THE SOCIOECOLOGY OF CHIMPANZEE FORAGING AND FOOD-ASSOCIATED CALLING BEHAVIOR

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Dedication

This dissertation is dedicated to my parents David and Linda O'Bryan for providing unwavering support throughout my graduate career and beyond.

Abstract

Social-living is complicated. Living in groups can provide greater protection from predators, promote discovery and defense of food sources and improve access to mates. On the other hand, it can increase susceptibility to predators or pathogens and incite competition for resources. Because of these trade-offs, social systems can display high levels of diversity, both on an evolutionary time-scale as well as in response to short-term variation in social and ecological pressures. In this dissertation I investigate the foraging and food-associated calling behavior of chimpanzees (*Pan troglodytes*) in order to better understand the causes and consequences of grouping behavior. Chimpanzee social groups display high levels of short-term variability in both size and composition. Furthermore, individuals produce specific vocalizations in foraging contexts that are believed to further modulate these parties. Thus, this system provides a prime opportunity to examine the costs and benefits of sociality and how individuals respond to these trade-offs. Using a combination of captive experiments and observational field studies, I examine chimpanzee foraging decisions, the trade-off between foraging and socialization and the social and ecological correlates of food-associated calling behavior. Results from these studies expand current understanding of the foraging and social behavior of chimpanzees and suggest an alternative function for their food-associated rough-grunt vocalization. Furthermore, they highlight the challenges and benefits of social-living and the tactics individuals can employ to manipulate their social landscape.

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INTRODUCTION

      Social-living is complicated. On the one hand, living in large groups can provide important benefits. Residing in close proximity to others can reduce the likelihood of predation and/or the amount of time needed to scan for predators (Delm, 1990). Furthermore, it can increase the likelihood of finding and acquiring food (Courchamp & Macdonald, 2001; Giraldeau & Caraco, 2000) and defending territories of higher quality resources (Wilson et al., 2012). In addition, it can improve access to mates and promote cooperative breeding (Emlen, 1978). On the other hand, living with others can be highly costly. Large groups of individuals may be targeted more by predators (Wrona & Dixon, 1991) or be more susceptible to pathogens (Langwig et al., 2012). Furthermore, more individuals in the vicinity means increased competition for both resources and mates (Widemo & Owensi, 1995).

      Because of these trade-offs, social systems can display high levels of variation (Smuts et al., 1987). Based on the relative costs and benefits of group-living, individuals can trade in their current social environment for a solitary existence or find another social group where they might be more successful. For these reasons, group size is often found to vary according to the trade-off between predation pressure and feeding competition (Janson & Goldsmith, 1995; Molvar & Bowyer, 1994; van Schaik, 1983). Furthermore, the distribution and abundance of resources and potential mates may influence both the social and mating system displayed by the population (Emlen & Oring, 1977; Wrangham, 1980). This variation can occur both on an evolutionary time-scale and in response to short-term changes in environmental and social factors (Getz et al., 1987). Understanding how individuals respond to the costs and benefits of social-living can promote a greater understanding of how and why these societies function the way they do.

      Organisms do not simply respond to their surroundings, they are also capable of changing them. A key way in which individuals can influence their social environment is through the production of signals. A signal is a specific form of behavior that evolved to influence the behavior of others, typically by providing information regarding the signaler's motivational or physiological state (Bradbury & Vehrencamp, 1998; Dawkins

& Krebs, 1978; Seyfarth et al., 2010). For instance, rather than physically challenging a competitor, animals can produce signals that advertise their aggressive intent. If receivers heed this signal, this communicative behavior saves both parties from a physically costly fight. Signals can be used to attract mates to oneself (Ward et al., 2013), to establish and maintain territory boundaries (McGregor, 1993; Wilson et al., 2001), to facilitate social interactions and even share valuable information about the environment with group members, such as the presence of a predator (Seyfarth et al., 1980). Thus, signals can be considered tools for influencing one's social surroundings.

While signaling behavior can provide many benefits to both signalers and receivers, it can also result in many costs. Signal production and reception typically requires developmental specializations and the use of time and energy. Furthermore, signals can often be highly conspicuous, making individuals more susceptible to predators or competitors (Ryan et al., 1982). Furthermore, while signals can be cooperative, conflicts of interest often exist between signalers and receivers, resulting in an arms race between increasingly manipulative signalers and skeptical receivers (Krebs & Dawkins, 1984; Silk et al., 2000). Nevertheless, the persistence of a given communicative interaction over evolutionary times suggests that neither party experiences a net cost from the interaction (Bradbury & Vehrencamp, 1998). Otherwise, individuals that do not produce the signal or who do not respond to the signal would out compete those that do.

For many of these reasons, the production of food-associated vocalizations by many bird and mammal species represents an evolutionary puzzle. Food-associated calls are vocalizations produced upon discovery of, or while consuming food. These signals are typically assumed to attract the attention of receivers and inform them about the presence of a food patch. This has obvious benefits for receivers as they can acquire a new food source. However, understanding why individuals should produce such vocalizations is more complicated. An obvious potential cost of this calling behavior is increased feeding competition for the signaler. However, as mentioned previously, there can also be a variety of benefits associated with forming groups. In order to understand

the function of food-associated calls, one must understand the interaction between ecological and social factors for the species in question.

Much recent research has focused on the food-associated calling behavior of chimpanzees (*Pan troglodytes*), one of our closest-living relatives (Kalan et al., 2015; Schel et al., 2013). Previous studies have reported that the food-associated "rough-grunt" vocalization of chimpanzees is produced upon discovery of high quality food (Hauser et al., 1993), and that variation in its acoustic properties may be capable of informing receivers about the properties of this food (Slocombe & Zuberbühler, 2005, 2006). These findings have attracted much interest from researchers interested in the evolutionary origins of human language due to their seeming ability to function in a word-like manner (Fedurek & Slocombe, 2011). However, why chimpanzees should produce such vocalizations remains unclear (Clay et al., 2012). Since attracting attention to a food source can increase feeding competition, signalers are presumed to gain some benefit from this calling behavior that outweighs this cost. Some researchers have suggested that chimpanzees trade information about food for social benefits such as coalitionary support or grooming (Brosnan et al., 2013). However, whether these vocalizations are sufficient to inform others about food and whether they function by attracting others to the food patch is still not well understood.

Another food-associated vocalization of chimpanzees, the food-arrival pant-hoot, has long been proposed to inform naïve community members about discovered food (Reynolds & Reynolds, 1965). Nevertheless, there is limited evidence that this vocalization actually functions in this manner. In contrast to rough-grunts, pant-hoots are not specific to foraging contexts and are produced in a variety of social situations (Goodall, 1986). Furthermore, one study did not find evidence that the pant-hoots produced in foraging contexts differ acoustically from pant-hoots produced in other social contexts (Clark & Wrangham, 1993), suggesting that this vocal behavior alone is not sufficient to inform others of food. Even more, there is mixed evidence that pant-hoots do attract others to the food source. Wrangham (1977) found that pant-hoot production was correlated with the arrival of estrous females while Clark and Wrangham (1994) found that pant-hoot production was not correlated with the arrival of extra-party

individuals (Clark & Wrangham, 1994). Thus, while it is tempting to assume that food-associated calls function by informing others about the food source, care must be taken in the interpretation of this calling behavior.

Understanding the function of food-associated calling behavior requires a thorough understanding of the social and ecological factors that influence individual foraging behavior. Furthermore, it requires understanding how call production influences the behavior of others. While most food-associated calls are presumed to attract others to the food patch (Elgar, 1986a), a wide variety of alternative functions have been discovered, including repelling others from the food. Thus, while many species production vocalizations in foraging contexts, the function of this calling behavior appears to vary according to the specific social and ecological challenges faced by each species (Clay et al., 2012). In this dissertation, I examine the function of chimpanzee food-associated calling behavior by exploring social and ecological influences on the foraging behavior of chimpanzees and their relationship with food-associated call production. These studies emphasize the function of the rough-grunt vocalization due to its specificity to foraging contexts. In order to best achieve my objectives I conducted both observational studies of wild chimpanzees and behavioral experiments with captive chimpanzees. My field studies enable me to understand the behavior of wild chimpanzees within their natural social and ecological environment. My captive studies enable me to explore chimpanzee behavior in more detail and isolate specific factors that influence their behavior. I conducted my experiments with captive chimpanzees since experimental manipulation of chimpanzee behavior was not permitted at Gombe National Park.

In Chapter 1, I describe my research sites and general methods, provide basic information about my study subjects and present key results that will facilitate a better understanding of the ensuing chapters. In Chapter 2, I discuss results from behavioral experiments in which I presented captive chimpanzees with a simple foraging task designed to reveal how chimpanzees make foraging decisions in the absence of environmental and social complexity. In Chapter 3, I examine social and ecological influences on the foraging behavior of wild chimpanzees, particularly with regards to the use of discrete food patches, in order to investigate the trade-offs chimpanzees may

experience in foraging contexts. In Chapter 4, I discuss a field study investigating social and ecological predictors of food-associated call production and patch-sharing in wild chimpanzees and a captive playback experiment designed to examine the effect rough-grunts have on listener behavior. Finally, in Chapter 5, I describe a preliminary analysis of the acoustic properties of rough-grunts in order to determine whether acoustic features of these vocalizations covary consistently with properties of wild foods.

Results from my captive foraging studies show that solitary chimpanzees follow predictions from optimal foraging models by demonstrating sensitivity to rate of energy intake and patch depletion. However, while optimal foraging studies predict that sharing a food patch with others will result in a social foraging cost due to more rapid patch depletion, I did not find evidence of such a cost in wild chimpanzees. Rather, I found evidence that the number of individuals feeding within a food patch is an indicator of patch quality and that satiation limits feeding duration in such high quality patches. Thus, sharing a high quality food patch with others does not appear to impose foraging costs. Furthermore, foraging with others opens the opportunity to socialize within the patch and reduces the likelihood that individuals will lose contact with one another over the course of the feeding bout. These findings suggest that chimpanzees adjust their grouping patterns so that they feed in groups when the benefits of doing so outweigh the costs.

When examining the function of food-associated calling behavior, I found that the production of food associated calls was better explained by social than ecological factors. Chimpanzees were more likely to produce rough-grunts when a higher ranking individual was present in their foraging party, regardless of abundance or quality of food. Furthermore, while food-associated call production was correlated with the arrival of others in the food patch, this arrival behavior was best explained by the total number of individuals already present in the vicinity, rather than by the production of food-associated calls. A preliminary acoustic analyses of rough-grunt vocalizations indicates that, rather than giving specific call types in different foraging contexts, chimpanzees often produce rough-grunts that cover the full range of acoustic variability within a single feeding bout. These findings indicate that food associated calls are unlikely to convey information about food properties, such as abundance and quality, and instead appear to

convey information about the motivational state of the signaler. Thus, rather than refer to food patch properties and attract others to a food patch, rough-grunts appear to mediate social interactions in foraging contexts when others are already coming together in a high quality food patch.

Together, these studies expand current understanding of the foraging, social, and communicative behavior of chimpanzees. Furthermore, they provide insights into the challenges and benefits of social-living and the mechanisms through which individuals can moderate their social landscape.

CHAPTER 1
RESEARCH SITES AND GENERAL METHODS

1.1 Introduction

In this section I describe the two research sites where I conducted my dissertation research. I conducted my captive work at the Michale E. Keeling Center for Comparative Research and Medicine (KCCMR), Bastrop, TX and my fieldwork at Gombe National Park (Gombe), Tanzania. In Section 1.2 I provide a description of both research sites. In Section 1.3 I provide a broad overview of the work I conducted at each site and a timeline for when I conducted these studies. Sections 1.4 and 1.5 focus specifically on the fieldwork I conducted at Gombe. In Section 1.4 I provide a detailed description of the methods I used to collect all field data. In Section 1.5 I present summary information on the quantity of field data I collected and present two results that are key to subsequent chapters of this dissertation. The first result explains why I focused my core fieldwork on adult male chimpanzees. The second justifies a key patch quality measure used throughout Chapters 3 and 4 of this dissertation.

1.2 Research Sites

KCCMR

I conducted experiments with captive chimpanzees housed at KCCMR. This site houses a large population of captive chimpanzees which reside in over 20 small multi-male, multi-female social groups. All groups have *ad libitum* access to an indoor and outdoor enclosure as well as to monkey chow and water. In addition, groups are fed four fresh produce meals a day and participate in food- and/or drink-related enrichment activities several times per week. Subjects were not deprived of food or water at any time during the research period and had access to chow and water throughout all experiments. While subjects did occasionally drink water, no subjects consumed chow during the experiments.

Gombe

I conducted field work at Gombe, a small (35 km^2) park in western Tanzania bordering the eastern shore of Lake Tanganyika. Inside the park live three communities of chimpanzees: the Mitumba community to the north, the Kasekela community in the center, and the Kalande community in the south. The field studies presented in this dissertation focus the Kasekela community, the largest community in the park, and the longest studied chimpanzee community in the world. Jane Goodall and her team have studied the Kasekela community since 1960 (Goodall, 1986). While the Kasekela community was provisioned with bananas from 1963 to 2000, regular feeding ended 9 years prior to the start of my fieldwork. At the start of my pilot fieldwork in 2009 the population consisted of 14 adult and 10 subadult males and 20 adult and 14 subadult females. At the start of my core fieldwork in 2012, the population consisted of 13 adult and 14 subadult males and 25 adult and 10 subadult females. I consider subadults to be all individuals below the age of 12 (Foerster et al., 2015; Murray, Gilby, Mane, & Pusey, 2008; Wroblewski et al., 2009).

1.3 Timeline

Michale E. Keeling Center for Comparative Research and Medicine

I conducted research at the KCCMR for a total of 10 months, including June-August 2010 and February-August 2011. In 2010 I conducted a playback experiment with chimpanzees housed in two social groups to assess the effect of food-associated call playbacks on individual feeding site choice. The specific methods followed in this experiment and results of this work are presented in Chapter 4 of this dissertation. In 2011 I conducted a foraging experiment with chimpanzees housed in four social groups in order to investigate their patch residence decisions. The specific methods followed in this experiment and results of this work are presented in Chapter 2 of this dissertation.

Gombe

I conducted fieldwork for a total of 14 months at Gombe: June-August 2009, February-July 2012 and January-June 2013. The work I conducted in 2009 was pilot fieldwork which helped to guide the development of the methods I used in my core

fieldwork. I conducted my core fieldwork during my 2012 and 2013 field seasons. All fieldwork focused on examining the foraging behavior of wild chimpanzees, social and ecological predictors of food-associated call production, the consequences of call production, and the acoustic properties of rough-grunt vocalizations. Results of this work are presented in Chapters 3, 4, and 5.

1.4 General Methods- Gombe

There is significant overlap in the methods I used to collect field data during my pilot and core field seasons. However, there are also some key differences, particularly in the style of focal follows I conducted and in the targets of these follows. To clearly differentiate the methods used in my pilot and core field seasons, I present these methods in the following two subsections. Only those data collected during my core field seasons are presented in Chapters 3, 4 and 5 of this dissertation.

Pilot Fieldwork

I spent the first month of my pilot field season (June 2009) becoming familiar with the park and its vegetation, learning the identities of the chimpanzees, observing their behavior and developing my observational research techniques. I collected pilot data from July-August 2009. The focal targets for my pilot fieldwork were all adult, adolescent and juvenile chimpanzees in the Kasekela community that I encountered regularly during the study period and which were habituated enough to the presence of humans that they could be followed relatively easily. This set of focal targets consisted of 14 adult, 2 adolescent and 3 juvenile males and 13 adult, 5 adolescent and 2 juvenile females. I conducted two-hour focal follows of all target individuals (Altmann, 1974). At the end of a given focal follow, I chose the next focal target from those available in the vicinity, giving precedence to those I had followed the least. I attempted to rotate through all available targets before repeating a focal follow of any given individual.

All pilot fieldwork was aided by Amri Alimasi, a Tanzanian from a village bordering the park who worked periodically as a field assistant for visiting researchers at Gombe. Due to this work, Alimasi was familiar with the park, the chimpanzees and the

vegetation within the park at the start of my study. At the beginning of the study I provided him with additional training on the specific research and data collection methods to be used in my study. In addition to aiding in navigation within the park and keeping track of my focal target, Alimasi also collected data on party composition. For my studies I considered all individuals within sight of the target to be in the target's party. In order to document party composition, Alimasi conducted party composition scans every 15 minutes during the focal follow. If an individual was seen at any point during a given 15 minute interval, Alimasi included that individual as being present during that interval.

I collected all other behavioral data myself. I conducted behavioral scan samples (Altmann, 1974) at regular intervals throughout the duration of the follow. Every five minutes, I recorded the target's behavioral state as either Travel, Feed, Wadge, Rest, Groom, Being Groomed, Mutual Groom, Other, Bad Observation or Out of Sight. If the target was in one of the three grooming states, I also recorded the identity of the target's grooming partner. During scans of the target's behavioral state, I also recorded the identity of the target's nearest neighbor and the neighbor's behavior using the same categories of behavioral states used for the focal target. During these scans I also recorded the identity of all individuals present less than 1 meter, 1-5 meters and 5-10 meters from the focal target. If I couldn't identify a given individual due to poor visibility, I recorded "X" to indicate that an unknown individual was present. If I could not reliably count the number of individuals present in a given distance category due to poor visibility, I recorded the identity or presence of all individuals that I could differentiate, if any, and indicated that the remainder were unknown.

If the target stopped to feed for a period of time longer than one minute I recorded the start and end time of the feeding bout to the nearest second. I considered the start time to be the time which the target first began feeding and the end time to be when the target last finished feeding. I only recorded the start and end time of feeding bouts lasting longer than one minute due to my inability to accurately record all relevant data for feeding bouts shorter than this duration. Thus, I did not record instances where the target grabbed single food items while traveling and discontinued recording data for any

feeding bouts where the target entered a food patch but departed before one minute had elapsed. Due to difficulty traveling through dense habitat, it was not uncommon for the target to arrive at a food patch before it was within my sight. If this occurred, I recorded the range of potential start times. For every feeding bout, I recorded the part of food being eaten by the target and the species of food, if known. Every time the target entered a new patch I recorded whether or not any other individuals were already feeding in that patch and recorded their identities, if present. If any individuals arrived while the target was feeding I recorded their identity and their arrival time to the nearest second.

I recorded all-occurrences of pant-grunts by or towards the target, noting the start time of the calling bout to the nearest second and the sender and receiver of the vocalizations, when known. I recorded these vocalizations since they are only produced towards individuals more dominant than the signaler (Goodall, 1986) and can thus be used to determine dominance relationships between individuals. I also recorded all occurrences of pant-hoots produced by the target and the time in which rough-grunts were first heard by the target during feeding bouts. When possible, I recorded vocalizations produced during feeding bouts by the target or any other party member with a Sennheiser ME66 shotgun microphone with K6 power module and Marantz PMD 671 recorder.

Alimasi and I regularly communicated throughout the data collection process to ensure accuracy of the data, particularly when visibility was low or there was uncertainty regarding the data to be documented.

Core Fieldwork

For my core fieldwork I focused on 10 adult males. I focused on adult males because results from my pilot study indicate that this age-sex class produces rough-grunts in the greatest proportion of feeding bouts (Section 1.5; Figures 1-1 and 1-2). For the same reasons, previous studies of food-associated calling behavior also have focused most intensely on this age-sex class (Fedurek & Slocombe, 2013; Slocombe et al., 2010). I chose my ten focal targets from the 13 available males due to their regular sightings during the study. Basic information for these focal targets is provided in Table 1-2. Age,

rank and maternal relatedness were determined from long-term observational data from Gombe Stream Research Centre (unpublished data). Relative rank was determined according to the direction of pant-grunt vocalizations between community members. These rank data were determined by Anne Pusey's research team from the long-term Gombe database hosted at Duke University. Pant-grunts are submissive vocalizations that are only directed towards higher ranking individuals (Goodall, 1986). By comparing the direction of pant-grunts produced between pairs of individuals, each individual's relative rank can be determined. No changes in rank between my focal targets were observed across the duration of my core fieldwork.

I aimed to conduct focal follows for up to 8 hours. Follows were terminated before achieving this duration if I lost the target and could not find him again or if the target built his night nest before the end of the focal follow- typically due to an extended amount of time spent searching for a focal target before the start of the follow. I continued follows for longer than 8 hours if nesting the focal target would aid in the acquisition of a new focal target the following day, which was the case if the focal target was traveling late in the day with another eligible target. I attempted to follow each focal target at least once every two weeks.

Kassimu Sadick assisted me during my 2012 field season and both Kassimu Sadick and Sadiki Haruna assisted me during my 2013 field season. Both are Tanzanians from villages bordering the park. Before beginning work on this study, Sadick periodically took tourists on guided tours through the park and Haruna and had trained for several months with Tanzanian field workers involved in long-term data collection efforts within the park. Thus, both Sadick and Haruna were familiar with the park, the chimpanzees and the vegetation within the park at the start of their involvement with this study. At the beginning of both the 2012 and 2013 field seasons I provided my assistant(s) with additional training on the specific research and data collection methods to be used during the study. Both field assistants aided in navigation within the park and helped keep track of my focal target. In addition, Sadick collected all scan samples of the target's behavior and the behavior and identity of the target's nearest neighbor. Party composition data was collected by Sadick in 2012 and Haruna in 2013. I hired Haruna to

collect party composition data in 2013 since it enabled Sadick to collect additional data on the behavior and proximity of the focal target's party members. Both myself and Sadick worked with Haruna at the beginning of my 2013 field season to ensure that he was properly trained in the methods used to collect party composition data during the 2012 field season.

For my studies I considered all individuals within sight of the target to be in the target's party. In order to document party composition, party composition scans were conducted every 15 minutes during the focal follow (by Sadick in 2012 and Haruna in 2013). If an individual was seen at any point during a given 15 minute interval, that individual was recorded as being present during that interval. Sadick conducted behavioral scan samples (Altmann, 1974) at regular intervals throughout the duration of all focal follows conducted during my core field season. Every five minutes, he recorded the target's behavioral state as one of the following: Travel, Feed, Wadge, Rest, Groom, Being Groomed, Mutual Groom, Other, Bad Observation or Out of Sight. "Feed" was restricted to the process of actively searching for and acquiring food while in a food patch. "Wadge" refers to holding food items in the lower lip and squeezing them against the teeth in order to extract juices (Goodall, 1986). Sadick only documented the target's behavior as wadging if he was sitting still and only performing this behavior. If the target was traveling, grooming or performing any other behavior while also wadging these behaviors were documented instead. "Bad Observation" was documented when the location of the target was known but we could not determine his behavior, for instance due to dense vegetation. "Out of Sight" was recorded if the target could not be seen at all, for instance, during periods in which we lost contact with him.

During scans of the target's behavioral state, Sadick also documented the identity of the target's nearest neighbor as well as the neighbor's behavior, using the same categories of behavioral states used for the focal target. In addition, he documented the nearest neighbor's distance as <1 meters, 1-5 meters, 5-10 meters or >10 meters from the focal target. During my 2013 field season Sadick also conducted behavioral scans of all individuals within 10 meters of the target. During these scans he documented the behavioral state and distance category of all individuals within this area. These

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behavioral categories were limited to "Travel", "Feed", "Rest", "Groom", "Other", or "Bad Observation". Distance categories were 0-1 meters, 1-5 meters and 5-10 meters. Group scans were not conducted while the target was traveling rapidly since the target's position relative to his party members was capable of changing rapidly before the relevant information could be documented.

I collected the remainder of the behavioral data. Throughout the follow I documented all occurrences of grooming behavior involving the target. These data provide a finer scale than that provided by behavioral scan data. For each grooming interaction, I recorded the direction of the grooming as well as the start and end time of the interaction to the nearest second. Each change in grooming direction was documented as a unique observation.

If the target stopped to feed for a period of time longer than one minute I documented the start and end time of the feeding bout to the nearest second. I considered the start time to be the time the target first contacted the substrate of the food patch (such as a tree, shrub, or liana) and the end time to by the time the subject broke contact with the food patch. I defined a food patch as an area of a single species where a chimpanzee would be capable of continuously feeding (White & Wrangham, 1988). While a patch could be comprised of a single tree, shrub or liana, it could also be comprised of multiple units growing very closely to one another. For all food patches I documented whether the boundaries of the patch were clearly identifiable. During the study, chimpanzees spent a relatively large proportion of their time feeding on food species distributed in patches that were difficult to define, for example, on the shrub *Monanthotaxis poggei* and the liana *Sabicea orientalis*. While feeding on these species, it was common for targets to continue traveling while selecting fruits from the vegetation as they passed. It was often difficult to remain in close proximity to the target in such patches. Thus, it was difficult to be certain whether the target did not produce any rough-grunts. Furthermore, it was difficult to determine whether other chimpanzees were within the same patch and when they arrived or departed. For this reason, I limited analyses to cases in which I could clearly determine the food patch.

I only documented feeding bouts lasting longer than one minute due to my inability to accurately record all relevant data for feeding bouts shorter than this duration. Thus, I did not record instances where the target grabbed single food items while traveling, and discontinued recording data for any feeding bouts where the target entered a food patch but departed before one minute had elapsed. Such abbreviated feeding bouts were not included in any analyses presented in this dissertation. Due to difficulty traveling through dense habitat, it was not uncommon for the target to arrive at a food patch before it was within my sight. If this occurred, I noted that the exact start time of the feeding bout was not observed. This is important since food-associated vocalizations often occur upon arrival at a food patch.

For every feeding bout I documented the part of food being eaten and the species of food, if known. I used six categories of food parts: fruit, leaves, flowers, pith, sap, unsure and mixed. I typically only documented "unsure" during feeding bouts were visibility was very poor. If the target was feeding on multiple food parts I recorded the food part as "mixed" and listed the food parts consumed. Table 1-3 displays the number of feeding bouts observed during my core field season in which the focal target consumed a given food species and part. These data are restricted to only those instances in which the boundaries of the food patch were clearly defined since this was a requirement of all analyses presented in this dissertation.

