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Sex Differences in the Use of Whinny Vocalizations in Spider Monkeys (*Ateles geoffroyi*).

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Sex Differences in the Use of Whinny Vocalizations in Spider Monkeys (*Ateles geoffroyi*).

by

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Abstract

Spider monkey social groups are characterized by male philopatry and high fission-fusion dynamics. Individuals form subgroups that temporally vary in size, composition, and spatial cohesion. Both sexes produce whinny vocalizations, which may allow close associates to maintain contact in dispersed subgroups. Females however do not form close bonds, therefore the use of their call remains unresolved. We investigate sex differences in the use of whinny vocalizations by the Yucatan spider monkey (*Ateles geoffroyi yucatanensis*) at Runaway Creek Nature Reserve, central Belize. Females called at higher rates than males in most behavioral contexts, particularly while foraging. The likelihood of female calling increased during subgroup fissions and fusions, and was positively correlated with the number of animals joining or leaving a subgroup. Neither behavioral context, nor changes in subgroup composition affected the likelihood of calling by males. These different patterns indicate that the call may function differently for each sex.

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CHAPTER 1: INTRODUCTION

1.1 Overview

As primates show increased levels of sociality relative to many other mammals, mechanisms for the maintenance of social ties likely have important fitness consequences. Vocalizations may play a key role in this respect, especially for species that live in spatially dispersed, or less cohesive social groups, as calls travel quickly over long distances and are less affected by physical barriers than other signalling methods (Kondo and Wantanabe 2009). A wide range of social functions have been attributed to different classes of vocalizations in non-human primates, including agonistic alliance formation (rhesus monkeys, *Macaca mulatta*: Gouzoules *et al.* 1984), reconciliation (adult female baboons, *Papio cynocephalus*: Cheney *et al.* 1995), and the maintenance of mate exclusivity (titi monkeys, *Callicebus moloch*: Robinson 1981). Some vocalizations also function to regulate the inter-individual distance of conspecifics within social groups (Boinski and Campbell 1995; Arnedo *et al.* 2010; Gros-Louis 2004), which is of particular interest to this study.

As social and ecological fitness challenges differ between the sexes (Trivers 1972; Wrangham 1979; Wrangham 1980), so too do patterns of acoustic communication in many primate species. Sex differences in the use of species-specific vocalizations may manifest themselves as differences in the overall rate of calling between males and females (eg. Diana monkeys, *Cercopithecus diana*: Shultz *et al.* 2003; Zuberbuhler *et al.* 1997), or the disproportionate use of specific calls by either sex; calls that best serve the social and/or ecological requirements of one sex may be used disproportionately by that sex (eg., Kitchen *et al.* 2003; Cheney and Seyfarth 1998; Arnedo *et al.* 2010).

Recent work has suggested that primate species can be characterised by their relative level of fission-fusion dynamics; social systems with high levels of fission-fusion dynamics are characterised by long lasting social relationships maintained between individuals in the context of perpetually shifting association patterns (Ramos-Fernandez 2005; Aureli *et al.* 2008). The dynamic nature of these social systems may require special mechanisms for the maintenance of social relationships after periods of separation. The process of maintaining these social relationships may be facilitated between conspecifics by the use of contact calls (Kondo and Wantanabe 2009), which are hypothesized to allow animals to monitor and regulate the spatial proximity of group members (Caine and Stevens 1990; Ramos-Fernandez 2005). As the benefits of regulating spatial proximity may be different for males and females (Wrangham 1979; Wrangham 1980), the use of contact calls is also likely to vary between sexes, as individuals attempt to optimize their spatial position in relation to social group members.

Spider monkeys live in large dispersed communities of related males and unrelated females (Chapman 1990; Aureli *et al.* 2008; Di Fiore *et al.* 2011). Their social system is characterized by high fission-fusion dynamics in which individuals of a larger group move between subgroups that vary in size, composition, and spatial cohesion (Chapman 1990; Aureli *et al.* 2008; Di Fiore *et al.* 2011). Spider monkeys exhibit male philopatry and female dispersal at sexual maturity, resulting in ‘male-bonded’ societies with high degrees of association and affiliation among adult males relative to females (Symington 1990; Di Fiore *et al.* 2009). Spatially dispersed individuals use mid- to long-range calls, known as ‘whinny’ vocalizations (Ramos-Fernandez 2005). As whinnies are frequently exchanged between individuals outside of each other’s visual range, they are hypothesized to function as ‘contact’ calls that allow group members to monitor the whereabouts of preferred social partners (Ramos-Fernandez 2005). If this is the case, we would

expect males to use whinnies more often than females, as socially-bonded males should be more motivated to stay in contact with close associates. This pattern has been reported in male-bonded chimpanzees (*Pan troglodytes*), whose pant-hoot vocalization is used primarily by the males of a community, particularly when separated from their close associates (Pepper *et al.* 1999; Mitani and Nichida 1993).

This study will focus on sex differences in the use of whinny vocalizations in the black handed spider monkey (*Ateles geoffroyi*). What little work has been done on the whinny vocalization suggests that whinnies are a ‘contact’ call used to maintain contact between close associates within and between dispersed subgroups (Ramos-Fernandez 2005), and that calling in feeding contexts is attractive to receivers, and therefore has implications for feeding competition (Chapman and Lefebver 1990). Male and female spider monkeys have different levels of association both within and between sexes, and suffer differing levels of costs associated with feeding competition, suggesting that the use of the whinny vocalization may have different implications for each sex. In this study, I explore differences in call rate, as well as the behavioural and social contexts in which whinnies are used by both sexes. Specifically, I attempt to determine whether the use of the call can be related to known differences in the association patterns that typify male and female spider monkeys. By doing this, I hope to further elucidate the functional significance of the call for males and females.

In what follows I outline relevant information about vocal communication. This review focuses on distance calls, with an emphasis on contact and food associated calls. I discuss sex differences in the use of vocal communication in other taxa, as well as proposed explanations for these differences. Finally, I review spider monkey social organization, and current hypotheses pertaining to the function of the whinny vocalization.

1.2 The use and proposed functions of distance calls

1.2.1 Contact calls

Distance calls are those used out of sight of recipients. There are many proposed ‘classes’ of distance calls, each relating to the proposed function of a particular vocalization. One of the most widely studied types of distance calls in birds and mammals is the contact call (Marler 2004, Rendall and Owren 2002). Generally speaking, contact calls are hypothesised to allow individuals to maintain spatial awareness of conspecifics, and they may be of great importance when visual contact is lost or hindered (Kondo and Watanabe 2009). The terms contact call, cohesion call, coordination call, isolation calls, advertisement call, and lost call are often used interchangeably, as they all denote calls that are thought to function in promoting spatial awareness and contact maintenance between group members. Contact calls may be important in group living species, as a means of maintain group cohesion. For example, the ‘coo’ calls of Japanese macaques (*Macaca fuscata*) play a role in the maintenance of contact between group members (Sugiura 1998, 2001). Koda *et al.* (2008) found that ‘coo’ calls were given at higher rates when visibility between individuals was restricted, further lending support to the hypothesis that the call functions in maintaining group cohesion. As primates tend to live in groups, contact calls are widespread within the order (eg.: ring tailed lemurs (*Lemur catta*): Petter and Charles-Dominique 1979, Macedonia 1986, gorillas (*Gorilla gorilla*): Harcourt *et al.* 1993, New World primates: Snowdon 1989).

Contact calls are found in other social animals as well. For example, the ‘rumble’ vocalizations of African elephants (*Loxodonta africana*) have been shown to mediate group

dispersion within a herd (Leighty *et al.* 2008). The emission of rumble vocalizations results in a decrease in space between the caller and their social partners. As African elephants live in highly fluid social groups, the use of these vocalizations allows individuals to mediate the distribution of these groups over distances of several kilometers (Leighty *et al.* 2008). Similarly, the use of whistle vocalizations by spinner dolphins (*Stenella longirostris*) increases as animals become separated by greater distances, suggesting that the vocalizations act to increase cohesion between individuals dispersed within a group (Lammers *et al.* 2006).

One key function of contact calls may be to help coordinate the movements of individuals in a group. For instance, capuchin monkeys (*Cebus capucinus*) use ‘trill’ vocalizations to initiate and coordinate group movement after periods of foraging or rest (Boinski 1993). The vocalization is given by adults at the periphery of the group, and conspecifics respond by traveling in the direction of the caller, who then ‘leads’ the group to a new location. Both adult male and female capuchins continue to give the vocalizations while at the leading edge of a group, and it is thought that these calls act as a guide for other group members (Boinski 1993). Similar patterns are evident in squirrel monkeys (*Saimiri oerstedii*); females who are either attempting to initiate group movement, or who are ‘guiding’ a group of conspecifics increase their rates of vocalization overall, with an increased use of twitter vocalizations relative to other call types (Boinski 1991). These group coordination calls function to maintain spatial cohesion, specifically in traveling contexts.

Numerous studies have used acoustic analysis to show that contact calls vary enough between individuals of a given population to allow receivers to identify a caller based on the acoustic properties of its vocalizations alone (reviewed in Rendall *et al.* 1998, 2000, ring-tailed lemurs: Macedonia 1986, chimpanzees: Marler and Hobbett 1975, flamingos (*Phoenicopterus*

ruber): Mathevon 1997, pygmy marmosets (*Cebuella pygmaea*): Snowdon and Cleveland 1980). Informing others of one's identity may be an effective way for callers to influence receivers, because the characteristics and frequency of social interactions between individuals is largely affected by the identities of the interactants (Rendall and Owren 2002). Rendall and Owren (2002) argue that a receiver's response to individually-specific variations in call structure should therefore vary based on their relationship with the caller. For example, in many colony-nesting bird species, individual discernible differences in call structure have been reported to allow individuals to recognise their mates (Silvereye, *Zosterops lateralis*: Robertson 1996, Zebra finches, *Taeniopygia guttata*: Miller 1979, Belted Kingfisher, *Ceryle alcyon*: Davis 1986). Kin recognition may also be facilitated through the use of contact calling. There are numerous examples of individual recognition of contact calls between parents and offspring in mammal and bird species where mothers and their offspring may be required to locate each other within large groups of individuals. Examples include: contact barks in baboons (Rendall *et al.* 2000), isolation calls in greater spear nosed bats (Bohn *et al.* 2007), contact calls in fur seals (Charrier *et al.* 2003), and advertising calls in king penguins (*Aptenodytes patagonicus*; Aubin and Jouventin 1998). Kin recognition through the use of contact vocalizations is not limited to mother offspring dyads however. Cooperative breeding long tailed tits (*Aegithalos caudatus*) are thought to use the 'churr calls' of individuals as a mechanism of kin recognition, allowing helpers to increase their inclusive fitness through kin-biased allocare (Sharp and Hatchwell 2005). Female rhesus macaques distinguish not only between the coo calls of kin and non-kin, but between the calls of individual kin as well, suggesting that their ability to identify callers exceeds simply recognising familial traits in call structure (Rendall *et al.* 1996).

Research suggests that individual-specific vocal characteristics may also play an important role outside of mating pairs or kin relationships. For example, the ability of animals to identify the relative dominance of a caller may affect how they respond to a vocalization. This has been observed in white-faced capuchin monkeys, where the dominance of callers correlates with the rate of response to vocalizations (Digweed *et al.* 2007). The contact calls of dominant individuals who become separated from a group are responded to more frequently by other group members than are the call of subordinate individuals. This allows dominant individuals who stray from their social group to rejoin faster than would a subordinate individual (Digweed *et al.* 2007). The ability of an individual to identify whether a call was emitted from a close associate or not may also affect the way the individual responds to a vocalization. In cotton top tamarins (*Saguinus oedipus*) for example, a series of playback experiments showed that cage mates could recognise each other's contact calls (Jordan *et al.* 2004). Cage mates tended to respond to playbacks of each other's vocalizations faster than other colony members who were kept in other cages (Jordan *et al.* 2004).

Mechanism behind Contact calls:

Contact calls do not always result in a vocal response from receivers. Adult female baboons (*Papio cynocephalus ursinus*) do not consistently exchange contact vocalizations after one is emitted (Rendall *et al.*, 2000). Playback studies revealed in fact that perceiving the contact call of an individual rarely results in a reciprocal call from receivers (Rendall *et al.* 2000; Cheney *et al.* 1996). Rendall *et al.* (2000) showed that although mothers approach the calls of their own infants more frequently than they did the infants of other females, they do not commonly exchange calls in either case. Mothers seem to call only when they themselves are at

risk of being separated from the rest of the group. These results are similar to another playback experiment, in which females did not respond vocally to the contact calls of their close relatives, unless they were at risk of being separated from the larger group themselves (Cheney *et al.* 1996). The results of both studies suggest that signalers call based on their own internal state, and not based on their assessment of the mental state of others. These findings bring into question the mechanisms by which contact calls function. For example, if contact calls are to function by informing receivers that a caller is 'lost' or 'separated' from the rest of the group, one must assume that receivers are able to attribute mental states to the signaler. However, for the above mechanism to work, receivers must 'understand' that the caller is lost. There is little evidence to suggest that monkeys are capable of understanding what another individual is experiencing (Byrne and Whiten 1990; Povinelli 1993). This suggests that monkeys should not be able to understand that another individual has become separated from the group, or that responding to the 'lost' individual's call would facilitate their rejoining the group (Cheney *et al.* 1996). Therefore, receivers might not be expected to call in response to the contact calls of others, as was observed by Cheney *et al.* (1996) and Rendall *et al.* (2000). Contact calls could still function to maintain group cohesion however, even if call production was controlled solely by an animal's internal state, as long as multiple individuals were often at risk of separation at the same time (Rendall *et al.* 2000). This might be the case, for example, when groups of animals are dispersed while feeding or traveling. Each individual would be calling based on their own risk of becoming separated from the group, but would be able to maintain its awareness of the other individuals by means of their calling.

1.2.2 Food Calls

Food calls in general are described as vocalizations associated with feeding or the discovery/presence of food (Clark and Wrangham 1994). This particular call type has been extensively studied in birds and mammals (eg. Chickens, (*Gallus gallus*): Evans and Marler 1994; Evans and Evans 1999, 2007; ravens, (*Corvus corax*): Bugnyar *et al.* 2001; tufted capuchins, (*Cebus paella nigritus*): Di Bitetti 2003; chimpanzees: Slocombe and Zuberbühler 2005; white-faced capuchins: Gros-Louis 2004; tufted capuchins: Di Bitetti 2005; Geoffroy's tufted-ear marmosets, (*Callithrix geoffroyi*): Kitzmann and Caine 2009; red-bellied tamarins, (*Saguinus labiatus*): Caine *et al.* 1995). Pollick *et la.* (2005) described two broad hypotheses as to why social animals would call in the presence of food: the 'food announcement' hypothesis, and the 'food ownership' hypothesis. The food announcement hypothesis relates to food calls that function to attract listeners. In many species, food calls seem to fit this description; the vocalizations are produced at large, divisible food sources, and appear to attract other group members to the caller's location at a feeding site (Dittus 1984, Gros-Louis 2004, Chapman and Lefebvre 1990). As these food calls tend to attract conspecifics, they are potentially costly to callers as a result of increased feeding competition (Clark and Wrangham 1994, Clay *et al.* 2012). Attracting conspecifics to food sources must provide some sort of benefits to callers to offset these costs (Clay *et al.* 2012). Krebs and Dawkins (1984) suggest that callers may be manipulating receivers to attain some sort of benefit intrinsic to increasing group size. Direct benefits of increasing group size in feeding contexts may include decreased predation risk (Sridhar *et al.* 2009, Elgar 1986, Caine *et al.* 1995), increased access to mates (Evans and Marler 1994, Marler *et al.* 1986, Van Krunkelsven *et al.* 1996), and the recruitment of allies (Heinrich 1988, Van Krunkelsven *et al.* 1996, Wilkinson and Boughman 1998).

In some species, food associated calling rarely results in an increase in the number of conspecifics at a food patch. Clark and Wrangham (1994), for example, noted that contrary to other studies, food arrival pant-hoots by chimpanzees did not affect the likelihood of other individuals joining callers at feeding sites. Moreover, food calls in some species are associated with the maintenance and/or increase of inter individual distance between callers and receivers, thereby functioning to reduce feeding competition between neighbors within a feeding patch (Boinski and Campbell 1996, Gros-Louis 2004). Pollick *et al.* (2005) suggest that these food calls support the ‘food ownership’ hypothesis, as the calls function to announce the possession of food without signifying a readiness to share. Boinski and Campbell (1996) found that capuchins increase the rate at which they use ‘huh’ vocalizations when feeding compared to when engaged in other contexts, and that the use of ‘huh’ vocalizations is associated with an increase in inter individual spacing. On average, the distance from a caller to its nearest neighbor increases by 3 meters within two minutes of the call (Boinski and Campbell 1996). Because calling subjects rarely change location within a bout of foraging, the increases in inter-individual spacing can be attributed to the movement of the neighbor, as opposed to the caller. This increase in inter individual spacing is not associated with any form of overt aggression from the caller, suggesting that the call itself is the sole trigger for the movement. Boinski and Campbell (1996) also showed that call rates of subjects increase when their nearest neighbor is closer than 10m away.

