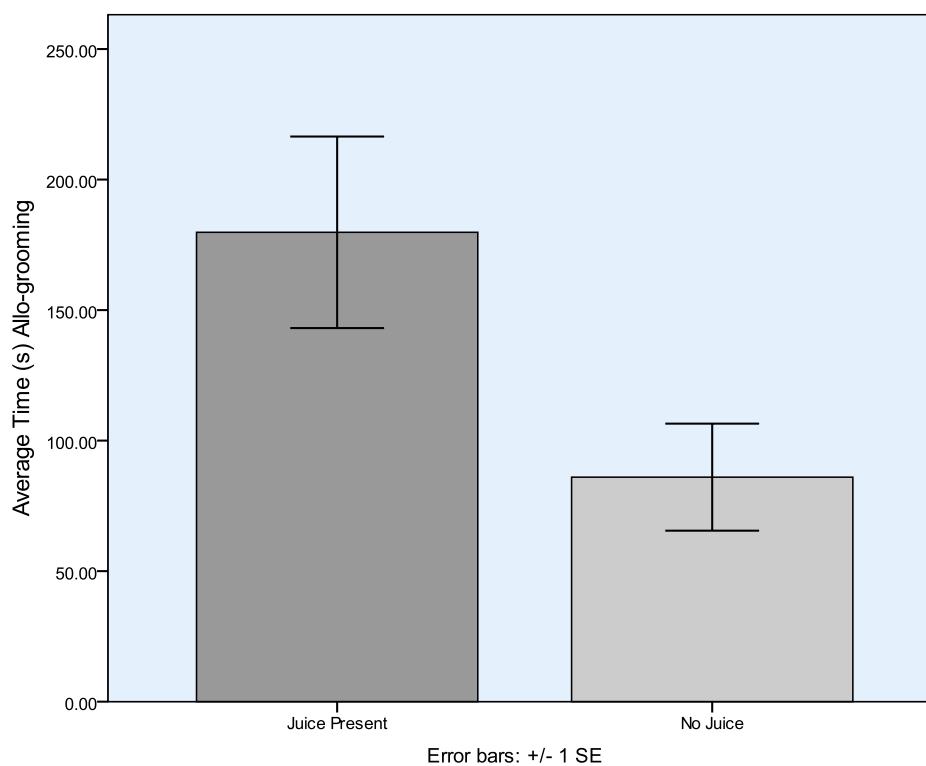


Figure 1. Decrease in Time Allocated to Allo-grooming. More time was allocated to allo-grooming when apple juice was present.

Time series analysis revealed significant decreases across the duration of the study for the frequency and duration of allo-grooming ($\beta = -0.103$, $t_{40} = -3.217$, $p = 0.003$; $\beta = -2.040$, $t_{40} = -3.233$, $p = 0.002$). Similar decreases in behavior were not observed for displacement or other agonistic interactions ($\beta = 0.199$, $t_{40} = 1.407$, $p = 0.167$; $\beta = -0.001$, $t_{40} = -0.040$, $p = 0.968$), and mutual grooming could not be analyzed across the duration of the study using a similarly modeled trend analysis due to multiple consecutive days of no observed interactions. Decreasing trends for the frequency and duration of allo-grooming are presented in Figures 2 and 3.

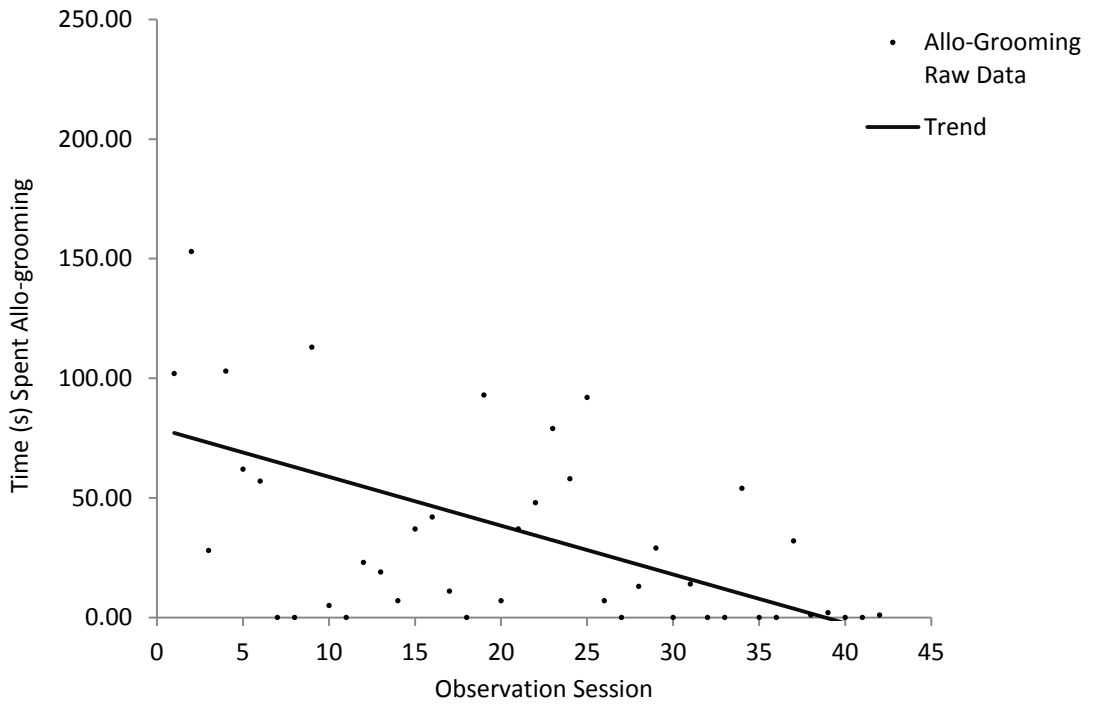


Figure 2. Decreasing Trend in Time (s) Spent Allo-grooming. Less time(s) was allocated to allo-grooming as the study progressed.

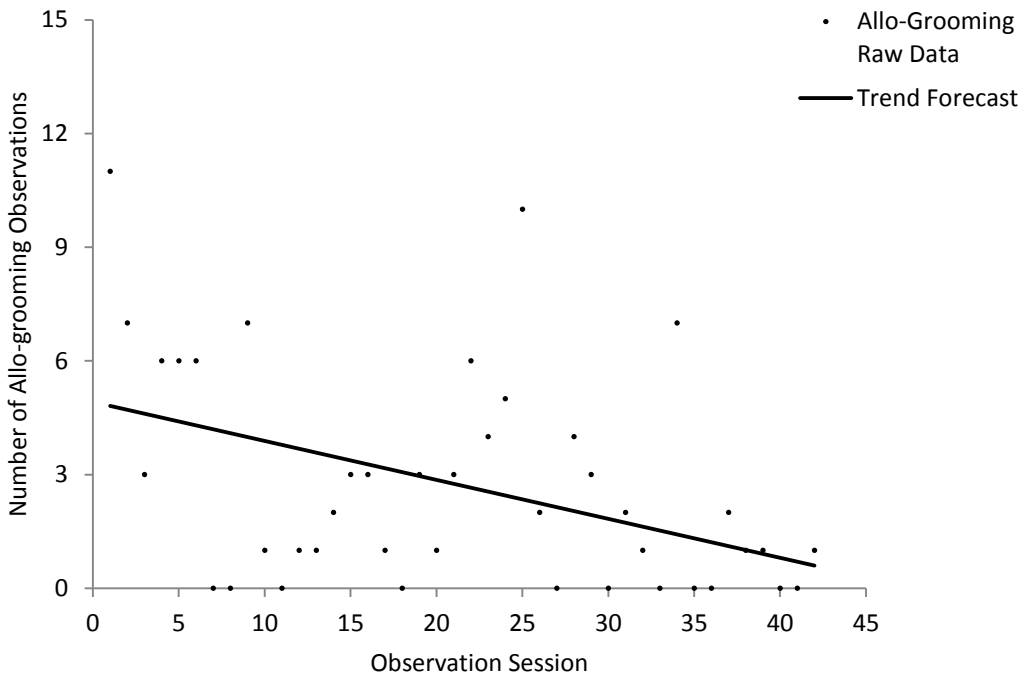


Figure 3. Decreasing Trend in the Prevalence of Allo-grooming. Fewer allo-grooming occurrences were documented as the study progressed.