For all clearly defined food patches I estimated the size of each patch at its widest diameter and assigned a size category of either <5m, 5-10, and >10m. I decided upon these size categories due to the relative ease of differentiating these categories by eye. When possible, I also measured the diameter at breast height (DBH) in centimeters of all trees in which the focal target fed. DBH is a reliable indicator of the overall size of the tree and a strong predictor of maximum possible output of fruit (Chapman et al., 1992). This measurement was taken at a height of approximately 1.4 meters or just above tree buttresses if they extended above this height. If the food patch in which the target was feeding consisted of more than one tree with merged crowns, I documented the DBH of each tree. For food patches consisting of more than one tree, the total DBH was calculated by calculating the area of the cross section at the DBH for each tree and

summing them together. I then determined the circumference of this area. For all tree species in which both DBH and size category estimations were taken (n=234) I determined the correlation between these two measurements using a Kruskal-Wallis rank sum test.

During my 2013 field season I conducted bite rate samples while the target was feeding on fruit, flowers or leaves. When visibility permitted, I conducted bite rate samples once every five minutes throughout the feeding bout. I aimed to conduct the first bite rate sample within the first five minutes of the feeding bout. I was not able to choose a specific time at which to record bite rate information since I often spent time at the beginning of the feeding bout acoustically recording food-associated vocalizations and recording other data such as the identities of those already in the food patch and the arrival times of those arriving after the target. For feeding bouts that lasted longer than 5 minutes, I conducted a new bite rate sample five minutes after the first sample and every five minutes thereafter. Bite rate samples lasted one minute. During this time period I documented all bites taken by the target. I did not consider wadging to be biting since wadging involves the processing of previously-acquired food. Bite rate samples were only conducted if the target was actively feeding during the time period of the intended bite rate sample. If he was not feeding at this point, I skipped the intended scan and attempted the next sample five minutes later. I coded skipped bite rate samples as null values rather than zeros since a zero would imply that the target was actively foraging but unable to find food to consume.

Every time the target entered a new patch I documented whether or not other individuals were already feeding in that patch and documented their identities if any were present. If any individuals arrived or departed from the patch while the target was feeding, I recorded their identity and their arrival/departure time to the nearest second. For each feeding bout, I documented whether the target produced any rough-grunts or pant-hoots. When possible, I recorded vocalizations produced during feeding bouts by the target or any other party member. For my core field season I used a Marantz PMD 620 recorder rather than the Marantz PMD 671 I used during my pilot season. I switched to

the PMD 620 since its small size allowed greater ease when navigating through dense vegetation while following my focal targets.

Sadick, Haruna and I regularly communicated throughout the data collection process to ensure accuracy of the data, particularly when visibility was low or there was uncertainty regarding the data to be documented.

1.5 Summary Statistics and Key Results- Gombe

During my pilot field season I conducted 121 2-hour focal follows, resulting in 242 hours of observation and (mean ± SE) 3.1 ± 0.1 focal follows per target. During this pilot field season I observed rough-grunt production by focal targets in only 7% of all feeding bouts (n=428 feeding bouts). For each focal target I calculated the proportion of feeding bouts in which any rough-grunts were documented. I found that adults produced rough-grunts in a greater proportion of feeding bouts than subadult individuals (Wilcox sign rank test, W=100, $p < 0.05$; Figure 1.1). Within adults, adult males produced rough-grunts in a greater proportion of feeding bouts than adult females (Wilcox sign rank test, W=41.5, $p < 0.05$; Figure 1.2). Due to the infrequency of rough-grunt production, I chose to focus my core fieldwork on the behavior of adult male chimpanzees in order to maximize the number of feeding bouts in which rough-grunt calling behavior might be observed. Furthermore, this focus enables me to compare my results to previous studies which have focused specifically on the rough-grunt calling behavior of adult male chimpanzees (Fedurek & Slocombe, 2013; Slocombe et al., 2010)

During my core field seasons I conducted 146 focal follows resulting in 1,030 hours of observation (mean ± SE: focal follow length (hours)= 7.0 ± 0.2; focal follows per target= 14.5 ± 1.3; hours of observation per target= 103 ± 8.5, Table 1.2). Focal targets frequently fed in food patches that were not trees and thus did not have definable DBH measurements (Table 1-3). In order to maximize the number of feeding bouts included in my analyses, I used size category measurements as my measure of patch size in all analyses rather than DBH. In order to justify this measure, I investigated the correlation between the DBH of a given tree and its assigned size category. I found that there was a significant positive correlation between these two measures (K=127.4,

p<0.001; Figure 1-3). This finding indicates that my size categories accurately represent differences in tree size, suggesting that this measure is a reliable indicator of patch size in general.

Due to the small number of observations in which targets fed in patches that had a diameter greater than 10 meters and that also had clearly defined boundaries (which I set as a requirement for all analyses), I combined the size categories 5-10m and >10 into the category >5m. This categorization is similar to that used by White and Wrangham (1988) in which they divided trees into the categories "small" and "large" according to whether they have a DBH of less than or greater than 50cm, respectively. These two size categories are used in the analyses presented in Chapters 3 and 4 of this dissertation.

1.6 Tables

Table 1-1. Experimental Subjects- KCCMR Basic information on the subjects that participated in my behavioral experiments at KCCMR. Each subject's sex (M=Male, F=Female), year of birth, age and social group ID are provided. Also included are data regarding which experiment(s) the subjects participated in (X= participated). Data on each subject's year of birth were obtained from records kept by staff members at KCCMR. Asterisks following the year of birth indicate that the date is estimated. Age is calculated with reference to the start of my captive work in 2010. Social group ID pertains to the social group in which each individual resided at the time of their participation in my experiments.

Name	Sex	Year Born	Age	Social Group	Playback Experiment	Foraging Experiment
Judumi	M	1990	20	D6	X	X
Patti	F	1969*	41	D6	X	
Kobi	M	1972*	38	D6	X	
Bernadette	F	1978	32	D6	X	
Tulik	F	1980	30	D6	X	X
Quincey	F	1971*	39	D6	X	
Bischk	F	1985	25	D8	X	
Gisoki	M	1983	27	D8	X	
Kukui	M	1984	26	D8	X	
Nahko	M	1986	24	D8	X	
Tahmia	F	1989	21	D8	X	
Kampani	F	1991	19	D8	X	
Ahni	F	1995	15	Q1		X
Gaygos	M	1991	19	Q1		X
Kelley	F	1966*	44	Q3		X
Martha	F	1966*	44	Q3		X
Akimel	M	1980	30	Q3		X
Gigi	F	1962*	48	Q4		X
Nick	M	1988	22	Q4		X
Ursula	F	1964*	46	Q5		X
Helga	F	1966*	44	Q5		X
Joey	M	1972*	38	Q5		X

Table 1-2. Focal Targets- Gombe Basic information on the focal targets for my core fieldwork- field seasons conducted in 2012 and 2013. Maternal relatedness, birth year, and rank were determined from long-term observational data from Gombe Stream Research Centre. The asterisk following the year of birth year of Zeus indicates that there is uncertainty regarding whether he was born in late 1993 or early 1994. Age is calculated according to the start of my core fieldwork in 2012. No changes in rank were observed across the duration of my core fieldwork. The number of focal follows and hours of observation are cumulative across the 2012 and 2013 field seasons.

Name	ID	Mother	Birth Year	Age	Sex	Rank	Number of Focal Follows	Hours of Observation
Apollo	AO	Athena	1979	33	M	7	13	88.4
Freud	FD	Fifi	1971	41	M	3	14	96.6
Ferdinand	FE	Fifi	1992	20	M	1	19	142.7
Faustino	FO	Fifi	1989	23	M	2	17	118.9
Frodo	FR	Fifi	1976	36	M	6	19	131.9
Fudge	FU	Fanni	1996	16	M	10	17	112.1
Sheldon	SL	Sparrow	1983	29	M	4	7	54.7
Sampson	SN	Sandi	1996	16	M	9	13	91.9
Titan	TN	Patti	1994	18	M	5	17	118.3
Zeus	ZS	Trezia	1993*	19	M	8	10	74.5

Table 1-3. Food Species and Parts Consumed- Gombe A table displaying the total number of feeding bouts in which the focal target consumed each food species and part. I also include the growth form of the species. These data are from my core field season only and are restricted to instances where the food patch had clearly defined boundaries- a requirement of all analyses (n=573). While these data represent the maximum number of feeding bouts that could be included in an analysis, most analyses had other restrictions which further limited the dataset. All requirements for a given analysis are described within the analysis sections of my chapters. The part "U" represents those food parts that were unknown (typically due to bad visibility). If the target consumed more than one food part during a given feeding bout, its part is displayed as "Mix".

Species	Form	Part							Total
		Fruit	Leaves	Flowers	Pith	Sap	U	Mix	
Albizia glabberima	tree	0	0	0	0	23	0	0	23
Antiaris toxicaria	tree	2	0	0	0	0	0	0	2
Antidesma venosum	shrub	11	0	0	0	0	0	0	11
Aspilia kotschyi	herb	1	0	0	0	0	0	0	1
Baphia capparidifolia	liana	0	4	0	0	0	0	0	4
Canthium crassum	tree	5	0	0	0	0	0	0	5
Canthium hispidum	tree	1	0	0	0	0	0	0	1
Dioscorea odoratissima	liana	0	15	0	0	0	0	0	15
Diplorhynchus condylocarpon	tree	25	2	0	0	0	0	0	27
Elaeis guineensis	tree	27	0	0	26	0	5	0	56
Ficus sansibarica sansibarica	tree	6	0	0	0	0	0	0	6
Ficus spp.	tree	3					0		36
Ficus trichopoda	tree	3	0	0	0	0	0	0	3
Ficus vallis-choudae	tree	21	21	0	0	0	3	8	53
Flacourtia indica	tree	1	0	0	0	0	0	0	1

Grewia platyclada	shrub	5	1	0	0	0	0	1	7
Harungana madagascariensis	shrub	13	0	0	0	0	0	0	13
Hypoestes verticillaris	herb	0	1	0	0	0	0	0	1
Landolphia lucida	liana	0	7	0	0	0	0	0	7
Monanthotaxis poggei	shrub	4	0	0	0	0	0	0	4
Parinari curatellifolia	tree	15	5	0	0	0	0	0	20
Pseudospondias microcarpa	tree	29	0	0	0	0	0	0	29
Pterocarpus tinctorius	tree	80	2	0	0	0	0	0	82
Saba comerensis var. florida	liana	4	0	0	0	0	0	0	4
Sabicea orientalis	shrub	1	0	0	0	0	0	0	1
Syzigium guineense	tree	0	0	0	0	1	0	0	1
Tabernaemontana holstii	tree	5	0	0	0	0	0	0	5
Tinospora caffra	liana	0	3	0	0	0	0	2	5
Uapaca kirkania	tree	0	0	2	0	0	0	0	2
Unknown	mixed	9	28	0	9	0	1	2	49
Uvaria angolensis	shrub	59	0	0	0	0	0	0	59
Vitex fischeri	tree	38	0	0	0	0	0	0	38
							Total:		571

1.7 Figures

Figure 1-1. Rough-grunt Production by Age Class Boxplots representing the proportion of feeding bouts in which focal targets produced rough-grunts during my pilot field season according to the age class of the focal target (n=39 focal targets). Boxes represent 1st-3rd quartiles. Points represent distinct focal targets and slight jitter is included around the x and y axis to promote visibility. Adults produced rough-grunts in a significantly greater proportion of feeding bouts than subadults (Wilcox test, $p<0.05$).

Figure 1-2. Rough-grunt Production in Adults by Age Class Boxplots representing the proportion of feeding bouts in which adult focal targets produced rough-grunts during my pilot field season according to the sex class of the focal target (n=25 focal targets). Boxes represent 1st-3rd quartiles. Points represent distinct focal targets and slight jitter is included around the x and y axis to promote visibility. Adult males produce rough-grunts in a significantly greater proportion of feeding bouts than adult females (Wilcox test, p<0.05).

Figure 1-3. Relationship Between Tree DBH and Assigned Size Category Boxplots
representing the diameter at breast height (1.4 meters) of trees assigned to three size
categories (<5 meters, 1-5 meters and 5-10 meters) (n=234 trees). I assigned a tree to a
given size category according to the estimated diameter of its crown at its widest point.
Boxes represent 1st-3rd quartiles. Points represent distinct trees and slight jitter is included
around the x and y axis to promote visibility. There is a positive correlation between
DBH and assigned size category (Kruskal Wallis test, p<0.001).
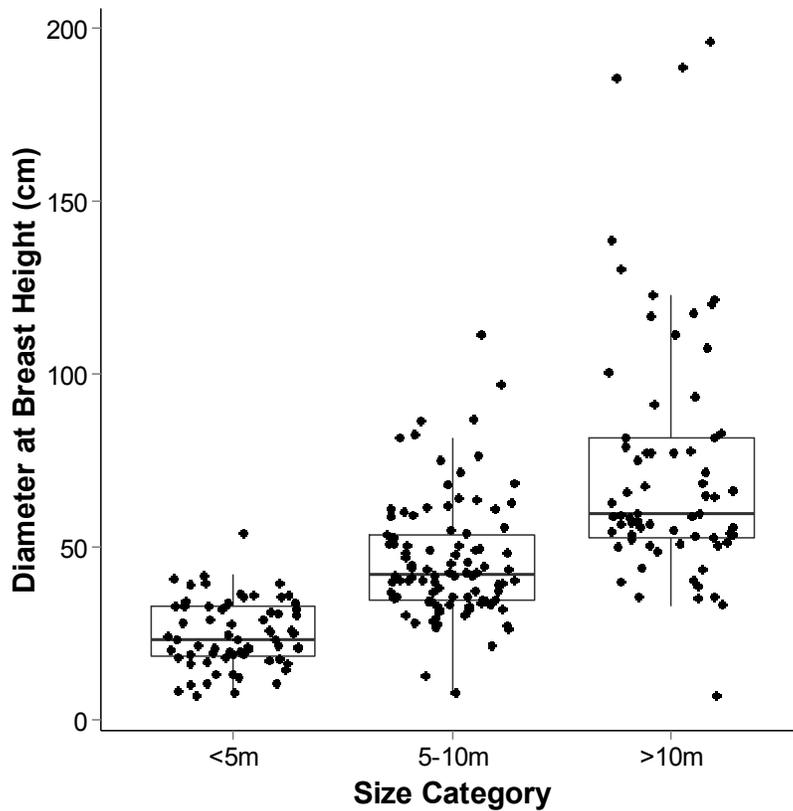
CHAPTER 2

CHIMPANZEES MAXIMIZE ENERGY INTAKE WITHIN A SIMPLE CAPTIVE FORAGING ENVIRONMENT

2.1 INTRODUCTION

Animals need energy to survive and reproduce, yet the time and resources needed to acquire this energy are limited. Thus, individuals that maximize their net long-term rate of energy intake should experience a selective advantage (Emlen, 1966; MacArthur and Pianka, 1966). Maximizing intake rate has the potential to either increase the total amount of energy acquired over a set amount of foraging time or minimize the amount of time required to obtain a set amount of energy (Schoener, 1971). These rate-maximizing strategies can enhance an organism's fitness by increasing the amount of energy or time available for activities such as gestation or mate advertisement that directly contribute towards reproductive success. Thus, genes that promote efficient foraging are expected to increase within the population over time.

Optimal foraging theory comprises a diverse set of mathematical models that predict how animals should behave in order to maximize their rate of energy intake while foraging. The utility of the optimal foraging framework is that it enables quantitative predictions for animal foraging behavior while requiring explicit statement of assumptions regarding the nature of the foraging decision, the currency being optimized and constraints on the forager's behavior. Optimal foraging models have promoted understanding of a range of foraging decisions, such as how to choose among available food items or food patches, how long to remain within a given patch and how to move between patches (Stephens & Krebs, 1986). Furthermore, modification of classic foraging models have provided insight into more nuanced scenarios such as how animals should balance foraging and the avoidance of predation (Lima et al., 1985) or how they should maneuver within a given social foraging environment (Giraldeau & Caraco, 2000).

Optimal foraging theory has played a strong role not only in the study of animal foraging behavior, but also the development of socioecological theory. This is

particularly true within primatology where extensive research efforts have been dedicated towards investigating the ecological factors responsible for the wide diversity of social systems displayed by this order (Mitani et al., 2012; Snaith & Chapman, 2005, 2007; Wrangham, 1980). For instance, levels of within-group scramble and contest competition incited by the distribution and abundance of food resources are believed to play a strong role in the both the long term and short term social structure of primate groups (Chapman et al., 1995). Despite this strong focus on foraging behavior, direct tests of optimal foraging theory have been rare in primates. This is partly because some investigators consider that primate foraging decisions, and those of many herbivores, are too complicated for simple rate-maximization models (Belovsky, 1984). Firstly, the nutritional content of plant foods can vary greatly between species, and even within species, depending upon the part of the plant being eaten or the point in its maturation cycle. Thus, rather than maximize rate of energy intake, primates and other herbivores may need to focus on eating a variety of foods in order to obtain an optimal balance of nutrients (Westoby, 1974) or to maximize one in particular (Mattson, 1980; Milton, 1979). Furthermore they may need to minimize the consumption of harmful plant toxins and substances that reduce digestibility (Rosenthal and Janzen, 1979). While these factors may discourage the application of optimal foraging models to the study of primate foraging behavior, Stephens (1986) argues that this emphasis on herbivore food quality has prevented us from discovering how complex, or simple, their foraging decisions actually are. In fact, there is evidence that even the most complex primate diets are explicable through relatively simple rate-maximization models (Barton & Whiten, 1994)

Nevertheless, even if researchers are interested in testing optimal foraging models in primates, doing so under natural conditions is highly challenging. Firstly, the dense foliage in which many primates live can make it logistically difficult to observe behaviors related to energy intake, such as bite rate (Nakagawa, 2009). Secondly, primates eat a wide diversity of foods that can vary greatly in energy composition on both spatial and temporal scales. Thus, even if bite rate can be measured, it is difficult to convert this measure into actual rate of energy intake (Conklin-Brittain et al., 2006). Captive foraging experiments have been key tools for reducing the complexity of animals' foraging

environments and enabling direct testing of optimal foraging models. Unfortunately, these experiments are typically conducted with species that are relatively easy to house, train, and/or engage in numerous trials, such as birds (Cowie, 1977; Krebs et al., 1974; Pyke, 1978), fish (Devries et al., 1989; Werner & Hall, 1974), insects (Hodges, 1981), and small mammals (Cassini et al., 1990; Giraldeau & Kramer, 1982; Newman & Caraco, 1987). Thus, how well primate foraging behavior adheres to predictions of optimal foraging theory is not well understood.

The current study fills this gap by experimentally examining the patch residency decisions of captive chimpanzees (*Pan troglodytes*) within an artificial foraging environment. Chimpanzees feed on a wide range of foods such as fruit, leaves, flowers, pith, insects, and vertebrates (Goodall, 1986). They tend to specialize on high quality food patches and display short-term variation in feeding party size, presumably to adjust to changes in food availability and feeding competition (White & Wrangham, 1988).

To test whether chimpanzee foraging decisions follow predictions from basic foraging theory, despite their complex and varied diet, I conducted experiments focused on the marginal value theorem. The marginal value theorem is a classic optimal foraging model that predicts optimal patch residence times in heterogeneous foraging environments such as that experienced by chimpanzees (Charnov, 1976). Specifically, it predicts that a forager should abandon a food patch once its instantaneous rate of energy intake drops to the average net intake rate within the environment as a whole. Qualitative predictions are that animals should spend more time in higher quality patches, they should deplete all patches to the same rate of energy gain and they should forage longer in all patches when the average quality of the environment is poor and/or average travel distance is high. In this study I presented captive chimpanzees with an artificial foraging environment consisting of two food patches of varying quality. Using this environment, I tested the qualitative and quantitative predictions of the marginal value theorem.

2.2 METHODS

Subjects in this experiment were 12 adult chimpanzees (5 male and 7 female) from four separate multi-male, multi-female social groups housed at KCCMR. For a

description of this research site and general research methods see Chapter 1 of this dissertation.

Experimental Set-Up

I used dried pineapple chunks (average weight: 2.71 g +/- 0.55) as food rewards in this experiment. Food rewards were presented to subjects within two artificial food patches comprised of solid square wooden boards, 60.7 cm in length and 1.8 cm in depth (Figure 2-1.). I created food compartments in these patches by drilling holes (3.2 cm in diameter) through each board. 30 compartments were positioned in 5 rows of 6 with 11 cm between columns and 11.9 cm between rows (measured from center to center of adjacent compartments). Each food compartment was hidden by a small, round, opaque cover, 5.8 cm in diameter. The top of each cover was attached to the board by a screw around which it could freely rotate. When rotated to either side, the contents of the food compartment would be revealed. Displaced covers fell back into place once released, concealing whether a given compartment had previously been searched. On the back of each patch (the side facing the experimenter), each food compartment was numbered from 1-30 from left to right and top to bottom. These numbers facilitated video coding by enabling easy identification of compartments. The backs of both patches were covered in transparent plexiglass which prevented food items from falling out the back of the device, while also enabling a video camera positioned behind each patch to document when each compartment was searched during the experiment and whether a food reward was extracted.

Based upon the number of compartments containing food rewards, patches could exist in either a high or low quality state. A low quality patch contained one food reward in 5 of the 30 compartments. A high quality patch contained one food reward in 20 of the 30 compartments. The quality of a patch was not visually apparent to subjects and could only be revealed by sampling the compartments. The foraging environment was comprised of two adjacent rooms within the indoor enclosure of each social group (Figure 2-2.). During the experiment, the subject remained alone within the foraging environment while its group members had free access to their outdoor enclosure as well

as the other indoor room(s) adjacent to, but visually separated from, the experimental area. The two rooms comprising the foraging environment were connected by a sliding door that the experimenter could manually open and close from outside of the experimental area. One wall of each room consisted of wire mesh to which one of the artificial food patches was attached with clips. The artificial patches were positioned so that the covers faced towards the subject. By sticking their fingers through the wire mesh and rotating the covers, subjects were able to search the compartments and retrieve food rewards.

Experimental Procedure

All subjects entered freely into the experimental area. At the beginning of the experiment, Patch 2 was attached to the wire mesh of Room 2. The subject was then isolated from the rest of its group and held in Room 1. At this point it did not yet have access to Room 2 or either food patch. I initiated the beginning of the experiment by attaching Patch 1 to the wire mesh of Room 1. As soon as the subject began feeding in Patch 1, I opened the sliding door leading to Room 2. At this point, the subject had full access to both patches. I removed Patch 1 from Room 1 once the subject finished feeding on this patch and stepped through the door leading to Room 2. This prevented the subject from returning to this patch. Once the subject finished feeding at Patch 2 and walked away from the patch, I removed Patch 2 from the wire mesh, ending the experiment.

Each subject experienced five training trials and 20 experimental trials. Each subject experienced no more than two trials per day during either the training or experimental period. Training trials were executed in the same manner as described above except that the door to Patch 2 was not opened immediately at the start of the trial. In the first training trial (t=1), the door to Patch 2 was only opened once the subject either found five food rewards or, if it did not find five rewards, when it abandoned Patch 1. In each subsequent training trial (t), the door was opened after the subject obtained (5-(t-1)) food rewards or whenever it finished foraging from the patch, whichever came first. This training period enabled subjects to become familiar with the foraging devices and to experience both patch types. It also taught them that they must forage in Patch 1 before

they could forage in Patch 2 and that they could not return to either patch upon departing. Video from training trials was not coded for analysis.

Overall, there was a 20% chance that a given patch was high quality and an 80% chance it was low quality. I designed the distribution of food rewards and relative abundance of high and low quality food patches to simulate primate foraging conditions in the wild. High quality food patches are relatively rare in the environment, but, when present, can include large quantities of food (Struhsaker, 1978). The qualities of Patches 1 and 2 were independent of one another. The 25 trials experienced by each subject were divided into five blocks of five trials. Patch quality treatments were randomized so that a given patch was high quality only once in every block of trials. The locations of food rewards were randomized before each trial. If a subject did not complete a given trial, the trial was repeated once more either on the same or a different day. A trial was not considered completed if the subject did not sample compartments from both Patch 1 and Patch 2, if it departed from Patch 1 as soon as the door to Patch 2 was opened, or if an outside occurrence distracted the subject from the foraging task (e.g. a fight within their social group). If the trial was not completed on the second try, it was discarded and the subsequently-scheduled trial was conducted during the next testing period. This was done to ensure that the ratio of experienced patch qualities did not substantially differ between individuals, for instance, due to a long period of incompletion for a given trial.

I remained outside of the experimental area, but within view of the subject, during all trials in order to manipulate the door between the two experimental rooms and to remove the patches at the appropriate time. Except for these actions, I remained still and stared straight ahead throughout the experiment in order to prevent interference with subject behavior.

Video Coding

All trials were video recorded with two Sony Handycam Cameras. One camera with tripod was focused on the back of each artificial food patch. Video was recorded at 30 frames/second. I only extracted behavioral data from video of Patch 1 since the primary function of Patch 2 was to provide motivation for subjects to depart from Patch 1

in an efficient manner. Video from Patch 2 was only utilized to estimate average travel time between patches. Video was coded using Quicktime version 7.7.4. From this video, the time the first cover started moving and the time the last cover stopped moving was extracted. In addition, I documented the order in which the compartments were searched. Subjects sometimes probed a given compartment multiple times in order to successfully extract a food reward. Accordingly, I did not include repeated, consecutive probes of the same compartment in my measure of foraging effort. If a compartment contained a food reward, I documented whether it was obtained during a given probe of that compartment. If a food reward was obtained on a given probe, I recorded the time the subject first touched the cover to that compartment on that probe. By synchronizing times between video from Patches 1 and 2, I calculated travel time as the start time of Patch 2 minus the end time of Patch 1. Travel times were extracted from a random subset of 20 trials. All times were documented with regards to frame number and converted to seconds by dividing the number by 30.