In a similar study, Gros-Louis (2004) found that capuchins who discover a food source are approached less frequently by other individuals if they emit a ‘huh’ vocalization, as opposed to remaining silent. Janson (1990) and Robinson (1981) note that decreases in inter individual spacing correlates with reductions in foraging success in capuchins. Increased inter individual spacing may decrease the amount of overlap between foraging individuals, thereby decreasing

direct competition for food, and minimizing the chances of entering areas within a patch where resources have already been depleted (Boinski and Campbell 1996). Evidence for these ‘food ownership’ calls have also been found in rhesus macaques (Hauser and Marler 1993), tufted capuchins (Di Bitetti 2005), and cottontop tamarins (Caine *et al.* 1995).

Food calls and referential signaling:

By definition, food calls are emitted in response to a specific environmental cue (ie: the presence or discovery of food), and they often evoke a response in listeners that suggests receivers associate the call with that specific stimulus. Stimulus specificity in call production and response specificity in receivers are the two criteria used to designate a signal as being functionally referential (Seyfarth *et al.* 1980; Marler *et al.* 1992; Macedonia and Evans 1993; Evans 1997; reviewed in Clay *et al.*, 2012). Essentially, food calls that attract individuals to a food source allow listeners to anticipate the presence of food without having seen the food themselves. This is only possible due to the close association between call production and the stimulus that elicits calling. As most animal calls are thought to be genetically predetermined, lacking the flexibility inherent to human language, calls are referred to as being ‘functionally’ referential because receivers respond ‘as if’ they interpret the call to contain specific information about the eliciting stimulus (Clay *et al.* 2012; Zuberbühler 2003; Seyfarth and Cheney 2010).

In many species, calls emitted while feeding may also be produced in other, non-feeding contexts. As these calls are not produced exclusively in the presence of food, it is possible that they do not directly reference the presence, abundance, or quality of food resources. For this

reason these calls are often described as food ‘associated’ calls (Clay *et al.* 2012). One mechanism by which food associated calls are thought to function is through indicating the motivational state of callers, be it hunger, or simply an elevated level of excitement resulting from the anticipation of feeding (Clay *et al.* 2012). Although food associated calls often attract conspecifics to the location of the caller, this does not indicate that the vocalizations refer specifically to food. That individuals move towards the call may simply indicate that these vocalizations serve a contact function (discussed above), and/or that animals are somehow attracted to the caller’s elevated level of excitement (Clay *et al.* 2012). This mechanism differs from that of a functionally referential signal, in that the lack of specificity between call emission and stimulus suggests that calling does not allow receivers to anticipate the presence of a specific environmental cue. For example, toque macaques (*Macaca sinica*) respond to food calls by immediately discontinuing their current behaviour, looking towards the location of the call’s emission, then running towards the origin of the call (Dittus 1984). Although on the surface, this response may seem to indicate that receivers of the call are responding to the presence of food, in reality this response differs very little than what has been observed in response to contact calls; the call seems to result in the recruitment of individuals. The contact calls and food calls of toque macaques are often associated in time, as contact calls are frequently emitted in response to these food calls. The two call types often grade into each other, and analysis of sonograms reveal structural similarities between each call type. Based on these acoustic similarities, as well as their association in time, Dittus (1984) goes as far as to liken these food associated calls to ‘intense contact calls’.

1.3 Sex differences in the use of distance vocalizations

Acoustic signaling in animals is subject to selective pressures as are any behavioural traits. As males and females are subject to different selective pressures (Trivers 1972), it is reasonable to expect that differences in the use of vocalizations might exist between males and females in many species (Green 1981). Differences in vocal patterns may range from the conspicuous use of sex-specific vocalizations, to more subtle differences, where the sexes use the same calls at different rates, or in different contexts.

The differential use of vocalization types by one sex or the other is exemplified in African elephants. Life histories of male and female African elephants differ substantially in regards to their social grouping patterns. Females live in multi-tiered societies consisting of family units, bond groups, and clans (Poole 1994). It is extremely rare to find females alone. Conversely, male elephants leave their family groups at about 14 years of age. Adult males spend much of their time alone or in small groups with other males. When in musth, interactions between males are highly aggressive. These differences in the level of sociality between the sexes are reflected in the vocal repertoires of male and female elephants. Of the 26 vocalizations used by African elephants, 19 are used exclusively by females. Many of these female-specific calls relate to the coordination of groups, including contact calls, lost calls, social greeting calls, and calls associated with elevated levels of social excitement. Conversely, there are only four vocalizations used exclusively by males, two of which are used as displays of dominance between individuals (Poole 1994).

The terms loud, and long calls are used synonymously to refer to species typical vocal signals which are used to communicate both between and within groups over long distances (Mitani and Stuht 1998). Such calls exist in the vocal repertoire of many New World monkeys

(Oppenheimer, 1977), Old World monkeys (Gautier and Gautier, 1977) and apes (Marler and Tenaza, 1977). Although loud calls may be produced by both males and females in some species (Zimmerman 1995), they are used primarily by males in many taxa (eg., Old World monkeys: Gautier and Gautier, 1977; chimpanzees: Marler and Tenaza, 1977; orangutans, (*Pongo pygmaeus*): Galdikas 1983; black howler monkeys (*Alouatta pigra*): Kitchen 2004). From this, it has been inferred that these vocalizations play a role in sexual selection (reviewed in Delgado 2006). At the individual level, loud calls vary sufficiently to allow receivers to assess the quality of callers as competitors in the case of male receivers, or mates in the case of female receivers (Delgado 2006). For example, baboon males give loud ‘whahoo’ calls when in aggressive interactions with other males, while chasing females, during intergroup interactions, and at dawn choruses (Kitchen *et al.* 2003a, 2003b; Fisher *et al.* 2004). High ranking males are more likely to engage in bouts of wahoo calling, and these bouts are longer than those produced by lower-ranking males (Kitchen *et al.* 2003a, 2003b). This reinforces the idea that males use wahoo calls to assess the competitive abilities of rival males. Long calls may also function to attract females. For example, male orangutans are less likely to call when in courtship with a female than when alone (Mitani 1985). Males call significantly more when they are temporarily out of consort with a receptive female, and females approach males when they give long calls (Mitra Setia and van Schaik 2007).

Sex related differences in vocalization patterns may be more subtle than the exclusive use of a call type by one sex. Both males and females may have the ability to produce a call, but may do so at different rates. This is because males and females could differ in the degree to which they benefit from a call’s specific function (Green 1981). For example, sexual dimorphism in the use of alarm calls has been observed in Belding’s ground squirrels

(*Spermophilus beldingi*, Sherman 1977). Female ground squirrels emit alarm calls in the presence of predators at higher rates than would be expected by chance. Males, on the other hand, call significantly less than would be expected by chance. These differences may be tied to the life histories of males and females of this species. Upon reaching sexual maturity, females do not leave their natal areas, nor do they leave between successive breeding seasons. As a result, females occupying a relatively small area show high levels of genetic relatedness. Contrary to this, males permanently leave their natal borrows to mate. Males do not defend a mating territory after having copulated, nor do they take part in the care of their progeny, as they leave when their mates give birth. These marked differences in the life histories of males and females suggest that females stand to gain more than males from alarm calling, as the benefits of warning kin may outweigh the costs of the increased risk of detection by predators incurred by calling (Sherman 1977). These differences in the costs/benefits of calling between the sexes are manifested in the relative frequency of call use.

Vocal communication is a mechanism by which squirrel monkeys coordinate group movement. The coordination of group movement falls predominantly on adult females. Adult females are thought to benefit more from moving to unused feeding patches than juveniles and adult males, who spend significantly less time feeding (Boinski 1988). By increasing the rate at which they vocalize at the periphery of a stationary group, females are able to initiate troop movement, and continue to vocalize at elevated rates as they 'lead' their group to the next undepleted feeding patch. Males and sub adult females do not routinely coordinate troop movement, and as a result, only vocalize intermittently in comparison to adult females (Boinski 1991). This illustrates a connection between the rates of vocalization, and differences in the optimum strategies of the different age-sex classes.

Chimpanzees emit a loud, distance call, referred to as a pant-hoot, which is primarily used by males to communicate with close male associates (Mitani and Nishida, 1993). Male chimpanzees pant-hoot more frequently when associates are close-by, than when those same associates are absent or accompanying the potential caller (Mitani and Nishida 1993). This indicates that males target pant-hoots to specific audiences within their group, which is thought to aid in maintaining contact between close associates and/or in recruiting allies (Mitani and Nishida 1993). The rate of pant-hoot vocalization in chimpanzees has been positively linked to dominance, with both lower ranking males and females using the vocalization less than high ranking males (Clark 1993). Female chimpanzees are able to produce all of the calls within the species vocal repertoire; however they were shown to use ‘non-submissive’ vocalizations, including the pant-hoot, at relatively low rates compared to males (Clark 1993; Marler and Tenaza 1977). This is perhaps the reason why the pant-hoots of females have been studied significantly less than those of males (King and Shanker 2003). Males outrank females within a community, and females may use pant-hoots less frequently as a strategy to avoid attracting both feeding competition and males who may potentially direct aggression toward them (Clark 1993). Based on the pant-hoot’s role in the maintenance of social bonds (Mitani and Nishida 1993), the low rate of pant-hoot use by female chimpanzees conforms to their relatively low levels of affiliation (Pepper *et al.* 1999).

1.4 Spider monkeys

1.4.1 Sex differences in spatial dynamics

Spider monkeys are ripe fruit specialists whose high energy food resources are distributed unevenly both temporally and spatially (Chapman *et al.* 1995; Link and Di Fiore 2006). Patchily

distributed resources have been associated with elevated levels of contest competition among females, requiring community members to break up into smaller subgroups to reduce feeding competition and travel time between food patches (Chapman *et al.* 1995; Wallace 2006). As a result, the uneven distribution of food patches has been cited as a strong factor in the development of the fluid, fission-fusion social system observed in spider monkeys (Chapman *et al.* 1995; Symington 1988; Symington 1990; Chapman 1990; Wallace 2006). As fission-fusion social systems vary along dimensions of spatial and temporal cohesion amongst subgroups, the term ‘fission-fusion dynamics’ has been proposed to describe the degree of variation in group membership and spatial cohesion over time (Aureli *et al.* 2008). Species with high levels of fission-fusion dynamics are characterized by flexible patterns of social organization where subgroups are formed and changed multiple times a day, varying in both composition and size (Chapman 1994; Norkonk and Kinzey 1990). High degrees of fission-fusion dynamics may have implications for signalling, communication, and the social evolution of a species (Aureli *et al.*, 2008). Fluid associations between individuals may require the development of complex communicative processes to manage social ties between individuals, who may spend long periods of time physically separated from one another (Ramos-Fernandez 2005; Aureli *et al.* 2008).

A community of spider monkeys consists of multiple males and females, with a pattern of male philopatry and female dispersal at sexual maturity (Di Fiore *et al.* 2009). Communities of black handed spider monkeys (*Ateles geoffroyi*) live in sex segregated societies, in which males and females range separately for the majority of the year (Hartwell *et al.* in press). Spider monkeys are male-bonded, with high degrees of association and affiliation among related adult males (Fedigan and Baxter 1984; Chapman 1990; Symington, 1990). Males frequently band

together and travel over large areas of their home range within the same subgroup, defending territorial boundaries from extra group males and potentially monitoring the reproductive status of females within the community (Chapman 1990; Shimooka 2005). Males associate with each other at levels that suggest active companionship, while females appear to aggregate randomly (Ramos-Fernandez *et al.* 2009). Females do not actively pursue any particular associations, aggregating primarily in feeding contexts (Ramos-Fernandez *et al.* 2009). Female-female associations are accordingly weaker than those between males (Chapman 1990; Symington, 1990). Females are generally less gregarious than males (Symington 1988; Chapman 1990; Fedigan and Baxter 1984, Aureli *et al.* 2008), potentially due to elevated levels of resource competition, which is thought to select for independent foraging by females. Male-female dyads show weaker associations than either same sex pairing (Ramos-Fernandez *et al.* 2009).

Male spider monkeys cooperate in the formation of coalitions, directing aggression towards females in the form of both non-contact chases as well as physical aggression (Slater *et al.* 2008). Female directed aggression by both males and females has been noted to take place in foraging contexts, where multiple individuals are feeding in the same tree (Slater *et al.* 2008 (males); Asensio *et al.* 2008 (females)). Female directed aggression is also associated with group fusions, being observed shortly after two subgroups come together (Aureli and Schaffner 2007).

1.4.2 The Whinny Vocalization

The spider monkey vocal repertoire consists of approximately 13 different vocalizations, which are distinguished based on their loudness, length, tonal qualities, and the presence/absence of frequency modulation (Eisenberg 1976). Of these vocalizations, the whinny has been studied

in the most detail. It is a frequency modulated call, consisting of 2-12 rapid rises and falls in pitch and a duration of 0.3 to 1.5 seconds (Ramos-Fernandez 2005). It has been described as sounding similar to the whinny of a horse, but quieter and at a higher pitch (Carpenter, 1935). Early research into the call's function yielded mixed ideas, but most studies implicate whinnies in playing a 'contact' function between spatially dispersed subgroups, as indicated by the observation that they tend to be produced immediately before or after a subgroup fusion (Carpenter 1935; Eisenberg 1976). The call is also associated with foraging, and as a result, some researchers propose that whinnies may provide information related to both food abundance, and location of feeding sites (Eisenberg 1976; Chapman and Lefebver 1990). Chapman and Lefebver (1990) suggest that call production at feeding sites may attract other subgroups or individuals, and note that there is a positive correlation between the frequency of calling by a subgroup and the number of individuals who then join the subgroup. Subgroups entering food trees do not call consistently however, and when calls are emitted, they are not consistently followed by fusion events (Chapman and Lefebver 1990).

Teixidor and Byrne (1999) suggested that the whinny may be comprised of discrete acoustic sub-types that are used in different contexts and which reference specific information about the caller's physical or social environment. The existence of distinct sub-types of whinny vocalization used in specific contexts could not be substantiated through acoustic analysis or playback experiments (Teixidor and Byrne 1999). Individuals may be able to discern the identity of a caller, however, based on the vocalization alone (Chapman and Weary 1990; Teixidor and Byrne 1999; Ramos-Fernandez 2005). Individual recognition of calls may allow receivers to make decisions about whether or not to respond to the call based on his/her relationship with the caller. Receivers may choose to ignore a call, respond to the call vocally

(with a whinny vocalization of their own), approach the caller, or move away from the caller. Through the use of playback experiments, Ramos-Fernandez (2005) showed that receivers are more likely to respond by approaching callers with whom they have higher level of association. Thus, whinnies may be essential for the maintenance of social ties. This may allow spider monkeys to be flexible in subgroup composition and size, as it would provide a means of managing social associations between dispersed individuals. Ramos-Fernandez (2005) suggested that the lack of predictability reported by Chapman and Lefebver (1990) concerning whether or not receivers joined callers in feeding contexts may have resulted from the failure to take into account the identity and the social relationship between callers and receivers. Based on their level of association, a receiver would be able to choose whether or not to approach a caller (Ramos-Fernandez 2005). The use of whinny vocalizations at feeding sites would thereby function to attract close associates of the caller, while non-associates may simply use the call to monitor the position of community members in the area.

1.4.3 Sex differences in the use of whinnies

Female spider monkeys have long been described as being less gregarious than males (Symington 1987; Chapman 1990; Aureli and Schaffner 2008). Recent work by Ramos-Fernandez *et al.* (2009) reported that although females do associate with other adults, their rates of association suggest little selectivity in regards to which individuals associate together. This is in stark contrast to the pattern observed between males, who associate at levels that suggest active companionship; while females may non-selectively associate with each other at feeding sites, males have actual preferred social partners. In his playback study, Ramos-Fernandez (2005) did not discuss the sex of either the caller or the receiver as a potential variable in the

response of receivers to a whinny vocalization. The interpretation of the data collected during that study suggested that whinnies were used by close associates to remain in contact while visually separated from each other. Taking this proposed function of the call into consideration, as well as the lack of preference for social partners exhibited by females (Fernandez *et al.* 2009), one would expect males to use the whinny vocalization more frequently than females. In fact, the vocalization is used by both sexes (Teixidor and Byrne 1999; Ramos-Fernandez 2005). Although little research has been done on sex differences in the use of the call, a six month field study in Guatemala reported that female spider monkeys vocalize at higher rates than do males overall, and emphasised that this difference was particularly true of the whinny vocalization (Fedigan and Baxter 1984). Somewhat at odds with this finding, Chapman and Lefebver (1990) indicated that there was no difference in the rate at which males and females whinny in feeding contexts.

Intra-sexual differences in vocalization patterns have been linked to differing levels of association between males and females in another atelid species, the muriqui (*Brachyteles hypoxanthus*)(Arnedo *et al.* 2010). As with spider monkeys, male muriquis are described as being more gregarious than females, spending a relatively higher proportion of their time in close proximity to other individuals (Strier 1990, Arnedo *et al.* 2010). The ‘neigh’ vocalization of the muriqui has been suggested to promote group cohesion, functioning as a contact call (Nishimura *et al.* 1988). In accordance with this suggestion, Arnedo *et al.* (2010) showed that after a ‘neigh’ vocalization was given, the number of conspecifics in close proximity with a caller increases. Based on the proposed function of the call as well as the elevated levels of gregariousness amongst males relative to females, the observation that male muriquis use the ‘neigh’ vocalization at higher rates than females was consistent with what would be expected, and what

was predicted by researchers (Arnedo *et al.* 2010). Conversely, female miquis use ‘staccato’ vocalizations at higher rates than males. After a ‘staccato’ vocalization is given, the number of conspecifics in close proximity with the caller *decreases*, suggesting that ‘staccato’ vocalizations function to increase interindividual spacing. ‘Staccatos’ have been suggested to reduce direct competition by allowing callers and receivers to maintain or increase inter-individual distances (Mendes and Ades 2004). As in many other primates species, female miquis spend a higher proportion of their time feeding in comparison to males, indicating that they have relatively higher energy requirements (Strier 1991). Thus, inter-sexual differences in the use of ‘staccato’ and ‘neigh’ vocalizations reflect the relative distribution and inter-individual spacing exhibited by each sex.