Feeding Behavior

Animals drank from the juice hopper 151 times for 3,470 s. While the juice was present, *O. garnettii* fed on chow 127 times for 4,479 s, and when juice was removed from the open field their feeding on chow increased to 227 times for 17,790 s. RM-ANOVA revealed the increases in frequency and duration to be significant ($F_{(1, 8)} = 7.860$, $p = 0.049$; $F_{(1, 8)} = 18.449$, $p = 0.013$). Furthermore, time series analysis did not reveal any significant decreases or increases in foraging behavior within treatments. Significant main effects for the frequency and duration spent foraging on chow are depicted in Figures 4 and 5.

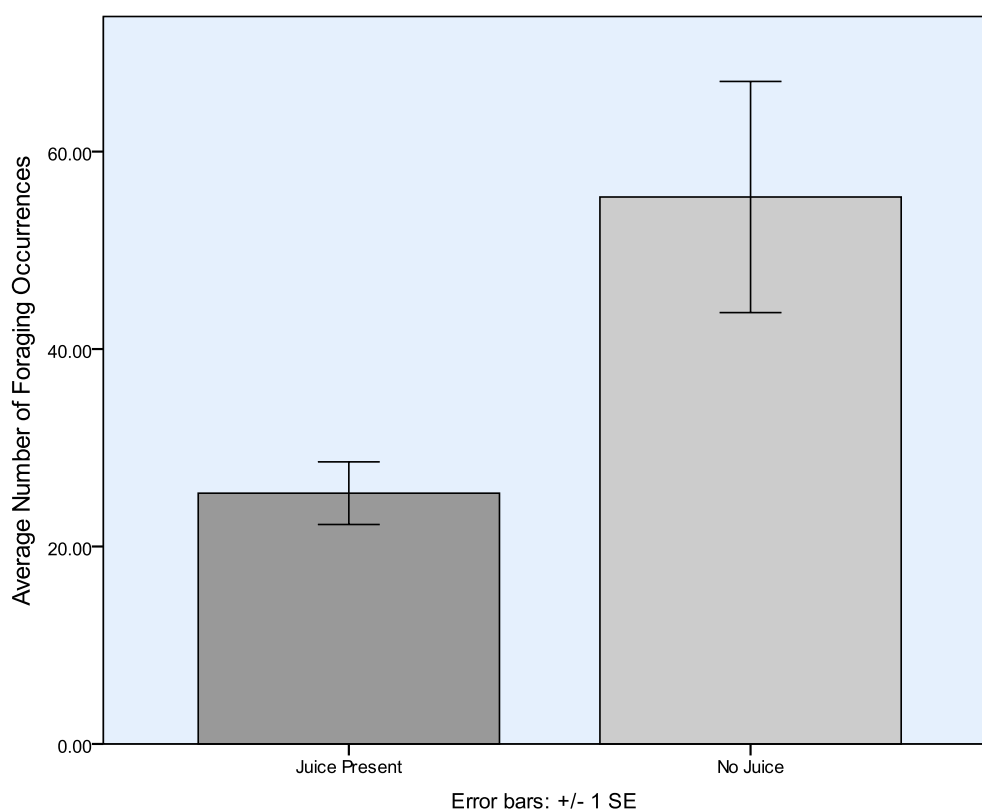


Figure 4. Chow Foraging Frequency. Animals foraged more frequently on chow when apple juice was present.

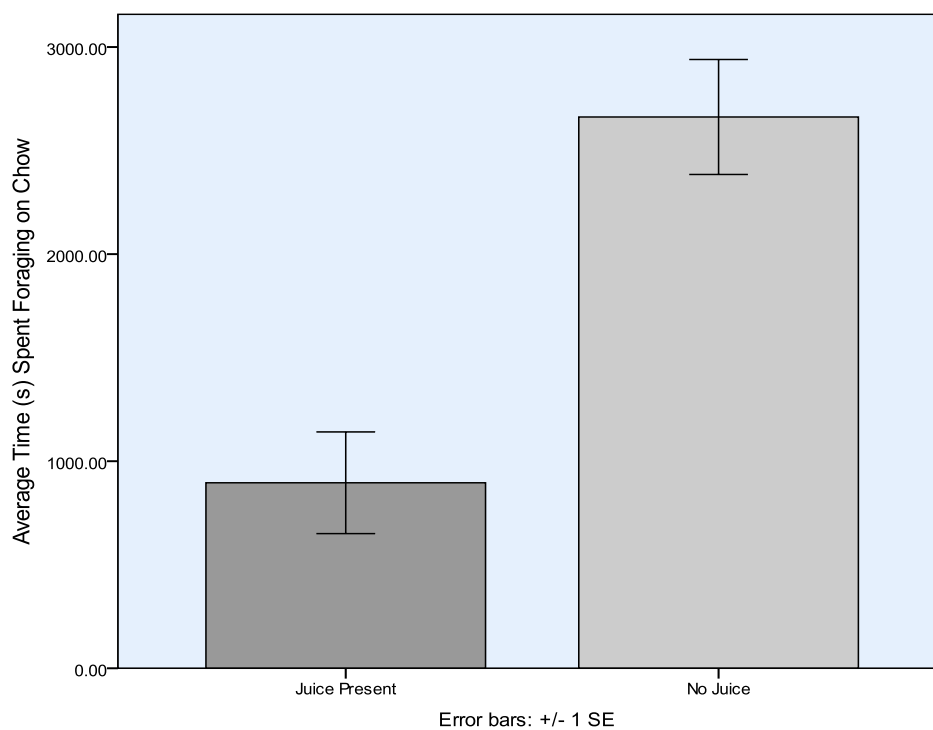


Figure 5. Time Allocated to Chow Foraging. More time was allocated to foraging on chow when apple juice was not present.

Directional Consistencies within Measures of Dominance

Displacement was the most frequent and reliable agonistic behavior across conditions and time blocks such that animals likely to displace conspecifics were likely to do so across conditions and time blocks. These correlations matrices are presented in Tables 1 and 2.

Average proportions (Actor/Total Interactions) could not be correlated across all time blocks and conditions for allo-grooming measures due to the absence of observed allo-grooming within one or more dyads. However, allo-grooming average proportions in the juice present and combined conditions could be computed and correlated. From these correlations, there appears to be consistency in the directionality of allo-grooming across conditions (see Tables 3).

Table 1

Consistency within the Displacement Measure across Time Blocks

Condition Names and Time Blocks	Juice	Juice	Juice Present	No Juice	No Juice	No Juice	Both	Both	Both
	Present 1	Present 2	3	1	2	3	1	2	3
Juice Present - 1	1.000								
Juice Present - 2	.900*	1.000							
Juice Present - 3	.800	.900*	1.000						
No Juice - 1	.900*	1.000**	.900*	1.000					
No Juice - 2	.800	.900*	1.000**	.900*	1.000				
No Juice - 3	.900*	1.000**	.900*	1.000**	.900*	1.000			
Both - 1	.900*	1.000**	.900*	1.000**	.900*	1.000**	1.000		
Both - 2	.800	.900*	1.000**	.900*	1.000**	.900*	.900*	1.000	
Both - 3	.800	.900*	1.000**	.900*	1.000**	.900*	.900*	1.000**	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Table 2

Consistency within the Displacement Measure between Conditions

Condition Name	Juice Present	No Juice	Both
Juice Present	1.000		
No Juice	1.000**	1.000	
Both	1.000**	1.000**	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Table 3

Consistencies within Allo-grooming Measures

Condition Names And Measure Type	Juice Present	Both	Juice Present	Both
	Frequency Measure	Frequency Measure	Duration Measure	Duration Measure
Juice Present – Frequency Measure	1.000			
Both – Frequency Measure	1.000*	1.000*		

Table 3 (continued).