2.3 ANALYSIS

I calculated the number of re-probes that each subject performed during its first thirty probes as a measure of foraging efficiency. A re-probe is defined as when the subject probed a compartment and then returned to that compartment after probing one or more other compartments. Foraging duration was calculated by subtracting the time the subject first touched the cover of the first food compartment from the time the subject released the cover of the last food compartment on a given patch. Since subjects may display longer foraging times in high quality patches simply due to the greater amount of time needed to extract and consume the additional food rewards, I also measured total foraging effort. Foraging effort was calculated by summing the total number of probes the subject made on a given patch. I summed the total number of food rewards obtained in each trial. Giving up density was calculated by subtracting the number of food rewards obtained from the total number of rewards hidden in the patch.

I conducted all analyses using the statistical program R (version 3.0.1). I found the median number of re-probes performed by each subject during its first 30 probes in

each patch type. I used one-sample Wilcoxon signed rank tests to compare these values to both zero (the number of re-probes expected if subjects were foraging completely systematically) and the number of re-probes expected by chance if subjects were foraging randomly. The number of re-probes expected of a random forager was calculated by generating 100 sets of 30 random values between 1 and 30. I used linear mixed-effects regression models to test the main effects of patch quality and trial number on the number of re-probes performed, foraging duration, foraging effort, and giving up density. Models were fit using the lme4 package (Bates et al., 2013). The number of re-probes, the number of compartment searches and the number of food rewards left behind were analyzed using models with a Poisson error structure and log link function while feeding duration data were analyzed using a model with a negative binomial error structure. All models included a random intercept for each subject (n=12) as well as a random slope for both trial number and patch quality within each subject.

I calculated the average gain curves for both low and high quality patches in both the first and last block of experimental trials (trials 1-5 and 16-20, respectively). I created these curves by calculating the average cumulative number of food rewards obtained by subjects within each 5-second interval during a foraging trial. Only data from time intervals with at least 10 observations were used to fit each curve. I fit a negative exponential function ($Y = Q(1-e^{-ax})$) to these data (Livoreil & Giraldeau, 1997) (Figure 2-4). In this equation, Y is the cumulative number of food rewards and x is time in the patch. The asymptote value Q was set at 5 for low quality patches and 20 for high quality patches. The value of a that produced the best fit was determined using least-squares methods. I then calculated the function for the average gain curve for the environment as a whole. I did this by multiplying the function for the low quality patch by 0.8, multiplying the function for the high quality patch by 0.2 and adding them together.

I found the equation of the line tangent to the average gain curve and intersecting the point ($-x_T$, 0) with $-x_T$ representing the average travel time in the environment. The slope of this line represents the average rate of gain within the artificial foraging environment and predicts the instantaneous intake rate at which subjects should abandon each patch. The x-values at which the derivative of the low and high quality gain curves

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are equal to this slope represent how long subjects should remain in each patch type. The y-values of the gain functions at these time points represent the total number of food rewards optimal foragers should have obtained by the time of departure (Figure 2-5). Using one-sample Wilcoxon signed rank tests I compared subjects' observed feeding duration and number of food rewards obtained in low and high quality patches to the values predicted by my models for both the first and last block of trials. For these tests I used each subject's only high quality trial and last low quality trial from each block for comparison. As a crude measure of the average observed giving up rate experienced by subjects, I found the derivative of each gain curve at the average foraging time for each patch in the corresponding block of trials. I also calculated the derivatives at the end points of the 95% confidence interval for feeding duration as a measure of precision for this estimate (Lima, 1984). I then determined whether the expected giving up rate fell within this observed confidence interval.

2.4 RESULTS

Subjects probed the compartments semi-randomly. The median number of re-probes performed by subjects during the first 30 probes was 6 (range: 4-8 re-probes) in low quality patches and 8.3 re-probes (range: 5-14) in high quality patches. The median numbers of re-probes performed by subjects in both patch types were significantly less than the 10.8 re-probes expected by chance (Low Quality: W=78, p<0.01; High Quality: W=78, p<0.01) but also significantly greater than zero (Low Quality: W=3.5, p<0.001; High Quality: W=302, p<0.01). There was a statistically significant effect of patch quality on the number of re-probes performed (β= 0.36, SE= 0.06, p<0.001, Figure 2a). Subjects re-probed more compartments in high quality than low quality patches. Trial number did not affect the number of re-probes performed (β = -0.01, SE= 0.01, p=0.30).

Subjects foraged longer and probed more compartments in high quality than low quality patches (Duration: β= 0.88, SE= 0.05, p<0.001, Figure 2b, Effort: β= 0.34, SE= 0.05, p<0.001, Figure 2c). Subjects foraged for (mean +/- SE) 80.68 +/- 38.77 seconds and probed 34.7 +/- 11.7 compartments in low quality patches and foraged for 199.89 +/- 75.29 seconds and probed 49.1 +/- 15.6 compartments in high quality patches. While

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mean foraging duration decreased across trials (β= -0.01, SE= 0.004, p<0.01), mean foraging effort did not (β=-0.01, SE=0.01, p=0.16). Subjects obtained (mean +/- SE) 4.6 +/- 0.7 out of 5 food rewards when feeding on low quality patches and 18.7 +/- 1.5 out of 20 food rewards while feeding on high quality patches. In addition to obtaining more food rewards in high quality patches, subjects also abandoned these patches at a higher giving up density (β=1.02, SE=0.29, p<.001, Figure 2d). Subjects left behind an average of 0.4 +/- 0.7 food rewards in low quality patches and 1.3 +/-1.5 food rewards in high quality patches. There was a significant decrease in giving up density across trials (β=-0.05, SE=0.02, p<0.05).

Observed patch residence times were significantly longer than those expected of optimal foragers in both the first and last block of trials (First: Low Quality: V= 73, p<0.01; High Quality: V= 53, p<0.01; Last: Low Quality: V=77, p<0.001; High Quality: V= 52, p<0.01). In the first block of trials, subjects foraged for (mean +/- SE) 38.26 +/- 44.06 seconds longer than the 31.22 seconds predicted for low quality patches and 94.85 +/-66.08 seconds longer than the 130.49 seconds predicted for high quality patches. In the last block of trials, subjects foraged for (mean +/- SE) 36.51 +/- 25.36 seconds longer than the 26.31 seconds predicted for low quality patches and 50.00 +/-44.97 seconds longer than the 107.27 seconds predicted for high quality patches. Accordingly, subjects also obtained more food rewards than that expected of optimal foragers in both the first and last block of trials (First: Low Quality: W = 77, p<0.01; High Quality: W= 55, p<0.01; Last: Low Quality: W = 78, p<0.01; High Quality: W= 55, p<0.01). In the first block of trials subjects obtained (mean +/- SE) 1.9 +/- 0.9 more food rewards than the 2.6 expected for low quality patches and 6.7 +/- 1.3 more food rewards than the 11.9 expected for high quality patches. In the last block of trials subjects obtained (mean +/- SE) 2.0 +/- 0.4 more food rewards than the 2.8 expected for low quality patches and 6.1 +/- 1.8 more food rewards than the 12.8 expected for high quality patches.

My model predicted that subjects should abandon both food patches once their intake rate fell to 0.056 food rewards/second in the first block of trials. The observed intake rate at the average departure time for low and high quality patches in the first block of trials (with 95% confidence interval) was 0.037 (0.021-0.048) and 0.029 (0.025-

0.044) food rewards/second, respectively. For the last block of trials my model predicted that subjects should abandon the food patch once their intake rate fell to 0.069 food rewards/second. The observed intake rate at the average departure time for low and high quality patches in the last block of trials was 0.041 (0.033-0.052) and 0.051 (0.040-0.067) food rewards/second, respectively. Within both the first and last block of trials there was substantial overlap in the 95% confidence interval for giving up rates in high quality and low quality patches suggesting they do not significantly differ. Nevertheless, none of these confidence intervals encompass the predicted giving up rate, with observed values being lower than predicted.

2.5 DISCUSSION

In this study I sought to determine whether chimpanzees employ a rate-maximization strategy as predicted by the marginal value theorem when utilizing patchy food resources within a controlled foraging environment. The marginal value theorem assumes that energy intake rate decreases over time within a patch due to the forager's depletion of the food supply and that this decrease in intake rate drives patch departure decisions (Charnov, 1976). If subjects were to have foraged completely systematically in the artificial food patches (i.e. not re-probe any compartments) patches would not be expected to have exhibited depression. Rather, intake rate would have remained stable until all food items had been obtained and then leveled off. I found that subjects foraged semi-randomly, re-probing more compartments than expected of a systematic forager but fewer than a completely random forager. Nevertheless, this level of deviation from systematic foraging resulted in negatively accelerating rates of energy intake, well-characterized by an exponential gain function.

Results from this study are consistent with qualitative predictions of the marginal value theorem. Subjects foraged significantly longer and demonstrated greater foraging effort in high quality than low quality food patches. Accordingly, subjects obtained more food rewards in high quality patches. Contrary to predictions, subjects abandoned high quality patches at a slightly, but statistically significant, higher giving up density than low quality patches. However, by using my model to estimate observed giving up rates at the

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average time of departure from both patch types, I found that the confidence intervals for giving up rates for high and low quality patches displayed significant overlap in both the first and last block of trials. While this is a coarse measure of giving up rate, it suggests that subjects experienced similar giving up rates in the two patch types at different giving up densities. This could be explained by the finding that subjects performed significantly more compartment re-probes in high quality than low quality patches. Thus, even when abandoning high quality patches at higher giving up densities, subjects' intake rates could have been similar to a low quality patch that had been depleted more thoroughly. The fact that subjects re-probed more compartments in high quality patches could be due to the greater frequency in which subjects had to extract food rewards between subsequent probes. Due to these interruptions, subjects may have been more likely to forget which compartments they had already probed. Many pros and cons have been suggested for using giving up density in studies of optimal foraging behavior (Bedoya-Perez et al., 2013). While this method can be a more efficient way to estimate giving up rate than calculating the intake rate of a forager, my findings suggest that giving up density may not always be a reliable measure of the final intake rate experienced by a forager.

Subject foraging duration decreased over time but foraging effort did not. These results suggest that, while subjects' foraging strategy did not change over time, they became faster at searching compartments- searching the same number of compartments in shorter amounts of time. This is reflected in the mean average intake rate increase from 0.056 to 0.069 food rewards/second as estimated by my gain curves for the first and last block of trials. While subjects became faster at searching compartments they did not become more efficient since the number of re-probes performed did not change over time.

The fact that subjects foraged longer in high quality than low quality patches is not surprising since qualitative support of the marginal value theorem is abundant in the literature (Stephens & Krebs, 1986). However, subjects could have theoretically employed a variety of relatively simple foraging strategies within their experimental environment. For instance, they could have foraged for a set amount of time in all patches ("Time Rule") or obtained a set number of food items ("Number Rule"), and thus spent

less time in higher quality patches (Krebs et al., 1974). In fact, the Time Rule can be the most profitable strategy when the distribution of prey between patches follows a Poisson distribution (Stewart-Oaten, 1982) while the Number Rule performs best when patches contain approximately the same number of food items. Rather, subjects utilized a strategy that biased their foraging behavior towards high quality patches. This strategy performs best when there is high variance in the number of food items between patch types, as there was in this experiment (Iwasa et al., 1981).

When examining quantitative predictions of the Marginal Value Theorem, I found that subjects foraged much longer than expected and depleted patches more fully in both high quality and low quality patches. Accordingly, I also found that their average giving up rate was lower for both patch types than that predicted by the marginal value theorem. While many studies are consistent with qualitative predictions of the marginal value theorem, quantitative predictions are less-often supported. In fact, subjects typically err on the side of remaining in food patches for longer than predicted (Nonacs, 2000). If differences between observed and expected behavior were based upon random errors, one would expect deviations to be equally likely in either direction. One possible reason for deviations between observed and expected behavior in my experiment could be that my view of the foraging environment was too restrictive. My model only takes into account the foraging environment within the experimental condition. However, subjects have access to a greater environment outside of this relatively brief experimental context, where they had ad libitum access to chow, regular meals of produce and occasional food-related enrichment activities. If subjects were factoring this greater environment into their foraging decisions and this environment is significantly lower quality than that estimated by my model, the marginal value theorem would predict longer residence times in all patches. Another potential explanation is that subjects were influenced by their energetic state- a factor not take into account by the marginal value theorem. State-dependent models tend to predict longer feeding durations than the marginal value theorem (Nonacs, 2000). In fact, a simulation by Nonacs (2000) found that high energy reserves are associated with staying in patches too long and reducing them to equal and very low giving up densities. This is very similar to the behavior observed in my experiment. The

diets of the chimpanzees housed at this research facility are closely monitored and efforts are taken to make sure they do not gain too much weight. However, the subjects in this study were never food-deprived at any point and are thus likely to have relatively high energy reserves.

The fact that the chimpanzees in this study displayed sensitivity to the quality of food patches is not surprising. The fission-fusion social structure exhibited by this species is believed to be strongly influenced by the abundance and distribution of foods in the environment (Wrangham, 1980). Furthermore, chimpanzees are believed to distribute themselves among patches according to the abundance level of food and the level of feeding competition between individuals (White & Wrangham, 1988; Wrangham, 1980). A unique trait of my foraging experiment is that subjects had no visual input as to the quality of the food patch while foraging. Rather, they only had information about their rate of food intake. The sensitivity of chimpanzees to changes in energy intake rate is not as well understood as their larger-scale foraging patterns. Under field conditions it can be challenging to obtain precise measures of patch quality, observe intake rate and differentiate between the multiple social and ecological factors that may be driving a given individuals' patch departure decision (Kazahari & Agetsuma, 2007; Kazahari, 2014). However, there is some evidence that chimpanzees are sensitive to subtle changes in intake rate. One field study found that chimpanzees had a slightly lower intake rate before departing from a food patch, suggesting that their departure decision may have been driven by patch depression (Chapman et al., 1995). Furthermore, results from a recent captive study indicate that subjects prompted extraction of hidden food rewards in a manner that maximized the rate at which they obtained energy (Sayers & Menzel, 2012). The fact that chimpanzees do display sensitivity to energy intake suggests that any observed deviations from predicted foraging behavior are likely not due to an individual's ability to accurately assess the quality of a food patch. This understanding can aid our interpretation of chimpanzee foraging behavior under natural conditions and help to identify potential causes for deviations from expected behavior. In Chapter 3 I examine chimpanzee foraging behavior under natural conditions by investigating both social and ecological influences on the foraging behavior of wild chimpanzees.

2.6 FIGURES

Figure 2-1. Diagram of Device Serving as a Single Foraging Patch a) The view of the patch from the perspective of the subject. Each round cover is attached to the board by a screw and hangs in front of a single food compartment. The upper left-hand corner of the diagram exemplifies how a cover can be rotated to the side about the screw in order to reveal whether a given compartment contains a food reward. b) The view of the patch from the perspective of the experimenter. Each food compartment is numbered from left to right and top to bottom. Compartment number 1 in the figure demonstrates how food rewards can be viewed through the clear backing of the patch. Compartment number 2 demonstrates what it looks like when the cover to a given compartment is moved to the side while the subject probes the compartment.

a.
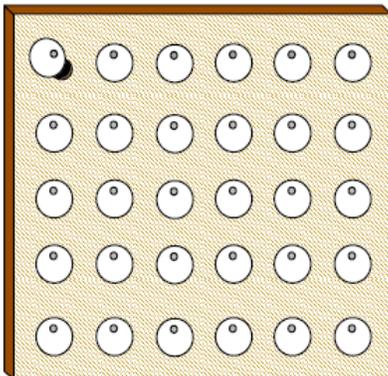
b.

Figure 2-2. **Diagram Representing Overhead view of Experimental Area** The experimental area consisted of Foraging Rooms 1 and 2. The subjects' group members had open access to the two rooms left of the Foraging Rooms as well as the outdoor area. Food Patch 1 was attached to the wire mesh of Foraging Room 1 and Food Patch 2 was attached to the wire mesh of Foraging Room 2. A video camera positioned in the human area focused on the back of each foraging patch. I stood in the human area while the subject was foraging on each patch in order to manipulate the door between Foraging Rooms 1 and 2 and to remove the patches from the wire mesh once the subject finished foraging.
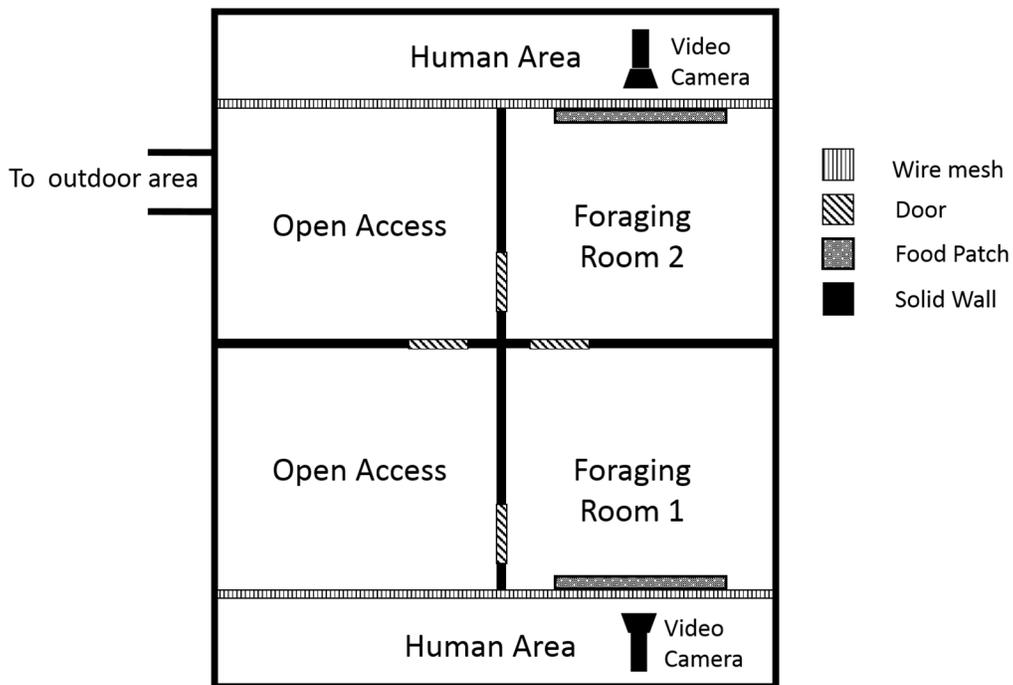
Figure 2-3. Compartment Re-probes by Patch Quality Scatterplots of a) compartment re-probes, b) foraging duration, c) foraging effort and d) giving up density by patch quality and trial number. For visualization purposes, lines represent simple linear regression functions. High quality patches and low quality patches are depicted by triangles and circles, respectively. Compartment re-probes, foraging duration, and foraging effort differed significantly by patch quality with higher values for all measures in high quality than low quality patches. Both foraging duration and giving up density decreased across trials.

a.
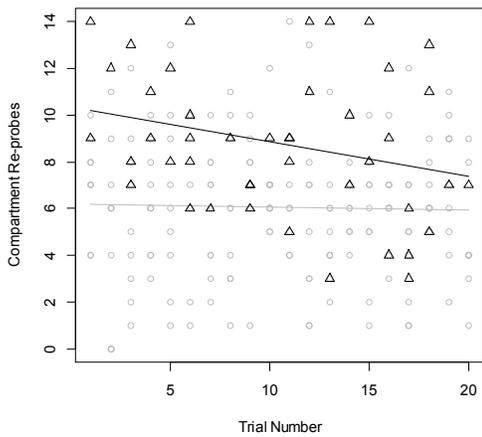
b.
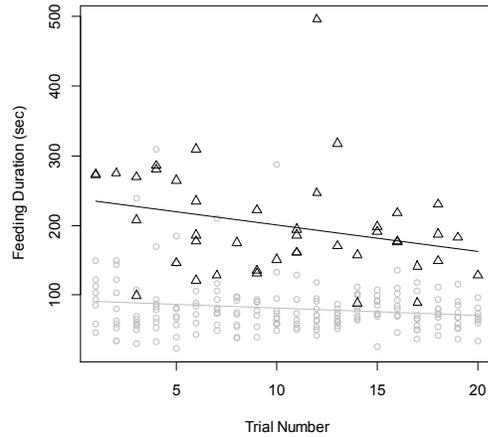
c.
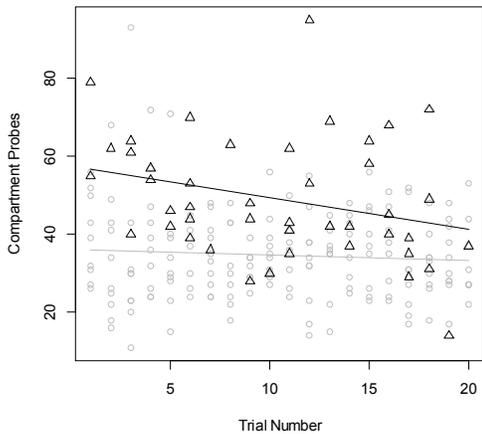
d.
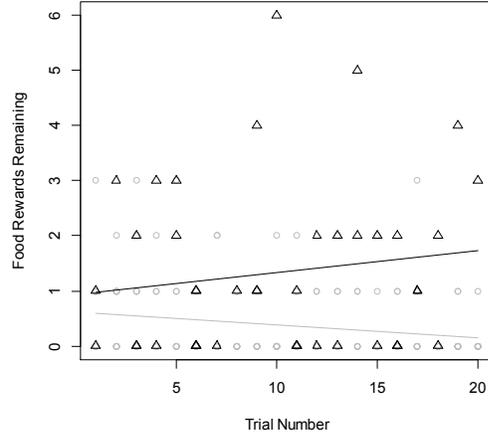
Figure 2-4. Fitted Gain Curves to Data on Cumulative Intake of Food Rewards

Mean number of food rewards obtained in each 5-second time interval in a,b) low quality and c,d) high quality patches. Figures 2-a and 2-c represent data from the first block of trials (trials 1-5) and Figures 2-b and 2-d represent data from the last block of trials (trials 16-20). Only time points with at least 10 observations are included. Error bars represent +/- 1 standard deviation. Solid lines represent the fitted negative exponential curve corresponding to the displayed equation.

a. Low Quailty- First Trial Block   **b. Low Quality- First Trial Block**
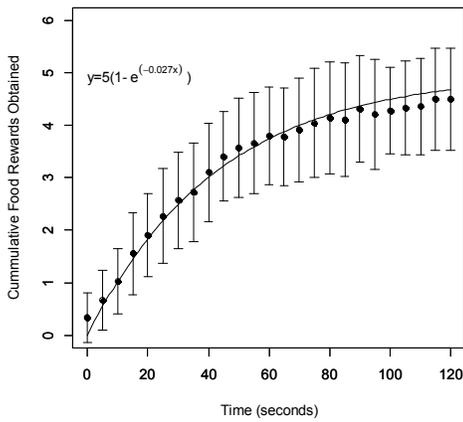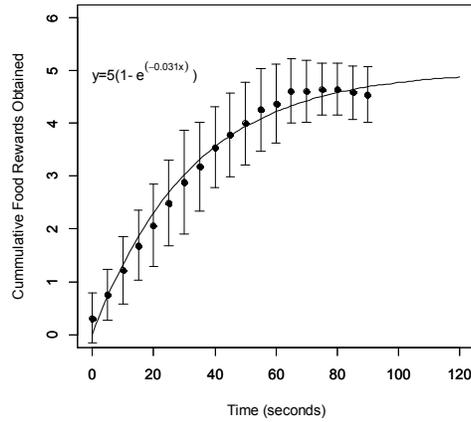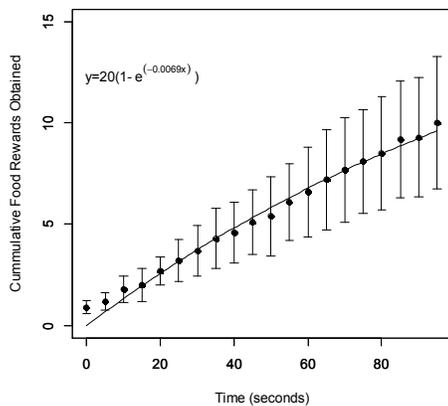
c. High Quality- Last Trial Block   **d. High Quality- Last Trial Block**
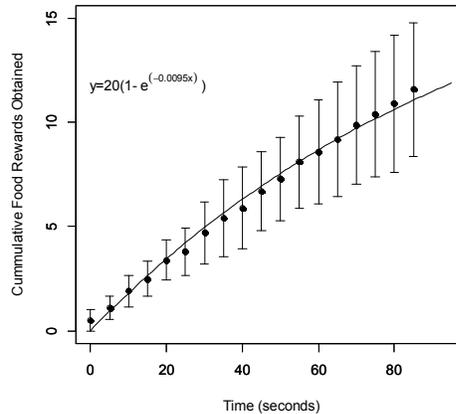
Figure 2-5. Marginal Value Model of Subject Foraging Environment Fitted curves for low quality and high quality food patches and their weighted average from a) the first block and b) the last block of trials. The slope of the dashed lines represent the optimal intake rate at which to abandon food patches determined by finding the line tangent to the average intake curve and intersecting the point $(-x_T, 0)$. The vertical dotted lines indicate the optimal residence times for the low quality and high quality food patches and the horizontal dotted lines indicate the optimal number of food rewards that should have been obtained at the point of departure.

a) First Trial Block
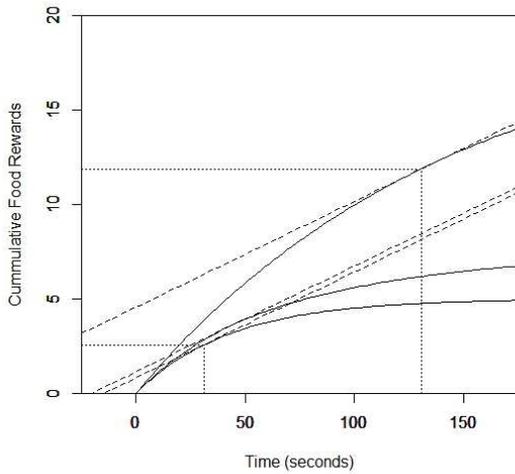
b) Last Trial Block
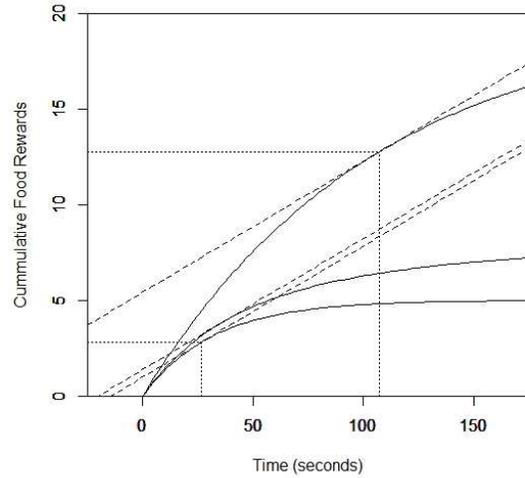
CHAPTER 3

LOW-COST PATCH SHARING PROMOTES SOCIALIZATION IN WILD CHIMPANZEES

3.1 INTRODUCTION

Optimal foraging theory focuses on how animals should behave while foraging in order to maximize their long-term rate of energy intake (Stephens & Krebs, 1986). Many studies of optimal foraging behavior have focused on the optimal use of patchy food resources. Central to patch use models is the assumption that a forager's rate of energy intake within a patch decreases over time due to depression of the food supply caused by the forager's feeding behavior. As discussed in Chapter 2, the marginal value theorem is a classic patch use model that has been central to many studies of animal foraging behavior (Charnov, 1976). This model predicts that animals can maximize their long-term rate of energy intake within patchy foraging environments by feeding within patches until their instantaneous rate of food intake drops to the average rate of intake within the environment as a whole. Qualitative predictions are that individuals will spend more time in high quality food patches, reduce all patches to the same giving up density and feed longer in all patches when the environment is poor and/or distance between patches is long.