On a general level, these findings suggest that atelid species use vocal mechanisms to control intragroup spacing. Moreover, these findings suggest that males and females exhibit different vocalization patterns as a means of optimising spatial associations specific to their sex. Like ‘neigh’ vocalizations in miquis, spider monkey whinnies have been associated with the fusion of two subgroups. The elevated rates of association reported in male-male dyads by many authors (Fedigan and Baxter 1984; Symington 1988; Chapman 1990; Ramos-Fernandez *et al.*, 2009) would again suggest that the whinny vocalization should be used at a higher rates by males.

Ramos-Fernandez (2005) suggests that the spider monkey whinny may serve a similar function to that proposed for the chimpanzee pant-hoot; namely that pant-hoots function to allow individuals to recruit and maintain contact with their close associates (Mitani and Nishida 1993). As adult male chimpanzees show elevated levels of association relative to females (Pepper *et al.* 1999), it follows that pant-hoots are used at higher rates by males (Marler and Tenaza, 1977).

Chimpanzees and spider monkeys show marked similarities in their social organization (Symington; 1990, Chapman *et al.*; 1995). In both taxa, males are more gregarious than females, social grouping patterns are highly dynamic, and male philopatry is the norm. Considering these similarities in social organization, and the similarities in the proposed role of whinnies and pant-hoots in regulating social associations in these taxa, one might expect that the two vocalizations will show similar patterns of use. Based on this, we would predict that male spider monkeys will whinny at higher rates than females, as is the case with pant-hoots in chimpanzees.

The prediction above assumes however that the primary function of the whinny is to maintain close bonds between individuals. Because the acoustic properties of whinny vocalizations vary between individuals, they are thought to be individually recognisable (Chapman 1990; Teixidor and Byrne 1999; Ramos-Fernandez 2005). As a result, the vocalization may simply announce the presence of a *specific* individual, allowing receivers to respond based on the identity of a caller. A receiver's response to individually-specific variations in call structure should therefore vary based on their relationship with the caller (Rendall and Owren 2002). As a result, whinnies have the potential to elicit different responses or reactions depending on the identity, or specifically the sex of the caller; whereas male calls may serve as a beacon for close associates to hone in on each other, female calls may, for instance, serve as a spacing mechanism, based on the less gregarious nature of female spider monkeys. If whinny vocalizations do in fact function differently for males and females, then presumably the context of call emission may vary between the sexes.

1.5 General Objectives:

The objective of this study is to address the question of whether there are differences in the use of the whinny vocalization by male and female spider monkeys at Runaway Creek Nature Reserve (RCNR) Belize. In the following chapter, I will describe RCNR and the field site where data were collected, and I will outline my general data collection methods. In chapter 3, I will attempt to determine whether calling by males and females is associated with any particular behavioural context(s). I will compare the overall rate of calling by males and females, and then determine whether the call is associated with different activity categories. I will also determine whether the activities with which the call is associated are consistent between males and females. In chapter 4, I will examine whether the calling behaviour of males and females is affected by the characteristics of their subgroup. Specifically, I will look at how the size, sex composition, and changes in subgroup composition affect an individual's likelihood of calling. I will also investigate whether these subgroup characteristics affect the calling behaviour of males and females differently. Chapter 5 will serve as a general discussion based on the results of the third and fourth chapters.

By determining what behaviours and subgroup characteristics are associated with calling for each sex, I hope to gain further insight into the ultimate function of the vocalization. The intent of this is not only to ascertain how and why the call is used by either sex, but also to better understand the behavioural differences between males and females in a sexually segregated species with a complex and dynamic social system.

CHAPTER 2: GENERAL METHODS

2.1 Study site

I collected Data for this study at the Runaway Creek Nature Reserve (RCNR), central Belize (88°35' W and 17°22'N). RCNR is managed by the non-government organization, Birds Without Borders (*Aves Sin Fronteras*), and is privately owned by the Foundation for Wildlife Conservation. Central Belize has a dry season from January through May, and a wet season from June through December. The mean annual rainfall in this area of Belize is estimated at 2000-2200 mm (Meerman, 1999). RCNR consists primarily of semi-deciduous, broadleaf tropical forest and pine savannah. The forest is continuous with those adjacent to the reserve. Limestone karst hills, low valleys, and seasonal swamps are found throughout the site. The site is relatively free of human disturbance, but has recently been disturbed by natural events; the site was struck by hurricane Richard on October 28th 2010, and by a fire in May of 2011. Two species of non-human primates inhabit the site; black handed spider monkeys and black howler monkeys (*Alouatta pigra*).

2.2 Study group

Ateles geoffroyi, commonly referred to as the black handed or Central American spider monkey, is distributed from its southern-most range in Ecuador, along the Choco Region of the pacific coast, through Central America to their northern-most distribution in Veracruz, Mexico (Collins and Dubach 2000; Rylands *et al.* 2006). The distribution of the Yucatan spider monkey (*Ateles geoffroyi yucatanensis*) is limited to Belize, north-eastern Guatemala, and the Yucatan Peninsula of southern Mexico (Kellogg and Goldman 1944). Prior to the establishment of the RCNR study site, the subspecies has been studied at Tikal National Park in Gutemala (Coehlo *et*

al. 1976; Cant 1977; Fedigan and Baxter 1984), and in Mexico at Punta Laguna Nature Reserve (Aureli *et al.* 2006; Valero *et al.* 2006; Slater *et al.*, 2009).

All data for this study were collected from a resident community of habituated black-handed spider monkeys that have been under observation by researchers at the University of Calgary since January 2008. The home range of the study group is approximately 114 hectares, and borders with the home range of a second community of spider monkeys to the north. All group members are identifiable by their facial features, the coloration of their pelage, or through identifiable characteristics of their genitalia. Since the onset of data collection in 2008, group size has varied from 33 to 37 individuals. Seventeen infants have been born into the community since 2008, four of which have subsequently gone missing before reaching adulthood. A total of 3 sub-adults are known to have immigrated into the group over the study, and 2 sub-adults are thought to have emigrated to other groups. Two adult females have disappeared since 2008. They are assumed to have either died, or have emigrated to a neighboring community. At last census in August 2012, the community consisted of 34 individuals: 7 adult males, 11 adult females, 1 sub-adult male, 2 sub-adult females, 3 juvenile males, 5 juvenile females, and 5 infants.

2.3 General data collection protocol

The majority of the data used for this study was collected over an eight month period from January 2012 until August 2012, although one part of the behavioural context analysis utilises data collected from May 2009 until August 2012 (see chapter 3). Full or part day follows of subgroups were used to collect behavioural data, including vocalization data. Because of their fluid social grouping patterns as well as the size of their home range, subgroups of

monkeys were sampled as they were encountered, and were followed throughout the day for as long as possible. Although no strict sampling roster was followed, we would leave a subgroup if it was comprised of individuals who were by chance overrepresented in the data. This was done in an attempt to even out observation time across all individuals. Subgroups were defined using a chain rule (Ramos-Fernandez 2005) of 50m; any individuals within 50m of any other individual within a subgroup were considered part of that same subgroup. In the event of subgroup fission, an attempt was made to follow the subgroup that contained the most under-sampled individuals.

Scan samples were recorded at 30 minute intervals once a subgroup had been located. The time, location, composition, spread, and the behavioural state of each member of the subgroup was recorded. Subgroup spread was measured using distance categories of 0m, <2m, 2-5m, 6-10m, 11-15m, 16-20m, 21-30m, 31-40m, 41-50m. Behaviours recorded during scan samples included all state behaviours listed in the attached ethogram (see Appendix A). If foraging, the plant species and plant part being fed on was recorded. When subjects were engaged in social behaviours, the identities of all individuals involved, and the direction of the interaction was recorded. For a list of behaviours considered to be social, see attached ethogram (Appendix A).

Between scan samples, focal animal sampling (Altmann 1974) was used to collect behavioural data on all adult individuals. Focal samples were 10 minutes in length. The same individual was not sampled twice within a 30 minute period to increase the independence of each sample. Behaviours recorded during focal samples are listed and described in the attached ethogram (see Appendix A).

CHAPTER 3: THE BEHAVIOURAL CONTEXTS OF WHINNYING BY MALE AND FEMALE SPIDER MONKEYS.

3.1 Overview

Signals are often interpreted based on the behavioural contexts with which they are associated. For example, one key feature that defines food calls are their association in time with feeding or the discovery of food (Clark and Wrangham 1994). Correspondingly, calls associated in time with the detection of specific predators have been described as alarm calls (Seyfarth et al. 1980), and calls that are emitted prior to, during, or just after copulation are often classified as copulation calls (Townsend *et al.* 2008). Researchers have often focused on the behavioural circumstances that elicit calling in an attempt to gain insight into the function of a particular vocalization. Alone, determining the context(s) of signal production cannot fully elucidate the ultimate function of that signal, but by determining these contexts, one can begin to generate hypotheses as to its ultimate function. Determining context can provide insight into the proximate triggers of signal production, which can be a useful first step when attempting to formulate hypotheses about how a signal may benefit a signaller. These hypotheses can subsequently be tested by observing the behaviours of receivers, and attempting to determine how those behaviours benefit the signaler.

One way of providing insight into the functional significance of the winny vocalization for male and female spider monkeys may be to determine whether each sex uses the winny vocalization at different rates in different behavioural contexts. In what follows, I will review research regarding the behavioural contexts associated with the use of the winny vocalization by the black handed spider monkey, and I will discuss how this work has generated hypotheses as to the function of the vocalization. I will then derive hypotheses as to the calling behaviour of

males and females based these proposed functions, taking into consideration what is known about the social and ecological differences between males and females of this species.

3.1.1 The Whinny and Behavioural context:

Much of the existing research on the vocal behaviour of spider monkeys has focused on the behavioural contexts associated with a particular call type (Eisenberg 1976; Chapman *et al.* 1989; Chapman and Lefebvre 1990; Teixidor and Byrne 1999). Whinnies are often emitted by spider monkeys entering feeding trees, and the call is emitted frequently by individuals as they forage (Klein 1972; Eisenberg 1976; Chapman and Lefebvre 1990). In a study examining the calling behaviour of foraging subgroups, Chapman and Lefebvre (1990) found a positive relationship between the frequency at which a subgroup emitted whinny vocalizations while feeding, and the number of animals that joined the foraging subgroup. The interpretation of these results was that the call functioned to attract others to a food source, and that the whinny was, in essence, a food call. The frequency of calling increased when subgroups were in larger feeding trees, and in times of relative resource abundance. The interpretation of this was that individuals called selectively based on the divisibility of resources within a patch; when a resource was not as easily divisible, animals would call at relatively lower rates. By calling at lower rates, a subgroup could avoid attracting unwanted competition from new individuals.

One limitation of Chapman and Lefebvre's 1990 study is that the authors only analysed whinnies that occurred in feeding contexts, despite the fact that whinnies are emitted in other contexts as well (Teixidor and Byrne 1999; Ramos-Fernandez 2005). In addition, Chapman and Lefebvre's assertion that calling by foraging subgroups functions to attract others was based on only 17 out of a possible 101 occasions in which foraging subgroups who called were joined by

other individuals. This suggests that the classification of ‘food call’ may be too narrow to capture the contextual relevance of whinnies. Teixidor and Byrne (1999) explored the possibility that the whinny vocalization was not a homogenous call type; ie., that acoustically discrete subtypes of whinny vocalization were produced in specific behavioural contexts. The existence of acoustic variants of a vocalization may allow receivers to interpret the behavioural and/or environmental context in which the caller is situated via the acoustic properties of the call alone, provided these variations are salient to receivers. A number of researchers have described animal calls as being referential, or semantic, suggesting that these vocalizations serve as acoustic ‘symbols’ that relay specific information to receivers (Macedonia and Evans 1993; Seyfarth *et al.* 1980; Slocumbe and Zuberbuhler 2005). For instance, acoustic subtypes of vervet alarm calls are produced in response to specific predator types and elicit appropriate escape tactics by receivers (Seyfarth *et al.* 1980; Cheney and Seyfarth 1981), and variants of chimpanzee food grunts produced at specific food types have been shown to elicit differential responses from naïve listeners (Hauser *et al.* 1993; Slocumbe and Zuberbueller 2005). The mechanism by which these so called ‘referential’ signals operate between signallers and receivers has been intensely debated (Rendall *et al.* 2009; Owren and Rendall 2001, Clay *et al.* 2012). What remains however is the fact that many call types across species do exhibit some acoustic variation that seems to correspond to specific contexts of production.

To explore the possibility that spider monkey whinnies are comprised of acoustic subtypes that are produced in specific behavioural or environmental contexts, Teixidor and Byrne (1999) conducted an acoustic analysis of a sample of whinnies across 6 behavioural contexts. They found that the acoustic properties of whinny vocalizations varied primarily among individuals, and not between contexts. In other words, variation in the acoustic

properties of the whinny across contexts was not consistent between individuals, suggesting that there is no consistent acoustic difference between, for example, a ‘feeding’ whinny and a ‘traveling’ whinny. This observation implies that whinnies emitted in different contexts may not be salient to receivers as distinct subtypes from which they can draw precise information about the signaller’s situation. Rather, receivers are more likely able to discern individual callers from a distance, and may react to a whinny based on their relationship to the caller (Ramos-Fernandez 2005, 2008).

3.1.2 Sex differences in the behavioural context of whinny vocalizations

Two aspects of the whinny vocalization that have yet to be examined analytically are whether the call is produced more often in certain behavioural contexts over others, and whether males and females call at the same rate in similar contexts. Research to date has been inconclusive on this point, as whinnies have been implicated in functioning primarily as both contact (Ramos-Fernandez 2005) and food calls (Chapman and Lefebvre 1990). Little research has focused on sex differences in calling. Also, the research that has been conducted into sex differences in calling has generated inconsistent results; Chapman and Lefebvre’s foraging study (1990) found that the presence of males within a foraging subgroup did not affect the rate of calling by that subgroup. The interpretation of this was that there was no difference in the rate of calling by males and females while foraging. This conflicts somewhat with the findings of Fedigan and Baxter (1984), which suggest that, overall, females call at elevated rates relative to males. These discrepancies may derive from the fact that Chapman and Lefebvre’s 1990 study looked at the call rate of entire subgroups of foraging individuals, as opposed to the rate of calling by individual monkeys in foraging contexts. Because of this, it is not clear whether

specific individuals or age/sex classes were responsible for the majority of calls within a subgroup, or whether the calls were produced at equal rates by all age/sex classes. The observation that mixed sex subgroups and all female subgroups called at the same rate while foraging should therefore not be taken as evidence that males and females call at the same rate while feeding; there is no way to determine whether both the males and the females within a mixed sex subgroup contributed equally to the calling based on the data collection methods used by Chapman and Lefebvre (1990).

As whinny vocalizations vary consistently between individuals (Teixidor and Byrne 1999), responses to the call may depend on a receiver's relationship to the caller (Ramos-Fernandez 2008), which in part might be determined by the caller's sex. Because of this, the functional significance of calling by males and females may differ by virtue of their distinct patterns of association (Ramos-Fernandez *et al.* 2009). For example, male vocalizations may allow close associates to locate each other within the environment. If this is the case, males might be expected to call more often while travelling as they attempt to monitor the whereabouts of male associates while moving through a habitat of reduced visibility. Mitani and Nishida (1993) found that pant-hooting by male chimpanzees was associated with traveling more often than would be expected by chance. Because pant-hooting was used at elevated rates by males who were traveling, and whose close associates were nearby, it was proposed that the pant-hoot functioned to communicate a caller's change in position with respect to these close associates. In this way, the call would be a means by which preferred social partners could maintain cohesion amidst their fluid social grouping patterns. The functional analogy between the chimpanzee pant-hoot and the spider monkey whinny (Ramos-Fernandez 2005) suggests that male spider monkeys may also call more while traveling.

As female-female and female-male dyads do not show association patterns consistent with active companionship however (Ramos-Fernandez *et al.*, 2009), predictions as to the behavioural contexts in which females will use the whinny are difficult to make. It is perhaps more feasible to consider contexts in which one would expect females to call at relatively low rates. As whinnies emitted while foraging have been suggested to have an attractive function (Chapman and Lefebvre 1990), and as the costs of feeding competition are thought to be greater for female spider monkeys (Chapman *et al.* 1995; Symington 1987; van Roosmalen and Klein 1988; Asensio *et al.* 2008; Slater *et al.* 2009), one would predict that females would call at proportionately lower rates than males while foraging to avoid increasing resource competition. Food calling behaviour has been shown to vary between individuals based on their sex in other primate species. For example, male tufted capuchins are quicker to give a food call upon finding food relative to females (Di Bitetti 2005). This is probably due to the fact that their food calls are attractive to receivers, and that increasing feeding competition through calling probably has higher fitness costs for females compared to males. Similarly, the increased fitness cost experienced by female spider monkeys suggests that they should whinny at lower rates than males while foraging. Regardless of context, both the proposed functions of the whinny vocalization as a food call (Chapman and Lefebvre 1990), and as a cohesion call used to allow close associates to maintain contact (Ramos-Fernandez 2005) suggest that males should call at higher rates than females overall.