Condition Names And Measure Type	Juice Present	Both	Juice Present	Both
	Frequency Measure	Frequency Measure	Duration Measure	Duration Measure
Juice Present – Duration Measure	.900*	.900*	1.000	1.000
Both – Duration Measure	.900*	.900*	1.000**	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed). Average proportions (Actor/Total Interactions) could not be computed for the no juice condition due to an absence of allo-grooming between Pebbles and Piper.

Mutual grooming showed consistency within both the frequency and duration measures in both the juice present and no juice conditions. Animals likely to participate in mutually grooming bouts were likely to do so across conditions (Table 4). Some consistencies were also observed across time blocks, but these consistencies were not as evident as those reported between conditions (see Appendix E).

Table 4

Consistencies across Conditions within the Mutual Grooming Measures

Condition Names and Measure Type	Juice Present	No Juice	Both	Juice Present	No Juice	Both
	Frequency Measure	Frequency Measure	Frequency Measure	Duration Measure	Duration Measure	Duration Measure
Juice Present – Frequency Measure	1.000					
No Juice – Frequency Measure	.900*	1.000				
Both – Frequency Measure	1.000**	.900*	1.000			
Juice Present – Duration Measure	1.000**	.900*	1.000**	1.000		
No Juice – Duration Measure	.900*	1.000**	.900*	.900*	1.000	
Both – Duration Measure	1.000**	.900*	1.000**	1.000**	.900*	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Correlation matrices produced evidence of consistencies across time blocks and between conditions for the feeding priority measure of first arrival to chow. *O. garnettii* likely to obtain chow first in block one of the juice present condition were less likely to

obtain chow first in blocks two and three of the same condition (Table 5). Furthermore, likelihood to arrive to chow first in the study was more closely related to the order of arrival to chow in the no juice conditions. No relationship was observed between the order of arrival to chow in the juice present or no juice conditions (Table 5).

Table 5

Inconsistency in the Order of Arrival to the Chow Patch across Time Blocks

Condition Names and Time Blocks	Juice Present	Juice Present	Juice Present	No Juice	No Juice	No Juice	Both	Both	Both
	1	2	3	1	2	3	1	2	3
Juice Present - 1	1.000								
Juice Present - 2	-1.000**	1.000							
Juice Present - 3	-1.000**	1.000**	1.000						
No Juice - 1	-.158	.158	.158	1.000					
No Juice - 2	.105	-.105	-.105	.789	1.000				
No Juice - 3	-.763	.763	.763	.237	.289	1.000			
Both - 1	.158	-.158	-.158	.895*	.947*	.079	1.000		
Both - 2	-.526	.526	.526	.632	.763	.763	.632	1.000	
Both - 3	-.975**	.975**	.975**	.154	-.051	.872	-.154	.564	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Table 6

Relationship between Order of Arrival to Chow in the No Juice and Combined Conditions

Time Block	Juice Present	No Juice	Both
Juice Present	1.000		
No Juice	.051	1.000	
Both	.154	.900*	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Correlation matrices for attacks, threats, and fights could not be produced from average proportions (Winner/Total Interactions) due to absences in observed agonistic interactions within one or more dyads. Even after collapsing the behavioral measures

into one category there were still missing dyadic interactions within each treatment. However, for the whole observation time each unique dyad interacted along one of these three behavioral dimensions at least once.

Directional Consistencies between Measures of Dominance

The direction of displacements was related to the observed direction in the frequency of allo-grooming, but not related to the duration of allo-grooming (Table 7).

O. garnettii likely to displace conspecifics frequently allo-groomed conspecifics;

however, they did not allo-groom for longer periods of time than other animals.

Directionality of displacements was also related with participation in mutual grooming such that animals more likely to displace conspecifics were less likely to participate in mutual grooming (Table 8).

Table 7

The Relationship between Displacement and Allo-Grooming

Condition Name and Behavioral Measure	Juice	No Juice	Both			Juice	Both
	D	D	D	Juice Gr(f)	Gr(f)	Gr(d)	Gr(d)
Juice – D	1.000						
No Juice – D	-1.000**	1.000					
Both – D	-1.000**	-1.000**	1.000				
Juice – Gr(f)	.900*	.900*	.900*	1.000			
Both – Gr(f)	.900*	.900*	.900*	1.000**	1.000		
Juice – Gr (d)	.700	.700	.700	.900*	.900*	1.000	
Both – Gr(d)	.700	.700	.700	.900*	.900*	1.000**	1.000

Note. D = Displacement, Gr(f) = Frequency measure of allo-grooming, and Gr(d) = Duration measure of allo-grooming. Unique coefficients that are not presented in other tables are lightly shaded grey. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

A consistent relationship between the frequency and duration of allo-grooming was observed, in that animals likely to allo-groom conspecifics were likely to allo-groom for longer than conspecifics that infrequently allo-groomed (see Table 3). No

relationships between allo-grooming and mutual grooming were detected (see Appendix G), nor were there any detected relationships between agonistic interactions and other behavioral measures of dominance (e.g., displacement, allo-grooming, and mutual grooming; see Appendix H).

Table 8

Relationship between Displacement and Participation in Mutual Grooming

Condition Names and Time Blocks	Juice	No Juice	Both	Juice	No Juice	Both	Juice	No Juice	Both
	D	D	D	MGr(f)	MGr(f)	MGr(f)	MGr(d)	MGr(d)	MGr(d)
Juice – D	1.000								
No Juice – D	-1.000**	1.000							
Both – D	-1.000**	-1.000**	1.000						
Juice – MGr(f)	-.900*	-.900*	-.900*	1.000					
No Juice – MGr(f)	-.700	-.700	-.700	.900*	1.000				
Both – MGr(f)	-.900*	-.900*	-.900*	1.000**	.900*	1.000			
Juice – MGr(d)	-.900*	-.900*	-.900*	1.000**	.900*	1.000**	1.000		
No Juice – MGr(d)	-.700	-.700	-.700	.900*	1.000**	.900*	.900*	1.000	
Both – MGr(d)	-.900*	-.900*	-.900*	1.000**	.900*	1.000**	1.000**	.900*	1.000

Note. D = Displacement, MGr(f) = Frequency measure of mutual grooming, and MGr(d) = Duration measure of mutual grooming. Unique coefficients that are not presented in other tables are lightly shaded grey. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Measures of feeding priority on juice were consistently related. Animals likely to arrive at the juice hopper early foraged more frequently ($r_s = -0.900$, $p = 0.037$) and for longer durations ($r_s = -1.000$, $p < 0.001$) on juice than conspecifics that arrived relatively late (see Table 9). Measures of feeding priority on juice were not related to other behavioral measures (Appendix I), nor were there any consistent relationships between the measures of feeding priority on chow with other behavioral measures (Appendix J).

Table 9

Consistency between Measures of Juice Foraging

Variable	1 st Arrival to Juice	Time (s) Foraging on Juice	Visits to Juice Hopper
1 st Arrival to Juice	1.000		
Time (s) Foraging on Juice	-.900*	1.000	
Visits to Juice Hopper	-1.000**	.900*	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Animals likely to feed first were less likely to feed frequently from chow when juice was not present. However, this relationship was not evident when juice was present. Furthermore, animals likely to feed from chow were not more or less likely to feed from chow for longer durations, nor were animals likely to feed frequently from chow more or less likely to feed on chow for longer durations. These relationships are presented in Table 10.