While the marginal value theorem traditionally models the behavior of a single forager, it can be modified to predict the behavior of individuals sharing a food patch with others (Parker, 1978). This model assumes that foragers feeding within the same patch do not directly interfere with one another's foraging behavior. However, since the feeding activities of multiple foragers will deplete a food patch more rapidly than a single forager, this model predicts that individuals will forage for shorter periods of time but deplete patches more thoroughly when foraging in larger groups. Thus, they will have lower feeding rates and leave the patch sooner than they would if they were foraging alone. Accordingly, individuals foraging within larger groups may have to spend more time traveling than solitary foragers, resulting in a substantial social foraging cost (Terborgh, 1983). Nevertheless, foraging in groups can provide other foraging benefits

that may out weight these costs, such as increasing the likelihood that food patches are discovered or decreasing the amount of time spent scanning for predators, and thus, increasing food intake rate.

While some social foragers may come together for the duration of a single feeding bout, others may remain cohesive for longer periods of time. Such groups may remain together due to the aforementioned foraging benefits, or other benefits such as improved defense of territories and access to mates. In groups where individuals remain in contact across feeding bouts, there is some evidence that individuals' patch residency decisions may be influenced by social factors beyond the effect they have on patch depletion. Particularly, there is evidence that individuals may alter their patch residence decisions in order to remain cohesive with group members. Much of this evidence comes from studies of primate foraging behavior. For instance, Kazahari (2014) found that the patch residence decisions of Japanese macaques (*Macaca fuscata*) were more influenced by the departure of other group members from the food patch than they were with a reduction in the rate of food intake. As another example, Alberts et al. (1996) found that male baboons display foraging patterns more typical of female baboons when in consortship with a sexually receptive female, suggesting that males adjust their foraging patterns to that of their consort partner. This behavior is not unique to primates. Social bird species also show signs of such social influences on foraging behavior. Hutto (1988) found that individuals feeding within mixed-species flocks manage to remain cohesive while foraging despite species-specific differences in feeding location and movement patterns. The author suggests that in order to accomplish this feat, individuals in some species must make adjustments to their typical foraging patterns.

Making patch residence decisions based upon factors unrelated to one's own foraging success has the potential to impose significant social foraging costs. A social foraging simulation by Valone (1993) suggests that patch departure decisions based upon the departure of others often results in under-utilization of food patches. This remains the case even if individuals follow a specific leader, rather than the first individual(s) to abandon the food patch (Valone, 1993). Thus, cohesive groups of social foragers may experience two types of social foraging costs: the cost associated with depleting a food

patch more quickly due to the foraging behavior of group members inside the patch and the cost associated with striving to maintain contact with those outside the food patch.

In this study I explore these social foraging costs by investigating social and ecological influences on the foraging behavior of wild chimpanzees (*Pan troglodytes*). Chimpanzees have a broad diet that includes fruit, leaves, flowers, pith, insects, and vertebrates (Goodall, 1986). Furthermore, they live in fission-fusion societies where the size and composition of their social groups can change multiple times throughout the day. For this reason, they are an excellent species with which to investigate the role social context plays in foraging behavior. Chimpanzees gain many benefits from socializing, such as access to potential mates and protection from neighboring chimpanzee communities (Tutin, 1979; Wilson et al., 2001). However, males and females differ greatly in their tendency to form groups (Wrangham & Smuts, 1980). Female chimpanzees spend most of their time alone or with dependent offspring and typically come together in larger groups when in estrous or when large patches of abundant fruit are available. Males are the philopatric sex and spend a greater portion of their time in parties with other adult chimpanzees. Adult male chimpanzees form strong relationships with other males which aid in the achievement of higher rank and access to fertile females (Gilby et al., 2013; Mitani, Merriwether, & Zhang, 2000). In fact, there is evidence that male chimpanzees coordinate their behavior in an effort to maintain contact with one another (Newton-Fisher, 1999). For these reasons I focus this investigation on the social forces influencing the foraging behavior of male chimpanzees.

I tested two hypotheses regarding chimpanzee foraging behavior and its relationship with social and ecological factors. The Optimal Foraging Hypothesis proposes that chimpanzee foraging behavior is determined by intake rate alone. This hypothesis predicts that patch residence time is positively correlated with the quality of the food patch and negatively correlated with the number of individuals within the food patch. The Coordination Hypothesis proposes that chimpanzees sacrifice foraging efficiency within patches in order to maintain contact with party members outside the food patch. This hypothesis predicts that an individual's patch residence time is negatively correlated with the number of party members outside the food patch due to the

tendency to monitor the behavior of these individuals and follow them should they leave the vicinity of the patch.

I tested these hypotheses by comparing models of chimpanzee foraging behavior in different social contexts using data obtained from an observational study of the behavior of wild chimpanzees. I also examined whether sharing a food patch with others results in a loss of foraging efficiency by comparing chimpanzee foraging behavior and feeding rate across different foraging contexts. Furthermore, I examined whether a tradeoff exists between foraging and maintaining contact with those outside the food patch by examining the relationship between patch residence time, patch sharing behavior and the likelihood of maintaining contact with party members.

3.2 ANALYSIS

I conducted an observational study of wild chimpanzees at Gombe where I studied the behavior of ten focal males. I collected data on the patch residence time of these focal targets, the properties of these food patches, the number of individuals that shared the patch with the target and the target's behavior throughout the feeding bout. For description of this research site and specific field methods see the Chapter 1.

I conducted all analyses of field data using the statistical program R v.3.0.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). The primary focus of analysis is on target patch residence times. However, I first investigated the relationship between target patch residence time and his behavior within the patch. Patch residence time was calculated by subtracting the start time of the feeding bout from the end time. I used a GLMM with a negative binomial error structure to investigate the correlation between feeding duration and the number of behavioral scans in which the target was performing feeding or non-feeding behaviors. I fit models using the glmmADMB package and included a random intercept for each focal target. Only those bouts where no more than one behavioral scan was documented as "Bad observation" were included in the analysis (n=176 feeding bouts). Bad observations were removed from the dataset before being analyzed. I also investigated changes in feeding behavior and bite rate over time. For analyses of feeding behavior, I only included those feeding

bouts in which at least three behavioral scans were taken (n=122 feeding bouts). I modeled the likelihood that the target's behavioral state was documented as "Feed" during a given behavioral scan using a GLMM with a binomial error structure and logit link function (Not Feeding=0, Feeding=1). As explained in Chapter 1, wadging was not considered in the category "Feed". The predictor variable considered in this analysis was the amount of time that had elapsed since the target first entered the food patch. Elapsed time was calculated by subtracting the start time of the feeding bout from the start time of the behavioral scan. To account for repeated observations per feeding bout, I included a random intercept for Feeding Bout ID in addition to the random intercept for Target ID. I conducted a similar longitudinal analysis of bite rate data. These data were modeled as an integer representing the number of bites the target took in one minute. For this analysis I including all feeding bouts in which at least three bite rate samples were conducted (n=26). I modeled bite rate data using a GLMM with a negative binomial error structure and log link function, and included random intercepts for both target and feeding bout ID.

I investigated the correlation between patch residence times, ecological variables and social influences outside and inside the food patch. Due to the presence of overdispersion in patch residence time data, I fit GLMMs with Poisson error structures and log link functions and included observation (e.g. each feeding bout) as a random intercept (Harrison, 2014; Marshall et al., 2013). To account for repeated observations of focal targets (n=10), I also included a random intercept for focal ID in all models. Models were fit using the lmer function in the lme4 package (Bates et al., 2013). To best isolate the effects of social influences outside and inside the food patch, I first focused analysis on only unshared food patches- those where the target was the only individual feeding in the patch for the full duration of the feeding bout (n=159). Patch quality parameters included patch size (*SIZE*: <5m, >5m) and food part (*PART*: leaves, flowers, fruit). The social parameter I examined was the total number of individuals outside the patch (*OUT*: count, numeric).

Using an information theoretic model selection framework (Burnham & Anderson, 2002), I considered a set of 8 models (Table 3-2a). This model set consisted of all combinations of patch quality parameters both with and without the parameter *OUT*.

A null model and a model consisting of *OUT* alone were also included. I then focused the analysis on target patch residence times in shared food patches- those where at least one other individual shared the patch with the target at some point during the feeding bout (n=93). The social parameter I examined in this context was the total number of individuals that shared the patch with the target (*IN*: count, numeric). I examined the same set of 8 models considered for target patch residence times in unshared food patches, except that the parameter *OUT* was replaced with *IN* (Table 3-2b). All model parameters are defined in Table 3.1. Model selection was carried out using the MuMIn package (K. Barton, 2013). Since the number of observations per parameter was lower than 40, models were ranked according to the Akaike information criterion adjusted for small sample sizes (AICc) (Burnham & Anderson, 2002). This criterion enables estimation of the best model among the set of candidate models while taking into account model complexity.

After examining shared and unshared food patches on their own, I then compared behavior between the two social contexts. I combined shared and unshared feeding bouts and investigated differences in the target's maximum and minimum bite rate according to the number of individuals sharing the food patch. Since there was high variation in bite rate between species and relatively few observations per species, I focused this analysis on the food species with the most observations, *Pterocarpus tinctorius*. *P. tinctorius* is a tree species found mostly in the drier upper slopes of the park. Chimpanzees feed on the fruit, leaves and flowers of this species. Both of my core field seasons spanned time periods of an abundant crop of *P. tinctorius* flowers. Not only do I have the most bite rate data for this species, it was also the only species for which sufficient observations were obtained across a range of feeding party sizes (n=21 feeding bouts). I using GLMMs with a negative binomial error structure and log link function to model the target's maximum and minimum bite rate during bouts of feeding on this species. The predictor variable I investigated was the number of individuals that shared the food patch with the target. In addition to this analysis of bite rate, I also compared patch residence times and target activity budgets between shared and unshared food patches. I used a GLMM with a Poisson error structure to compare patch residence times between shared and unshared

patches (n=252). In this model I included a fixed effect for social context (Unshared/Shared). In order to account for repeated measures of focal targets I also included a random effect for focal ID. Due to overdispersion in patch residence time data, I also included observation (e.g. each feeding bout) as a random intercept (Harrison, 2014; Marshall et al., 2013). Finally, I calculated the target's activity budget using data from feeding bouts in which no more than one bad observation of the target's behavior occurred (n=176). I used bar plots to visualize the global breakdown in target activity in the two social contexts. I then collapsed behavioral categories into "Feeding" and "Not Feeding". Again, "Wadging" was included in the "Not Feeding" category since chimpanzees were capable of wadging and performing other activities such as traveling and grooming. For each feeding bout, I calculated the proportion of time the target spent feeding. I then used a Wilcox rank-sum test to compare these distributions between the two social contexts.

Lastly, I investigated the relationship between patch residence time, patch sharing and the maintenance of contact with party members. Due to high variation in the number of individuals present in the target's party across feeding bouts (median: 3, range: 1-25), I randomly selected one party member present at the start of each feeding bout to include in the analysis (n=132 unique feeding events). The response variable I considered is whether or not the chosen individual was also documented in the party composition scan conducted in the 15 minutes after the end of the feeding bout (No=0, Yes=1). The predictor variables I considered were the (log-transformed) duration of the target's patch residence time (*DURATION*, continuous, numeric) and whether that party member shared the target's food patch at any point during the feeding bout (*SHARE*, No/Yes). I modeled these data using a GLMM with a binomial error structure and logit link function. To account for repeated observations of both focal targets and party members, I included a random intercept for both focal ID and party member ID.

3.3 RESULTS

Chimpanzees resided in patches for a median 969 seconds (range: 60-19,380 seconds). The number of behavioral scans in which the target was documented to be

feeding, as well as not feeding, was positively correlated with target patch residence time (Feeding: $\beta=-3.9\times10^{-4}$, SE=3.9×10^{-5}, p<0.001, Not feeding: $\beta=-4.5\times10^{-4}$, SE=4.9×10^{-5}, p<0.001; Figure 3-1). I found that the likelihood of feeding decreased over time spent in the food patch ($\beta=-2.4\times10^{-4}$, SE=5.8×10^{-5}, p<0.001; Figure 3-2). Bite rate did not change over time spent in the patch ($\beta=3.8\times10^{-5}$, SE=2.4×10^{-5}, p=0.11; Figure 3-3).

Of the models I considered for target patch residence time when foraging in unshared patches, all those including the parameter *SIZE* outcompeted all models without this parameter (Table 3-2a). Furthermore, each model including *OUT* was less supported than the corresponding model without this parameter. The top model consisted of both *SIZE* and *PART* (Akaike weight (w_i)= 0.67). These results indicate that the number of individuals outside the food patch (*OUT*) did not influence target foraging behavior but both the size of the food patch (*SIZE*) and the food part being eaten (*PART*) did influence target behavior. Model averaged parameters (Table 3-3a) indicate that chimpanzees spent longer in larger patches and when feeding on flowers and fruit. The 95% confidence intervals for OUT included zero indicating it does not have a strong effect on target behavior.

For shared feeding bouts, the number of individuals sharing the patch with the target ranged from 1 to 17, with a median of two individuals. Of the 8 models I considered for target patch residence times in these patches, no one model received substantial support (Table 3-2b). However, most models including *IN* outcompeted most models without this parameter, and the top model consisted of *IN* alone (Akaike weight (w_i)= 0.32). These results indicate that when chimpanzees shared patches with others, the amount of time they spent feeding depended not on the size of the food patch or food part but were instead correlated with the number of individuals within the target's food patch (*IN*). In contrast to expectations that the presence of more feeding competitors would decrease patch residence time, model averaged parameters (Table 3-3b) indicate that *IN* is positively associated with target patch residence time, indicating that targets stay longer when more individuals are in the food patch (Figure 3-4). The 95% confidence intervals for all other parameters included zero. There was one feeding bout with a particularly large number of individuals in the food patch (17 individuals) and where the

target had a relatively long patch residence time. Re-running the analysis without this data point did not substantially change the results, though it did reduce the importance of the parameter *IN*. Nevertheless, the best model again consisted of *IN* alone (w_i=0.24). Within this model set, the 95% confidence intervals for all parameters include zero (Table 3-3c) but maintained similar trends as before, including a slight positive association between *IN* and patch residence time. I found that neither maximum nor minimum bite rate significantly varied according to the number of individuals sharing a patch of flowers (β=0.004, SE=0.02, p=0.82; β=-0.04, SE=0.02, p=0.10).

Target patch residence times are significantly longer in shared than unshared food patches (β=0.97, SE=0.16, p<0.001; Figure 3-5). Nevertheless, the proportion of time spent feeding in the two contexts did not significantly differ (W=3488.5, p=0.89; Figure 3-6). The breakdown in activity budget between the two contexts is also similar (Table 3-4, Figure 3-7). However, there are notable differences when it comes to the categories Wadging and Grooming. Since there are no other individuals in the food patch in unshared feeding bouts, the target did not spent any time grooming in this context. In contrast, grooming represented 10% of the activity budget of targets feeding in shared patches. Wadging represented 16% of the activity budget in unshared patches and 9% in shared patches.

A given party member remained cohesive with the focal target across the duration of 71 out of 132 (53.8%) feeding bouts. I found that the patch residence time of the focal target was significantly, negatively correlated with the likelihood of maintaining contact with a given party member (β=-0.39, SE=0.16, p<0.05). On the other hand, sharing the food patch with that individual was significantly positively correlated with the likelihood of maintaining contact (β=2.3, SE=0.61, p<0.001; Figure 3-8).

3.4 DISCUSSION

The aim of this study was to better understand chimpanzee foraging behavior under natural conditions and examine the costs and benefits of sharing a food patch with party members. In unshared food patches, individuals foraged as predicted by the marginal value theorem- residing longer in larger patches and in patches of fruit and

flowers. Fruit has a high energy content compared to other primate foods and can be consumed at a relatively high rate (Nakagawa, 2009). Thus, individuals in this study resided longer in food patches where their rate of energy intake is higher and food is more abundant– factors that increase the time to which the food patch is depleted to its marginal value (Charnov, 1976). Since more foragers feeding within a patch will deplete the patch to its marginal value more quickly than would occur with a single forager, optimal foraging models also predict that patch residence time should decrease as the number of foragers within the patch increases (Parker, 1978). In contrast to this prediction I found that the number of foragers feeding within the food patch was positively correlated with patch residence time. Even more, the number of foragers within the patch was a better predictor of patch residence time in shared patches than properties of the food patch, such as food part and patch size. Thus, while chimpanzee foraging behavior adhered to predictions of the Optimal Foraging Hypothesis in unshared patches, at first glance, it did not appear to adhere to these predictions in shared patches.

However, the positive correlation between patch residence time and feeding party size is likely explained by the idea that the number of individuals in the food patch provides additional information about patch quality that my patch quality measures do not capture. Chimpanzees are known to distribute themselves among patches according to food availability (Symington, 1988; Wrangham, 1980). In fact, the amount of time and number of individuals feeding in a food patch is a commonly-used measure of patch quality for chimpanzees (sometimes termed "chimp minutes") (White & Wrangham, 1988). Thus, the presence of more individuals in the food patch likely indicates that more food is also available. In addition, I did not find a correlation between bite rate and foraging party size or a difference in the proportion of time spent feeding in shared and unshared food patches. These findings indicate that the number of individuals within the patch is not correlated with decreased foraging efficiency.

I found that the likelihood of feeding decreased over time in a food patch but that feeding rate did not. As noted in Chapter 1, I only conducted feeding rate scans when focal targets were actively foraging. These data indicate that individuals become increasing less likely to feed over time in a patch yet are capable of obtaining food at a

similar rate. These data provide strong support for the idea that satiation limits feeding duration in high quality food patches. There is evidence from other primate species that patch depletion does occur in lower quality patches but not in patches that exceed the intake capacity of foragers (Tombak et al., 2012). The relatively long spacing of my behavioral and bite rate samples limited my ability to study short-term changes in feeding behavior over time. Thus, it is possible that individuals do depress low quality food patches, within which they feed for shorter periods of time, but not high quality patches. Nevertheless, if satiation limits the amount of food individuals can consume in high quality food patches, sharing these patches with others will not negatively impact an individual's foraging success.

I did not find substantial differences in individuals' activity budget between shared and unshared food patches. On average, individuals actively foraged during only 60-70% of the time they spent in food patches. Thus, in patches of sufficient quality, individuals may spend a relatively long amount of time performing behaviors such as processing or digesting food. Comparison of the activity budget between shared and unshared patches reveals that individuals spend an approximately equal proportion of time wadging in unshared patches as they do in the combined categories of wadging and grooming in shared patches. The seemingly reduced proportion of time spent wadging in shared food patches is likely a result of the order of priority given to different behavior states (Altmann, 1974). Since wadging is a relatively passive behavior, this behavioral state was assigned a lower priority, and thus only recorded when the target was not engaged in high priority behavior states. When individuals were engaged in other activities, such as traveling or grooming, I recorded these behaviors instead. Thus, it is possible that individuals spend the same proportion of time wadging when in shared patches but that part of this time is also spent grooming others.

The Coordination Hypothesis proposes that sharing a food patch with others reduces the need to abandon a food patches prematurely in order to maintain contact with those individuals outside the patch (Kazahari & Agetsuma, 2007; Kazahari, 2014; Nakagawa, 1990). I did find a negative association between patch residence time and the likelihood of maintaining contact with party members and that sharing a food patch with

others reduces the likelihood of losing contact with party members. This suggests that there is a tradeoff between foraging duration and the maintenance of contact with party members outside the patch. However, I did not find a correlation between the size of the party outside the food patch and feeding duration within the patch, suggesting that individuals do not sacrifice foraging behavior in order to remain in contact with these party members.

My results indicate that if individuals are motivated to feed for long periods of time and do so alone, there is a high likelihood that they may lose contact with party members. Furthermore, I show that sharing high quality food patches with others does not impose a substantial foraging cost since feeding duration is limited by satiation and shared food patches are associated with an abundance of food. Thus, sharing high quality food patches with others could be a cost-effective strategy for reducing the trade-off between foraging and the maintenance of social contact. Furthermore, since foragers spend a substantial amount of time resting and processing food during long feeding bouts, sharing the patch with others could facilitate time for additional socialization with party members. Thus, permitting others to feed in one's food patch, or even facilitating patch-sharing through the production of food-associated calls, could be the most effective strategy when arriving at a high quality food patch in the presence of important social partners. In Chapter 4 I explore the socioecological context of food-associated call production in chimpanzees and whether these vocalizations are capable of facilitating the sharing of food patches between foragers.

3.6 TABLES

Table 3-1. Definition of Model Parameters- Target Patch Residence Time Definition of the parameters included in models of target patch residence time.

Parameter	Definition
SIZE	A factor representing the size category of the food patch. Factor levels include <5 meters and >5 meters
PART	A factor representing the food part being eaten in the patch. Factor levels include leaves, flowers, and fruit.
IN	A numeric variable representing the number of individuals that fed in the target's food patch at some point during the feeding bout
OUT	A numeric variable representing the number of individuals outside the target's food patch but in the vicinity of the patch

Table 3-2. Model Selection Tables: Target Patch Residence Time Model selection table for target patch residence time when feeding in a) unshared food patches (n=159 feeding bouts) and b) shared food patches (n=93 feeding bouts). Parameter estimates are provided for numeric parameters present in a given model, including the intercept (B). +'s indicate whether a given factor variable was present a given model. K represents the number of parameters in each model, including the intercept. Δ_i represents the difference in the Akaike information criterion (AICc) between the ith and best model. w_i represents the probability that a given model is the best model among the candidate set.

a) Unshared Food Patches

Model	B	OUT	PART	SIZE	K	Δ_i	w_i
PART + SIZE	5.6		+	+	3	0	0.67
FULL	5.6	-0.003	+	+	4	2.2	0.23
SIZE	6.0			+	2	4.5	0.07
OUT + SIZE	6.0	-0.01		+	3	6.4	0.03
PART	6.0		+		2	24	0.00
OUT + PART	6.1	-0.01	+		3	26	0.00
NULL	6.4				1	28	0.00
OUT	6.4	-0.02			2	30	0.00

b) Shared Food Patches

Model	B	IN	PART	SIZE	K	Δ_i	w_i
IN	7.0	0.10			2	0.0	0.32
IN + SIZE	6.9	0.09		+	3	0.8	0.22
IN + PART	7.0	0.11	+		3	1.7	0.14
SIZE	7.0			+	2	2.1	0.11
FULL	6.8	0.10	+	+	4	2.8	0.08
NULL	7.3				1	2.8	0.08
PART + SIZE	7.0		+	+	3	4.7	0.03
PART	7.3		+		2	5.0	0.03

Table 3-3. Model Averaged Parameters: Patch Residence Time Model averaged parameter estimates for target patch residence time when feeding in a) unshared food patches (n=159 feeding bouts) and b,c) shared food patches (n=93 feeding bouts). Tables 3-3b and c display parameter estimates with (b) and without (c) the data point from the feeding bout with a relatively large number of individuals (17) in the food patch. Food part was coded using deviation coding where the mean of the dependent variable at each factor level is compared to the grand mean of the dependent variable.

a) Unshared Food Patches

Parameter	Reference Level	Factor Level	Parameter Estimate	2.5%	97.5%
SIZE	<5m	>5m	0.92	0.58	1.3
PART	*grand mean	leaves	-0.47	-0.77	-0.16
		flowers	0.48	0.58	1.3
		fruit	-0.02	0.10	0.86
OUT	NA	NA	-0.004	-0.05	0.05

b) Shared Food Patches

Parameter	Reference Level	Factor Level	Parameter Estimate	2.5%	97.5%
SIZE	<5m	>5m	0.35	-0.16	0.87
PART	*grand mean	leaves	-0.29	-0.66	0.07
		flowers	0.13	-0.24	0.50
		fruit	0.17	-0.16	0.50
IN	NA	NA	0.1	0.009	0.19

c) Shared Food Patches (Data Point Removed)

Parameter	Reference Level	Factor Level	Parameter Estimate	2.5%	97.5%
SIZE	<5m	>5m	0.37	-0.15	0.88
PART	*grand mean	leaves	-0.29	-0.66	
					0.08
		flowers	0.13	-0.17	0.49
		fruit	0.16	-0.17	0.49
IN	NA	NA	0.1	-0.02	0.22

Table 3-4. Target Activity Budget in Shared and Unshared Food Patches The global activity budget of target individuals feeding in shared and unshared food patches (n=176 feeding bouts). Decimal values represent the proportion of time the target spent in each activity within a given social context. Numbers in parentheses represent the total number of behavioral scans in which a target individual was documented in each activity state.