3.1.3 Objectives:

To better understand sex differences in the use of the winny vocalization, I will first determine whether the call is used at different rates by males and females in general. I will then determine whether the call is used at different rates across several activity categories, and I will determine if the use of the call across these categories is different for each sex. By determining the behavioural contexts that elicit calling by males and females, I hope to gain insight into the functional significance of the call for each sex.

3.1.4 Hypotheses and Predictions:

The central hypothesis that I am testing is that male and female spider monkeys will winny at different rates overall, and at different rates in different contexts. I will test three main predictions. First, I predict that the winny vocalization will be used at a higher rates by males than by females overall. Secondly, based on the hypothesis that the winny vocalization functions to allow close associates to maintain contact, I predict that males will winny at elevated rates while traveling relative to females, allowing them to monitor the whereabouts of preferred social partners. Finally, based on the hypothesis that winny vocalizations emitted in feeding contexts serve the general function of attracting conspecifics, I predict that females will call at lower rates while foraging compared to males.

3.2 Methods:

3.2.1 General data collection protocol

The general data collection protocol for this study is in most regards similar to what was described in chapter 2. Where possible this study utilises project data collected from May 2009 until August 2012. Standardised data collection procedures over this time period allowed data collected by multiple researches to be included in some aspects of this study. Where this was not possible, data collected from January 2012 until August 2012 were used (see below).

3.2.2 Behavioural context data:

Whinny vocalization data were collected during 10 minute focal animal samples. All whinny vocalizations emitted by a focal animal were associated with one of four possible behavioural contexts: foraging, socializing, inactivity or traveling. The context of ‘foraging’ was defined as handling, inspecting, ingesting, searching for a food item, or drinking at the time of call production. ‘Social’ contexts were defined as sitting in body contact or within a two meter radius of another individual, engaged in social play, or participating in social grooming. ‘Travel’ was defined as moving within the canopy, excluding movements within the crown of a tree while foraging. The context ‘inactive’ was assigned to calls emitted while an individual was sitting, laying in a resting position, or grooming themselves outside the two meter radius prescribed for context ‘social’. If a focal animal changed behaviours at the onset of the whinny, the call was assigned to the behaviour directly following the whinny.

3.2.3 Analysis: *Effects of sex and behavioural context*

The behavioural context of calling by male and female spider monkeys was analysed using two separate two-way repeated measures ANOVAs on two sets of data. In both analyses, the rate of calling by male and female spider monkeys across various behavioural contexts was compared to determine the effect of sex and activity on an individual's rate of calling. Specifically, the analyses were used to determine whether there was an effect of sex, individual activity, or a sex by activity interaction effect on an individual's rate of calling. Only adult and sub-adult monkeys of known identity were included in the analyses.

The first ANOVA utilised a data set that included all focal samples collected from May 2009 until August 2012. A total of 2820 whinnies were recorded during focal animal samples over this period. As this analysis utilised the longest period of data collection, it will be referred to as the *long term analysis*. This long term analysis was included to increase sample size, specifically on males. As there are fewer adult males in the study community, and because males are known to travel faster and further throughout the day (Klein 1972; Symington 1987), collecting large amounts of data on males can be difficult (Campbell 2002). Including the long term analysis therefore allows for a more accurate depiction of the differences in vocal behaviour between the sexes.

The second analysis utilised data collected from January through August 2012. Of the 658 whinnies that were recorded over this period, I removed all vocalizations that were emitted during focal samples that were associated with a subgroup fission or fusion. This left a total of 526 whinny vocalizations for this analysis. The short term analysis was done to control for the possible effects of subgroup composition changes on an individual's rate of calling (see chapter 4). I took this into consideration because changes in subgroup composition may occur at

elevated rates in certain contexts. For example, fusions may occur at relatively high rates in feeding trees, as the result of two or more subgroups converging on a single feeding patch. One would therefore expect individuals to be involved in subgroup fusions more frequently while foraging than when engaged in other activities. Because of this, the effects of an individual's activity on its rate of calling cannot be unequivocally separated from the effects of subgroup stability using the long term analysis exclusively. By removing the confounding factor of fissions and fusions in the short term analysis, then comparing the results to long term analysis, the direct effects of activity on call rate can be more accurately assessed. This second analysis utilised the shorter data collection period to assure that subgroup fissions and fusions were recorded consistently across both the behavioural context analysis and the subgroup characteristics analysis (see following chapter). This second analysis will be referred to as the *short term analysis*, as it utilised the short term data set.

In both behavioural analyses, I applied the Greenhouse-Geisser correction when data violated the assumption of sphericity. Post-hoc simple effects analyses were performed to compare the rates of calling between the four behavioural contexts within sexes, and between sexes within each behavioural context. An adjustment for multiple comparisons was made using the Bonferroni correction (Holm 1979).

3.3 Results: Sex and individual activity

3.3.1 Long term analysis:

The rate of whinny vocalizations differed significantly by sex ($F(1, 21) = 25.849, p < 0.001$), with females calling at higher rates than males overall. Call rate differed significantly between activity categories as well ($F(1.920, 40.325) = 30.438, p < 0.001$), and there was a significant sex by activity interaction effect ($F(3, 63) = 9.780, p < 0.001$), indicating that the effect of an individual's activity on its rate of calling varied with the sex of the caller.

Simple effects analysis of female whinnies in different behavioural contexts indicated a significant difference in the rates of calling between all activities. Females whinnied at a significantly higher rate while foraging (9.75 ± 0.87 calls/hour; Table 1) in comparison to other activities (social $p < 0.001$; inactive $p = 0.010$; travel $p < 0.001$; Table 2A; Fig 1A). The next highest rate of calling by females was while inactive, (7.26 ± 0.61 calls/hour) then while traveling (5.01 ± 0.53 calls/hour), and finally while in social contexts (1.99 ± 0.34 calls/hour). Males showed no significant differences in their rate of calling between any activity category (foraging 3.17 ± 1.19 ; social 0.87 ± 0.47 ; inactive 1.88 ± 0.83 ; traveling 1.65 ± 0.73 ; Table 2B).

Table 1: Descriptive statistics summary for long term analysis

Sex	Total Observation hours	Activity/ Behavioural context	Observation hours per activity	Frequency of calling per activity	Weighted Mean Rate of calling (calls/hour)	Std. Error
Male	88.9	Forage	22.18	58	3.17	1.187
		Social	21	22	.87	.468
		Inactive	25.66	40	1.88	.833
		Travel	15.38	25	1.65	.729
Female	424.67	Forage	122.67	1093	9.75	.867
		Social	75.28	151	1.99	.342
		Inactive	147.64	1071	7.26	.609
		Travel	73.15	360	5.01	.532

Table 2A: Pairwise comparisons of call rate across activities in females

Compare activity A	Compare activity B	Mean Difference (A-B)	Std. Error	Sig.b
Forage	Social	7.76*	0.814	0*
Forage	Inactive	2.49*	0.692	0.01*
Forage	Travel	4.74*	0.822	0*
Social	Inactive	-5.28*	0.521	0*
Social	Travel	-3.02*	0.427	0*
Inactive	Travel	2.25*	0.429	0*

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table 2B: Pairwise comparisons of call rate across activities in males

Compare activity A	Compare activity B	Mean Difference (A-B)	Std. Error	Sig.b
Forage	Social	2.30	1.115	0.311
Forage	Inactive	1.29	0.948	1
Forage	Travel	1.52	1.125	1
Social	Inactive	-1.01	0.713	1
Social	Travel	-0.78	0.584	1
Inactive	Travel	0.22	0.587	1

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Call rate was significantly higher for females in comparison to males in foraging ($F = 20.015$, $df = 1$, $p < 0.001$), inactive ($F = 27.251$, $df = 1$, $p < 0.0001$) and traveling contexts ($F = 13.833$, $df = 1$, $p = 0.001$; Table 3; Fig 1B). There was no significant difference in the rate of calling between males and females in social contexts ($F = 3.699$, $df = 1$, $p = 0.068$; Table 3; Fig 1B).

Table 3: Pairwise Comparisons of call rate across sexes for each behavioural context

Activity/Behavioural context	Mean Difference (Female-Male)	Std. Error	Sig. ^b	95% Confidence Interval for Difference ^b	
				Lower Bound	Upper Bound
Forage	6.58*	1.470	.000*	3.520	9.635
Social	1.12	.580	.068*	-.091	2.321
Inactive	5.39*	1.032	.000*	3.241	7.532
Travel	3.36*	.903	.001*	1.480	5.234

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

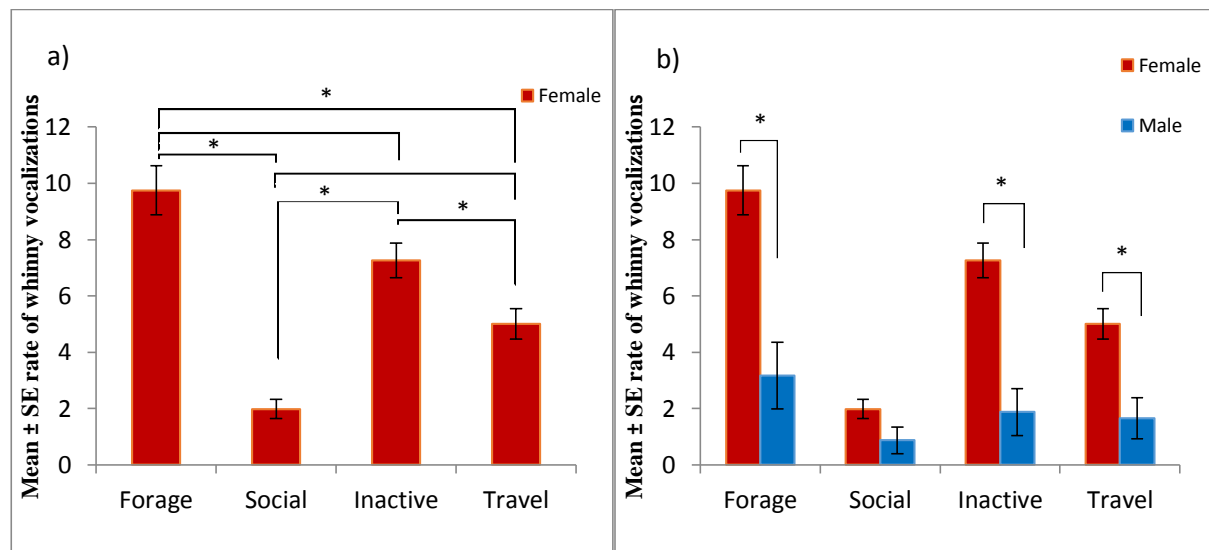


Fig. 1: Rates of whinny vocalizations by sex and activity over 40 months of data collection. The significance levels of Post-hoc pair wise comparisons (a) between behavioural activities for females, and (b) between sexes within behavioural activities are indicated by asterisks. Bars connected by an asterisk are significantly different ($p < 0.05$).

The results of the long term analysis showed that females called at higher rates than males in all behavioural contexts, except for while engaged in social activities. When comparing call rates across activities within each sex, females called at significantly different rates between each of the four activity categories; their highest rate of calling was while foraging, and their lowest rate of calling was while engaged in social activities. Males showed no differences in their rate of calling across the four activity categories.

3.3.2 Sex and individual activity – short term analysis:

The results of the short term analysis were comparable to the results of the long term analysis in most respects. The rate of whinny vocalizations differed significantly by sex ($F(1, 18) = 5.408, p = 0.032$), and by individual activity ($F(1.724, 31.030) = 5.504, p = 0.012$). As with the long term analysis, females called at a higher rate than males overall. There was a significant sex by activity interaction effect ($F(1.724, 31.030) = 3.696, p = 0.042$), indicating that the effect of an individual's activity/behavioural state on its rate of calling varied with the sex of the caller.

Simple effects analysis of female whinnies in different behavioural contexts indicated a significant difference in the rates of calling between all activities. Females whinnied at a significantly higher rate while foraging (8.26 ± 1.11 calls/hour; Table 4) in comparison to any other activity (social $p = 0.006$; inactive $p = 0.001$; travel $p = 0.001$; Table 5A; Fig 2A). The next highest rate of calling by females was while inactive, (4.02 ± 0.64 calls/hour) then while traveling (3.46 ± 0.56 calls/hour), and finally while in social contexts (1.12 ± 1.38 calls/hour). Males showed no significant differences in their rate of calling between any activity category (foraging 3.23 ± 1.36 ; social 2.92 ± 1.68 ; inactive 1.50 ± 0.78 ; traveling 1.05 ± 0.68 ; Table 5B).

Table 4: Descriptive statistics summary for short term analysis

Sex	Total Observation hours	Activity/ Behavioural context	Observation hours per activity	Frequency of calling per activity	Weighted Mean Rate of calling (calls/hour)	Std. Error
Male	17.14	Forage	3.30	11	3.23	1.358
		Social	3.58	4	2.92	1.684
		Inactive	4.30	8	1.50	.778
		Travel	3.90	6	1.05	.682
Female	111.59	Forage	54.24	212	8.26	1.109
		Social	51.23	22	1.12	1.375
		Inactive	101.13	174	4.02	.636
		Travel	65.97	88	3.46	.557

Table 5A: Pairwise comparisons of call rate across activities in females for the short term analysis (fissions and fusion removed)

Compare activity A	Compare activity B	Mean Difference (A-B)	Std. Error	Sig.b
Forage	Social	7.14*	1.815	.006*
Forage	Inactive	4.25*	.846	.001*
Forage	Travel	4.81*	1.012	.001*
Social	Inactive	-2.90	1.557	.476
Social	Travel	-2.34	1.578	.935
Inactive	Travel	.56	.686	1.000

Based on estimated marginal means

*, The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table 5B: Pairwise comparisons of call rate across activities in males for the short term analysis (fissions and fusion removed)

Compare activity A	Compare activity B	Mean Difference (A-B)	Std. Error	Sig.b
Forage	Social	.31	2.223	1.000
Forage	Inactive	1.73	1.036	.675
Forage	Travel	2.18	1.240	.578
Social	Inactive	1.42	1.907	1.000
Social	Travel	1.87	1.932	1.000
Inactive	Travel	.45	.841	1.000

Based on estimated marginal means

*, The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Call rate was significantly higher for females in comparison to males in foraging ($F = 8.242$, $df = 1$, $p = 0.010$), inactive ($F = 6.267$, $df = 1$, $p = 0.022$) and traveling contexts ($F = 7.460$,

$df = 1, p = 0.014$; Table 6; Fig 2B). There was no significant difference in the rate of calling between males and females in social contexts ($F = 0.685, df = 1, p = 0.419$; Table 6; Fig 2B).

Table 6: Pairwise Comparisons of call rate across sexes for each behavioural context for the short term (fissions and fusion removed)

Activity/Behavioural context	Mean Difference (Female-Male)	Std. Error	Sig. ^b	95% Confidence Interval for Difference ^b	
				Lower Bound	Upper Bound
Forage	5.04*	1.754	.010*	1.350	8.719
Social	-1.80	2.174	.419	-6.367	2.768
Inactive	2.52*	1.005	.022*	.404	4.627
Travel	2.41*	.880	.014*	.555	4.254

Based on estimated marginal means

*, The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

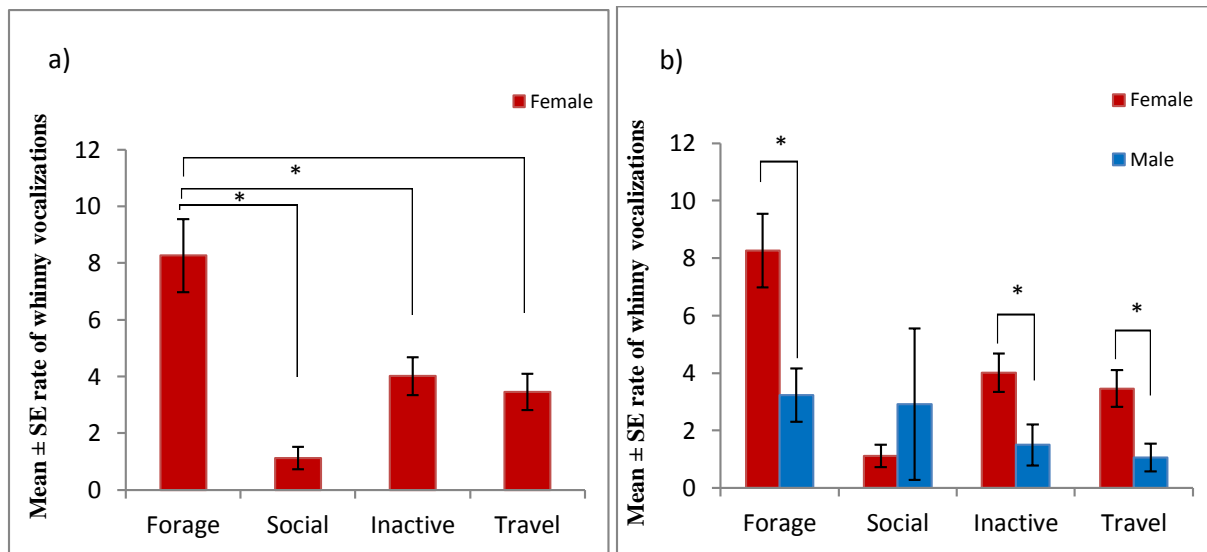


Fig. 2: Rates of whinny vocalizations by sex and activity over 8 months of data collection. Results depicted are from the short term data set, with all focal samples associated with a subgroup fission or fusion removed from the analysis. The significance levels of Post-hoc pairwise comparisons (a) between behavioural activities for females, and (b) between sexes within behavioural activities are indicated by asterisks. Bars connected by an asterisk are significantly different ($p < 0.05$).