Table 10

Consistency between Measures of Chow Foraging

Condition Names and Behavioral Measure	Juice	No Juice	Both	Juice	No Juice	Both	Juice	No Juice	Both
	1 st Arrival	1 st Arrival	1 st Arrival	C(f) Measure	C(f) Measure	C(f) Measure	C(d) Measure	C(d) Measure	C(d) Measure
Juice – C 1 st	1.000								
No Juice – C 1 st	.051	1.000							
Both – C 1 st	.154	.900*	1.000						
Juice – C(f)	-.763	-.359	-.616	1.000					
No Juice – C(f)	.359	-.900*	-.700	-.051	1.000				
Both – C(f)	-.051	-1.000*	-.900*	.359	.900*	1.000			
Juice – C(d)	-.154	-.800	-.900*	.462	.600	.800	1.000		
No Juice – C(d)	.308	.400	.300	-.462	-.300	-.400	.100	1.000	
Both – C(d)	-.410	.100	.000	.103	-.300	-.100	.400	.700	1.000

Note. C 1st and C 1st Arrival = Average order of arrival to the chow patch, C(f) = Frequency measure of foraging on chow, and C(d) = Duration measure of foraging on chow. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Hierarchy Formation

Posterior rank orderings were constructed from the direction of displacement interactions and allo-grooming since these measures showed high degrees of consistency within and between measures. Dominance indexes were also constructed from displacement and allo-grooming interactions. These indexes are presented in Appendixes K through M. Means and the 95% credibility intervals of the posterior rank distributions from each measure, across each condition, are reported in Appendixes N, O, and P.

Documented in Tables 11 through 13 are the potential rank orderings constructed from the direction of displacement interactions (reference Appendix K and N). When juice was present Pebbles outranked all animals 100% of the time. Furthermore, across the duration of the study, Pebbles and Sybil were determined to outrank the other *O. garnettii* 100% of the time.

Table 11

Possible Rank Orderings from Displacement Interactions in the Juice Present Condition

Individual Rank Order	Posterior Probability	Cumulative Probability
Pebbles > Sybil > Piper > Sam > Brandine	0.4298	0.4298
Pebbles > Sybil > Sam > Piper > Brandine	0.2467	0.6765
Pebbles > Piper > Sybil > Sam > Brandine	0.0997	0.7762
Pebbles > Sybil > Piper > Brandine > Sam	0.0720	0.8483
Pebbles > Sam > Sybil > Piper > Brandine	0.0500	0.8983
Pebbles > Piper > Sybil > Brandine > Sam	0.0187	0.9170
Pebbles > Sybil > Sam > Brandine > Piper	0.0186	0.9355
Pebbles > Sybil > Brandine > Piper > Sam	0.0175	0.9530

Note. Posterior probabilities indicate the likelihood of that rank ordering, and cumulative probabilities indicated the likelihood of all probable rank ordering up to the rank order of interest. All rank orders within the 95% credibility set are reported.

Table 12

Possible Rank Orderings from Displacement Interactions in the No Juice Condition

Individual Rank Order	Posterior Probability	Cumulative Probability
Pebbles > Sybil > Piper > Brandine > Sam	0.5044	0.5044
Pebbles > Sybil > Piper > Sam > Brandine	0.4604	0.9647

Note. Posterior probabilities indicate the likelihood of that rank ordering, and cumulative probabilities indicated the likelihood of all probable rank ordering up to the rank order of interest. All rank orders within the 95% credibility set are reported.

Table 13

Possible Rank Orderings from all Displacement Interactions in Both Conditions

Individual Rank Order	Posterior Probability	Cumulative Probability
Pebbles > Sybil > Piper > Sam > Brandine	0.8364	0.8364
Pebbles > Sybil > Piper > Brandine > Sam	0.1630	0.9994

Note. Posterior probabilities indicate the likelihood of that rank ordering, and cumulative probabilities indicated the likelihood of all probable rank ordering up to the rank order of interest. All rank orders within the 95% credibility set are reported.

Rank orders formed from the direction in the frequency of all-grooming bouts are presented in Tables 14 through 16, and those formed from the direction in the duration (s) of all-grooming bouts are presented in Tables 17 through 19. Similar rank orderings to those constructed from the displacement measure were documented. Pebbles and Sybil occupied the top two ranks with Pebbles typically outranking Sybil. Piper tends to occupy the middle rank while Brandine and Sam frequently reverse ranks near the bottom of the hierarchy.

Table 14

Possible Rank Orderings from the Frequency of Allo-Grooming Interactions in the Juice Present Condition

Individual Rank Order	Posterior Probability	Cumulative Probability
Pebbles > Sybil > Piper > Brandine > Sam	0.5302	0.5302
Pebbles > Piper > Sybil > Brandine > Sam	0.1734	0.7036
Sybil > Pebbles > Piper > Brandine > Sam	0.1197	0.8234
Pebbles > Sybil > Piper > Sam > Brandine	0.0654	0.8887
Pebbles > Sybil > Brandine > Piper > Sam	0.0218	0.9105
Pebbles > Piper > Sybil > Sam > Brandine	0.0203	0.9308
Sybil > Pebbles > Piper > Sam > Brandine	0.0169	0.9477
Piper > Pebbles > Sybil > Brandine > Sam	0.0164	0.9641

Note. Posterior probabilities indicate the likelihood of that rank ordering, and cumulative probabilities indicated the likelihood of all probable rank ordering up to the rank order of interest. All rank orders within the 95% credibility set are reported.

Table 15

Possible Rank Orderings from the Frequency of Allo-grooming Interactions in the No Juice Condition

Individual Rank Order	Posterior Probability	Cumulative Probability
Pebbles > Sybil > Piper > Brandine > Sam	0.2784	0.2784
Pebbles > Sybil > Piper > Sam > Brandine	0.1535	0.4318
Pebbles > Sybil > Brandine > Piper > Sam	0.1267	0.5585
Sybil > Pebbles > Piper > Brandine > Sam	0.1249	0.6834
Sybil > Pebbles > Piper > Sam > Brandine	0.0739	0.7573
Pebbles > Sybil > Sam > Piper > Brandine	0.0653	0.8226
Sybil > Pebbles > Brandine > Piper > Sam	0.0544	0.8770
Pebbles > Sybil > Brandine > Sam > Piper	0.0321	0.9091
Sybil > Pebbles > Sam > Piper > Brandine	0.0304	0.9395
Pebbles > Sybil > Sam > Brandine > Piper	0.0291	0.9686

Note. Posterior probabilities indicate the likelihood of that rank ordering, and cumulative probabilities indicated the likelihood of all probable rank ordering up to the rank order of interest. All rank orders within the 95% credibility set are reported.

Table 16

Possible Rank Orderings determined from the Frequency of all Allo-Grooming Interactions in Both Conditions

Individual Rank Order	Posterior Probability	Cumulative Probability
Pebbles > Sybil > Piper > Brandine > Sam	0.6714	0.6714
Sybil > Pebbles > Piper > Brandine > Sam	0.1540	0.8254
Pebbles > Sybil > Piper > Sam > Brandine	0.1003	0.9257
Pebbles > Sybil > Brandine > Piper > Sam	0.0309	0.9566

Note. Posterior probabilities indicate the likelihood of that rank ordering, and cumulative probabilities indicated the likelihood of all probable rank ordering up to the rank order of interest. All rank orders within the 95% credibility set are reported.

Table 17

Possible Rank Orderings from the Duration of Allo-Grooming Interactions in the Juice Present Condition

Individual Rank Order	Posterior Probability	Cumulative Probability
Pebbles > Sybil > Brandine > Piper > Sam	0.5399	0.5399
Pebbles > Sybil > Piper > Brandine > Sam	0.4601	1.000

Note. Posterior probabilities indicate the likelihood of that rank ordering, and cumulative probabilities indicated the likelihood of all probable rank ordering up to the rank order of interest. All rank orders within the 95% credibility set are reported.

Table 18

Possible Rank Orderings from the Duration of Allo-grooming Interactions in the No Juice Condition

Individual Rank Order	Posterior Probability	Cumulative Probability
Sybil > Pebbles > Brandine > Piper > Sam	0.6801	0.6801
Sybil > Pebbles > Piper > Brandine > Sam	0.3102	0.9902

Note. Posterior probabilities indicate the likelihood of that rank ordering, and cumulative probabilities indicated the likelihood of all probable rank ordering up to the rank order of interest. All rank orders within the 95% credibility set are reported.

Table 19

*Possible Rank Orderings determined from the Duration of all Allo-Grooming**Interactions in Both Conditions*

Individual Rank Order	Posterior Probability	Cumulative Probability
Pebbles > Sybil > Piper > Brandine > Sam	0.6022	0.6022
Pebbles > Sybil > Brandine > Piper > Sam	0.3973	0.9995

Note. Posterior probabilities indicate the likelihood of that rank ordering, and cumulative probabilities indicated the likelihood of all probable rank ordering up to the rank order of interest. All rank orders within the 95% credibility set are reported.