	Social Context	
Activity	Unshared	Shared
Feed	0.68 (306)	0.63 (287)
Travel	0.06 (25)	0.05 (23)
Rest	0.10 (44)	0.13 (59)
Groom	0.00 (0)	0.10 (46)
Wadge	0.16 (73)	0.09 (40)

3.7 FIGURES

Figure 3-1. Patch Residence Time and Non-feeding Behavior Correlation between target patch residence time and the number of behavioral scans in which he was documented to be performing a non-feeding behavior (n= 176 feeding bouts). Slight jitter is added to data point location in order to promote visibility of individual observations. Regression line represents a simple linear regression between the two variables and is provided for visual purposes only. Data were analyzed using a GLMM with a negative binomial error structure and a random intercept for each focal target. There was a significant, positive correlation between feeding duration and the number of scans spent not feeding (GLMM, $p < 0.001$).
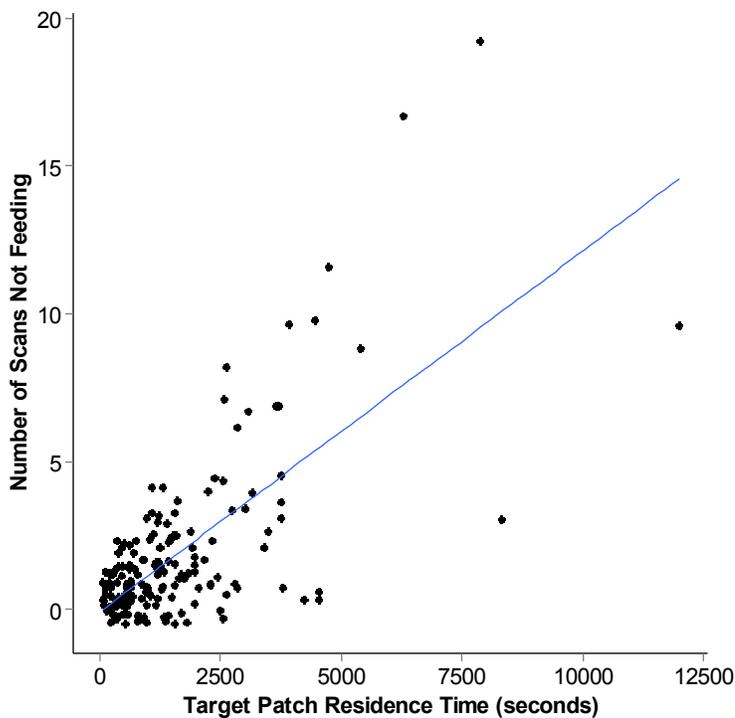
Figure 3-2. Likelihood of Feeding According to Time in Patch Correlation between the likelihood that the focal target was documented to be feeding during a given behavioral scan (Not Feeding=0, Feeding=1) according to the amount of time that had elapsed since the target entered the food patch (n= 122 feeding bouts). Jitter is included around data point location in order to promote visibility of individual observations. Regression line represents a simple GLM smoothing function of the binomial family and is provided for visual purposes only. Data were analyzed using a GLMM with random intercepts included for repeated measures of both feeding bout and target ID. There was a significant negative correlation between elapsed time the likelihood of feeding (GLMM, p<0.001).
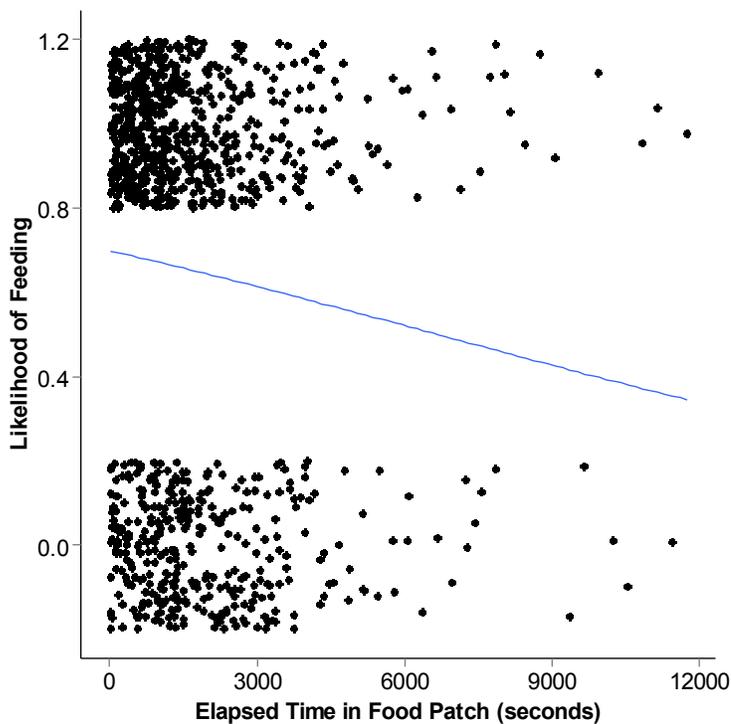
Figure 3-3. Bite Rate According to Time in Patch Correlation between target bite rate in patches of *P. tinctorius* and the amount of time that had elapsed since the target entered the food patch. Data points with the same shape represent data points from the same feeding bout. Lines represent simple linear regression functions calculated separately for each feeding bout and are provided for visual purposes only. Data were analyzed using a GLMM with a negative binomial error structure and log link function with random effects included for repeated measures of both feeding bout and target ID. There was not a significant correlation between bite rate and elapsed time in the patch (n= 26 feeding bouts, GLMM, p=0.10).
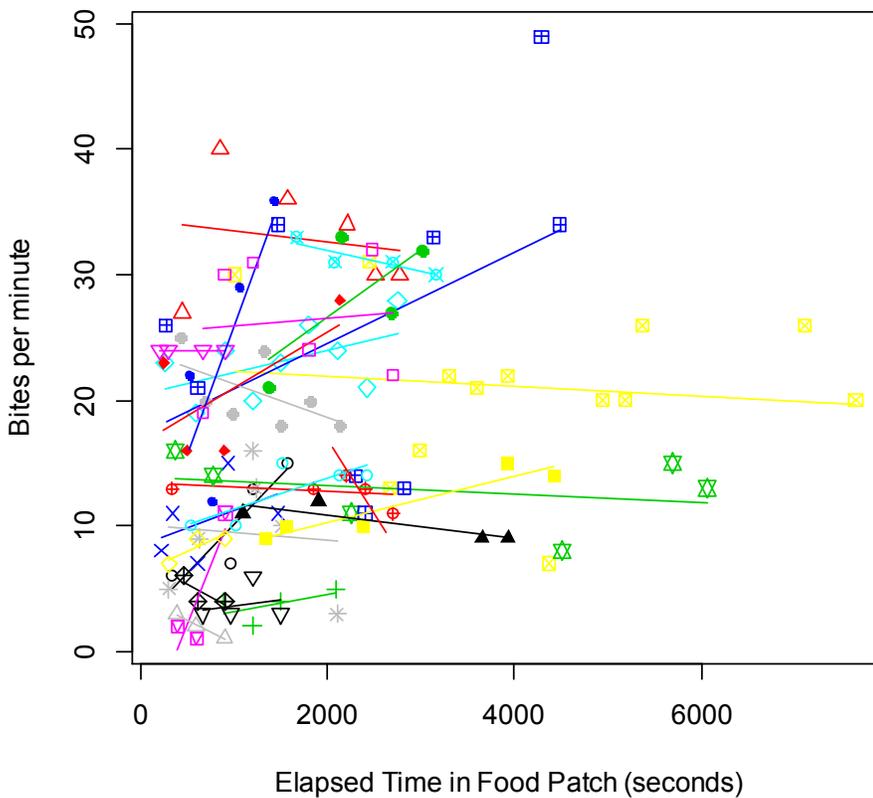
Figure 3-4. Target Patch Residence Time by Number of Individuals in Food Patch
Correlation between target patch residence time and the number of individuals that shared
the food patch with the target at some point during the feeding bout (n=93 feeding bouts).
Slight jitter is included around the position of data points in order to promote visibility of
individual observations. The lines represent simple linear regression functions for the two
variables and are provided for visual purposes only. Data were analyzed using a GLMM
with Poisson error structure and long link function with random intercepts included for
target and observation ID. Models including different combinations of ecological and
social predictors were compared using a model selection approach. Model averaged
parameters indicate that the number of individuals inside the food patch is positively
associated with target patch residence time.
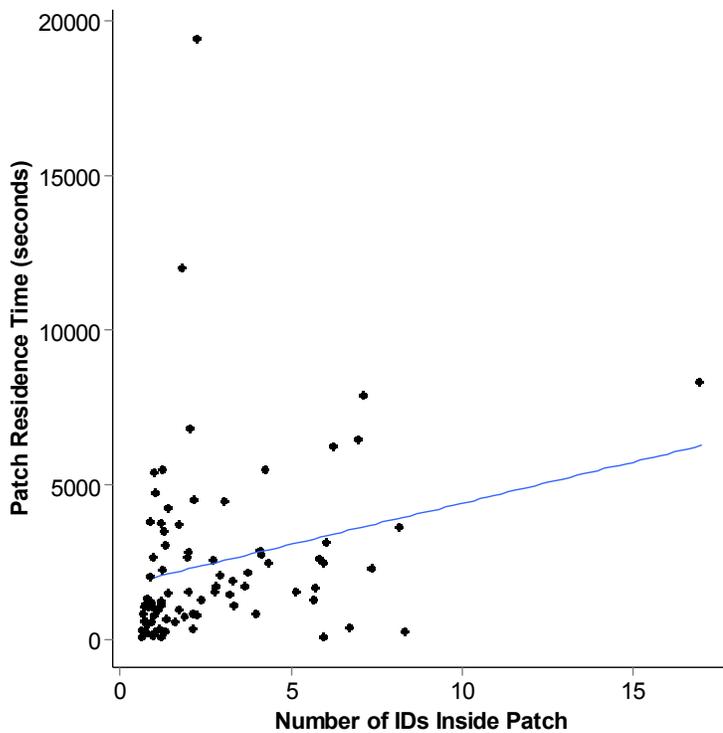
Figure 3-5. Patch Residence Time in Shared and Unshared Patches Boxplots
representing the distribution of patch residence times in shared and unshared food patches
(n=252 feeding bouts). Boxes represent 1st-3rd quartiles. Points represent individual
feeding bouts with slight jitter around the x and y axis to promote visibility. Data were
analyzed using a GLMM with Poisson error structure and log link function with random
intercepts for target ID and feeding bout ID. Patch residence times were significantly
longer in shared than unshared food patches (GLMM, p<0.001).
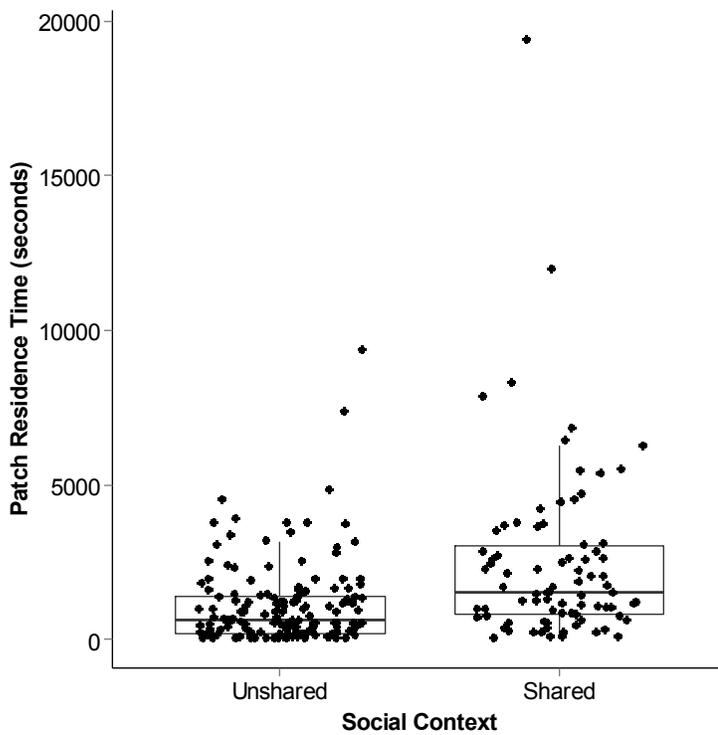
Figure 3-6. Proportion of Patch Residence Time Spent Feeding by Social Context
Boxplots representing the distribution of patch residence times in shared and unshared food patches. Boxes represent 1st-3rd quartiles. Points represent individual feeding bouts with slight jitter around the x and y axis to promote visibility. Proportion of time spent feeding was significantly longer in shared than unshared food patches (n=176, Wilcox rank sum test, p<0.001).
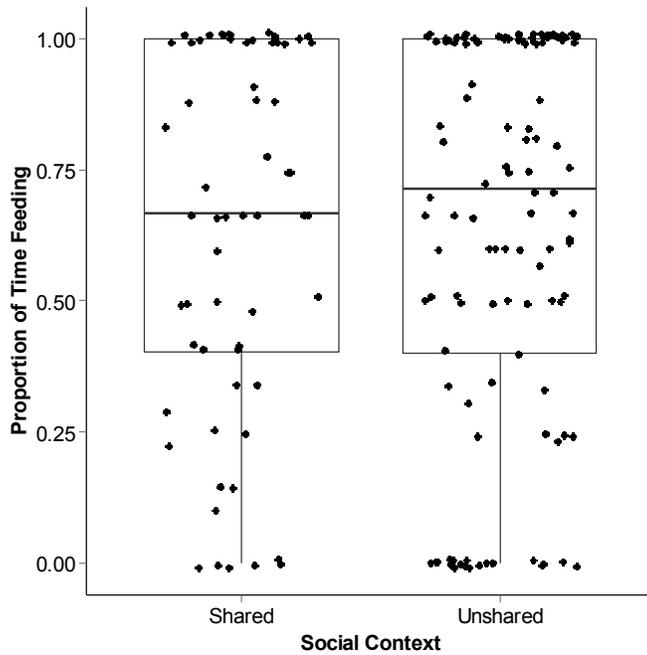
Figure 3-7. Activity Budget in Shared and Unshared Food Patches Global activity budget of target individuals in shared and unshared food patches (n=176 feeding bouts). All behavioral scans in which the target was performing each activity were summed for each social context and divided by the total number of behavioral scans in that context.
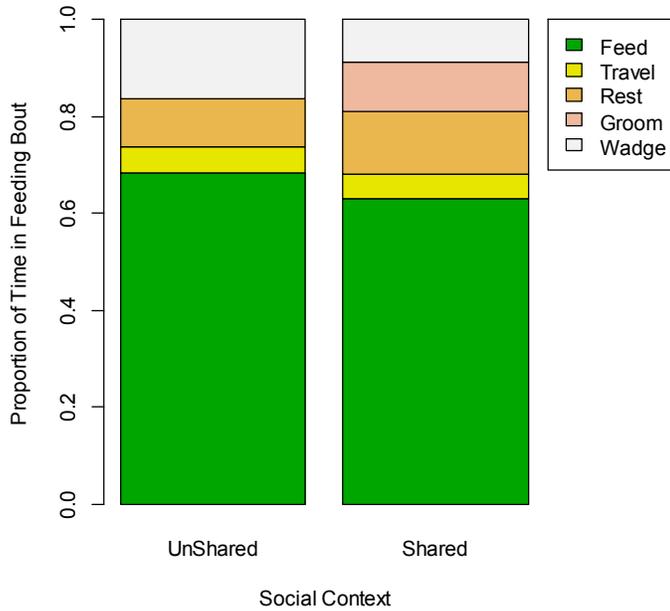
Figure 3-8. Likelihood of Maintaining Contact with Party Members Correlation between the likelihood that a given party member present at the beginning of a feeding bout was still documented in the target's party by the end of the feeding bout (Not Present=0, Present=1) according to the target's patch residence time and patch sharing behavior (n=132 feeding bouts). Figures 3-8a and b display data for individuals that shared (a) and did not share (b) the food patch with the target at some point during the feeding bout. Slight jitter is included around data point location in order to promote visibility of individual observations. Regression line represents a simple GLM smoothing function of the binomial family and is provided for visual purposes only. Data were analyzed using a GLMM with random effects included for repeated measures of both target and party member ID. There was a significant negative correlation between the likelihood of cohesion and target patch residence time ($p<0.05$) and a significant positive correlation with patch sharing ($p<0.001$).

a) Shared Patches
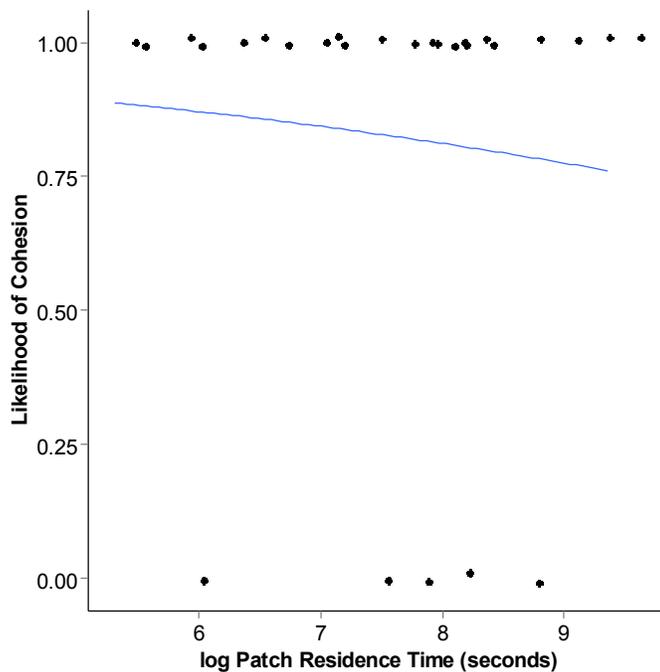
Figure 3-8 continued.

b) Unshared Patches
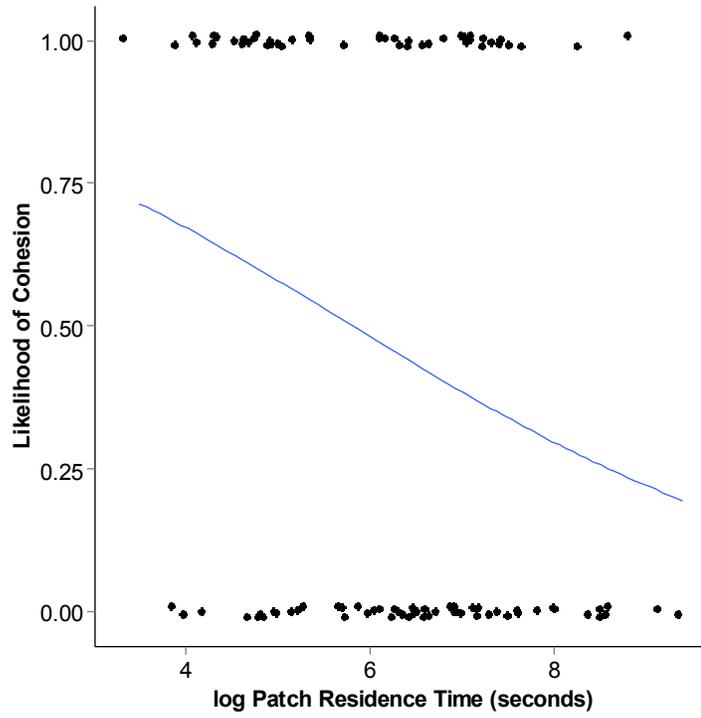
CHAPTER 4

PATCH SHARING AND FOOD-ASSOCIATED CALLING BEHAVIOR IS BEST EXPLAINED BY SOCIAL FACTORS

4.1 INTRODUCTION

Many species of birds and mammals produce specific vocalizations in foraging contexts. These calls represent an evolutionary puzzle since drawing attention to a food source can increase feeding competition for the signaler. Thus, much research effort has focused on the function of these vocalizations (Clay et al., 2012). The presumed function of most "food-associated calls" is that they increase the likelihood that others approach the discovered food. This could occur via general recruitment or by explicitly informing receivers about the presence and/or properties of the food. There is evidence that the production of food-associated calls can promote food-searching behavior (Evans & Evans, 2007), increase the likelihood that others approach the discovered food (Chapman & Lefebvre, 1990; Elgar, 1986a; Heinrich, 1988), reduce the amount of time it takes for others to arrive at the food patch (Chapman & Lefebvre, 1990; Elgar, 1986a), and increase the total number of individuals that arrive (Brown et al., 1991; Hauser & Marler, 1993b; Laidre, 2005). Attracting others to a food patch is presumed to benefits signalers if the benefits gained by increasing proximity to others outweigh the cost of increase feeding competition. Suggested benefits include a reduced risk of predation (Chapman & Lefebvre, 1990; Elgar, 1986b), increased feeding rate due to lower levels of vigilance, increased mating (Dibitetti, 2005; Evans & Marler, 1994) or other social opportunities (Fedurek & Slocombe, 2013), or increased ability to defend food.

While the majority of studies have found evidence that food-associated calls elicit an attractive response, a few have found mixed or contrasting evidence. For example, pant-hoots of chimpanzees (*Pan troglodytes*) have been reported to be produced in situations of high food abundance (Hauser et al., 1993) but field studies have found no evidence that these calls convey information about properties of the discovered food (Clark & Wrangham, 1993, 1994). Furthermore, one study found that pant-hoot production was not correlated with arrival of extra party individuals (Clark & Wrangham,

1994) while another found that pant-hoot production was correlated with the arrival of estrous females (Wrangham, 1977). As another example, a food-associated vocalization of pied babblers (*Turdoides bicolor*) does not recruit others to the food source, but rather reduces the likelihood that other foragers approach the signaler (Radford & Ridley, 2008). Similarly, the production of food-associated "huh" vocalizations by white-faced capuchins (*Cebus capuchinus*) is correlated with an increase in spacing between foragers (Boinski & Campbell, 1996) and a reduction in the likelihood that the signaler is approached, or receives aggression, by other foragers (Gros-Louis, 2004b). Thus, rather than attract others to the food patch, some food-associated vocalizations may rather function by mediating social interactions during foraging contexts in which others are already feeding.

Some researchers propose that food-associated calls advertise an increased likelihood of defending food (Gros-Louis, 2004b), a claim supported by findings that food-associated calls are positively correlated with hunger level in some species (Hauser & Marler, 1993a) and that call production is correlated with a lower likelihood of receiving aggression from dominant individuals (Gros-Louis, 2004b; Hauser & Marler, 1993b). Interestingly, playbacks of the capuchin 'huh' vocalization that appears to repel other foragers within the patch, attracts those who are unaware of the food patch (Gros-Louis, 2004a). There is mounting evidence that receivers can show great flexibility in the information they can obtain from vocalizations (Marler et al., 1992). Thus, receivers may be able to gain information about discovered food when hearing food-associated calls, despite the fact that these calls serve an alternative function from the signaler's perspective.

A food-associated call that has been subject to much recent investigation is the "rough-grunt" vocalization of chimpanzees. In contrast to pant-hoots, which are produced in a variety of contexts, rough-grunts are specific to foraging contexts (Goodall, 1986). Rough-grunts can range from low-pitch grunts to high-pitched barks (Slocombe & Zuberbühler, 2006) and calling bouts can vary from one to many vocalizations (Brosnan & de Waal, 2002). Previous studies have reported that these calls are produced upon discovery of high quality food (Hauser et al., 1993; Slocombe et al., 2010), and recent

studies have reported that acoustic properties vary according to properties of the discovered food (Kalan et al., 2015; Slocombe & Zuberbühler, 2005), and that receivers can gain specific information about discovered food when hearing these vocalizations (Kalan et al., 2015; Slocombe & Zuberbühler, 2005). In a captive playback study, researchers trained the single experimental subject to expect either bread or apples from one of two artificial food trees. Researchers then presented the subject with playbacks of rough-grunt vocalizations. Depending on the trial, the researchers presented the subject with rough-grunts that had been recorded from individuals discovering either bread or apples. Researchers found that the subject searched longer for food beneath the artificial food tree corresponding with the food type that had elicited the broadcast rough-grunts (Slocombe & Zuberbühler, 2005). However, this effect was limited to only the first few trials after which the subject developed a more general search strategy, potentially due to the fact that no food was ever discovered during playback trials.

While many studies have focused on the relationship between rough-grunt production and properties of discovered food, recent studies suggest that social context is just as, or more important, than food properties in the production of rough-grunts. Some studies indicate that chimpanzees are more likely to call when in the presence of others (Brosnan & de Waal, 2002), particularly when in the presence of socially significant individuals such as grooming partners (Fedurek & Slocombe, 2013; Slocombe et al., 2010) and high ranking individuals (Schel et al., 2013). Thus, despite suggestive evidence that rough grunts provide information about food properties, they may rather serve as a means of mediating social interactions in foraging contexts.

I conducted an observational study of wild chimpanzee behavior in order to compare two hypotheses for the function of rough-grunt calling behavior. The Functionally Referential Hypothesis proposes that food-associated calls advertise properties of discovered food to others in the vicinity, attracting them to the food patch. Alternatively, the Social Facilitation Hypothesis proposes that food-associated calls mediate social interactions during foraging contexts in which many individuals are already feeding together. In order to test these two hypotheses I investigated social and ecological predictors of rough-grunt production and the arrival of others in the target's

food patch. The Functionally Referential Hypothesis predicts that individuals will be more likely to produce rough-grunts at high quality food patches, presumably to inform others of the discovered food. Furthermore, it predicts that rough-grunt production increases the likelihood that others will arrive in the signaler's food patch. The Social Facilitation Hypothesis predicts that rough-grunt production is best explained by the social context during arrival at the food patch and that individuals arrive at food patches for reasons other than food-associated calling behavior. The two alternative factors I am considering for the arrival of others in the target's food patch are the number of individuals in the vicinity of the food patch and the quality of the patch. I predict that others are more likely to share the food patch with the target when more individuals are in the vicinity and/or when the target is feeding in a high quality food patches since these patches are capable of supporting more individuals (see Chapter 3). While the focus of this study is on rough-grunt production, the production of pant-hoots is also taken into account since both may influence the behavior of others in foraging contexts.