3.3.3 Individual activity/behavioural context– Review:

The results of both the long term and the short term analyses showed that females called at higher rates than males overall. When broken down by context, both analyses showed that females called at higher rates than males while feeding, traveling and while inactive. Call rate was not significantly different between males and females when engaged in social activities. When comparing call rates across activities within sexes, both analyses indicated that females called at significantly higher rates while foraging in comparison to any other activity. Female call rate was lowest when engaged in social activities, though the difference in call rate between social, traveling, and inactive contexts were only significant in the long term analysis. Males showed no differences in their rate of calling across the four activity categories in either analysis. Despite the removal of all samples that were associated with a fission or a fusion in the short term data set, the results of the two analyses were largely similar.

3.4 Discussion:

The results of both behavioural analyses indicated that overall, females call at higher rates than males. This difference in rate is consistent across all activities except social, where males and females call at a similar rate. Males and females also differ in the degree to which behavioural context affects their call rate. Male calling does not differ significantly across activity categories; females however call at significantly higher rates while foraging relative to any other behavioural context. Although this association between the use of the whinny vocalizations and foraging has been described previously (Klein 1972; Eisenberg 1976; Chapman and Lefebver 1990), this is the first time that a difference in call rate between the sexes has been demonstrated in this context. As the results of both the long and the short term analyses were consistent, it can be inferred that the effects of behavioural context on call rate revealed by the long-term analysis are legitimate, and are not merely the result of differential rates of fissions or fusions across the four behavioural categories. The long term analysis also indicated that call rate by females was significantly lower while engaged in social activities when compared to any other behavioural context. Although call rate by females was also lowest in social contexts in the short term analysis, the difference in call rate between social, travel, and inactive contexts were not significant.

The elevated rate of calling by females in the context of foraging does not support the idea that the whinny vocalization simply functions to attract listeners for two reasons. Firstly, one would expect females to call at lower rates than males in feeding contexts if whinnies were consistently attractive to listeners. It has been suggested that the tendency for female spider monkeys to forage independently is a response to the patchy distribution of the contestable, high quality resources they exploit (Symington, 1988; Aureli *et al.* 2008; Aureli and Schaffner 2007).

It therefore seems counter intuitive that females would whinny at elevated rates in feeding contexts if the primary function of the vocalization was to attract other individuals with whom callers would have to compete with for resources. Secondly, females are less gregarious than males, and do not form close associations with other individuals (Fedigan and Baxter 1984; Symington 1990; Chapman 1990; Slater *et al.* 2009; Ramose Fernandez *et al.* 2009), nor do they have close kin within the community as they disperse at sexual maturity. There are therefore few individuals within a community with whom a female should be tolerant of sharing food resources, apart from their own offspring. If calling served an attractive function, one would predict females to call at lower rates in feeding contexts compared to philopatric males, who show active levels of companionship between each other.

That females call at elevated rates while foraging suggests that calling may function differently than previously proposed. For example, whinnies emitted by females may be a means by which an individual can announce their presence, potentially promoting or maintaining inter-individual spacing. Because the whinny vocalization is individually recognisable, calling by females may simply inform others as to the caller's presence, identity, and location. By virtue of the fact that females are less gregarious than males, forage independently due to elevated levels of resource competition (Symington 1988; Chapman 1990; Fedigan and Baxter 1984, Aureli *et al.* 2008), and do not actively pursue association with adults of either sex (Ramos-Fernandez *et al.* 2009), it is reasonable to assume that their relatively high rate of calling does not serve to attract conspecifics. Because a receiver's response to the whinny of a specific individual should vary based on their relationship with the caller (Rendall and Owren 2002; Ramos-Fernandez 2005, 2008), listeners may perceive a female's call as an indication that an individual with whom they are not closely associated is nearby, allowing them to space themselves out

accordingly. Ramos-Fernandez *et al.* (2009) suggested that females aggregate randomly, primarily in feeding contexts. It is possible that without some mechanism for maintaining inter-individual spacing, these random aggregations at feeding trees would result in excessive amounts of competition and aggression over resources. Given the hypothesis that females use the whinny to promote optimal inter-individual spacing, the elevated rate of calling by females in foraging contexts is more easily explained. The whinny vocalization may be one mechanism by which the independent foraging that is characteristic of female spider monkeys is achieved and mediated.

Pollick *et al.* (2005) described two hypotheses as to the function of food calling by social primates. The first was termed the ‘food announcement’ hypothesis. This applies to calls that are attractive to receivers, and suggests that food calls function to alert conspecifics to feeding opportunities (reviewed in Pollick *et al.* 2005). The second hypothesis is called the ‘food ownership’ hypothesis. As with the former hypothesis, it suggests that food calling functions to inform others that a caller has found food, but unlike food announcement calls, signaling is meant to secure the callers possession of a resource, and does not suggest a readiness to share by the signaler. Because the whinny vocalization is not strictly used in feeding contexts, it may not fit altogether into either category, though I propose that calling by females shares some functionality with ‘food ownership’ category of calls. If females can inform other individuals with whom they are not closely associated that they are feeding within a patch, listeners may respond by spacing themselves out from the caller. This in turn would allow callers to maintain exclusive access to small areas within a larger feeding patch, thereby decreasing direct competition over resources. Because whinny vocalizations are often responded to through antiphonal calling (Ramos-Fernandez 2008), females can continually monitor each other’s

positions while foraging, allowing them to avoid unnecessary competition or confrontations in this context.

Another surprising finding of this analysis was that in contrast to females, the calling behaviour of males was not affected by behavioural context. I had predicted that males would call at elevated rates while traveling as a means of maintaining contact. One possible explanation is that closely associated males stay within visual range of each other as they travel in the same subgroup, and may not rely heavily on the use of the whinny to locate each other. In the next chapter, I will examine the relationship between calling by males and females and various characteristics of their subgroup. Although males do not seem to use the whinny vocalization at elevated rates while traveling, it is possible that they use the call more often when their chances of being separated from their close associates is greater. Specifically, I will examine the effects of subgroup size, subgroup sex composition, and changes in subgroup composition on the likelihood of calling by males and females.

CHAPTER 4: THE EFFECTS OF SUBGROUP SIZE, COMPOSITION AND STABILITY ON THE USE OF WHINNIES BY MALE AND FEMALE SPIDER MONKEYS.

4.1 Overview

Because the composition of a spider monkey's subgroup is continually changing in a habitat of reduced visibility, maintaining contact with preferred social partners might be difficult if not for mechanisms for locating specific individuals. Whinny vocalizations may play a role in this respect, as calling may allow closely associated individuals to identify and locate each other both within and between the dispersed subgroups that characterize spider monkey grouping patterns. This hypothesis has received empirical support through the use of playback experiments (Ramos-Fernandez 2005). When recordings of whinnies from known individuals were played to subjects, those who had a higher degree of association with the caller were the only ones to approach the playback speaker. It was inferred from this that the call functioned to allow close associates to locate and maintain contact with each other. It should be noted however that this study did not make a distinction between male and female callers or receivers.

If whinnies function to allow close associates to maintain contact with each other, then the observed association patterns within and between each sex would suggest that males would be more motivated to call than females. This is because males show active levels of companionship with other males, while females show patterns of either passive association or active avoidance with other adult members of their group (Ramos-Fernandez *et al.* 2009). The fact that both males and females make use of the whinny vocalization (Fedigan and Baxter 1984; Chapman and Lefebvre 1990; Teixidor and Byrne 1999; Ramos-Fernandez 2005), and that females call at higher rates than males in most behavioural contexts (see chapter 3), suggests that

the vocalization may provide female callers with alternative benefits; males may use the call to maintain contact with close associates, while calling by females may have a different functional significance.

4.1.1 Vocal signaling and social context

In addition to determining the behavioural or ecological contexts that surround call production, it is important to consider the effects of social context on an individual's use of a signal. Not only might call production be triggered by a specific social context, but the use of a call associated with a specific ecological or behavioural context (eg., food calling, copulation calling) may be influenced by specific social cues. For example, it has been shown that chickens (*Gallus gallus*) modify their food calling behaviours based on the identities of potential receivers (Marler *et al.* 1986 a,b; Evans and Marler 1994). Specifically, rates of food calling by males increase when in the presence of a hen, and decrease when in the presence of another male. Hens respond to these calls by approaching the male. As a result, calling has been proposed to signify a male's willingness to allow females access to resources, thereby increasing the males access to that female. Although sharing access to food has obvious costs associated with it, the social factors that mediate calling in chickens give some clue as to the fitness benefits that counterbalance these costs. Determining the social contexts surrounding the production of many classes of vocal signal in multiple species of birds and mammals has proven useful in further understanding the functional significance of the call (eg., alarm calls: Karakashian *et al.* 1988; Heinrich and Marzluff 1991; contact calls: Mitani and Nishida 1993; Striedter *et al.* 2003; copulation calls; Townstead *et al.* 2008; food calls: Di Betetti 2005; Slocombe *et al.* 2010; Pollick *et al.* 2005).

Social factors such as group size (capuchin food calls: Pollick *et al.* 2005), the presence of important social partners (chimpanzee loud calls: Mitani and Nishida 1993; chimpanzee food calls: Slocombe *et al.* 2010), the presence of potential mates (chicken food calls: Marler *et al.* 1986a,b; Evans and Marler 1994), or the distance from (capuchin food calls: Di Betti 2005), or rank of (chimpanzee copulation calls: Townsend *et al.* 2008) potential receivers have been shown to influence the vocal signaling behaviour of many species. That social factors influence an individual's call rate, likelihood of calling, or latency between a stimulus (such as the discovery of food) and calling, may give insight into the ultimate function of a particular signal. Determining the degree to which a class of vocalization is produced in a specific social context may be a useful step in assessing the ultimate function of a call.

One class of vocalization, contact calls, are often classified almost purely by the social factors that accompany their use. Vocalizations are often classified as contact calls if they are used at elevated rates when individuals are spread out, or inter-individual visibility is restricted (Koda *et al.* 2008; Boinski 1993; Boinski and Campbell 1995; Wrangham 1977; Ghilieri 1984). As previous research has suggested that whinnies serve a contact function (Carpenter 1935; Eisenberg 1976; Ramos-Fernandez 2005), it follows that various social factors may have an effect on an individual's calling behaviour. The fluid grouping patterns characteristic of spider monkeys make this an interesting area of study, as neither the size, nor the composition of an individual's subgroup remain stable throughout the day (Aureli *et al.* 2008). As a result, the membership or stability of an individual's subgroup may affect an individual's calling behaviour, and may be an important consideration when attempting to understand the functional significance of the whinny vocalization.

4.1.2 Sex differences in sociality, and implications for signaling behaviour

The species typical loud vocalization of chimpanzees, known as the pant-hoot, is used at elevated rates by individuals when in large, dispersed subgroups. Pant-hoots have thus been hypothesized to serve a contact function, allowing for the formation and maintenance of chimpanzee subgroups (Wrangham 1977; Ghilieri 1984). Upon noting that males call more frequently when their alliance partners or close associates were nearby (as opposed to in their company or completely absent), Mitani and Nishida (1993) proposed a more explicit function of the call; that pant-hoots may allow closely associated males to recruit and maintain contact with allies and preferred social partners. Although both males and females use the call, it is used more frequently by males (Marler and Tenaza, 1977). Male chimpanzees are philopatric, form long-term social relationships with each other, and are generally the more gregarious sex, which may explain why males pant-hoot at higher rates than females.

Of particular interest to this study are the potential differences in calling behaviour by male and female spider monkeys across various social contexts. Early descriptive research into the vocal repertoire of spider monkeys suggested that the whinny was consistently produced in association with subgroup fusions (Klein, 1972). Chapman and Lefbvre (1990) suggested that whinnies attracted listeners in nearby subgroups to the location of the caller, thereby resulting in subgroup fusions. Ramos-Fernandez (2005) showed that whinnies are indeed attractive to receivers, but only when callers and receivers are preferred social partners. If preferred social partners are to coordinate their movements, the whinny vocalization may be one mechanism by which they are able to maintain vocal contact when visual contact is lost or hindered. This may be the case when associates are dispersed in larger subgroups, or during periods of subgroup instability (ie; during subgroup fissions or fusions). The close social bonds and high rates of

affiliative behaviour characteristic of male-male relationships (Fedigan and Baxter 1984; Symington 1988; Chapman 1990; Ramos-Fernandez *et al.* 2009) suggests that one important function of the whinny for males may be to facilitate regrouping or contact maintenance between social partners; male spider monkeys may call more frequently during periods of subgroup instability as a mechanism of maintaining contact, despite the increased chance of separation from their close male associates. This in many ways parallels the function of the chimpanzee pant-hoot, as proposed by Mitani and Nishida (1993).

Because female spider monkeys are not thought to have preferred social partners (Ramos-Fernandez *et al.* 2009), it is reasonable to assume that they would use the whinny vocalization at lower rates than males, as is the case with female chimpanzees and the pant-hoot vocalization. The results described in the previous chapter however show that in most behavioural contexts, females call at higher rates than males. The discrepancy between the function of the call as proposed by Ramos-Fernandez (2005) and the social behaviours of females presents a challenge; if females do not use the call to attract close associates, what is the functional significance of the whinny vocalization for females?

Here, I attempt to gain further insight into the function of the whinny vocalization for male and female spider monkeys by determining what social contexts elicit calling by either sex. I will examine the use of the call while taking into consideration subgroup size, composition, and changes to that composition through subgroup fissions and fusions. The implication of the call as a means of maintaining contact with preferred social partners would suggest that the call should be used by males in contexts where maintaining visual contact with close associates would be difficult, such as during subgroup fissions or fusions, or when in larger subgroups containing other males. Because female spider monkeys are the less gregarious sex, females

should have less reason to vocalize in association with either increased subgroup size or changes in subgroup composition, provided that the primary function of the whinny is to maintain contact between preferred social partners. If however females do call in association with larger subgroups or changes in subgroup composition, one might infer that calling by females serves an alternate function.

4.1.3 Objectives:

In this section, I hope to first determine whether winny vocalizations are associated with any specific subgroup characteristics. The first three subgroup characteristics I investigate relate to the effects of subgroup size and composition on calling. These subgroup characteristics include the size of a subject's subgroup, and the number of males or females in the subgroup. The next 6 subgroup characteristics relate to the stability of the subgroup. Subgroup stability here will refer to the number of individuals joining (in association with a fusion), or leaving (fission) a subject's subgroup. I will determine if an individual's likelihood of calling is related to the number of individuals joining or leaving a subject's subgroup, the number of females joining or leaving a subjects subgroup, and the sex of individuals joining or leaving a subjects subgroup. Finally, I will determine whether these subgroup characteristics affect the calling behaviour of both males and females to the same degree.

4.1.4 Predictions:

I will test the effect of 9 subgroup characteristics on the calling behaviour of male and female spider monkeys. Based on the proposal that the winny functions to allow close associates to maintain contact while dispersed within or between subgroups, I predict that the calling behaviour of males will be affected by these subgroup characteristics more than that of females. For a list of my predictions for males and females, see Table 7.

Table 7: Predicted calling behaviour for males and females for 9 subgroup characteristics

Subgroup characteristic	Prediction (Females)	Prediction (Males)
The size of an individual's subgroup	will not affect its likelihood of calling	Males will be more likely to call when in larger subgroups
The number of females in an individual's subgroup	will not affect its likelihood of calling	will not affect its likelihood of calling
The number of males in an individual's subgroup	will not affect its likelihood of calling	Males will be more likely to call when in subgroups containing other males
The number of individuals joining a subject's subgroup	will not affect its likelihood of calling	Males will be more likely to call when more individuals are joining their subgroup
The number of females joining a subject's subgroup	will not affect its likelihood of calling	will not affect its likelihood of calling
The sex of individuals joining a subject's subgroup	will not affect its likelihood of calling	Males will be more likely to call when males are joining their subgroup
The number of individuals leaving a subject's subgroup	will not affect its likelihood of calling	Males will be more likely to call when more individuals are leaving their subgroup
The number of females leaving a subject's subgroup	will not affect its likelihood of calling	will not affect its likelihood of calling
The sex of individuals leaving a subject's subgroup	will not affect its likelihood of calling	Males will be more likely to call when males are leaving their subgroup

4.2 Methods

4.2.1 Vocalization and Subgroup characteristic data

During 10 minute focal animal sampling periods, the time and behavioural context of all whinny vocalizations emitted by the focal animal were recorded. Behavioural contexts were state behaviours, and included foraging, inactive, social activities and traveling (see chapter 3 on the behavioural contexts of calling for details). The age and sex of the focal animal, as well as the age/sex class of all other individuals within the focal animal's subgroup were recorded at the onset of each 10 minute sample. Subgroup fissions and fusions were recorded on an 'all

observed occurrence' basis. In order to capture the possible effects of subgroup fissions and fusions that may have occurred immediately preceding or after a focal sample, focal samples were considered a 'fission' or 'fusion' focal if individuals joined or left the subgroup during, or within a 4 minute time interval around the sample (2 minutes before or after the 10 minute focal sample). This ensured that vocalizations that may have been associated with a subgroup composition change immediately before a focal sample were included as associated with that fission or fusion event. Similarly, I observed that the monkeys often called at the detection of approaching animals before I was aware that a fusion was occurring. Therefore, I considered all fissions or fusions two minutes after the end of a focal sample to be connected with that sample in order to capture calls that may have been associated with an impending arrival of others that the monkeys detected, but that I did not initially. The identity and age/sex classes of all individuals joining or leaving the subgroup were recorded. To separate the effects of fissions and fusion on the probability of a subject calling, focal samples that were associated with both a fission and fusion were discarded from the analysis.