CHAPTER IV

DISCUSSION

Dominance Hierarchy Formation

From the directionality of displacement and allo-grooming interactions, it was concluded that female *O. garnettii* have the behavioral capacity to construct dominance hierarchies. The strength of these hierarchies and distribution of different types of agonistic interactions (e.g., relatively high rates of approach-avoidance behaviors but low rates of overt agonism) resembled those exhibited by the grey-cheeked mangabey (*Lophocebu albigena*; Chancellor & Isbell, 2009) and gorilla (*Gorilla beringei*; Robbins, 2008), as expected (see Erhart & Overdorff, 2008).

Relationship between Displacement and Grooming Measures

Some interesting consistencies between the directionality of displacement, allo-grooming, and mutual grooming interactions were observed. Since the directionality of displacement interactions is a common indicator of dominance (Drews, 1993), and the current data indicated animals more likely to displace conspecifics more frequently allo-groomed conspecifics, it appears female *O. garnettii* groomed down the hierarchy. Furthermore, high ranking *O. garnettii* were less likely to participate in mutual grooming interactions. These combined findings suggest grooming between female *O. garnettii* is agonistic in nature.

The brown capuchin (*Cebus paella*), a new world nonhuman primate species, was also found to direct grooming down the hierarchy (Parr et al., 1997). This phenomenon, however, is extremely uncommon. Therefore, it is possible that displacement and grooming interactions may serve a function completely unrelated to the dominance

concept in *O. garnettii*. Although this is a possibility, an article by Drews (1973) showed a similar relationship between the direction of displacement and allo-grooming interactions.

Drews (1973) descriptively illustrated that captive female *Galago crassicaudatus* likely to displace conspecifics were less likely to receive grooming. Similarly, animals less likely to receive grooming were more likely to win agonistic interactions. Although these relationships were not found to be statistically significant, nor did Drews discuss them in great detail, they nonetheless provide supporting evidence for the current conclusion that displacement and grooming are agonistic behaviors related to the dominance concept in female *O. garnettii*.

Agonistic Behavior and the Dominance Concept

It is unclear whether agonistic behaviors, other than displacement and grooming interactions (e.g., threats, attacks, pursuits, and fights), are related to the dominance concept due to the extremely low frequency of these behaviors during the current investigation. To determine this relationship in a similar captive setting the observation time would need to be substantially longer in order to safely increase the number of agonistic interactions between the animals. Future investigations looking for the function of overt agonistic behavior may not be warranted if displacement and grooming interactions are valid indicators of dominance status since these behaviors occur more frequently than threats, attacks, pursuits, or fights. However, if displacement and grooming interactions serve a different function unrelated to the dominance concept in *O. garnettii*, then future research is needed to determine the function of displacement and grooming behavior in this species.

Feeding Priority and the Dominance Concept

The current findings do not provide evidence that feeding priority is related to the dominance concept in *O. garnettii*. This is consistent with findings in other research (e.g., Drews, 1973; Welker, & Witt, 1982) and may be due to the relatively brief manipulation period (see Berger, 1988; Sterck et al., 1997). However, the manipulation did have an effect on allo-grooming and feeding behavior (e.g., *O. garnettii* fed more on chow when the juice was absent than when it was present). Therefore, if feeding priority was related to the dominance concept in this species, there is reason to believe the manipulation was long enough to impact that relationship.

O. garnettii in the current research were provided ample food and adequate nutrition. It may be possible to reveal the relational strength of feeding priority to the dominance concept by means of food deprivation. However, since there is little evidence here to suggest that feeding priority relates at all to the dominance concept in *O. garnettii*, future investigations of feeding priority's relationship to the dominance concept may not be warranted.

Some expected relationships between the measures of feeding priority on juice were revealed. For example, animals likely to drink first from the juice hoppers were more likely to visit and spend more time drinking from the hoppers. Likewise, animals likely to visit the juice hoppers spent more time drinking from them. Similar consistencies were not observed while the animals were foraging on chow. Future investigations are needed to further understand the relationship between various measures of feeding priority and the functions of these feeding behaviors within complex social systems.

Socio-Ecological Theory and the Dominance Concept

Although the juice manipulation was successful at effecting allo-grooming and foraging behavior in female *O. garnettii*, it had little to no effect on other social behaviors. The frequency of allo-grooming decreased across conditions but was confounded due to a general decrease across time. Displacements, overt agonistic behavior, the frequency of allo-grooming, and mutual grooming showed no decreases between conditions. Once again this may be due to the relatively brief manipulation and/or observation period (see Berger, 1988; Sterck et al., 1997). However, this is improbable because foraging behavior should be more strongly controlled by genetic influences and less plastic than social behavior. Phylogenetic inertia, being the alternative to socio-ecological theory, is therefore a more viable explanation.

Female social behavior has been shown to be strongly influenced by phylogenetic pressures (Di Fiore & Rendall, 1994; Thierry et al., 2000). Strong consistencies and general stability in the frequency and duration of displacement and grooming interactions gathered here provides evidence that *O. garnettii* social behavior is more likely under the control of phylogenetic influences than socio-ecological pressures. Similarly, but beyond the scope of the current research, temperament and personality factors may also relate to dominance concept (e.g., McGuire, Raleigh, & Pollack, 2005). Understanding the complexities of *O. garnettii* social behaviors as they relate to phylogeny, socio-ecological pressures, temperament, and personality will require much more investigation.

Conclusion

Research on *bushbabies* during the 1970's and early 1980's revealed much about bushbaby social behavior, but left much unresolved about how these behaviors relate to

the dominance concept (e.g., Drews 1973; Rosenson, 1973; Welker, & Witt, 1982).

Some researchers postulated bushbabies were capable of forming dominance hierarchies but were unable to show sufficient evidence due to low interaction rates and inconsistent relationships between various dominance related behavioral measures (e.g., Drews, 1973). Other researchers suggested that such sophisticated social behavior could not be exhibited by the bushbaby (e.g., Welker, & Witt, 1982).

Evidence gathered here demonstrated that female *O. garnetti* are in fact capable of constructing dominance hierarchies and these dominance relationships strengthen with time. Whether this capacity is unique to female *O. garnettii* or can be generalized to the male sex, or other species of bushbaby, will require further investigation. Likewise, further investigation is needed to determine the function of dominance related behaviors and the degree to which these behaviors are influenced by phylogenetic factors, socioecological pressures, temperament and personality. Understanding the primitive, yet complex, social organizations of this species may provide researchers with new insights into the origins of primate social behavior and organization.

APPENDIX A

IACUC PROTOCOL APPROVAL

**THE UNIVERSITY OF SOUTHERN MISSISSIPPI**

Institutional Animal Care and Use Committee

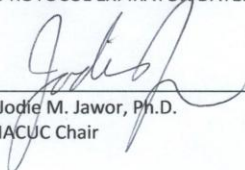
118 College Drive #5147
 Hattiesburg, MS 39406-0001
 Phone: 601.266.4063
 Fax: 601.266.4377

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER: **11102704**
 PROJECT TITLE: **Bushbaby Social Behavior**
 PROPOSED PROJECT DATES: **October 2011 – September 2014**
 PROJECT TYPE: **New**
 PRINCIPAL INVESTIGATOR(S): **Sheree Watson**
 DEPARTMENT: **Psychology**
 FUNDING AGENCY/SPONSOR:
 IACUC COMMITTEE ACTION: **Full Committee Approval**
 PROTOCOL EXPIRATION DATE: **September 30, 2014**


 Jodie M. Jawor, Ph.D.
 IACUC Chair

3/26/2013
 Date

*The original letter has been misplaced. The protocol was approved in the minutes of October 27, 2011. This letter will serve as a replacement.