In addition to this observational study, I conducted a series of playback experiments with captive chimpanzees. These experiments tested whether rough-grunts elicit an attractive response after controlling for knowledge of food and food patch properties.

4.2 METHODS

I conducted both an observational study of wild chimpanzees and behavioral experiments with captive chimpanzees. I conducted my fieldwork at Gombe where I studied the behavior of ten focal males. I collected data on the socioecological context of rough-grunt production by these focal targets and their sharing of food patches with others. For description of this research site and specific field methods see Chapter 1. I conducted experiments at KCCMR. Subjects were 12 adult chimpanzees (7 female and 5 male) from two multi-male, multi-female social groups. For description of this research site see Chapter 1. Details of the experiment are described below.

Experimental Set-Up

The foraging environment consisted of each social group's three adjacent indoor rooms positioned in a row (Figure 4-1). Each room had a sliding door between it and its adjacent room(s), as well as the outdoor area. All doors could be manipulated by the experimenter from outside of the experimental area. The wall of each room between the experimental area and the human area was largely made of wire mesh. This enabled me to observe and document the subject's behavior from outside the experimental area. The center room is where the subject first entered the experimental area from the outdoor enclosure and is where the subject resided during the playback. The two side rooms are where the subject was able to access the food patches and from where the acoustic stimuli were broadcast.

Food patches consisted of 60 grapes in troughs composed of a PVC pipe cut in half length-wise. Grapes are a preferred food in this population of captive chimpanzees (Hopper et al., 2013). The food patches could be attached to the wire mesh with clips, enabling the subject to retrieve the grapes by sticking its fingers through the mesh. Vocalizations were played back to the subject through speakers (Mackie SRM 350v2) placed outside of each side room and angled towards the center room. Each speaker was placed on top of a crate so that its center was positioned approximately at the height of a chimpanzee's head at resting level. One video camera on a tripod was positioned in the human area outside of each of the three rooms and focused on the center of each room. This enabled the subject's activity to be documented as it traveled in and between each room. The sliding doors between the adjacent rooms could be opened from the human area by pulling straight back on the handles in line with the plane of the door. Since the handles to the two sliding doors were positioned at a distance greater than arms reach, a pull bar was used in order to open both doors at the same time. This bar had clasps on either end connected to chains. The end of each chain was clipped to the handle of each door. By pulling back on the bar, I could simultaneously open both doors. A laptop containing the stimulus sound files was placed in the human area outside the view of the subject. I was able to initiate each playback by pressing play on a small remote control held in my pocket.

At the start of the experiment all doors in the experimental area were in the closed position. A subject was brought into the experimental area by opening the door between the outdoor enclosure and the center room. Once the subject was inside, the door was closed behind it. At the time of the subject's entry, the two food troughs were lying next to one another on the ground just outside of the center room (Figure 4-1) in clear view of the subject. The pull bar was positioned on the ground behind the troughs. Once the subject had entered the room and the door was closed, I brought one food trough to one of the side rooms and clipped it onto the wire mesh at the front of the room at a comfortable feeding height. I then attached the other trough to the other room in the same manner. The order in which I attached the right vs. left trough was randomized before each trial. I positioned the food troughs and attached them to the rooms in plain sight of the subject in an attempt to reduce uncertainty regarding differences in quality between the two food patches. Once the food was placed, the playback was initiated.

There were three treatment levels: Silence, Rough-grunt and Control Call. Each subject experienced all three treatment levels in a random order. For a given subject, the identity of the individual producing the rough-grunt and control call was kept consistent. The rough-grunt condition was used to determine whether and how rough-grunts influence the subjects' foraging decisions. The silent condition was used to determine whether subjects had a significant side bias. Since it is possible that the subjects' responses to the rough-grunt could simply be due to the presence and general vocal activity of the signaler, I also included a condition in which subjects were presented with a vocalization that was not a rough-grunt.

During both the Rough-grunt and Control Call conditions, a rough-grunt or control call was broadcast from one of the two speakers. The side from which the rough-grunt or control call was broadcast was randomly selected before each trial. I initiated the playback while standing in the human area in the middle of the center room. Once the playback was completed I pulled back on the pull bar, simultaneously opening the doors to the two side rooms. At this point, subjects were free to feed from both troughs as desired. Once all of the food was consumed, one of the doors to the outdoor area was

opened so that the subject could return to the outdoor area. The silent condition was carried out in the same manner as the Rough-grunt and Control Call conditions except that no stimulus was broadcast from either speaker.

Recording Playback Stimuli

I recorded all playback stimuli with a Sennheiser ME66 shotgun microphone with K6 power module and a Marantz PMD670 recorder. Most vocalizations were recorded *ad libitum* during normal social interactions within the group. However, rough-grunts were occasionally elicited by placing food inside the chimpanzees' enclosure. Stimuli were recorded from four different individuals, two from each social group. One rough-grunt and one control call were recorded from each individual. Unfortunately, I was not able to obtain a consistent control call from all subjects. Two of the control calls were pant-grunts: calls produced by lower ranking chimpanzees to higher ranking chimpanzees (Goodall, 1986). One of the control calls was a pant-hoot: a long-distance call produced in a variety of contexts, including a foraging context (Fedurek et al., 2014). The other control call was a raspberry, a vocalization frequently produced in captive environments to catch the attention of humans (Hopkins et al., 2007). While ideally the same type of control call would be presented to all subjects, these calls still controlled for the fact that the subject heard the vocalization of another chimpanzee in the room next to them. Three subjects from each group were presented with one of the four unique Rough-grunt/Control Call stimulus pairs. Stimuli were left unedited except for being reduced to a duration of 6 seconds. Stimulus files were edited in Praat and played back through Windows Media Player.

4.3 ANALYSIS

Gombe

I conducted all analyses using the statistical program R v.3.0.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). I restricted all analysis of field data to those feeding bouts where the entire duration was observed, the

boundaries of the food patch were clear and it was known whether or not the target produced at least one rough-grunt at any point during the feeding bout (n=176).

I used an information theoretic approach (Burnham & Anderson, 2002) to compare hypotheses for the likelihood of rough-grunt production by target individuals. Rough-grunt production was modeled using a GLMM with binomial error structure and logit link function (No Rough-grunt=0, Rough-grunt=1). Patch quality parameters included patch size (*SIZE*: <5m, >5m) and PART (leaves, flowers, fruit). Social parameters included the number of individuals documented in the party composition scan that was conducted in the fifteen minutes prior to the target's arrival at the food patch (*PARTY*: count, numeric), the presence of a higher ranking individual in the target's party during this scan (*RANK*: No/Yes) and the presence of an important social partner in the target's party during this scan (*GROOM*: No/Yes). All parameters included in models of target rough-grunt production are defined in Table 4.1. In the analysis I included only those feeding bouts in which all social and ecological parameters were known (n=108, occurrences of rough-grunt production= 46).

Dominance rank was determined from long-term data collected at Gombe on the direction of submissive pant-grunt vocalizations between individuals (See Chapter One, Table 1-1). As my focal targets are all adult males, they out-rank all other individuals in the community. However, each focal target has at least one other individual whom out ranks itself, except for the alpha male. No changes in rank between adult males were observed across my two core field seasons.

I found important social partners for all focal targets. Using the all-occurrences (Altmann, 1974) grooming data I collected during my field studies, I summed the total amount of time the target spent grooming each member of the community and divided this value by the total amount of time these two individuals were observed to be in the same party. These measures were calculated separately for each field season. I then identified all individuals whose relative grooming score fell two standard deviations above each target's mean score. The number of important social partners identified for each focal target in this study (median= 3, range= 2-5) is similar to the number identified

in previous studies of chimpanzee rough-grunt calling behavior (Fedurek & Slocombe, 2013; Slocombe et al., 2010).

I compared a set of eight models which consisted of a full model containing all predictor variables, a null model, and univariate models consisting of each predictor variable on its own (Table 4-3). Furthermore, I included one model with the combination of *PART + SIZE*. Models were fit using the lme4 package (Bates et al., 2013). Since the number of parameters per observation were lower than 40, models were ranked according to the Akaike information criterion adjusted for small sample sizes (AICc) (Burnham & Anderson, 2002). This criterion allows estimation of the best model among the set of candidate models while taking into account model complexity. Model selection was carried out in R using the MuMIn package (Barton, 2013).

In addition to modeling the likelihood of rough-grunt production, I also examined its relationship with the arrival of others in the food patch. An individual was considered to arrive in the target's food patch if it arrived in the patch at any point after the target but before the target abandoned the food patch. I used a chi-squared test to investigate the correlation between rough-grunt production by the target (No/Yes) and whether or not any individuals arrived in the patch after him (but before he abandoned the patch) (No/Yes). I also used an independent Mann-Whitney U test to test the correlation between rough-grunt production by the target (No/Yes) and the total number of arrivals (count, numeric). Dependent offspring were not counted in this analysis as their arrival is likely dependent upon the arrival of their mother. I used a chi-squared test to examine the relationship between the production of rough-grunts and the production of pant-hoots using data from all feeding bouts for which target vocal production was known with respect to both call types (n=157). With these data I also used chi-squared tests to examine the relationship between rough-grunt and pant-hoot production by the target and the occupancy of the food patch upon arrival (Empty/Occupied).

It is possible that a positive relationship between rough-grunt production and arrivals could come about because rough-grunts facilitate arrival or because rough-grunts are produced in contexts where more arrivals are likely. Rough-grunt production is correlated with other variables that may promote patch-sharing such as the quality of the

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patch (Brosnan & de Waal, 2002), pant-hoot production (Hauser et al., 1993), and the presence of individuals in the target's party at the start of the feeding bout (Fedurek & Slocombe, 2013; Slocombe et al., 2010). Thus, I used an information theoretic approach (Burnham & Anderson, 2002) to compare hypotheses for the likelihood of arrivals after the target. The Functionally Referential Hypothesis predicts that the likelihood of another arrival in a food patch is best explained by the quality of the food patch. The Social Facilitation Hypothesis predicts that the arrival of others is best explained by other factors such as the social context prior to arrival at the patch or the quality of the food patch.

I first modeled arrivals in all patches where all relevant parameters were known (n=99). I then restricted the analysis to only those instances where the target arrived at an empty food patch (n=87). This controls for the fact that no other individuals would have produced any vocalizations before the target arrived. Due to the relatively few instances of arrivals (Figure 4-2) I modeled arrival behavior as a binary response (No Arrivals/Arrival(s)) using a GLMM with a binomial error structure and logit link function. To account for repeated observations of focal targets (n=10) I included a random intercept for focal ID. Model selection was carried out in the same manner as described above. Due to the small sample size, I combined the food parts leaves and flowers into a single category. The factor level listed first for each of my predictor variables represents the reference category. The factor level listed second is expected to have a positive effect on the likelihood of arrival. Patch quality parameters were food patch size (*SIZE*: <5m, >5m) and food part (*PART*: leaves/flowers, fruit). Food-associated call parameters were rough-grunt production by the target (*RG*: No/Yes) and pant-hoot production by the target (*PH*: No/Yes). The parameter representing social context was the target's party size in the 15 minutes prior to arrival at the food patch (*PARTY*: count, numeric). All parameters included in models of arrival behavior are defined in Table 4.2. Due to the small number of observations where arrivals actually occurred (All Social Contexts: n=97, Arrivals: No=75, Yes=24; Empty Patches: n=87, Arrivals: No=70, Yes=17) I restricted the maximum number of model parameters (k) to two. This keeps the number of events per parameter above 10 for the first social context

and just below 10 (8.5) for the second social context. Restricting model size is important in order to reduce biases of regression coefficients which can result due to small event per parameter ratios (Peduzzi et al., 1996). The final model set consisted of 10 models (Table 4-5) which include a null model, univariate models consisting of each predictor variable on its own, and bivariate models with each of the patch quality and food-associated call predictors in combination with party size. Party size is included in some models representing the Functionally Referential Hypothesis since rough-grunt vocalizations are within-group signals and likely cannot influence the behavior of others if there are no individuals in the area to hear them.

KCCMR

For the silent condition I used chi-squared tests to test whether the number of subjects that investigated, entered, and fed in the left vs. right room first differed significantly from chance. A subject was considered to investigate a room if it either entered the room or walked to the door of the room and peered inside. For the rough-grunt and control call conditions I used chi-squared tests to test whether the number of subjects that investigated, entered, and fed in the stimulus room first differed significantly from chance. I also used a McNemar's chi-squared test to compare each subject's response to the rough-grunt vs. control call condition.

4.4 RESULTS

Gombe

Target individuals produced rough-grunts in 42.6% of feeding bouts (n=108). Of the eight models compared for the likelihood of rough-grunt production, three fell into the 95% confidence set (Table 4-3). Two of the models belong to the Social Facilitation Hypothesis while the other was the full model. The top model included *RANK* alone and was substantially supported above all other models (Akaike model weight, $w_i = 0.81$), indicating that the presence of a high ranking individual in the target's party was the best predictor of rough-grunt production. Model averaged parameters indicate that the presence of a higher ranking individual is strongly positively correlated with the

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likelihood of rough-grunt production (Table 4-4, Figure 4-3). The 95% confidence estimates of all other parameters include zero. Nevertheless, there was a slight positive association between rough-grunt production and the presence of an important social partner, as well as feeding on flowers. A post-hoc test indicates that a focal target's linear rank (1-10, integer) was not significantly correlated with the proportion of feeding bouts in which he produced rough-grunts (n= 179, Spearman rank correlation, S=146, p=0.76, Figure 4-4).

Rough-grunt production by the target was significantly correlated with the arrival of at least one individual in the food patch after the target (n=166, χ= 8.5, df=1, p<.01) as well as with the total number of individuals arriving (n=156, W=2305, p<.001). Another individual arrived in the patch after the target in 16 out of 99 (16.2%) feeding bouts when he did not produce rough-grunts and 25 out of 67 (37.3%) bouts when he did. The median number of arrivals was zero (range: 0-2) when rough-grunts were not produced and zero (range: 0-12) when they were produced (Figure 4-5).

Rough-grunts and pant-hoots were not distributed randomly with respect to one another (χ=37.9, p<0.001). When a focal target produced rough-grunts, there was an approximately equal likelihood he would produce a pant-hoot as well. However, when a focal target did not produce any rough-grunts, the production of a pant-hoot was unlikely (Figure 4-6). Both rough-grunts and pant-hoots were produced more often upon arriving in an occupied food patch than an unoccupied patch, but this tendency only reached significance for pant-hoots (Rough-grunt: χ=2.1, p=0.15; Pant-hoot: χ=6.3, p<0.01). Rough-grunts were produced in 46.7% of feeding bouts when arriving at an occupied food patch and 30.6% of feeding bouts when arriving at an empty food patch. Pant-hoots were produced in 40% of feeding bouts when arriving at an occupied food patch and 16.9% of feeding bouts when arriving at an empty food patch.

Out of the 10 models I considered for the likelihood of another's arrival in the target's food patch (regardless of whether the patch was occupied or empty upon the target's arrival), 4 fell into the 95% confidence set (Table 4-5a). All models within this set included the parameter *PARTY*. In fact, all models including this parameter out performed all models without it. The 95% confidence set consisted of two models

belonging to the Social Facilitation Hypothesis and one model belonging to the Functionally Referential Hypothesis. The top performing model was the patch quality model consisting of the parameter *PART* alongside *PARTY*. This model was supported 4.9 times more (evidence ratio = w_i/w_j = 0.68/0.14 = 4.9) than the second-best model consisting of the food-associated call variable *PH* alongside *PARTY*. These results indicate that the number of individuals present in the target's party at the beginning of the feeding bout (*PARTY*) is the best predictor of the arrival of others in the target's food patch. Model averaged parameters calculated across all models indicate that party size is positively correlated with the arrival of an individual in the target's food patch (Table 4-6a, Figure 4-7). The 95% confidence intervals for all other parameters zero.

I found similar results when I re-ran the analysis on the reduced dataset where the target was the first to arrive in the food patch. In this analysis, five models fell into the 95% confidence set (Table 4-5b). As before, the best model was the patch quality model consisting of *PART* and *PARTY*. However, this model had over half the model weight as before (w_i=0.3), suggesting greater uncertainty in model selection. The second best model in this model set included *PARTY* alone. Again, the only parameter whose 95% confidence interval did not encompass zero is *PARTY* (Table 4-6b).

KCCMR

In the silent condition, the number of subjects that investigated, entered, and fed first in the left room vs. the right room did not differ from chance (Investigate: Left:Right=5:7, χ^2= 0.33, df=1, p-value=0.56; Enter: L:R=6:6, χ^2=0, df=1, p-value=1.00; Feed: L:R=6:6, χ^2=0, df=1, p-value=1.00). Also in the silent condition, the number of subjects that investigated, entered, and fed first in a given room was not correlated with the side on which I first attached the food patch (Investigate: χ^2= 0.33, df=1, p-value=0.56; Enter: χ^2=0, df=1, p-value=1.00; Feed: χ^2=0, df=1, p-value=1.00)

Significantly more subjects than expected by chance investigated the stimulus room first in the rough-grunt condition (Stimulus:Non-Stimulus=10:2, χ^2= 5.33, df=1, p-value=0.02) but not the control call condition (S:NS=7:5, χ^2= 0.33, df=1, p-value=0.56). However, in both the rough-grunt and control call conditions the number of subjects

entering the stimulus room first did not differ from chance (Rough-grunt: S:NS=8:4, χ^2= 1.33, df=1, p-value=0.25; Control Call: S:NS=8:4, χ^2= 1.33, df=1, p-value=0.25). Similarly, in the both the rough-grunt and control call conditions, the number of subjects that fed first in the stimulus room did not differ from chance (Rough-grunt: S:NS=6:6, χ^2= 0, df=1, p-value=1.00; Control Call: S:NS=8:4, χ^2= 1.33, df=1, p-value=0.25). I found that subject response did not significantly differ between the rough-grunt and control call condition for any of the behavioral measures (Investigate: χ^2= 1.78, df=1, p-value=0.18; Enter: χ^2= 0.75, df=1, p-value=0.39; Feed: χ^2= 0.07, df=1, p-value=0.79).

4.5 DISCUSSION

The purpose of this study was to gain insight into the function of chimpanzee food-associated calling behavior by weighing evidence for the causes and consequences of call production. When comparing social and ecological models of rough-grunt calling behavior, I found most support for the Social Facilitation Hypothesis which predicts that rough-grunt production is best explained by the social context during arrival at a food patch. I found that rough-grunt production by a focal target was best predicted by the presence of a higher-ranking individual in his party. This finding is consistent with several recent studies of chimpanzee food-associated calling behavior indicating that social context is an important predictor of rough-grunt production (Brosnan & de Waal, 2002; Fedurek & Slocombe, 2013; Slocombe et al., 2010) and particularly with a recent playback study conducted with wild chimpanzees (Schel et al., 2013). In this study, a focal subject feeding in a food patch alone was more likely to produce rough-grunts in response to the playback of another individual's pant-hoot if that individual was substantially higher ranking than the subject or if there was a strong affiliative relationship between them. I did not find that rough-grunt production was correlated with the dominance status of the signaler, indicating that this result is not due to lower ranking individuals calling more than higher ranking individuals. These results suggest that chimpanzees produce rough-grunts in order to communicate with high ranking individuals during foraging contexts.

The Functionally Referential Hypothesis predicted that rough-grunts would be best predicted by the quality of the food patch. While models representing this hypothesis were not well supported, there was evidence that call production was less likely when arriving at patches of fruit and more likely when arriving at patches of flowers. This is contradictory to expectations since chimpanzees are considered ripe fruit specialists and food-associated calls have previously been reported to be associated with arrival at high quality food patches (Hauser et al., 1993). However, while some studies have found a negative correlation between fruit and flower consumption (Lima et al., 1999) suggesting that flowers are a fallback food, flowering trees are reported to be important food sources for other primates such as vervets (*Chlorocebus pygerythrus*) and are capable of supporting large foraging parties (Whitten, 1998). Each of my field seasons spanned time periods with substantial crops of flowers of the species *Pterocarpus tinctorius*. While both young leaves and flowers contain fewer calories compared to fruit, they contain higher amounts of protein (Nakagawa, 2009), which may be a limiting nutrient for primates and other herbivores (Felton, Felton, Lindenmayer, & Foley, 2009; Mattson, 1980). Thus flowers may have been an important food source during the time period of my study.

I found that rough-grunt production positively correlates with the likelihood that at least one other individual arrived in the food patch after the target and also with the total number of individuals arriving. These findings are consistent with the Functionally Referential Hypothesis and are similar to results from other field studies of food-associated calling behavior in other primates (Chapman & Lefebvre, 1990). However, when comparing models for the likelihood of arrival, I found that party size was the most important predictor of arrivals in a food patch. Even more, models including party size and food part performed better than models including food-associated calls. These results strongly support the Social Facilitation Hypothesis since they indicate that rough-grunt production is correlated with arrivals in the food patch but factors others than food-associated call production promote arrival. In fact, I found that rough-grunts, and particularly pant-hoots, were produced more often when arriving at occupied, rather than empty, food patches. These results are inconsistent with previous studies reporting a

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negative correlation between food-associated call production and the number of individuals in the food patch in other species (Chapman & Lefebvre, 1990; Elgar, 1986a) but consistent with the idea that some food-associated calls function by mediating social interactions in foraging contexts (Brosnan & de Waal, 2002; Evans & Marler, 1994).

It is possible that the association between arrivals and food part is due to the food-associated calling behavior of others already in the food patch. As mentioned previously, focal targets in this study were more likely to produce rough-grunts in patches of flowers compared to other food parts. In the analysis of arrival behavior, I also found that patches of flowers and leaves were positively associated with arrivals. Thus, the fact that food properties were a better predictor of arrivals than the food-associated calling behavior of the target could be attributed to the food-associated calling behavior of other party members. However, while the relative weight of the top model was reduced by over half when examining only empty food patches, the relative weight of models including food-associated call parameters remained low. This finding indicates that food-associated calls do not have a strong effect on the arrival of others even when the target arrives at an empty food patch.

It was surprising that I did not find a strong correlation between food patch size and the likelihood of arrivals since larger food patches are typically associated with larger foraging parties (White & Wrangham, 1988) (though see (Chapman et al., 1995). Large food patches are capable of containing more food and can also provide a greater number of foraging sites (e.g. large branches). Thus, they are capable of holding more individuals while also reducing the level of feeding competition between co-feeders. The lack of a correlation between patch size and the occurrence of arrivals could be attributed to the fact that I had to limit my response to a binary measure rather than model the total number of arrivals. While large food patches may be more capable of hosting large foraging parties compared to small patches, they may be no more capable of hosting two individuals.

Findings indicating that rough-grunts are produced more in the presence of higher ranking individuals and that factors other than food-associated calls promote arrival in food patches support the Social Facilitation Hypothesis. It is possible that chimpanzees

produce food-associated calls in order to claim their food or repel others, similar to the proposed function of food-associated calling in capuchin monkeys (*Cebus capuchinus*). This interpretation is supported by a previous study suggesting that food-arrival pant-hoots of chimpanzees advertise the dominance status of the signaler (Clark & Wrangham, 1994). However, results from my playback experiment suggest that chimpanzee rough-grunts are not repulsive vocalizations. Subjects had the chance to approach a presumably empty food patch or one where an individual was producing rough-grunts. If rough-grunts are an aggressive signal, or are generally repulsive, I would expect subjects to immediately choose the silent food patch. While it is difficult to determine why individuals approached the stimulus, this behavior suggests that these calls do attract the receiver's attention and that subjects felt comfortable enough to reduce proximity. Looking behavior is a common response measured in primate playback studies that is used to assess the significance of the stimulus (Fischer et al., 2001). Even if the primary function of rough-grunts is to attract the visual attention of the listener, this could be enough to provide them with information regarding the signaler's behavior and/or the presence and properties of the food patch. However, while rough-grunts did appear to attract the subject's attention more than chance, they did not necessarily attract more attention than other species-specific vocalizations. This could be due to the small sample size and/or because pant-hoots were used as one of the control calls in the experiment. Both my field study and previous food placement experiments (Hauser et al., 1993) indicate that the production of rough-grunts and pant-hoots may occur within the same contexts. Thus, these two call types could provide similar information to receivers. Interpretation of subject behavior could be improved by extending this experiment in the future by testing more subjects and including control stimuli representing known repulsive and attractive stimuli.

The main goal of this experiment was to examine the effect rough-grunts have on receiver behavior after controlling for knowledge about the presence of food. In my study, subjects were no more or less likely to enter or feed first in the room from which rough-grunts were broadcast. This may be because the effect of the treatment was eliminated once subjects looked in the room and saw that there was no signaler or saw

that the food in this room was no different than the food presented at the beginning of the experiment. The absence of a strong behavioral response with knowledge of food could indicate that these two pieces of information are redundant. A study of food-associated calling behavior in chickens (*Gallus gallus*) showed that subjects were less likely to search the substrate for food when presented with food-associated calls after they had recently been fed (Evans & Evans, 2007). Extending this experiment by manipulating subject knowledge regarding the presence of food could be one way to determine whether this factor strongly influences receiver response. However, if social context is the main determinant of arrival in food patches in wild chimpanzees, producing vocalizations that inform others of food would be unnecessary. Rather, the production of appeasing vocalizations that facilitate patch sharing in a potentially volatile social situation could be highly useful. Overall, better comprehending the information conveyed by these vocalizations can promote a greater understanding of their function, a topic I discuss in Chapter 4.

4.7 TABLES

Table 4-1. Definition of Model Parameters- Likelihood of Rough-grunt Production
Definition of the parameters included in models of rough-grunt production by target individuals.