4.2.2 Analysis: Effects of sex and subgroup characteristics

Focal animals were classified as either having called or not called during a sampling period. Although individuals sometimes called multiple times during a given focal sample, each sample was classified as either a 'whinny' focal or 'non-whinny' focal. This was done to decrease the risk of erroneously treating multiple whinnies within a single sample as independent events. Only focal samples in which subjects remained in sight for ≥ 8 minutes were included in the analysis.

A total of nine *Generalized Estimating Equation* (GEE) models were constructed to determine whether any specific subgroup characteristic(s) elicited a whinny response from males

or females. GEEs are a variant of generalized linear models (GLM) that control for repeated measures on the same subjects over time. The nine GEE models were divided into two groups: one group looking at the effects of subgroup size and composition on calling, and the next group testing for the effects of subgroup fissions and fusions (subgroup stability) on calling. Each of the models was used to predict the likelihood that a subject would call based on its sex, and one of nine independent variables relating to characteristics of their subgroup. In all of the models, the dependant variable was the presence or absence of a whinny vocalization emitted by a focal animal during a sampling period. All 9 GEE models are summarised in Table 8.

Table 8: Summary of 9 GEE models. All models test the effects of the three predictor variables on the likelihood of a focal subject calling during a given focal sample. * indicates an interaction between two variables.

Name of model		Predictor variable 1	Predictor variable 2	Predictor variable 3 (interaction effect)	Number of Focal samples per model
Effects of subgroup size and composition	Group size model 1	Sex of focal subject	Number of adults in subject's subgroup	Sex of focal subject * Number of adults in subject's subgroup	674
	Group size model 2	Sex of focal subject	Number of adult females in subject's subgroup	Sex of focal subject * Number of adult females in subject's subgroup	674
	Group size model 3	Sex of focal subject	Number of adult males in subject's subgroup	Sex of focal subject * Number of adult males in subject's subgroup	674
Effects of subgroup stability	Fission model 1	Sex of focal subject	Number of adults leaving subject's subgroup	Sex of focal subject * Number of adults leaving subject's subgroup	810
	Fission model 2	Sex of focal subject	Number of females leaving subject's subgroup	Sex of focal subject * Number of females leaving subject's subgroup	802
	Fission model 3	Sex of focal subject	Sex of individuals leaving subject's subgroup	-	48
	Fusion model 1	Sex of focal subject	Number of adults joining subject's subgroup	Sex of focal subject * Number of adults joining subject's subgroup	810
	Fusion model 2	Sex of focal subject	Number of females joining subject's subgroup	Sex of focal subject * Number of females joining subject's subgroup	795
	Fusion model 3	Sex of focal subject	Sex of individuals joining subject's subgroup	-	65

The nine subgroup characteristics organised by model group were: A) Subgroup size and composition models: 1) The total number of adults in a focal animal's subgroup, 2) the number of adult females in a focal animal's subgroup, 3) the number of adult males in a focal animal's subgroup. B) Fission Models: 1) the number of adults leaving a focal animal's subgroup during a subgroup fission, 2) the number of adult females leaving a focal animal's subgroup 3) the sex of individuals leaving a focal animal's subgroup. C) Fusion models: 1) the number of adults joining a focal animal's subgroup at a subgroup fusion, and 2) the number of adult females joining a focal animal's subgroup 3) the sex of individual's joining a focal animal's subgroup. I was not able to analyse the effects of males leaving or joining a subgroup specifically as there were too few focal samples that fit the criteria for those analyses. Instead, the third variables listed under both the fission and fusion models above were used to determine whether the sex of individual's joining or leaving a subgroup affected the likelihood of calling by individuals within that subgroup.

The first model group focused on subgroup size (see Table 8). In the first of these models, the independent variables were the sex of the focal animal as well as the number of adults (excluding the focal animal) in the focal animal's subgroup. In the second and third models, the number of adult females and adult males in the focal animal's subgroup were analyzed separately. This was done to determine whether subjects responded differently to the presence of females or males. For all three subgroup size models, only focal samples in which subgroup composition remained constant throughout the sample were used in the analysis, i.e., focal samples in which either a fission or a fusion occurred were not used in the analysis. In all three models, I tested for an interaction between both independent variables and the likelihood that the focal animal emitted a whinny vocalization.

The next model group dealt with subgroup stability. The 6 subgroup stability models were broken into two categories: 3 models dealing with subgroup fissions, and three models dealing with subgroup fusions (see table 8). In the first fission model (Fission model 1), the independent variables were the sex of the focal animal and the total number of adults who left the focal animal's subgroup in association with that focal sample. Similarly, in the first fusion model (Fusion model 1), the independent variables were the sex of the focal animal and the total number of adults who *joined* the focal animal's subgroup in association with that focal sample. In the second fission model, I specifically considered the total number of females that left a focal animal's subgroup. This was also done for the second fusion model, with the number of females that joined a subgroup being considered specifically. I did this to determine whether subjects responded differently at fissions or fusions based on the sex of individuals leaving or joining their subgroup. Focal samples in which both males and females left or joined the focal animal's subgroup were discarded in these second models. This allowed for the effects of females coming and going from a focal animal's subgroup to be examined separately from males. In all four of these fission-fusion models (Fission model 1, fission model 2, fusion model 1, fusion model 2), I also tested for an interaction between the sex of the focal animal and the second independent variable on the focal animal's likelihood of calling.

As previously mentioned, I could not analyse the effects of just males leaving or joining a subgroup using the same analytical methods described above. To address this issue, I ran two more GEE models on smaller subsets of the data (fission model 3, fusion model 3). For these analyses, only focal samples that were associated with a) a fission, or b) a fusion were analysed. As was done in fission model 2 and fusion model 2, focal samples in which both males and females left or joined the focal animal's subgroup were discarded in these last analyses. These

models were used to determine whether there was a difference in the likelihood of calling by a focal subject at a fission or fusion, based on the sex of the animals joining or leaving their subgroup.

4.3 Results: Sex and Subgroup characteristics

4.3.1 Subgroup size

Subgroup size across focal samples varied from 0 to 10 adult individuals. The mean subgroup size across samples was 1.38 adults, excluding the focal animal. The number of females in a subgroup ranged from 0 to 7 individuals with an average subgroup containing 1.01 female adults excluding the focal animal. The number of males in a subgroup ranged from 0 to 4 individuals, with an average subgroup containing 0.28 male adults excluding the focal animal. For a breakdown of audience size by the sex of the focal animal, see Table 9. Of the 714 focal samples on females, 124 were associated with either a fission, a fusion, or both, leaving a total of 590 focal samples on females for the group size analysis. Of the 106 focal samples on males, 22 were associated with either a fission, a fusion, or both, leaving a total of 84 focal samples on males for the group size analysis.

Table 9: Breakdown of subgroup size by sex

focal animal	Total number of focal samples (N)	Number of adults in subgroup (excluding focal subject)			Number of adult females in subgroup (excluding focal subject)			Number of adult males in subgroup (excluding focal subject)		
		Minimum	Maximum	Average	Minimum	Maximum	Average	Minimum	Maximum	Average
Male/Female Combined	674	0	10	1.38	0	7	1.01	0	4	0.28
Female	590	0	7	1.29	0	7	1.12	0	3	0.17
Male	84	0	10	1.98	0	6	0.92	0	4	1.06

When considering male and female subgroup members together, results of the GEE model showed no relationship between the likelihood of calling and the sex of the focal animal ($\beta = 0.901, p = 0.140$), subgroup size ($\beta = 0.143, p = 0.555$), or the interaction between the sex of the focal animal and the size of its subgroup ($\beta = -0.152, p = 0.566$). The same held true when considering females in the subgroup specifically (group size model 2), and when considering only male subgroup members (model 3); Neither GEE model showed a relationship between the likelihood of calling and the sex of the focal animal (Group size model 2: $\beta = -0.080, p = 0.666$; Group size model 3: $\beta = 0.845, p = 0.074$), the number of females or males in the subgroup (Group size model 2: $\beta = 0.059, p = 0.828$; Group size model 3: $\beta = 0.225, p = 0.360$), or the interaction between the sex of the focal animal and the number of females or males in the subgroup (Group size model 2: $\beta = -0.074, p = 0.808$; Group size model 3: $\beta = -0.90, p = 0.521$). For a table of the results of the subgroup size analyses, see appendix B

4.3.2 The effects of Subgroup stability – Fission and fusions

In five of the six subgroup stability models, the results of the GEE showed that the sex of the focal animal significantly predicted its likelihood of calling during a sample period (Fission model 1 $\beta = 0.728$, $p = 0.011$; fission model 2 $\beta = 0.783$, $p = 0.007$; fusion model 1 $\beta = 0.768$; $p = 0.014$; fusion model 2 $\beta = 0.756$, $p = 0.014$; fusion model 3 $\beta = 2.894$, $p = 0.003$). Female subjects were more likely to call during a focal sample than were males in these five models, regardless of subgroup stability. The only subgroup stability model that did not suggest females were more likely to call than males overall was fission model 3 (i.e. sex of the individual leaving the focal group; $\beta = 1.620$, $p = 0.098$).

Fissions

Of the 714 focal samples on females, 57 were associated with subgroup fissions by adults of either sex. Of those 57 samples, 8 were also associated with a subgroup fusion, and were therefore excluded from this analysis. Of the 106 focal samples on males, 9 were associated with subgroup fissions by adults of either sex. Two of those samples were not used in the analysis as they were also associated with a subgroup fusion. For the second fission model, all fissions that involved males were discarded, leaving a total of 699 focal samples on females, and 103 focal samples on males. Of the focal samples on females, 42 were associated with subgroup fissions that did not also include fusions, and 6 of the focal samples on males were associated with subgroup fissions that did not also include fusions. For a complete breakdown of the samples used in these analyses, see table 10.

Table 10: Breakdown of sample sizes for fission GEE models. Samples marked with an asterix were too small for statistical analysis.

Sex	Total number of focal samples (model 1)	Number of focal samples associated with a subgroup fission (model 1)	Total number of focal samples (model 2)	Number of focal samples associated with a subgroup fission in which only females left (model 2)	Number of focal samples associated with a subgroup fission in which only males left *	Number of focal samples associated with a subgroup fission (model 3)
Female	706	49	699	32	10	42
Male	104	7	103	4	2	6
Total	810	56	802	36	12*	48

Fission model 1 - Total number of adults leaving the subgroup during a focal sample:

When looking at subgroup fissions with males and females simultaneously, results of the GEE model showed that the likelihood of a subject calling during a focal sample was not significantly influenced by the number of adults leaving a focal animal's subgroup when the sex of the focal animal was not taken into account ($\beta = -0.767$, $p = 0.133$). There was a significant interaction effect between the sex of the focal animal and the number of adults leaving a subgroup ($\beta = 1.055$, $p = 0.041$). Females were significantly more likely to call as the number of adults leaving the subgroup increased ($\beta = 0.288$, $p < 0.001$; Fig 3). The number of adults leaving the subgroup did not significantly influence the likelihood of calling in males ($\beta = -0.703$, $p = 0.175$).

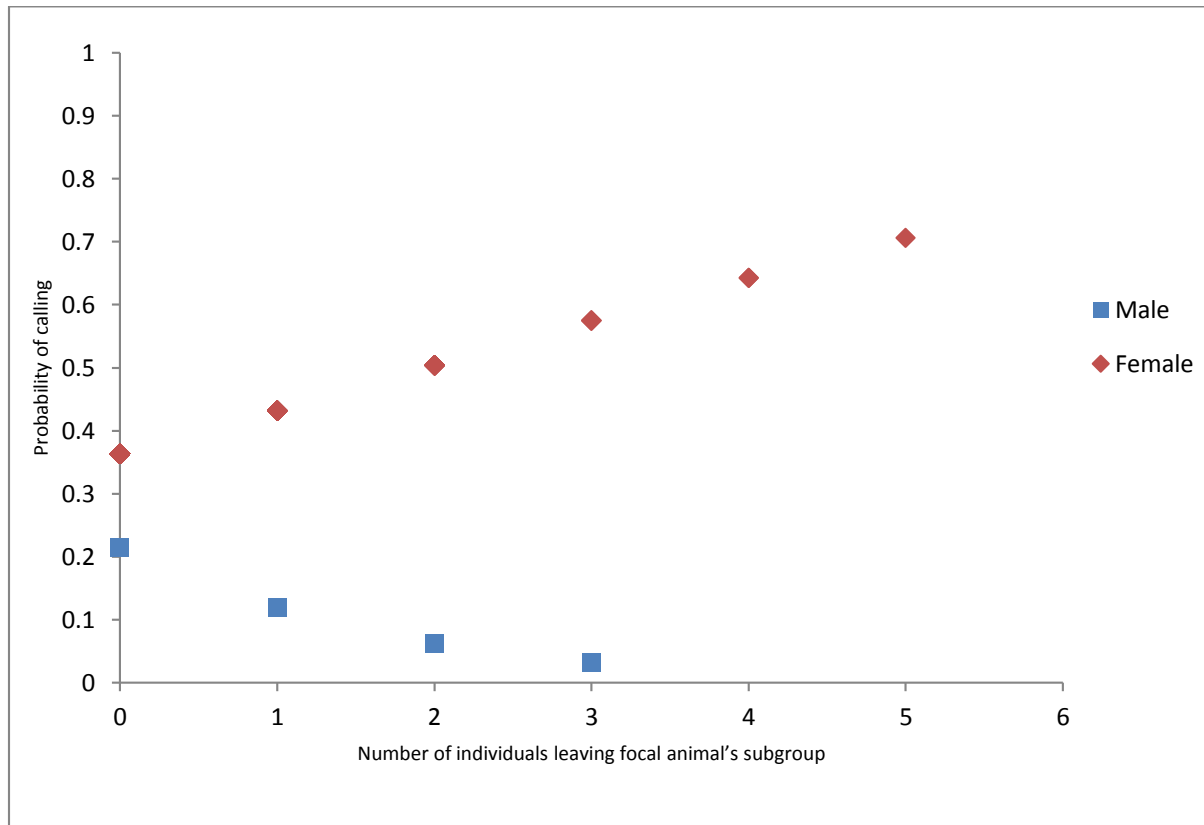


Fig 3: Predicted probability of calling by males and females for a given number of individuals leaving a subject's subgroup. Females were significantly more likely to call as the number of adults leaving the subgroup increased ($\beta = 0.288, p < 0.001$).

Fission model 2 - Total number of females leaving the subgroup during a focal sample:

Results of the GEE model showed that the likelihood of a subject calling during a focal sample was not significantly influenced by the number of females leaving a focal animal's subgroup when the sex of the focal animal was not taken into account ($\beta = -0.347, p = 0.397$).

There was no significant interaction effect between the sex of the focal animal and the number of females leaving ($\beta = 0.575, p = 0.243$).

Fission model 3 – Sex of adults leaving the subgroup during a fission:

Analysis of the 48 focal samples that were associated with a fission with either females or males (mixed sex fusions were removed) revealed that the likelihood of a focal animal calling was not affected by the sex of the individuals that left the subgroup ($\beta = -0.038$, $p = 0.953$).

Summary: Effects of subgroup fissions on the likelihood of calling:

In the first 2 models, the sex of the focal animal was a significant predictor of whether a subject called during a sample when the stability of their subgroup was not taken into account (fission model 1; $p = 0.011$, fission model 2; $p = 0.007$, fission model 3; $p = 0.098$). In both models, focal samples on females were more likely to contain a whinny vocalization than focal samples on males. When looking at the effect of subgroup fissions on a subject's probability of calling, the first model showed that the probability of a female emitting a whinny vocalization increased significantly as the number of adults leaving the subject's subgroup increased. This did not hold true for males. The third model showed that the probability of an individual calling in association with a subgroup fission was not dependent on the sex of the animals that left the focal animal's subgroup. Results are summarized in Table 11.

Table 11: Results from three GEE models showing interactions between the likelihood of calling and the sex of the focal subject, as well as the number and sex of adults fissioning from a focal subject's subgroup. Independent variables are the sex of a subject, the number of adults (Fission model 1), the number of females (Fission model 2), or sex of individuals (Fission model 3) leaving a subject's subgroup during a focal sample. The dependant variable is the presence/absence of a whinny vocalization emitted by a focal animal.

Model	Effect	β	P	Females		Males	
				β	p	B	P
Fission model 1	Sex of subject	0.728	0.011 *	na	na	Na	Na
	Number of adults leaving subject's subgroup	-0.767	0.133	na	na	Na	Na
	Sex of subject* Number of adults leaving subject's subgroup	1.055	0.041 *	0.288	<0.001*	0.703	0.175
Fission model 2	Sex of subject	0.783	0.007 *	na	na	Na	Na
	Number of females leaving subject's subgroup	-0.347	0.397	na	na	Na	Na
	Sex of subject* Number of females leaving subject's subgroup	0.575	0.243	-	-	-	-
Fission model 3	Sex of subject	1.620	0.098	na	na	Na	Na
	Sex of individuals leaving subject's subgroup	-0.038	0.953	na	na	Na	Na

Fusions

Of the 714 focal samples on females, 75 were associated with subgroup fusions, though 8 of these were removed as they were also associated with a fission. Of the 106 focal samples on males, 15 were associated with subgroup fusions. Two of these samples were not used in the analysis as they were also associated with a subgroup fission. For the second fusion model, all fusions that involved males were discarded, leaving a total of 694 focal samples on females, and 101 focal samples on males. Of the focal samples on females, 55 were associated with subgroup fusions that did not also include fissions, and 10 of the focal samples on males were associated with subgroup fusions that did not also include fissions. For a complete breakdown of the samples used in these analyses, see table 12.