APPENDIX B
BEHAVIORAL ETHOGRAM

Ethogram

Category	Behavior	Description
Displacement	Displacement	Approaching animal comes within one body length of a stationary conspecific, and the conspecific moves a body length or more away within 5 seconds of the approach; no escalation of aggression.
Agonistic Behaviors	Threat	Lunging at a conspecific without making contact or retaliation from the conspecific, as well as standing in a bipedal posture with both arms raised over their head while facing a conspecific.
	Attack	Animal bites or claws at a conspecific without retaliation from the conspecific.
	Fight	Reciprocated agonism between two or more animals, that is, conspecifics retaliate with a threat or attack within five seconds of the initial threat or attack.
	Pursuit	Animal chases a conspecific for more than 5 seconds and the chase ends with a threat, attack, or fight.
Grooming	Allogrooming	Animal licks a conspecific without reciprocation from the conspecific.
	Mutualistic Grooming	Animal licks of a conspecific with reciprocation from the conspecific, that is, the conspecific reciprocates by licking within 5 seconds of the animal desisting grooming behavior.
Feeding Priority	Preferential Access (Order of Arrival)	The sequential order, from the start of a session, in which animals lick or chew food items, will be documented.
	Preferential Access (Duration Measure)	When an animal consistently obtains food for a longer total time than other conspecifics. This will be determined by recording the amount of time animals are licking or chewing on resources.
	Preferential Access (Frequency Measure)	When an animal consistently obtains food more frequently than other conspecifics. This will be determined by recording the number of times animals lick or chew on food items. Ceasing licking or chewing behavior for five or more seconds will constitute a stop.

APPENDIX C

FREQUENCY OF BEHAVIOR ACROSS TIME BLOCKS WITHIN CONDITIONS

Table C1

Agonistic Behavior

Measure	<u>Juice Present Condition</u>			<u>No Juice Condition</u>		
	<i>Block 1</i>	<i>Block 2</i>	<i>Block 3</i>	<i>Block 1</i>	<i>Block 2</i>	<i>Block 3</i>
Displacements	80	92	59	178	131	115
Attacks	4	5	8	4	9	6
Fights	6	4	3	5	2	5
Threats	0	1	4	0	4	1
Pursuits	0	2	1	0	0	0

Table C2

Grooming Behavior

Measure	<u>Juice Present Condition</u>			<u>No Juice Condition</u>		
	<i>Block 1</i>	<i>Block 2</i>	<i>Block 3</i>	<i>Block 1</i>	<i>Block 2</i>	<i>Block 3</i>
Allo-	25	17	23	31	11	7
Mutualistic	5	10	4	11	3	3

Table C3

Feeding Behavior

Measure	<u>Juice Present Condition</u>			<u>No Juice Condition</u>		
	<i>Block 1</i>	<i>Block 2</i>	<i>Block 3</i>	<i>Block 1</i>	<i>Block 2</i>	<i>Block 3</i>
Juice	118	21	12	X	X	X
Chow	60	35	32	182	48	47

APPENDIX D
DURATION (SECONDS) OF BEHAVIOR ACROSS TIME BLOCKS
WITHIN CONDITIONS

Table D1

Grooming Behavior

	<u>Juice Present Condition</u>			<u>No Juice Condition</u>		
Measure	<i>Block 1</i>	<i>Block 2</i>	<i>Block 3</i>	<i>Block 1</i>	<i>Block 2</i>	<i>Block 3</i>
Allo-	364	240	295	253	116	61
Mutualistic	109	347	79	210	67	61

Table D2

Feeding Behavior

	<u>Juice Present Condition</u>			<u>No Juice Condition</u>		
Measure	<i>Block 1</i>	<i>Block 2</i>	<i>Block 3</i>	<i>Block 1</i>	<i>Block 2</i>	<i>Block 3</i>
Juice	3186	234	50	X	X	X
Chow	2033	1073	1373	9721	1937	1653

APPENDIX E
CORRELATION MATRICES ILLUSTRATING INCONSISTENCIES
WITHIN MEASURES OF SOCIAL BEHAVIOR

Table E1

Consistency in Total Time Spent Mutual Grooming Across Time Blocks

Condition Names and Time Blocks	Juice Present	Juice Present	Juice Present	No Juice	No Juice	No Juice	Both	Both	Both
	1	2	3	1	2	3	1	2	3
Juice Present - 1	1.000								
Juice Present - 2	.900*	1.000							
Juice Present - 3	.667	.564	1.000						
No Juice - 1	.564	.667	.895*	1.000					
No Juice - 2	.667	.872	.684	.895*	1.000				
No Juice - 3	.051	.051	.158	.158	.000	1.000			
Both - 1	.900*	.700	.872	.667	.546	.205	1.000		
Both - 2	.900*	1.000**	.564	.667	.872	.051	.700	1.000	
Both - 3	.700	.600	.975**	.872	.667	.359	.900*	.600	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Table E2

Consistency in the Number of Observed Mutual Grooming Events across Time Blocks

Condition Names and Time Blocks	Juice Present	Juice Present	Juice Present	No Juice	No Juice	No Juice	Both	Both	Both
	1	2	3	1	2	3	1	2	3
Juice Present - 1	1.000								
Juice Present - 2	.900*	1.000							
Juice Present - 3	.949*	.791	1.000						
No Juice - 1	.632	.791	.667	1.000					
No Juice - 2	.667	.872	.649	.973**	1.000				
No Juice - 3	-.354	-.354	-.559	-.559	-.544	1.000			
Both - 1	.975**	.975**	.892*	.730	.789	-.363	1.000		
Both - 2	.900*	1.000**	.791	.791	.872	-.354	.975**	1.000	
Both - 3	.975**	.821	.973**	.649	.632	-.363	.921*	.821	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

APPENDIX F

INCONSISTENCIES ACROSS TIME BLOCK

WITHIN MEASURES OF FORAGING ON CHOW AND JUICE

Table F1

Inconsistency in the Time Allocated to Chow Foraging

Condition Names and Time Blocks	Juice Present	Juice Present	Juice Present	No Juice	No Juice	No Juice	Both	Both	Both
	1	2	3	1	2	3	1	2	3
Juice Present - 1	1.000								
Juice Present - 2	.000	1.000							
Juice Present - 3	-.300	.700	1.000						
No Juice - 1	.462	-.051	-.154	1.000					
No Juice - 2	-.500	-.500	-.100	.410	1.000				
No Juice - 3	.000	-.500	-.900*	-.154	.000	1.000			
Both - 1	.600	.100	-.100	.975**	.200	-.200	1.000		
Both - 2	-.500	.500	.600	.359	.500	-.500	.300	1.000	
Both - 3	-.200	.300	.700	-.667	-.400	-.600	-.600	-.100	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Table F2

Inconsistency in the Number of Observed Bought of Chow Foraging

Condition Names and Time Blocks	Juice Present	Juice Present	Juice Present	No Juice	No Juice	No Juice	Both	Both	Both
	1	2	3	1	2	3	1	2	3
Juice Present - 1	1.000								
Juice Present - 2	-.600	1.000							
Juice Present - 3	-.700	.600	1.000						
No Juice - 1	-.300	-.100	.500	1.000					
No Juice - 2	-.112	.224	.335	.783	1.000				
No Juice - 3	-.100	.800	.500	.000	.447	1.000			
Both - 1	-.300	-.100	.500	1.000**	.783	.00	1.000		
Both - 2	-.564	.821	.872	.410	.574	.821	.410	1.000	
Both - 3	-.308	.872	.667	.103	.459	.975**	.103	.921*	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Table F3

Inconsistency in the Order of Arrival to the Juice Patch across Time Blocks

Time Block	1	2	3
1	1.000		
2	.872	1.000	
3	.763	.410	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Table F4

Inconsistency across Time Blocks in the Foraging on Juice measures

Measure Type and Time Block	Juice Present 1	Juice Present 2	Juice Present 3	No Juice 1	No Juice 2	No Juice 3
Duration (s) - 1	1.000					
Duration (s) - 2	.100	1.000				
Duration (s) - 3	.900*	.300	1.000			
Frequency - 1	.700	.100	.600	1.000		
Frequency - 2	.300	.600	.500	.700	1.000	
Frequency - 3	.821	.359	.975**	.410	.410	1.000