Parameter	Description
SIZE	A factor representing the size category of the food patch. Factor levels include <5 meters and >5 meters
PART	A factor representing the food part being eaten in the patch. Factor levels include leaves, flowers, and fruit.
RANK	A factor representing the presence of a higher ranking individual in the target's party prior to arrival at the food patch. Factor levels include the presence or absence of a higher ranking individual.
GROOM	A factor representing the presence of a higher ranking individual in the target's party prior to arrival at the food patch. Factor levels include the presence or absence of a higher ranking individual.
PARTY	A numeric variable representing the total number of individuals present in the target's party prior to arrival at the food patch

Table 4-2. Definition of Model Parameters- Likelihood of Arrival Definition of the parameters included in models of arrival behavior in the target's food patch.

Parameter	Description
Size	A factor representing the size category of the food patch. Factor levels include <5 meters and >5 meters
Part	A factor representing the food part being eaten in the patch. Factor levels include leaves/flowers, and fruit.
RG	A factor representing whether the focal target produced any rough-grunts during the feeding bout. Factor levels include rough-grunt and no rough-grunt
PH	A factor representing whether the focal target produced any pant-hoots during the feeding bout. Factor levels include pant-hoot and no pant-hoot
Party	A numeric variable representing the total number of individuals present in the target's party prior to arrival at the food patch

Table 4-3. Model Selection Table: Likelihood of Rough-grunt Production Model
selection table for the likelihood of rough-grunt production by a focal target (n=108
feeding bouts). Parameter estimates are provided for numeric parameters present in a
given model, including the intercept (B). +'s indicate whether a given factor variable was
present in the given model. K represents the number of parameters in each model
(including intercept). Δ_i represents the difference in the Akaike information criterion
(AICc) between the ith and best model. w_i represents the probability that a given model is
the best model among the candidate set.

Model	B	PART	SIZE	PARTY	RANK	GROOM	K	Δ_i	wi
RANK	-0.72				+		2	0.0	0.81
FULL	-0.70	+	+	0.04	+	+	6	4.6	0.08
PARTY	-0.71			0.19			2	5.1	0.06
GROOM	-0.53					+	2	6.3	0.03
PART	0.00	+					2	10	0.01
NULL	-0.23						1	10	0.00
SIZE	-0.43		+				2	12	0.00
SIZE + PART	-0.15	+	+				3	12	0.00

Table 4-4. Model Averaged Parameters: Likelihood of Rough-grunt Production
Model averaged parameter estimates for the likelihood of rough-grunt production by
target individuals obtained by averaging across all models (n=104 feeding bouts).

Parameter	Reference Level	Factor Level	Parameter Estimate	2.5%	97.5%
SIZE	<5m	>5m	0.15	-0.79	1.1
PART	*gran mean	leaves	-0.03	-0.87	0.83
		flowers	0.67	-0.17	1.5
		fruit	-0.63	-1.3	0.0006
PARTY	NA	NA	0.11	-0.11	0.33
RANK	NA	NA	2.0	0.77	3.3
GROOM	NA	NA	0.80	-0.65	2.3

Table 4-5. Model Selection Table: Likelihood of Arrival Model selection table for the likelihood of another's arrival in the food patch after the target's own arrival. Table 4-5a displays results from the analysis of all feeding bouts (n=99) while table 4-5b displays results from the analysis of only empty food patches (n=87). Parameter estimates are provided for numeric parameters present in a given model. +'s indicate whether a given factor variable was present in the given model, including the intercept (B). K represents the number of parameters in each model (including intercept). Δ_i represents the difference in the Akaike information criterion (AICc) between the ith and best model. w_i represents the probability that a given model is the best model among the candidate set.

a) All Food Patches

Model	B	PARTY	SIZE	PART	RG	PH	K	Δ_i	w_i
PARTY + PART	-1.6	0.36		+			3	0	0.68
PARTY + PH	-2.4	0.30				+	3	3.2	0.13
PARTY	-2.3	0.35					2	4.5	0.07
PARTY + RG	-2.6	0.32			+		3	4.8	0.06
PARTY + SIZE	-2.6	0.35	+				3	5.1	0.05
PH	-1.5					+	2	12.7	0.00
PART	-0.4			+			2	14.4	0.00
RG	-1.7				+		2	15.7	0.00
NULL	-1.1						1	19.9	0.00
SIZE	-1.5		+				2	19.9	0.00

b) Empty Food Patches Only

Model	β	PARTY	SIZE	PART	RG	PH	K	Δ_i	w_i
PARTY + PART	-1.9	0.33		+			3	0	0.30
PARTY	-2.5	0.32					2	0.3	0.26
PARTY + SIZE	-2.9	0.32	+				3	0.9	0.19
PARTY + RG	-2.6	0.29			+		3	1.8	0.12
PARTY + PH	-2.5	0.28				+	3	1.9	0.12
PH	-1.7					+	2	9.3	0.00
RG	-1.9				+		2	9.5	0.00
PART	-0.9			+			2	11	0.00
NULL	-1.4						1	12	0.00
SIZE	-1.8		+				2	12	0.00

Table 4-6. Model Averaged Parameters: Likelihood of Arrival Model averaged parameter estimates obtained by averaging across all models included in the model selection analysis for the arrival of others in the food patch after the target. Table 4-6a displays results from the analysis of all feeding bouts (n=99) while table 4-6b displays results from the analysis of only empty food patches.

a) All Food Patches

Parameter	Reference Level	Factor Level	Parameter Estimate	2.5%	97.5%
SIZE	<5m	>5m	0.66	-0.44	2.0
PART	leaves/flowers	fruit	-1.4	-2.2	0.24
RG	No Rough-grunt	Rough-grunt	0.74	-0.72	1.8
PH	No Pant-hoot	Pant-hoot	1.2	-0.93	2.3
PARTY	NA	NA	0.35	0.11	0.52

b) Empty Food Patches Only

Parameter	Reference Level	Factor Level	Parameter Estimate	2.5%	97.5%
SIZE	<5m	>5m	0.77	-0.44	2.0
PART	leaves/flowers	fruit	-0.97	-2.2	0.24
RG	No Rough-grunt	Rough-grunt	0.53	-0.72	1.8
PH	No Pant-hoot	Pant-hoot	0.68	-0.93	2.3
PARTY	NA	NA	0.31	0.11	0.52

4.8 FIGURES

Figure 4-1. Experimental Set-up for Captive Playback Experiment Experimental set-up used in the captive playback experiment. This diagram specifically represents the experimental set-up as it existed when the subject first entered the experimental area from the outdoor enclosure. At this point all doors were closed, containing the subject in the Subject Holding Room. Each food patch consisting of 60 grapes was in clear view of the subject. Prior to playback each food patch was attached to the wire mesh on the front was of each Food Presentation Room by each speaker. Following silent trials or the playback of a given stimulus from one of the speakers the pull bar was used to simultaneously give the subject access to both food presentation rooms. At this point the subject was free to move between all three rooms in the experimental area and feed on the food. Once all food had been consumed the door leading to the outdoor enclosure was opened, enabling the subject to leave the experimental area.
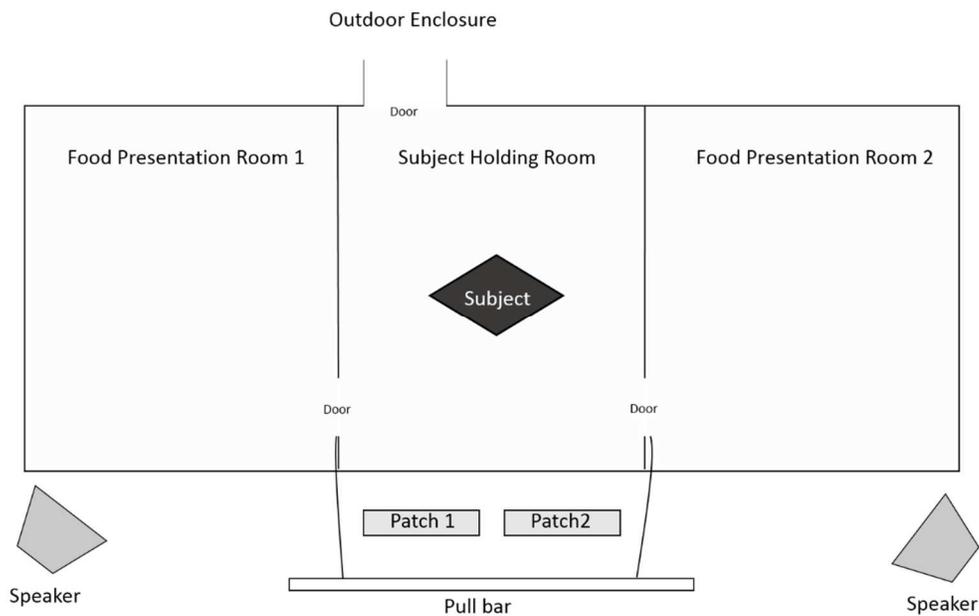
Figure 4-2. Number of Arrivals Observed in Each Feeding Bout Frequency of the
number of individuals arriving in the patch after the target in all feeding bouts where the
relative arrivals times of all individuals in the patch were known (n=156)
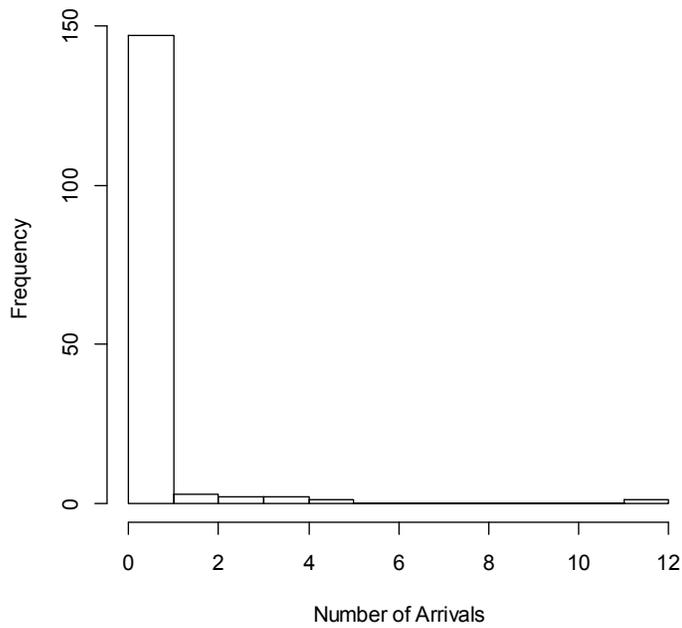
Figure 4-3. Likelihood of Rough-grunt Production by Social Context Bar plot representing the proportion of feeding bouts in which focal targets produced rough-grunts according to whether or not a higher ranking individual was present in the target's party (n=104 feeding bouts). The numbers in the middle of each bar represent the total number of observations per social context. Results of model selection analysis identify the presence of a higher ranking individual to be the most important predictor variable of rough-grunt production. Focal targets were more likely to produce rough-grunts when a higher ranking individual was present in his party.
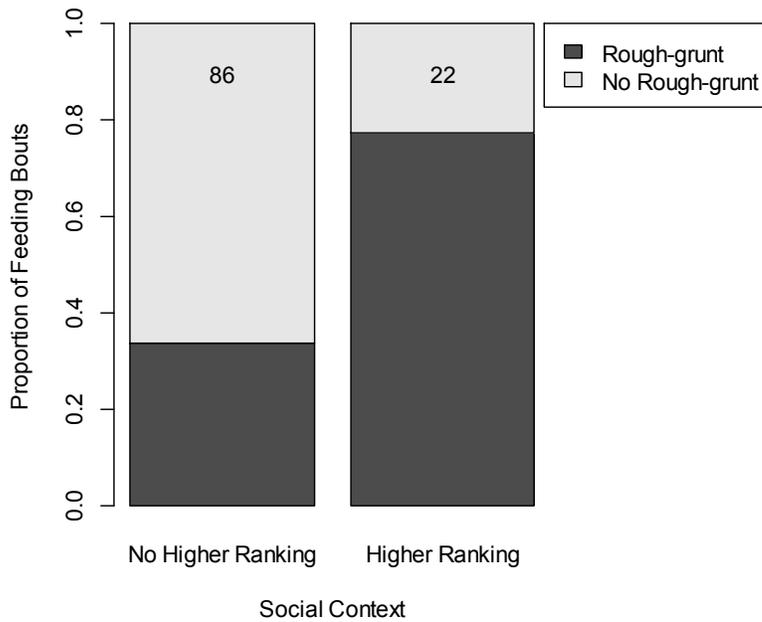
Figure 4-4 Rough-grunt Production by Target Rank The proportion of feeding bouts in which target individuals produced rough-grunts. The x-axis displays the 2-letter code for each focal target. From left to right, targets are listed in order of decreasing rank. Numbers represent the total number of feeding bouts included in the analysis for each focal target. Only feeding bouts in which the entire bout was observed, the nature of the food patch was clear, and the target's vocal production was known are included (n=179). The small number of observations for ZS is due to the relatively few number of observations for this individual, the high level of difficulty following him (and thus of observing the full duration of the feeding bout), and a relatively high number of feeding bouts in undifferentiated food patches. There was not a significant correlation between target rank and the likelihood of rough-grunt production (Spearman rank correlation, p=0.76)

Figure 4-5. Number of Arrivals by Target Rough-grunt Production The number of individuals arriving in a food patch after the target according to whether he did or did not produce rough-grunts during the feeding bout. Analysis is restricted to those feeding bouts where the arrival times of all individuals relative to the target are known (n=156). Boxes represent 1st-3rd quartiles. Points represent individual feeding bouts with slight jitter around the x and y axis to promote visibility. Rough-grunt production by target individuals is correlated with the arrival of significantly more individuals in the food patch (Mann-Whitney U, p<0.001).

Figure 4-6. Co-occurrence of Rough-grunt and Pant-hoot Production Vocal production by target individuals according to whether they did or did not produce rough-grunts or pant-hoot(s) at any point during a given feeding bout (n=157). Rough-grunt and pant-hoot production were not independent of one another (Chi-square test, p<0.001).
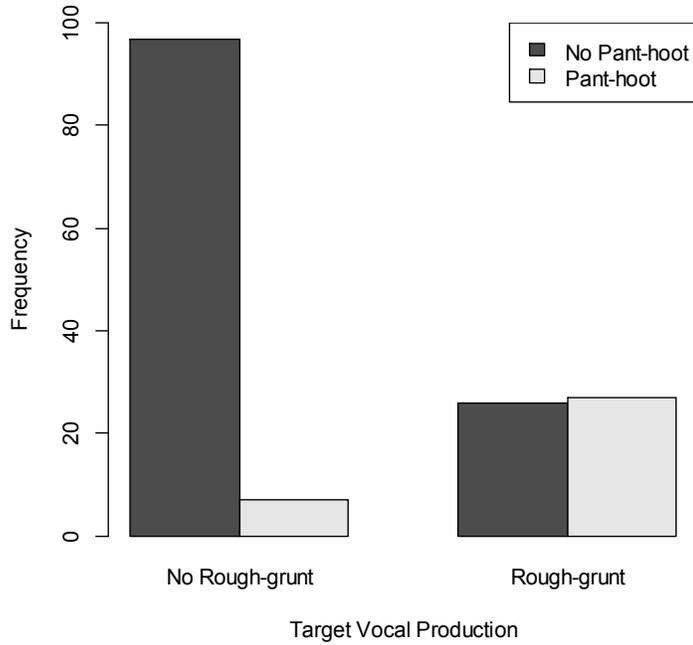
Figure 4-7. Arrival Behavior According to Social and Ecological Variables Arrival behavior plotted against each predictor variable included in the model selection analysis for observations in which the target arrived at either an occupied or empty food patch (n=99). Figure 4a displays whether another individual arrived in the food patch after the target in a given feeding bout (Arrival(s)=1, No Arrival(s)= 0) according to the size of the target's party in the 15 minutes prior to arrival at the food patch. Regression line represents a simple binomial smoothing function. Figures 4b-f display the proportion of feeding bouts in which another individual arrived after the target according to the parameter of interest (b,c: food part, d: target rough-grunt production, e: target pant-hoot production, f: food patch size). Dark gray sections represent the number of feeding bouts with arrival(s) and light gray sections represent the number of feeding bouts with no arrival(s). The numbers inside each bar represent the total number of observations for that factor level. For Figures 4b,d,e,f the factor level presented on the left represents the reference category for factor coding. Figures 4b,c display arrival data according to 4b) the combined food part categories used in the analysis as well as 4c) separated into more distinct categories. Data was reduced to 81 observations for figure 4c due to uncertainty in some feeding bouts regarding whether the target was feeding on ripe or unripe fruit.

Figure 4-7 continued.

**a) Party Size**
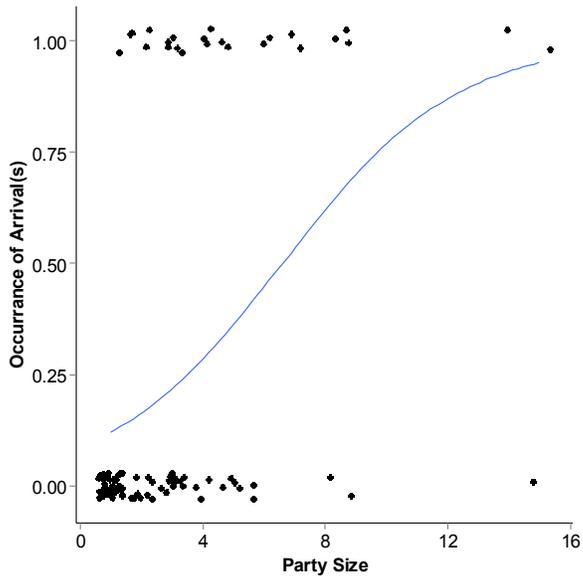
b) Food Part
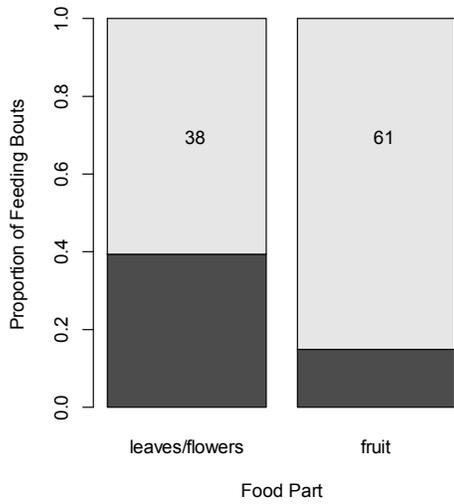
c) Food Part (break down)
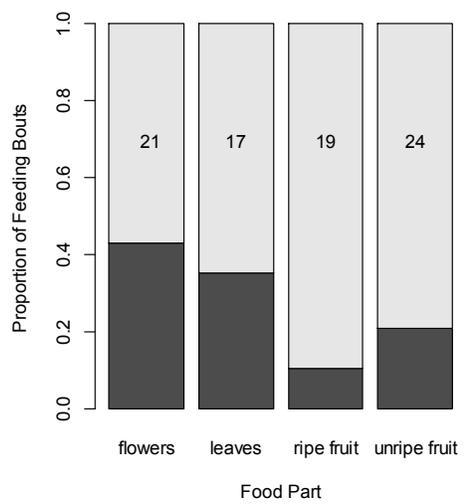
Figure 4-7 continued.

d) Rough-grunt
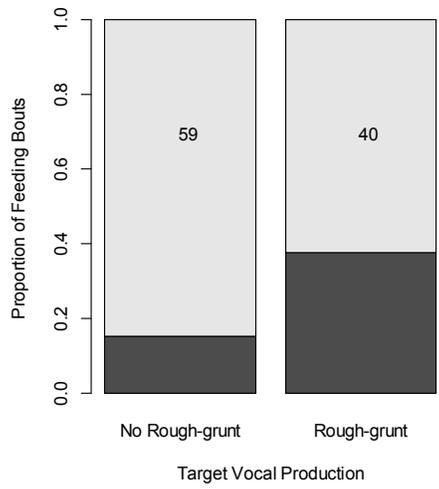
e) Pant-hoot
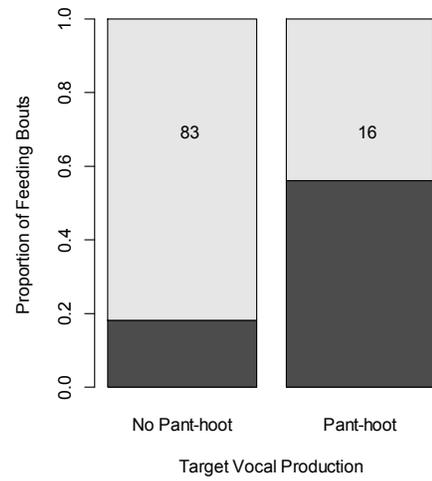
f. Food Patch Size
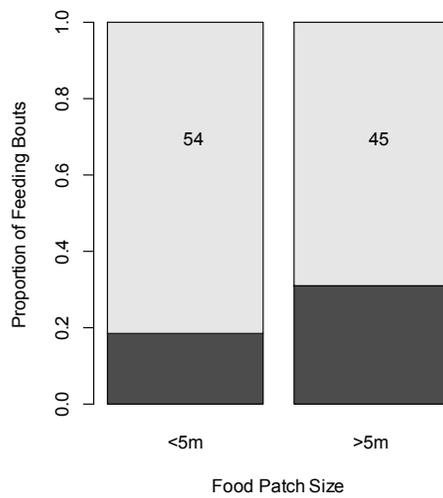
CHAPTER 5

PRELIMINARY ACOUSTIC ANALYSIS: ROUGH-GRUNTS DISPLAY HIGH LEVELS OF ACOUSTIC VARIATION WITHIN FEEDING BOUTS

5.1 INTRODUCTION

The landmark discovery that predator-specific alarm calls alone elicit the appropriate escape strategies in vervet monkeys (*Chlorocebus pygerythrus*) was a turning point in animal communication research (Seyfarth et al., 1980). Prior to this study, it was widely believed that animal signals were only capable of reflecting the signaler's motivational or physiological state and not information about the external environment. Due to their ability to function in an apparently word-like manner, these "functionally referential signals" have attracted much attention from researchers interested in the evolutionary origins of human language. Since then, much research effort has been spent looking for other such signals in the vocal repertoires of a variety of species (Evans & Evans, 2007; Marler et al., 1992). Naturally, substantial research effort has focused on our closest-living relatives due to their potential to provide insight into the communicative abilities of a shared common ancestor (Fedurek & Slocombe, 2011; Zuberbühler, 2003).

One class of signals that has attracted considerable interest is the acoustically graded food-associated "rough-grunt" of chimpanzees (*Pan troglodytes*). Captive studies have reported that individuals are more likely to produce rough-grunts upon discovery of large quantities of food (Hauser & Wrangham, 1987), and that individuals produce more grunts in response to larger and more divisible food sources (Brosnan & de Waal, 2002; Hauser et al., 1993). More recently, another captive study has reported that the acoustic and temporal properties of these calls can vary according to the preference level, and even identity, of the food, with higher preference foods eliciting longer calls with higher peak and fundamental frequencies (Slocombe & Zuberbühler, 2006). These findings suggest the existence of functionally referential communication in our evolutionary cousins, and have prompted speculations regarding the importance of reciprocal

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information-sharing within chimpanzee society (Brosnan and de Waal 2003; Slocombe et al., 2010).

Nevertheless, studies of rough-grunt calling behavior in wild chimpanzees have produced mixed evidence that these vocalizations function in a referential manner in natural socioecological contexts. Consistent with findings from captive studies, in some studies, wild chimpanzees have been found to be more likely to produce rough-grunts upon arrival at large food sources, presumably because these patches contain more food (Slocombe et al., 2010). Furthermore, they are more likely to produce these vocalizations upon arriving in patches of ripe fruit and young leaves, compared to low-quality terrestrial herbaceous vegetation, and before feeding for long periods of time (Fedurek & Slocombe, 2013). However, the same researchers who found acoustic differences between foods in captivity were not able to find such differences between calls produced to the three food species consumed most often by wild chimpanzees living in Budongo Forest Reserve in Uganda (Slocombe & Zuberbühler, 2006). Moreover, a recent field study conducted at Taï National Park, Cote d'Ivoire found that call duration did not vary according to tree size, food species or fruit count, and only one food species was associated with a difference in call pitch (Kalan et al., 2015). This one species displayed a greater range in call pitch- a combined measure reflecting multiple frequency measurements, than the others, with pitch appearing to vary according to the size of the tree. However, while a captive study found that higher frequency calls are produced to more preferred foods (Slocombe & Zuberbühler, 2006), this study found that call pitch was actually lower in larger food patches (Kalan et al., 2015). Nevertheless, these authors suggest that this acoustic variability may still be capable of providing meaningful information to receivers.

In Chapter 4 I show that rough-grunt production is best predicted by social context rather than properties of discovered food suggesting that rough-grunts may not be a reliable source of information about this food. In this study, I built upon these findings by conducting a preliminary acoustic analysis of rough-grunts produced by wild chimpanzees foraging on natural foods at Gombe. In order to function referentially, signals must display consistent acoustic variation to a given stimulus (Marler et al.,

1992). Since many rough-grunts may be produced during a given feeding bout (Brosnan & de Waal, 2002; Fedurek & Slocombe, 2013), I focus this initial examination on the level of acoustic variation present within feeding bouts rather than between them.

5.2 ANALYSIS

I conducted an observational study of wild chimpanzees at Gombe where I studied the behavior of ten focal males. I acoustically recorded all vocalizations produced by these focal targets during feeding bouts, when possible, as well as the vocalizations of other individuals within the target's food patch. For description of this research site and specific methods see the Chapter One.

I processed all acoustic data using the acoustic analysis program Praat version 5.3.63 using the following settings: window length: 0.005 seconds; dynamic range: 70 dB. I identified and extracted all rough-grunts which I could reliably attribute to a given signaler and which did not overlap with other acoustic signals or environmental noise. Since the focus of my recording efforts was on call production by my ten focal males, calls produced by these individuals make up the majority of this dataset. However, other community members are also represented since I took *ad libitum* recordings of vocalizations produced by other chimpanzees feeding within the target's food patch. This preliminary analysis only focuses on calls produced by my ten focal males, regardless of whether they were the focal target at the time of the recording. If calls from multiple signalers were identified within a given feeding bout, only calls produced by one of the signalers were considered in this analysis, with priority given to the focal target.