Table 12: Breakdown of sample sizes for fusion GEE models. Samples marked with an asterisk were too small for statistical analysis.

Sex	Total number of focal samples (model 1)	Number of focal samples associated with a subgroup fusion (model 1)	Total number of focal samples (model 2)	Number of focal samples associated with a subgroup fusion with females only (model 2)	Number of focal samples associated with a subgroup fusion with males only *	Number of focal samples associated with a subgroup fusion (model 3)
Female	706	67	694	41	14	55
Male	104	13	101	9	1	10
Total	810	80	795	50	15*	65

Fusion model 1 - Total number of adult joiners associated with a focal sample:

When considering fusions in which both males and females join a focal subject's subgroup, results of the GEE model showed that the probability of a subject calling during a focal sample was not significantly influenced by the number of adults that joined ($\beta = 0.059$, $p = 0.883$). There was no significant interaction effect between the sex of the focal animal and the number of adult joiners on the probability of calling ($\beta = 0.418$, $p = 0.322$). Females were more likely to call than males, but the likelihood of an individual calling during a focal sample was not influenced by the number of other monkeys joining the subgroup.

Fusion model 2 - Total number of female joiners associated with a focal sample:

Results of the GEE model showed that the likelihood of a subject calling during a focal sample was not influenced significantly by the number of females joining a focal animal's subgroup when the sex of the focal animal was not taken into account ($\beta = -0.278$, $p = 0.365$).

There was a significant interaction effect between the sex of the focal animal and the number of female joiners ($\beta = 1.118, p = 0.006$). Females were significantly more likely to call as the number of females joining the subgroup increased ($\beta = 0.840, p = 0.002$). This did not hold true for males ($\beta = -0.276, p = 0.370$; Fig 4).

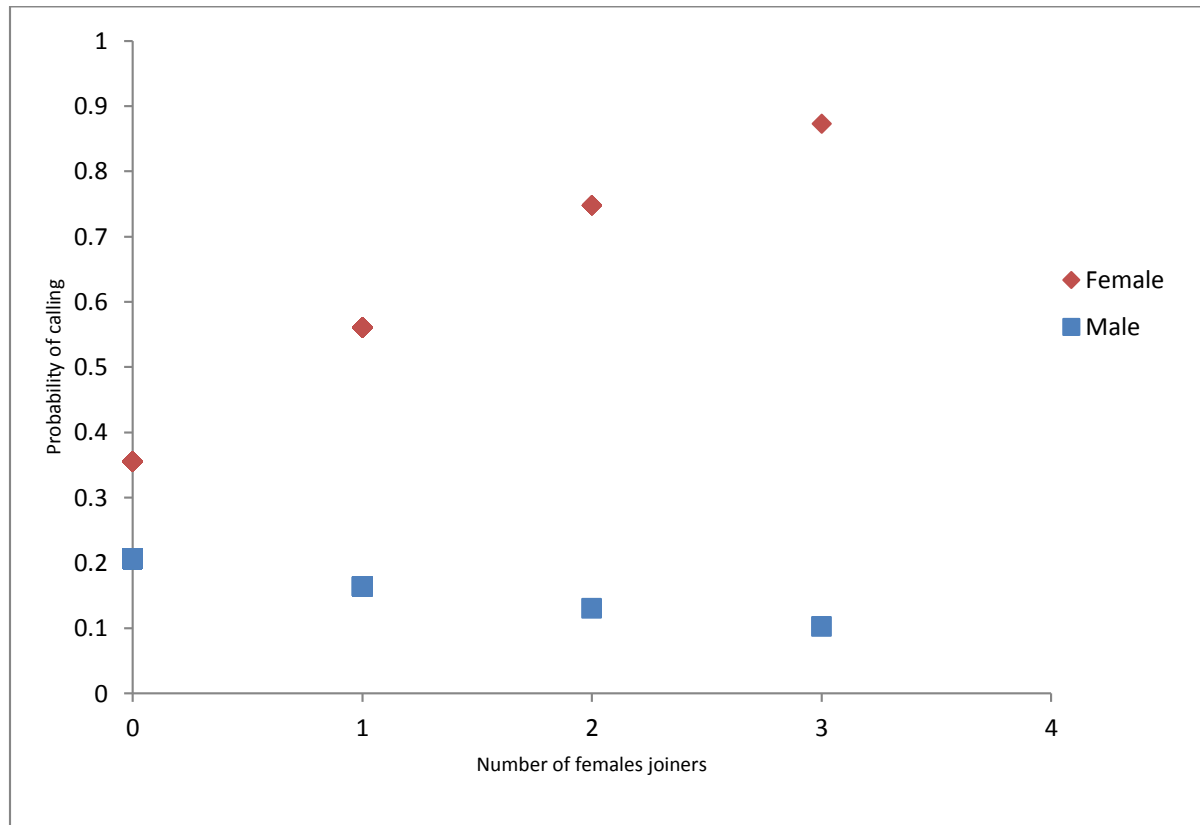


Fig 4: Predicted probability of calling by males and females for a given number of females joining a subject's subgroup. Females were significantly more likely to call as the number of females joining the subgroup increased ($\beta = 0.840$, $p = 0.002$).

Fusion model 3 – Sex of adults joining the subgroup during a fusion:

Analysis of the 65 focal samples that were associated with a fusion with either females or males (mixed sex fusions were removed) revealed that the likelihood of a focal animal calling was not affected by the sex of the individuals that joined the subgroup ($\beta = 0.330$, $p = 0.505$).

Summary: Effects of subgroup fusions on the likelihood of calling:

In all three fusion models, the sex of the focal was a significant predictor of whether a subject called during a sample; ie., females were more likely to call during a focal sample than were males (Fusion model1; $p = 0.014$, Fusion model 2, $p = 0.014$, Fusion model 3, $p = 0.003$).

When looking specifically at the effect of female joiners on a subject's probability of calling, the model showed that females were more likely to produce a whinny vocalization as the number of females joining their subgroup increased. This did not hold true for males; neither the number of adults, or adult females joining a subgroup affected the likelihood that males would emit a whinny vocalization during a focal sample. The third model showed that the probability of an individual calling in association with a subgroup fusion was not dependent on the sex of the animals that joined the focal animal's subgroup. Results are summarized in Table 13.

Table 13: Results from three GEE models showing interactions between the likelihood of calling and the sex of the focal subject, as well as the number and sex of adults joining a focal subject's subgroup. Independent variables are the sex of a subject, and the number of adults (Fusion model 1), the number of females (Fusion model 2), or sex of individuals (Fusion model 3) joining a subject's subgroup during a focal. The dependant variable is the presence/absence of a whinny vocalization emitted by a focal animal.

Model	Effect	β	p	Females		Males	
				β	P	B	P
Fusion model 1	Sex of subject	0.768	0.014 *	na	Na	Na	Na
	Number of adults joining subject's subgroup	0.059	0.883	na	Na	Na	Na
	Sex of subject* Number of adults joining subject's subgroup	0.418	0.322	-	-	-	-
Fusion model 2	Sex of subject	0.756	0.014 *	na	Na	Na	Na
	Number of females joining subject's subgroup	-0.278	0.365	na	Na	Na	Na
	Sex of subject* Number of females joining subject's subgroup	1.118	0.006 *	0.840	0.002 *	-0.276	0.370
Fusion model 3	Sex of subject	2.894	0.003 *	na	Na	Na	Na
	Sex of individuals joining subject's subgroup	0.330	0.505	na	Na	Na	Na

4.4 Discussion:

The analyses presented above tested whether winny vocalizations are associated with any specific subgroup characteristics. First, I tested whether the size and sex composition of an individual's subgroup affects its likelihood of emitting a winny vocalization. The results of the subgroup size analysis suggest that, regardless of its sex, the likelihood of a focal animal emitting a winny vocalization is not dependent on the total number of adults in its subgroup. This also holds true when the total number of adult males or adult females in the subgroup are considered separately. My predictions, that males would be more likely to call when in larger subgroups and in subgroups where other males were present, were not supported by these results. It is possible that once within a subgroup with a stable composition, spider monkeys do not rely heavily on the winny vocalization to continually monitor the whereabouts of other individuals.

The second section of the analysis tested whether the stability of an individual's subgroup affects its likelihood of emitting a winny vocalization. I tested whether an individual's calling behaviour is affected by the number of individuals joining its subgroup (in association with a fusion), or the number of individuals leaving its subgroup (in association with a fission). I also tested whether the sex of the individuals joining or leaving a subject's subgroup has an effect on its likelihood of calling. Finally, I tested whether these effects are different if the focal subject is male or female. My results show that the vocal behaviour of females is affected by both subgroup fissions and fusions, whereas the vocal behaviour of males is not. As the number of adult females joining a focal animal's subgroup increases, it becomes more likely that female focal animals will emit a winny vocalization (fusion model 2). Females are also more likely to call as the number of adults leaving their subgroup increases (fission model 1). Both fission model 3 and fusion model 3 suggest that the likelihood of a focal animal calling in association

with a fission or a fusion is not dependent on the sex of the animals joining or leaving the focal animal's subgroup. Although previous researchers have noted that whinny vocalizations are often emitted in association with subgroup fusions (Eisenberg 1976; Ramos-Fernandez 2005), this is the first study to examine the differential use of the call by males and females in this context. Additionally, the present study is the first to note the association between calling by females and subgroup fissions.

My central prediction as to the effect of subgroup stability on the calling behaviour of each sex was that males would be more likely to call than females in association with both fissions and fusions. This prediction was based on two assumptions: First, that whinnies function primarily to allow preferred social partners to maintain contact and coordinate their movements (Ramos-Fernandez 2005, 2008), and secondly, that while males associate at rates that suggest active companionship, females are not thought to form close associations (Symington 1988; Chapman 1990; Fedigan and Baxter 1984, Aureli *et al.* 2008; Ramos-Fernandez *et al.* 2009). The results of this study do not support my prediction, bringing into question the previously proposed function of the call.

My results show that the sex of the focal animal is a significant predictor of whether or not an animal called during a given sampling period; female focal animals are more likely to call than males, regardless of any changes in subgroup composition. That the likelihood of an individual calling during a given sampling period is significantly higher if the focal subject is female is consistent with the results of the behavioural context analysis presented in the previous chapter; that females call at a higher rate than males overall. It is possible that females call at elevated rates relative to males simply because they tend to be more separated throughout their home range, thereby requiring the ability to locate each other using a vocal, as opposed to a

visual method. As males tend to travel through their range together, there may be little need to call, as visual contact is more easily maintained. This explanation suggests that females call at elevated rates as a means of locating conspecifics that they cannot see, and that their increased likelihood of calling relates to their being less gregarious, and more spatially isolated than males. Although this explanation may in part explain the increased tendency to call by females compared to males, it ignores the proposal that calling is used primarily to maintain contact with specific, preferred social partners. Furthermore, the fact that females are more likely to call in association with changes to subgroup composition is not explained based on this rationale alone. The positive association between the probability of calling, and the number of individuals leaving or joining a female's subgroup does not substantiate my predictions as to the calling behaviour of females. The tendency for non-socially bonded females to call in association with subgroup fissions and fusions suggests that, at least for females, whinny vocalizations serve an alternate function than what has been proposed by previous researchers.

The playback experiments of Ramos-Fernandez (2005) demonstrate that the individual specific variation in the acoustic properties of the whinny vocalization are both conspicuous and salient to receivers, at least when callers and receivers are close associates. What has yet to be explored is how non-closely associated individuals use this information. Because whinnies are individually recognisable (Chapman 1990; Teixidor and Byrne 1999), receivers have the ability to respond to each other's calls based on their own social identity, or their social relationship with the caller. This means that the functional significance of the whinny vocalization may be dependent on the relationship between callers and receivers (Ramos-Fernandez 2008); that is, if calling simply informs listeners to the presence of a specific individual, the effect of calling is likely determined by the nature of the relationship between a caller and the receiver(s). Calling

by males may therefore function to announce their presence, thereby allowing a caller's close associates to locate them within the active space of the vocalization. Calling by females may also inform receivers that a caller is nearby, although the outcome may differ from that of male calling; the outcome would be dependent on the relationship between that female and the individual(s) who perceive the call.

Because females show association patterns that suggest either passive association or active avoidance (Ramos-Fernandez *et al.*, 2009), it seems likely that receivers would be more likely to avoid female callers, or be indifferent to them. It is therefore possible that by announcing their presence, females can better space themselves out, thereby maintaining inter-individual spacing. This might explain their tendency to call when the composition of their subgroup changes. It has been noted that aggression was often observed in association with subgroup fusions (Klein 1974; Aureli and Schaffner 2007). In particular, females risk receiving aggression from conspecifics who join their subgroup during a subgroup fusion. The ability to maintain inter-individual spacing relative to new 'joiners' using the vocal mode may prove beneficial, as it would allow females to 'announce' their presence without having to come too close to potential aggressors. The results described in the previous chapter (chapter 3) indicated that females call at elevated rates while foraging as well. Asensio *et al.* (2008) reported that female spider monkeys direct aggression towards other females in feeding contexts, and Slater *et al.* (2009) found coalition formation and aggression amongst females were more common in feeding contexts than expected based on the observed feeding time. Females might call in contexts where there is an elevated risk of receiving aggression which may function as a spacing mechanism, thereby allowing callers to avoid aggressive interactions.

Mechanisms for decreasing aggression at subgroup fusions have been suggested prior to the present study. Aureli and Schaffner (2007) noted that following subgroup fusions, members of a subgroup act aggressively towards individuals joining their subgroup at higher rates than they do towards individuals who are in their subgroup pre-fusion. The rate of embraces between individuals increases within this same period as well. Because individuals who embrace do not aggress towards each other, it was inferred that embraces may be one mechanism by which individuals reduce tension associated with fusions. These findings support the findings of Schaffner and Aureli (2005), which suggest embraces may signify a benign disposition between individuals at fusions, or in other potentially ‘tense’ situations. The association between the use of the whinny vocalization and changes in subgroup composition by females may suggest that calling is another mechanism by which aggression at fusions may be avoided, although I propose that the mechanism by which this may function differs somewhat from that of the embrace; while embraces may function to signify benign intent at a fusion, whinnying may allow individuals to make appropriate choices as to whether or not they should approach specific individuals based on their relationship with that particular individual. Taken together, the fact that whinnies are individually recognisable may allow receivers to decide whether to approach (males) or avoid the caller (females) depending on the relationship between them. Females may call at higher rates than males as they stand to incur more costs by approaching non-associates, as demonstrated by the elevated rates of female directed aggression observed at subgroup fusions (Link *et al.* 2009).

In regards to males, my results showed that the probability of calling did not increase in association with subgroup fissions or fusions. Because male-male dyads are characterised by active companionship, I had predicted that a male’s likelihood of calling would increase when

subgroup composition was unstable. In this way, closely associated males could maintain contact and coordinate their movements despite changes in subgroup composition. One possible explanation for why I did not observe this is that closely associated males are more likely to be within visual range of each other as they travel in the same subgroup. As a result, there may not be a heavy reliance on vocal mechanisms to maintain contact in most cases. When males do whinny, it may function to bring associates within a caller's subgroup closer, which would still be in accordance with the findings of Ramos-Fernandez (2005), but would not have been detected using the data collection methods of the present study. This is because spider monkey subgroups are highly variable with respect to spatial cohesion over time, and it is therefore difficult to reliably monitor the whereabouts of multiple individuals relative to a focal animal over extended periods. As a result, it was not possible to accurately assess a receiver's change in position relative to callers within a subgroup in most instances. It should also be noted that due to a small sample size, I was not able to analyse the effect of subgroup fissions or fusions involving males specifically on the likelihood of calling by either males or females. It is therefore possible that males do increase their likelihood of calling specifically when changes in subgroup composition involve the arrival or departure of other males.

The elevated use of the whinny vocalization specifically by females in association with subgroup fissions and fusions may suggest that females use the whinny vocalization to serve a function apart from what has been previously described. Proposals as to the function of the call by females should take the context in which they use the call into consideration, as well as what is known about the behaviours that typify females of this species.

CHAPTER 5: GENERAL DISCUSSION

5.1 Results Summary

The results of this study suggest that the use of whinnies differs substantially between male and female spider monkeys at RCNR. Overall, female spider monkeys call at higher rates than males in almost all activities. When broken down by activity category, females call at elevated rates while foraging compared to any other context. The lowest rate of calling by females was when individuals were engaged in social activities, although call rate in this context was only significantly lower than inactive and traveling contexts in the long term analysis. The rate at which females called while engaged in social activities was not statistically different from the consistently low rates of calling by males in either of the behavioural context analyses.