Note. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

APPENDIX G
 RELATIONSHIP BETWEEN ALLO-GROOMING
 AND MUTUAL GROOMING MEASURES

Table G1

No Relationship between the Direction of Allo-grooming and Participation in Mutual Grooming

Condition Names and Behavior	Juice MGr(f)	No Juice MGr(f)	Both MGr(f)	Juice MGr(d)	No Juice MGr(d)	Both MGr(d)
Juice – Gr(f)	-.700	-.600	-.700	-.700	-.600	-.700
Both – Gr(f)	-.700	-.600	-.700	-.700	-.600	-.700
Juice – Gr(d)	-.600	-.700	-.600	-.600	-.700	-.600
Both – Gr(d)	-.600	-.700	-.600	-.600	-.700	-.600

Note. Gr(f) = Frequency measure of allo-grooming, Gr(d) = Duration measure of allo-grooming, MGr(f) = Frequency measure of mutual grooming participation, and MGr(d) = Duration measure of mutual grooming participation. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

APPENDIX H

RELATIONSHIPS BETWEEN THE DIRECTION OF AGONISTIC INTERACTIONS
AND OTHER MEASURES

Table H1

No Relationship between the Direction of Agonism and Displacement

Condition Names and Behavioral Measure	Juice - D	No Juice - D	Both - D
Both - AI	-.400	-.400	-.400

Note. D = Displacement. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Table H2

No Relationship between the Direction of Agonism and Grooming

Condition Names and Behavior	Juice	Both	Juice	Both	Juice	No Juice	Both	Juice	No Juice	Both
	Gr(f)	Gr(f)	Gr(d)	Gr(d)	MGr(f)	MGr(f)	MGr(f)	MGr(d)	MGr(d)	MGr(d)
Both - AI	-.200	-.200	.100	.100	.300	.000	.300	.300	.000	.300

Note. Gr(f) = Frequency measure of allo-grooming, Gr(d) = Duration measure of allo-grooming, MGr(f) = Frequency measure of mutual grooming participation, and MGr(d) = Duration measure of mutual grooming participation. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Table H3

No Relationship between the Direction of Agonism and Foraging on Juice

Condition Names and Behavioral Measure	Juice	Juice	Juice
	1 st Arrival	Frequency Measure	Duration Measure
Both - AI	-.100	.100	.000

Note. D = Displacement. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

Table H4

No Relationship between the Direction of Agonism and foraging on Chow

Condition Names and Behavior	Juice	No Juice	Both	Juice	No Juice	Both	Juice	No Juice	Both
	1 st Arrival	1 st Arrival	1 st Arrival	Frequency	Frequency	Frequency	Duration	Duration	Duration
Both - AI	.718	-.100	-.200	-.410	.300	.100	.400	.700	.200

Note. Gr(f) = Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

APPENDIX I

INCONSISTENT RELATIONSHIPS BETWEEN FORAGING ON JUICE
AND OTHER BEHAVIORAL MEASURES

Table I1

Inconsistency in the Preferential Access to the Juice Patch with Other Measures

Condition Names Behavioral Measures	Juice 1 st Arrival	Juice Frequency Measure	Juice Duration Measure
Juice – D	-.200	.200	-.100
No Juice – D	-.200	.200	-.100
Both – D	-.200	.200	-.100
Juice – Gr(f)	-.100	.100	-.300
Both – Gr(f)	-.100	.100	-.300
Juice – Gr(d)	.200	-.200	-.600
Both – Gr(d)	.200	-.200	-.600
Juice – MGr(f)	.000	.000	.200
No Juice – MGr(f)	-.300	.300	.500
Both – MGr(f)	.000	.000	.200
Juice – MGr(d)	.000	.000	.200
No Juice – MGr(d)	-.300	.300	.500
Both – MGr(d)	.000	.000	.200
Juice – C 1 st Arrival	.205	-.205	-.462
No Juice – C 1 st Arrival	.700	-.700	-.400
Both – C 1 st Arrival	.500	-.500	-.300
Juice – C(f)	-.051	.051	.154
No Juice C(f)	-.600	.600	.200
Both – C(f)	-.700	.700	.600
Juice – C(d)	-.700	.700	.600
No Juice – C(d)	-.100	.100	.300
Both – C(d)	-.500	.500	.800

Note. D = Displacement, Gr(f) = Frequency measure of all-grooming, Gr(d) = Duration measure of allo-grooming, MGr(f) = Frequency measure of mutual grooming, MGr(d) = Duration measure of allo-grooming, C 1st Arrival = Average order of arrival to the chow patch, C(f) = Frequency measure of foraging on chow, and C(d) = Duration measure of foraging on chow. For the relationship between agonistic interactions and foraging on juice measures see Appendix H. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

APPENDIX J
 INCONSISTENT RELATIONSHIPS BETWEEN FORAGING ON JUICE
 AND OTHER BEHAVIORAL MEASURES

Table J1

Inconsistency in the Preferential Access to the Chow Patch with Other Measures

Condition Names	No			No			No		
	Juice	Both	Both	Juice	Juice	Both	Juice	Juice	Both
Behavioral Measures	1 st Arrival	1 st Arrival	1 st Arrival	Frequency Measure	Frequency Measure	Frequency Measure	Duration Measure	Duration Measure	Duration Measure
Juice – D	.205	-.300	.100	-.359	.500	.300	-.300	-.600	-.600
No Juice – D	.205	-.300	.100	-.359	.500	.300	-.300	-.600	-.600
Both – D	.205	-.300	.100	-.359	.500	.300	-.300	-.600	-.600
Juice – Gr(f)	.359	-.500	-.200	-.205	.700	.500	-.100	-.700	-.800
Both – Gr(f)	.359	-.500	-.200	-.205	.700	.500	-.100	-.700	-.800
Juice – Gr(d)	.667	-.300	-.100	-.359	.600	.300	-.200	-.500	-.900*
Both – Gr(d)	.667	-.300	-.100	-.359	.600	.300	-.200	-.500	-.900*
Juice – MGr(f)	-.359	-.100	-.500	.667	-.200	.100	.600	.300	.500
No Juice – MGr(f)	-.667	-.300	-.600	.821	-.100	.300	.700	.100	.600
Both – MGr(f)	-.359	-.100	-.500	.667	-.200	.100	.600	.300	.500
Juice – MGr(d)	-.359	-.100	-.500	.667	-.200	.100	.600	.300	.500
No Juice – MGr(d)	-.667	-.300	-.600	.821	-.100	.300	.700	.100	.600
Both – MGr(d)	-.359	-.100	-.500	.667	-.200	.100	.600	.300	.500

Note. D = Displacement, Gr(f) = Frequency measure of all-grooming, Gr(d) = Duration measure of allo-grooming, MGr(f) = Frequency measure of mutual grooming, MGr(d) = Duration measure of allo-grooming, C 1st = Average order of arrival to the chow patch, C(f) = Frequency measure of foraging on chow, and C(d) = Duration measure of foraging on chow. For the relationship between agonistic interactions and foraging on juice measures see Appendix H. For relationships between foraging measures on chow and juice refer to Appendix I. Significant correlations at an alpha level of 0.05 are indicated by *, and significant correlations at an alpha level of 0.01 are indicated by ** (2-tailed).

APPENDIX K
DOMINANCE INDEXES CONSTRUCTED FROM
DISPLACEMENT INTERACTIONS

Table K1

Dominance Index from Displacement Interactions in the Juice Present Condition

Names	Pebbles	Sybil	Piper	Brandine	Sam
Pebbles	-	11	83	24	18
Sybil	5	-	15	7	11
Piper	4	11	-	6	8
Brandine	0	3	3	-	3
Sam	1	12	3	3	-

Note. Winners are presented in rows and losers are presented in the columns. For example, Pebbles displaced Sybil 11 times and was displaced by Sybil 5 times when the juice was present.

Table K2

Dominance Index from Displacement Interactions in the No Juice Condition

Names	Pebbles	Sybil	Piper	Brandine	Sam
Pebbles	-	6	85	44	22
Sybil	7	-	53	57	79
Piper	0	8	-	14	22
Brandine	1	1	7	-	4
Sam	1	3	3	7	-

Note. Winners are presented in rows and losers are presented in the columns. For example, Pebbles displaced Sybil 6 times and was displaced by Sybil 7 times when the juice was not present.