In order to reduce low and high frequency noise in the recordings, I applied a band-pass filter to all extracted calls. This filter had a lower frequency of 50 Hz, an upper frequency of 3500 Hz and a smoothing frequency of 100 Hz. The two acoustic measures I examined in this preliminary acoustic analysis were call duration and peak frequency. Call duration is defined as the time in seconds from the beginning to the end of the main acoustic energy of the call. Peak frequency is defined as the frequency at which most acoustic energy is present across the duration of the call. I used a Spearman's rank correlation to examine the correlation between peak frequency and call duration.

All analyzed calls were matched to the feeding bout in which they were produced using data on the time of call production and the start and end times of the focal target's feeding bouts. For all feeding bouts for which at least two rough-grunts were extracted (n=30), I calculated the within-bout range in peak frequency and call duration. This was done by subtracting the minimum value for each of these measures within a given feeding bout from the maximum value within the same bout. Acoustic variation within feeding bouts was examined by producing boxplots for all feeding bouts with at least 10 calls (n=10). For feeding bouts consisting of at least 10 calls produced by the focal target (n=5), I calculated the time of call production relative to the target's arrival in the food patch. I visualized these data using scatterplots to examine temporal structure in acoustic properties over time.

5.3 RESULTS

From m recordings I extracted 446 identifiable rough-grunts produced by ten focal males. These rough-grunts were produced in 32 distinct feeding bouts. This represents approximately 60% of the total available dataset consisting of calls produced by all individuals. Peak frequency displayed a bimodal distribution with peaks at approximately 225 Hz and 725 Hz (Figures 5-1,2). Distinct bimodality was not observed in the distribution of call durations (Figure 5-3). There was not a significant correlation between peak frequency and call duration (Spearman correlation, $S = 1.4 \times 10^7$, p=0.13; Figure 5-4). The number of identifiable calls per feeding bout ranged from 1 to 74 with a median of 5 calls per bout. The median range (max-min) in frequency within a given feeding bout was 593.9 Hz (range: 10.6-1884.8 Hz) (Figure 5-5a). The median range in duration was 0.05 seconds (range: 0.01-0.25 seconds) (Figure 5-5b). There is no obvious temporal structure to variation in peak frequency or call duration across a given feeding bout (Figure 5-6a,b).

5.4 DISCUSSION

The purpose of this study was to obtain a preliminary look at the potential for rough-grunts to function referentially by informing listeners about properties of the discovered food. Referential signals must display high levels of production specificity in order for receivers to learn the association between the acoustic properties of the signal and the properties of the stimulus (Marler et al., 1992). I found that peak frequency had a bimodal distribution, with a relatively large number of calls at both low and high frequencies. While there was not a significant correlation between peak frequency and call duration, these two measures were positively correlated with one another. Upon first inspection, these results appear consistent with the idea that rough-grunts display high levels of acoustic variability that could provide meaningful information about different food types (Slocombe & Zuberbühler, 2006). However, I found that high levels of variation in both peak frequency and call duration existed within single feeding bouts. In fact, the level of variation observed within a single bout was just as much or greater than the level of acoustic variation observed between food types in captivity (Slocombe & Zuberbühler, 2006). This finding is inconsistent with the idea that food-associated calls inform receivers about specific properties of discovered food.

Since chimpanzees feeding in a food patch likely deplete it over time, it could be possible that changes in call acoustics reflect the changing quality of the food patch. If this were the case, peak frequency and call duration would be expected to decrease over time spent in the food patch. However, I did not find consistent variation in acoustic properties over time. In fact, calls with high frequencies or durations often occurred within seconds of calls with low frequencies or durations. This suggests that changing patch quality is not a driver of this acoustic variation. These results are similar to the finding that bonobos (*Pan paniscus*) produce a mixture of food-associated call types in foraging contexts (Clay & Zuberbühler, 2009). While this suggests low call-specificity, the authors suggest that chimpanzees produce different combinations of calls to foods from different food preference categories and that this information is meaningful to receivers (Clay & Zuberbühler, 2011). Indeed, a previous study has reported that rough-grunts of higher frequency are often produced within bouts with many calls while very low frequency calls are often produced in bouts with few calls (Fedurek & Slocombe,

2013). While, it is possible that receivers can extract meaningful information from rough-grunts at the level of the calling bout, this type of signaling substantially differs from the idea of functional reference first proposed for animal signals (Marler et al., 1992; Seyfarth et al., 1980) as well as from human language. Furthermore, such investigations of functional reference likely tell us more about the cognitive abilities of receivers than they do about the function of these vocalizations from the signaler's perspective.

Morton (1977) describes common acoustic properties displayed by the vocalizations of animals from a wide variety of species when experiencing different motivational states. This paper describes how call frequency and structure can shift with changing levels of appeasement, fear or hostility experienced by the signaler. High-pitched, tonal calls tend to be produced by nervous or appeasing animals while low, harsh sounds tend to be produced by those feeling more aggressive. Interestingly, the "chevron" shape displayed by calls that fall within the center of these conflicting motivations is one commonly taken by rough-grunts. The observed changes in rough-grunt frequency over the course of a feeding bout are consistent with the idea that these calls reflect the fluctuating motivational state of signalers during feeding events. Since these calls are associated with feeding bouts in which many individuals are feeding within a single food patch (Chapter 3), they could be valuable sources of information regarding the likely next behavior of the signaler. This information could be more valuable to a nearby forager than potentially unreliable or redundant information regarding the properties of food within the food patch. Thus, I argue that in order to better understand the function of food-associated vocalizations, as well as other non-human vocal signals, it would be useful to focus less effort searching for language-parallels and instead return to more basic principles of animal behavioral ecology (Owren & Rendall, 2001).

5.5 FIGURES

Figure 5-1. Histogram of Peak Frequency Distribution of peak frequencies for all extracted vocalizations (n= 446). Bin width is equal to 50 Hz.
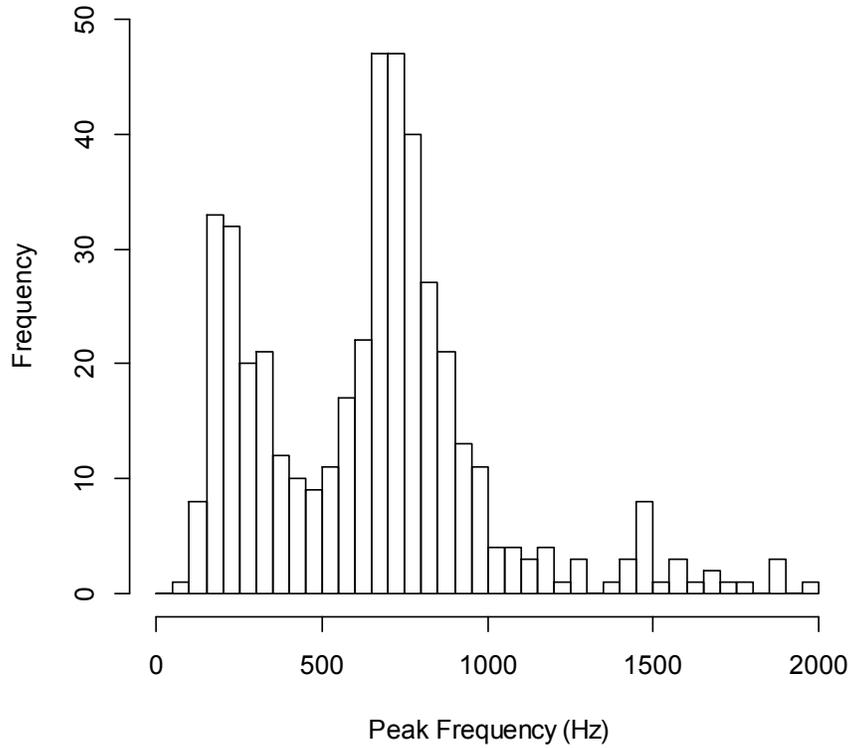
Figure 5-2. Visualization of Rough-grunt Frequency Variation Spectrograms of two rough-grunts representing acoustic variants with relatively low and high peak frequencies. Figure 5-2a displays a rough-grunt with a peak frequency of 133 Hz and a duration of 0.15 seconds. Figure 5-2b displays a rough-grunt with a peak frequency of 712 Hz and a duration of 0.13 seconds.
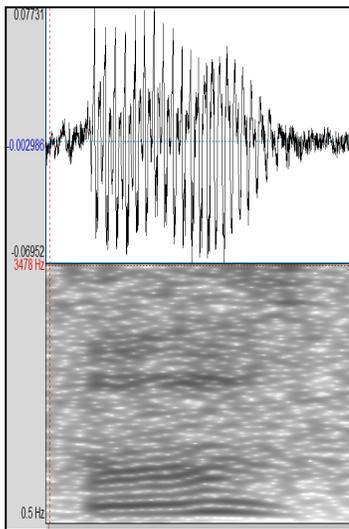
**a.**   **b.**
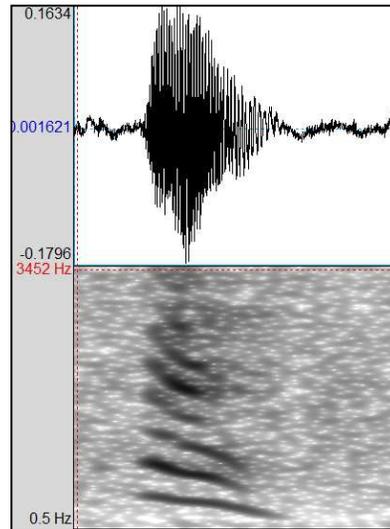
Figure 5-3. Histogram of Call Duration Distribution of call durations for all extracted vocalizations (n= 446). Bin width is equal to 0.01 seconds.
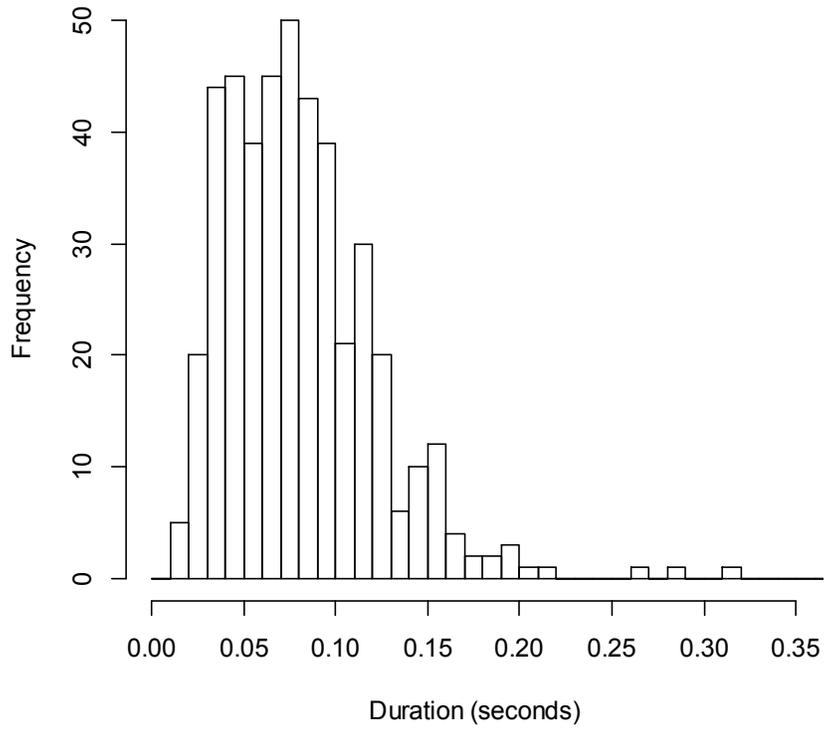
Figure 5-4. Correlation Between Peak Frequency and Call Duration Scatterplot of Peak frequency against call duration. There is not a significant correlation between these measures (Spearman correlation; p=0.13).
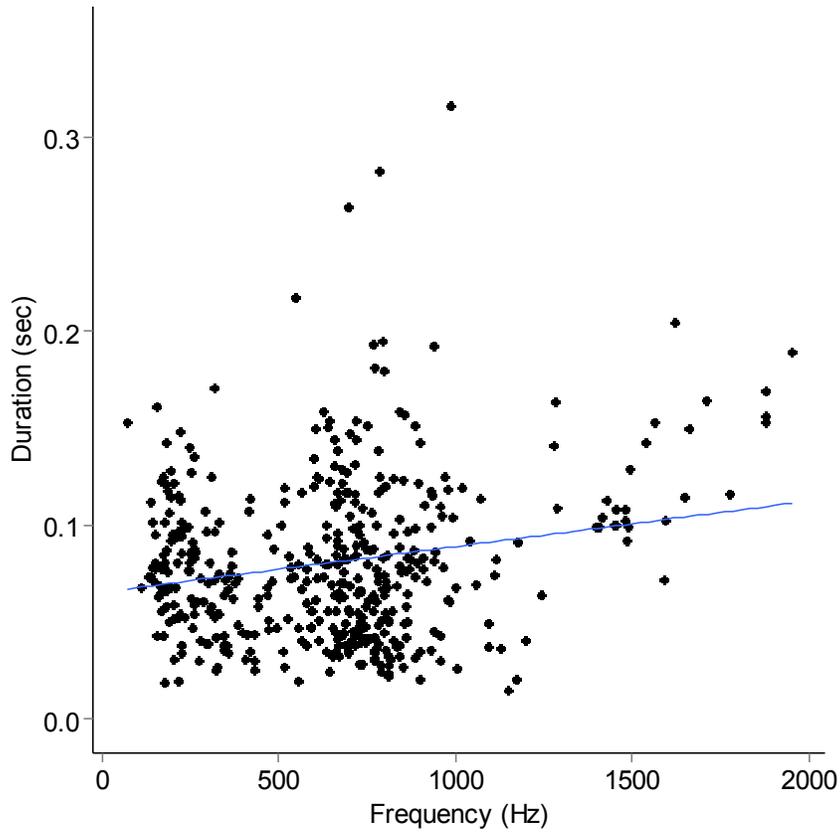
Figure 5-5. Peak Frequency Within and Across Feeding Bouts Boxplots displaying the a) peak frequency and b) duration of all calls produced during feeding bouts where at least 10 calls were produced (n=10 feeding bouts, 364 calls). Boxes represent 1st-3rd quartiles.

a) Peak Frequency
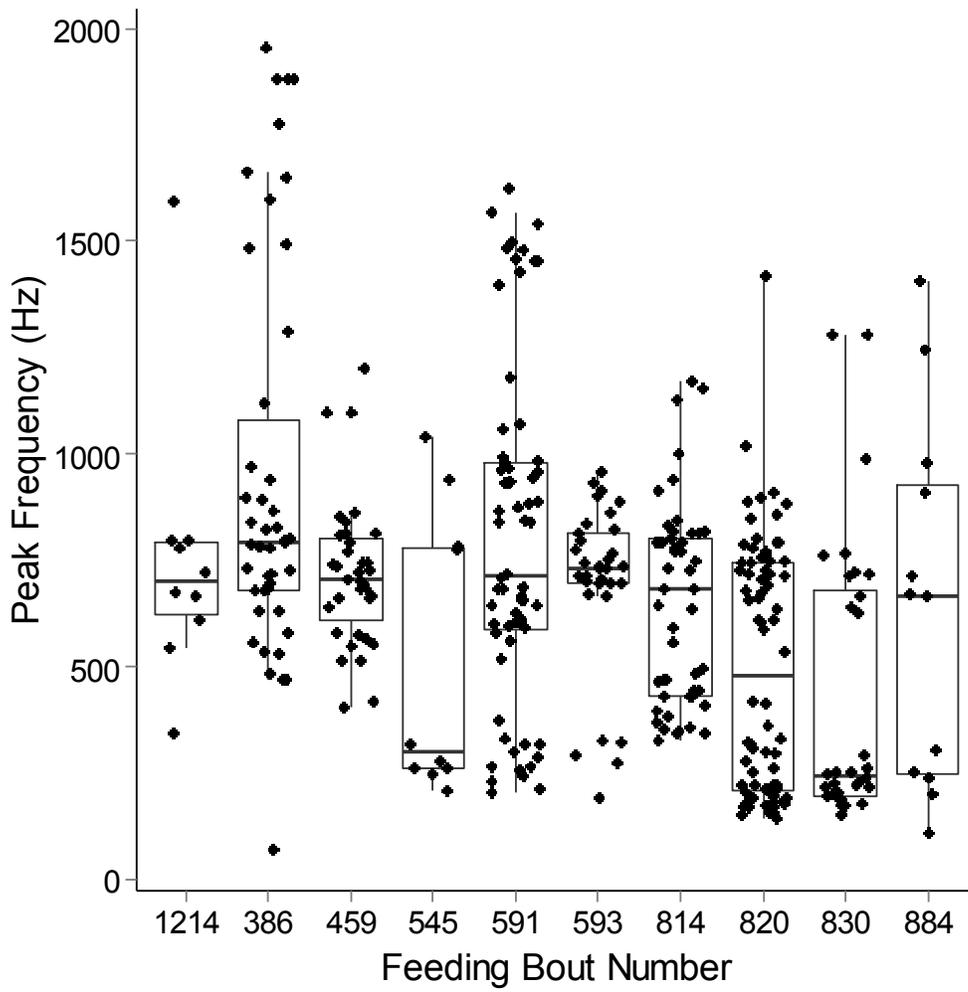
Figure 5-5 continued.

b) Call Duration
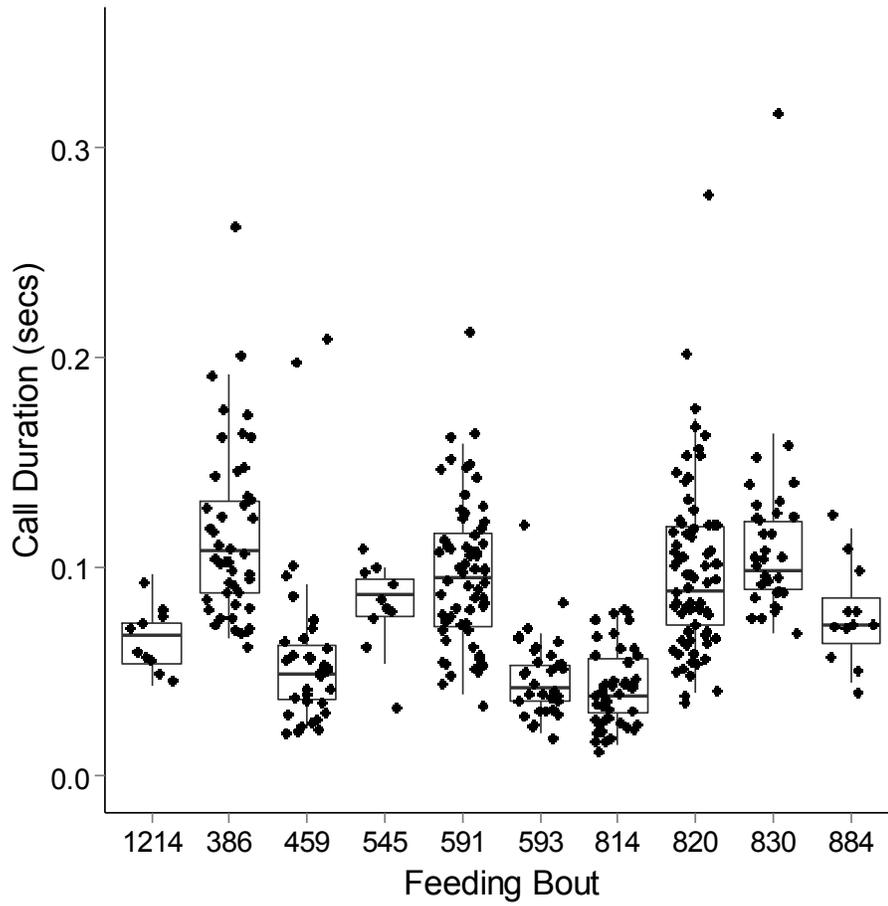
Figure 5-6. Temporal Structure of Call Acoustics a) Peak frequency and b) call duration of rough-grunts produced over time within feeding bouts. Each call produced within a given feeding bout has the same shape and can be matched to the corresponding feeding bout number in the legend. Only feeding bouts with calls produced by the focal target are included in order to relate each call to the total amount of time the signaler had spent in the food patch at the time of production.

a) Peak Frequency
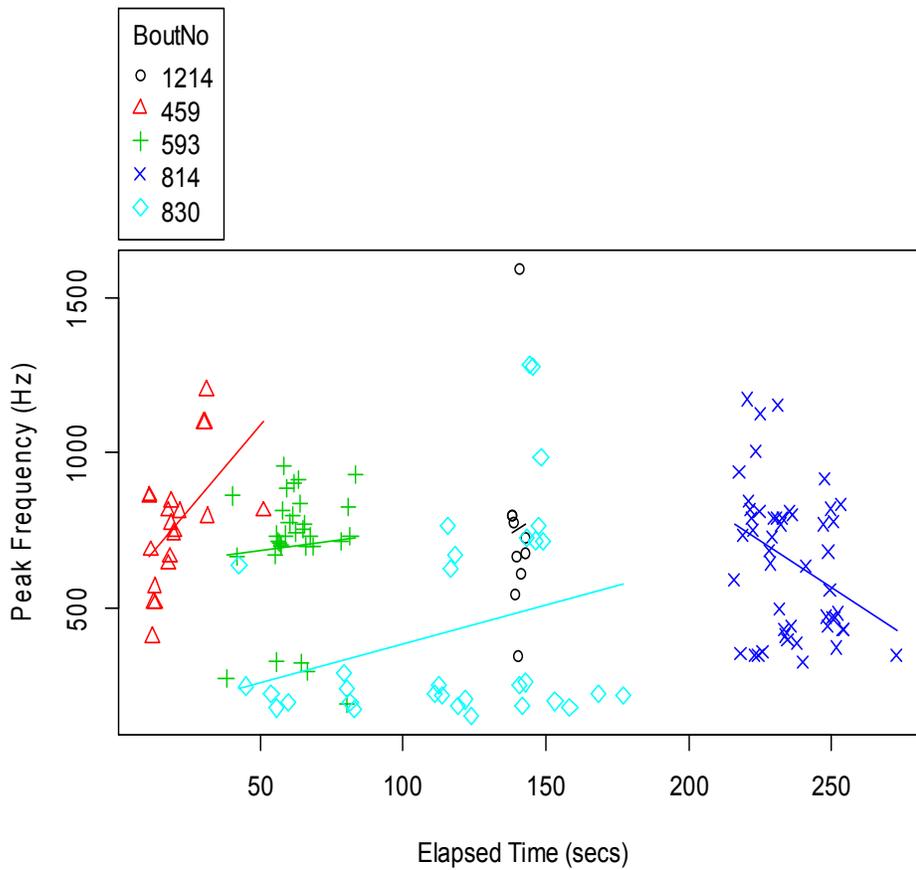
Figure 5-6 continued.

b) Call Duration
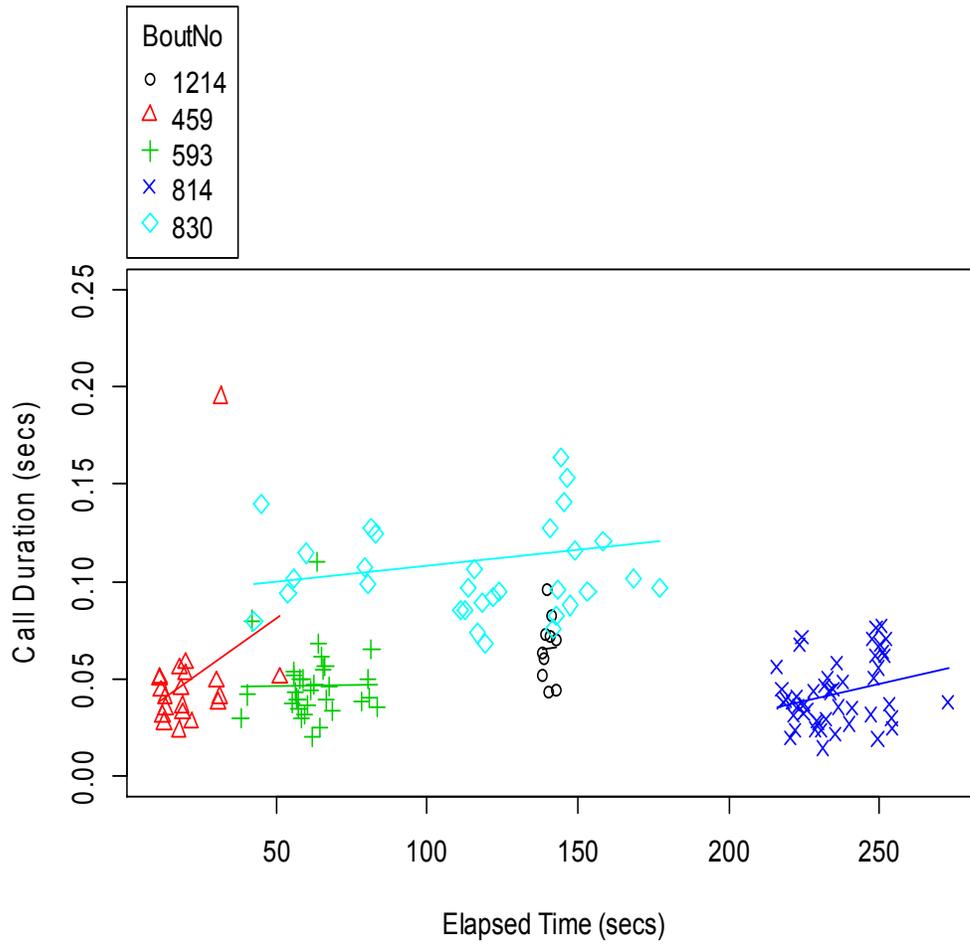
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