Table K3

Dominance Index from Displacement Interactions in Both Conditions

Names	Pebbles	Sybil	Piper	Brandine	Sam
Pebbles	-	17	168	68	40
Sybil	12	-	68	64	90
Piper	4	19	-	20	30
Brandine	1	4	10	-	7
Sam	2	15	6	10	-

Note. Winners are presented in rows and losers are presented in the columns. For example, Pebbles displaced Sybil 17 times and was displaced by Sybil 12 times throughout the study.

APPENDIX L

DOMINANCE INDEXES CONSTRUCTED FROM

THE FREQUENCY MEASURE FOR ALLO-GROOMING

Table L1

Dominance Index from the Frequency of All-Grooming Interactions in the Juice Present

Condition

Names	Pebbles	Sybil	Piper	Brandine	Sam
Pebbles	-	2	3	12	5
Sybil	3	-	2	2	5
Piper	0	2	-	6	6
Brandine	0	1	2	-	8
Sam	1	1	1	3	-

Note. Winners are presented in rows and losers are presented in the columns. For example, Pebbles allo-groomed Brandine 12 times but was never allo-groomed by Brandine when the juice was present.

Table L2

Dominance Index from the Frequency of Allo-Grooming Interactions in the No Juice

Condition

Names	Pebbles	Sybil	Piper	Brandine	Sam
Pebbles	-	1	0	6	1
Sybil	1	-	2	6	5
Piper	0	0	-	5	7
Brandine	0	1	7	-	1
Sam	0	0	1	5	-

Note. Winners are presented in rows and losers are presented in the columns. For example, Pebbles allo-groomed Brandine 6 times but was never all-groomed by Brandine when there was no juice.

Table L3

Dominance Index from the Frequency of Allo-Grooming Interactions in Both Conditions

Names	Pebbles	Sybil	Piper	Brandine	Sam
Pebbles	-	3	3	18	6
Sybil	4	-	4	8	10
Piper	0	2	-	11	13
Brandine	0	2	9	-	9
Sam	1	1	2	8	-

Note. Winners are presented in rows and losers are presented in the columns. For example, Pebbles allo-groomed Brandine 18 times but was never allo-groomed by Brandine throughout the study.

APPENDIX M

DOMINANCE INDEXES CONSTRUCTED FROM THE DURATION MEASURE
FOR ALLO-GROOMING

Table M1

Dominance Index from the Duration of Allo-Grooming Interactions in the Juice Present

Condition

Names	Pebbles	Sybil	Piper	Brandine	Sam
Pebbles	-	14	81	106	75
Sybil	22	-	44	8	127
Piper	0	18	-	104	76
Brandine	0	28	71	-	75
Sam	12	2	31	5	-

Note. Winners are presented in rows and losers are presented in the columns. For example, Pebbles allo-groomed Brandine for 106 seconds but was never allo-groomed by Brandine when the juice was present.

Table M2

Dominance Index from the Frequency of Allo-Grooming Interactions in the No Juice

Condition

Names	Pebbles	Sybil	Piper	Brandine	Sam
Pebbles	-	1	0	77	23
Sybil	7	-	6	22	117
Piper	0	0	-	29	45
Brandine	0	0	53	-	24
Sam	0	0	4	22	-

Note. Winners are presented in rows and losers are presented in the columns. For example, Pebbles allo-groomed Brandine for 77 seconds but was never allo-groomed by Brandine when the juice was not present.

Table M3

Dominance Index from the Frequency of Allo-Grooming Interactions in Both Conditions

Names	Pebbles	Sybil	Piper	Brandine	Sam
Pebbles	-	15	81	183	98
Sybil	29	-	50	30	244
Piper	0	18	-	133	121
Brandine	0	28	124	-	99
Sam	12	2	35	27	-

Note. Winners are presented in rows and losers are presented in the columns. For example, Pebbles allo-groomed Brandine for 183 seconds but was never allo-groomed by Piper throughout the study.

APPENDIX N
POSTERIOR DISTRIBUTION DATA FROM
THE DISPLACEMENT MEASURE

Table N1

Node Statistics for the Displacement Measure in the Juice Present Condition

Name	2.5%	Mean	97.5%	Standard Deviation
Pebbles	1.959	2.608	3.340	0.352
Sybil	-0.282	0.325	0.935	0.311
Piper	X	0	X	X
Sam	-0.873	-0.148	0.568	0.368
Brandine	-1.586	-0.693	0.152	0.444

Table N2

Node Statistics for the Displacement Measure in the No Juice Present Condition

Name	2.5%	Mean	97.5%	Standard Deviation
Pebbles	2.403	3.147	3.996	0.406
Sybil	1.772	2.405	3.099	0.339
Piper	X	0	X	X
Sam	-1.194	-1.203	-0.528	0.358
Brandine	-1.168	-1.179	-0.473	0.373

Table N3

Node Statistics for the Displacement Measure in the Both Conditions

Name	2.5%	Mean	97.5%	Standard Deviation
Pebbles	2.316	2.801	3.329	0.258
Sybil	1.072	1.470	1.885	0.208
Piper	X	0	X	X
Sam	-1.230	-0.752	-0.283	0.242
Brandine	-1.596	-1.044	-0.523	0.273

APPENDIX O

POSTERIOR DISTRIBUTION DATA FROM THE FREQUENCY OF ALLO-
GROOMING MEASURE

Table O1

Node Statistics for the Frequency of Allo-grooming in the Juice Present Condition

Name	2.5%	Mean	97.5%	Standard Deviation
Pebbles	-0.140	1.259	2.802	0.751
Sybil	-0.837	0.539	1.991	0.722
Piper	X	0	X	X
Sam	-3.142	-1.771	-0.558	0.659
Brandine	-2.345	-1.113	0.017	0.600

Table O2

Node Statistics for the Frequency of Allo-grooming in the No Juice Present Condition

Name	2.5%	Mean	97.5%	Standard Deviation
Pebbles	0.989	3.924	8.081	1.817
Sybil	0.923	3.169	6.460	1.415
Piper	X	0	X	X
Sam	-1.765	-0.537	0.616	0.605
Brandine	-1.359	-0.321	0.694	0.523

Table O3

Node Statistics for the Frequency of Allo-grooming in the Both Conditions

Name	2.5%	Mean	97.5%	Standard Deviation
Pebbles	0.678	1.873	3.221	0.647
Sybil	0.254	1.333	2.518	0.578
Piper	X	0	X	X
Sam	-1.969	-1.100	-0.290	0.427
Brandine	-1.419	-0.661	0.070	0.379

APPENDIX P
 POSTERIOR DISTRIBUTION DATA FROM
 THE DURATION OF ALLO-GROOMING MEASURE

Table P1

Node Statistics for the Duration of Allo-grooming in the Juice Present Condition

Name	2.5%	Mean	97.5%	Standard Deviation
Pebbles	1.668	2.061	2.472	0.206
Sybil	0.702	1.060	1.433	0.187
Piper	X	0	X	X
Sam	-1.746	-1.404	-1.076	0.171
Brandine	-0.240	0.013	0.265	0.129

Table P2

Node Statistics for the Duration of Allo-grooming in the No Juice Present Condition

Name	2.5%	Mean	97.5%	Standard Deviation
Pebbles	4.466	8.812	13.26	2.452
Sybil	6.305	11.03	14.8	2.428
Piper	X	0	X	X
Sam	-1.446	-0.946	-0.467	0.249
Brandine	-0.295	0.096	0.489	0.200

Table P3

Node Statistics for the Duration of Allo-grooming in the Both Conditions

Name	2.5%	Mean	97.5%	Standard Deviation
Pebbles	1.949	2.318	2.705	0.193
Sybil	1.264	1.611	1.972	0.181
Piper	X	0	X	X
Sam	-1.598	-1.317	-1.044	0.141
Brandine	-0.242	-0.029	0.182	0.108

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