The calling behaviour of males and females also varied significantly when taking into account various subgroup characteristics. First, changes in subgroup composition had an effect on the likelihood of calling by females, but not by males. Notably, I show that females are more likely to call as the number of females joining their subgroup (during a subgroup fusion) increases. Similarly, females are more likely to call as the total number of adults leaving their subgroup (during a subgroup fission) increases. The tendency for female subjects to call during both fissions and fusions suggests an association between shifts in subgroup membership, and the use of the whinny vocalization. Interestingly, the size of a subject's subgroup did not affect the likelihood of calling in either sex. Not only did this hold true when the total number of adults in a focal subject's subgroup was taken into account, but also when the number of adult females, or number adult males were considered separately. This suggests that the sex composition of an individual's subgroup also does not affect its likelihood of calling. My results suggest that it is

not subgroup membership, but changes in membership that affect an individual's tendency to call.

5.2 Implications for the functional significance of the whinny

The results of this study raise further questions about the function of the whinny vocalization, particularly given what is known about the social patterns of the sex (females) that appears to make use of the call most frequently. If whinnies function to allow individuals to maintain specific associations, as proposed by Ramos-Fernandez (2005), then individuals who have stronger associations (males) should use the call more often. One might also expect males to increase their rate of calling in contexts likely to involve separation from their close associates; namely, when traveling, and/or during periods in which the composition of their subgroup is changing (ie., fissions or fusions). This does not seem to be the case.

Just as surprising is the elevated use of whinnies by females, both while foraging and in association with changes in subgroup composition. As females are thought to forage independently as a means of decreasing feeding competition, their use of the vocalization at elevated rates in feeding contexts is surprising based on previous work that has suggested the call is attractive to receivers (Chapman and Lefebvre 1990). Also, the association between changes in subgroup composition and calling by females is unexpected, as females are not thought to form the same kinds of affiliative relationships with each other as are males, with whom they might coordinate their movements (Ramos-Fernandez *et al.* 2009). Due to these incongruities, one might surmise that the functional significance of the whinny vocalization is different than what has been proposed previously, at least in the case of females.

5.2.1 Are whinnies “cohesion” calls?

Studies by both Chapman and Lefebvre (1990) and Ramos-Fernandez (2005) imply that whinnies are attractive to conspecifics. In addition, other researchers have observed that during subgroup fusions, individuals from both subgroups often exchange whinnies (Eisenberg 1976; Ramos-Fernandez 2005; personal observation). One question that arises from this latter observation however is whether calling results in a subsequent fusion (which is consistent with the proposal above that the whinny is an “attractive” call), or whether it is the fusion itself that triggers the calling. The methods used in Chapman and Lefebvre’s (1990) study, for example, may not have been sensitive enough to make this distinction. By using a playback design however, Ramos-Fernandez (2005) was able to show that individuals may be attracted to each other’s whinnies, though this only seems to be the case when the caller and receiver are preferred social partners. It seems plausible then that calling by an individual may result in a subsequent fusion, but only if the caller and the receiver(s) are close associates. However, my analysis shows that it is females who call at elevated rates both in foraging contexts, and during changes in subgroup composition. As females do not appear to have consistent and preferred social partners (Ramos-Fernandez *et al.* 2009), it raises the question of whether whinnies emitted by females are attractive to other group-members and lead to fusions.

My analyses also suggest an additional contextual dimension whereby spider monkeys (females in particular) are likely to call in association with subgroup fissions. The positive association between the number of individuals leaving a subject’s subgroup, and the subject’s likelihood of calling is inconsistent with the theory that whinnies act to attract conspecifics. Rather, whinnies may be produced in response to any changes in subgroup composition, perhaps

as a result of a sudden increase in anxiety in response to an abrupt change in social environment. That whinnies may be associated with increased arousal is also suggested by my own observation that the call is often given in response to sudden noises, such as breaking branches, falling trees, or loose rocks rolling down hillsides. These sudden noises may in some way simulate the movement of conspecifics within audible range, yet out of sight of the caller, as would be the case during both fissions and fusions. The fact that individuals respond to these sudden noises with a whinny vocalization is more in line with the idea that the call is given as a response to the arrival or departure of another monkey, as opposed to acting to attract conspecifics.

5.3 Motivation, Mechanism and Function

An animal signal, such as a vocalization, can be broken down into four principal components. These components are the *signal* itself, the *motivation* that elicited the signaling behavior from the actor, the *mechanism* by which the signal affects a receiver(s), and the ultimate *function* of the signal; ie., how the signal benefits the signaler (Smith 1977). The signal itself is the only component which is directly observable, while motivation, mechanism and function must be inferred from the context(s) eliciting a signal, or the behaviours of both signalers and receivers following signal production. Previous work on the whinny vocalization has focussed primarily on the function of the call (Chapman and Lefebvre 1990; Ramos-Fernandez 2005), and on the mechanism by which the call may function (Teixidor and Byrne 1999; Ramos-Fernandez 2005, 2008). As discussed above, my results suggest that, at least for females, the functional significance of the whinny vocalization may differ from what has been

previously proposed. Here, I will discuss the motivation, mechanism and function of the whinny vocalization based on the results of my study.

5.3.1 Motivation: the proximate triggers of calling

The term motivation is used to refer to the internal state of an animal which elicits signaling. For example, an animal may emit a vocalization in response to fear, sexual arousal, or excitement. Motivation must be inferred by observing the context of signal production, or the behaviour of the signaler at the time of signal production. Thus far, no research on the whinny vocalization has focused on the motivation for calling.

One interesting finding of my study is that females call in contexts in which they are at a higher risk of receiving aggression. Klein (1974) noted that aggression in spider monkeys was often observed in association with both subgroup fusions, and in feeding contexts. Females in particular risk receiving aggression from conspecifics who join their subgroup during a fusion event (Klein 1974; Aureli and Schaffner 2007). Additionally, although it is less common than female directed aggression by males, female-female aggression occurs primarily in feeding contexts (Fedigan and Baxter 1984; Symington 1990). The observation that calling by females seems to be associated with contexts that are linked to female directed aggression suggests that on a motivational level, calling may be a response to elevated levels of stress or anxiety. Intragroup aggression in spider monkeys is primarily directed toward females, and this may be one reason why females tend to call more than males. Also, because females are more solitary than males, and do not have strong social alliances, females may ultimately experience relatively high levels of stress. Further supporting this proposal is the fact that spider monkeys call at the sudden onset of noises, and upon first noticing researchers as they approach in the field (personal

observation, Teixidor and Byrne 1999). It is interesting to note that my results show reduced rates of whinnying in females when they were engaged in social activities. Here, `social activities` refer to both affiliative and passive social behaviours, such as when individuals were sitting in body contact, engaged in social play, or participating in social grooming. Because grooming (Boccia *et al.* 1989; Aureli *et al.* 1999; Gust *et al.* 1993; Shutt 2007), as well as these other behaviours are presumably periods of reduced stress for an individual, the fact that females call at reduced rates in these contexts is further evidence that calling may be triggered at the proximate level by elevated levels of arousal and anxiety.

5.3.2 Mechanism

Although my analysis did not focus on the mechanism by which whinnies affect receivers, the work of previous researchers have suggested that the whinny vocalization contains sufficient individual specific variation in acoustic properties to allow receivers to determine the identity of a caller (Chapman and Weary 1990; Teixidor and Byrne 1999; Ramos-Fernandez 2005). Rendall and Owren (2002) suggest that in highly social species, advertising one's identity might be an effective way of influencing the behaviour of others. Essentially, they suggest that the caller's relationship to those around them is paramount for any adaptive benefits of a communication signal to be realized. Because the qualities of male and female spider monkey associations differ so dramatically (Ramos-Fernandez *et al.* 2009), it is possible that the mechanism by which whinnies affect receivers' behaviour is by simply advertising a caller's identity, or sex. As a result, a whinny from a male versus a female caller may ultimately function differently, as a receiver would presumably react differently to the call of a close associate versus an individual who they tend to avoid.

5.3.3 Possible functions of whinnies

I propose that the whinny vocalization may, on a proximate level, function to simply alert receivers to a caller's presence and identity. This in turn would allow receivers to anticipate the presence of a specific caller in spite of the fluid grouping patterns characteristic of spider monkeys. Without a mechanism for advertising one's presence, individuals (especially females) would potentially experience unanticipated and potentially costly encounters with each other throughout their range. Because receivers often respond to each other's calls with a whinny of their own (Ramos-Fernandez 2008), calling may be a way by which individuals can rapidly determine what other individuals are present, while advertising their own presence at the same time. This could prove adaptive for both callers and receivers, as individuals would be able to make appropriate decisions as to who they should approach, or potentially avoid. Although my analysis did not focus on the ultimate function of calling, some possible benefits to announcing one's presence are discussed below.

Reduce Feeding Competition

A benefit of advertising one's presence may be to reduce feeding competition. Gros-Louis (2004) noted that capuchins emit 'huh' vocalizations at elevated rates in feeding contexts, and that these calls serve a spacing mechanism, whereby individuals are able to influence the position of others relative to themselves. In this way, these calls seem to fit the 'food ownership hypothesis' as described by Pollick *et al.* (2005), whereby calling does not function to advertise the availability of food, so much as it serves to decrease direct competition over a particular resource. One mechanism by which this could work would be by simply announcing one's

presence within a feeding patch. By announcing their presence, callers may deter others from approaching an area by simply informing receivers that a space is already occupied by a foraging animal. This would not only benefit the caller by decreasing the amount of competition over a resource, but would benefit receivers for the same reason.

In a similar fashion, female spider monkeys may inform others of their presence in a food patch by whinnying. Receivers not associated with a female caller may be motivated to maintain a minimum distance from the caller in order to avoid direct competition. Gros-Louis (2004) also found that compared to males, female capuchins were more likely to give a food-associated call when first encountering a food item, and that they called at higher rates while feeding. One explanation for this was that in capuchin social groups, males tend to be of a higher rank than females. As a result, males are rarely challenged for food, and would therefore not need to announce their presence, as would a female. Correspondingly, male spider monkeys have been described as being dominant relative to females (Fedigan and Baxter 1984; Symington 1987), and may therefore not experience as much anxiety over feeding competition. Males would therefore not need to announce their presence in feeding contexts through whinnying to the same extent as females.

Reduce the risk of receiving aggression

Increased levels of feeding competition may result in elevated levels of aggression over access to a particular resource. If whinnying functions to alert receivers to a caller's presence, calling may allow individuals to better space themselves out in contexts where they risk receiving aggression. Calling may therefore be a mechanism by which callers can avoid engaging in costly agonistic interactions that may arise in feeding contexts, or as subgroups

become larger. Slater *et al.* (2009) found that coalition formation and aggression amongst female spider monkeys were more common in feeding contexts than expected based on the observed feeding time. Although the rates of female-female aggression are low in other species who show high levels of fission fusion dynamics coupled with male philopatry (Chimpanzees: Muller 2002; Muller and Mitani 2005) and in other atelid species (Muriquis: Printes and Strier 1999), the majority of aggressive interactions between females in these species occur in feeding contexts as well. If females are at risk of receiving aggression while feeding, whinny vocalizations may be produced in response to elevated levels of anxiety; this could function as a spacing mechanism that would decrease the rate of confrontations between individuals over resources. As female directed aggression frequently occurs at subgroup fusions, the tendency for females to call as subgroup composition changes may also relate to elevated levels of anxiety over the increased risk of receiving aggression. Calling would be adaptive if it allowed individuals to space themselves out appropriately, thereby decreasing the risk of aggressive encounters.

5.5 Directions for Future research

In order to test the possibility that calling by males is attractive to their close associates while calling by females functions to space individuals out, it is necessary to determine how specific individuals respond to the whinnies of specific callers. Although Ramos-Fernandez's 2005 play-back study showed that close associates are attracted to each other's calls, no information was given as to the sex of the individuals being tested. What remains is to test whether the whinnies of females cause receivers to either maintain or increase inter-individual

spacing. One way to test this is through the use of playback studies similar to those of Ramos-Fernandez (2005). By distinguishing between the responses of males and females to played-back whinnies from each sex, it would be possible to evaluate differential responses based on the sex of the caller and the receiver. Alternatively, other researchers have explored the effects of vocalizations on inter-individual spacing using naturalistic observations. This was done by measuring the distance from a focal animal to its nearest neighbour at regular intervals, and determining whether this distance changes predictably after the production of a call (see Boinski and Campbell 1996; Gros Louis 2004; Arnedo *et al.* 2010).

It would also be beneficial to determine whether rates of aggression between females in feeding contexts or immediately after subgroup fusions could be predicted based on whether or not individuals produce a whinny vocalization, or based on their rates of calling. This was difficult to measure in my study for two reasons. First, female-female aggressive interactions have been described as being subtle compared to the overt chases and displays seen in female direct aggression (FDA) by males (Link *et al.* 2009). It is perhaps for this reason that FDA by males has received more attention than female-female aggression in this species; the overall rarity of female-female aggression, coupled with its subtle nature may make it an easily missed form of interaction. Secondly, the Runaway Creek Nature Reserve was struck by hurricane Richard on October 28th 2010, and by a fire in May of 2011. These natural disturbances altered the composition of the forest, and affected both the travel routes as well as feeding trees utilised by the monkeys. Since these disturbances, the monkeys at RCNR have showed a significant decrease in their overall rates of aggression (Champion *et al.* in press). Because of this, rates of aggression from January 2012 through August 2012 were extremely low, making comparisons between vocal behaviour and rates of aggression impossible.

It is important to note that because males were less frequently encountered in the field, I was unable to analyse the effect of subgroup fissions or fusions involving only males on an individual's likelihood of calling. Subgroup fissions and fusions involving only males were relatively rare, as the study community is comprised of fewer adult males than adult females. For this reason, more longitudinal data will be required to analyse the specific effects of males joining or leaving an individual's subgroup on its calling behaviour. Anecdotal evidence however suggests that fusions involving males do affect the calling behaviour of females. On numerous occasions in the field, while observing a subgroup comprised of mostly females and their dependant offspring, multiple adult males would approach rather quickly and fuse with the female's subgroup. The females appeared distressed, and would produce multiple whinny vocalizations. The females would often climb down to lower branches, and were extremely vigilant of the newly arriving males. On some occasions, some of the males would chase the females, who would emit 'scream' vocalizations and continue to show obvious signs of anxiety. Often, after these chases, the females would produce multiple whinnies before eventually returning to the higher parts of the canopy. The proximate trigger of the calling in these instances appeared to be the anxiety caused by the newly arriving males, or from the aggressive interactions that followed.

The results of my fusion analysis suggested that females were more likely to call as the number of *females* joining their subgroup increased. Fusion model 1 shows however that when the sex of the joining individuals was not taken into account, the likelihood of calling by females was not affected by the number of individuals joining their subgroup. However, this should not be taken as evidence that females do not call in response to fusions involving males. The third models in both the fission and fusion model groups show that the likelihood of a female calling

in association with a subgroup fission or fusion was not dependent on the sex of the individuals joining or leaving the subgroup. This suggests that when males either leave or join a subgroup, there is an impact on the calling behaviour of other individuals. To directly test these effects, more longitudinal data is needed.

REFERENCES

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*. 227-267.
- Anderson, J. R. (1998). Sleep, sleeping sites, and sleep-related activities: Awakening to their significance. *American Journal of Primatology*. **46**(1): 63-75.
- Arnedo, L. F., Mendes, F. D. C., Strier, K. M. (2010). Sex differences in vocal patterns in the northern muriqui (*Brachyteles hypoxanthus*). *American Journal of Primatology*. **72**:122–128.
- Asensio, N., Korstjens, A. H., Schaffner, C. M., Aureli, F. (2008). Intragroup aggression, fission–fusion dynamics and feeding competition in spider monkeys. *Behavior*. **145**: 983-1001.
- Aubin, T., Jouventin, P. (1998). Cocktail–party effect in king penguin colonies. *Proceedings of the Royal Society of London. Series B: Biological Sciences*. **265**(1406): 1665-1673.
- Aureli, F., Preston, S. D., de Waal, F. (1999). Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): A pilot study. *Journal of Comparative Psychology*. **113**(1): 59.
- Aureli, F., Schaffner, C. M. (2007). Aggression and conflict management at fusion in spider monkeys. *Biology Letters*. **3**: 147–149.
- Aureli, F., Schaffner, C. M., Verpooten, J., Slater, K., Ramos-Fernandez, G. (2006). Raiding parties of male spider monkeys: insights into human warfare?. *American Journal of Physical Anthropology*. **131**(4): 486-497.
- Aureli, F., Schaffner, C., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., DiFiore, A., Dunbar, R. I. M., Henzi, P. S., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B., van Schaik, C. P. (2008). Fission–fusion dynamics: new research frameworks. *Curr Anthropol* **49**: 627– 654.
- Boccia, M. L., Reite, M., & Laudenslager, M. (1989). On the physiology of grooming in a pigtail macaque. *Physiology & Behavior*. **45**(3): 667-670.
- Bohn, K. M., Wilkinson, G. S., Moss, C. F. (2007). Discrimination of infant isolation calls by female greater spear-nosed bats, *Phyllostomus hastatus*. *Animal behaviour*. **73**(3): 423-432.
- Boinski, S. (1988). Sex differences in the foraging behavior of squirrel monkeys in a seasonal habitat. *Behavioral Ecology and Sociobiology*. **23**(3): 177-186.
- Boinski, S. (1991). The coordination of spatial position: a field study of the vocal behaviour of adult female squirrel monkeys. *Animal Behavior*. **41**: 89-102.
- Boinski, S. (1993). Vocal coordination of troop movement among white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*. **30**(2): 85-100.

- Boinski, S., Campbell, A. F. (1995). Use of trill vocalizations to coordinate troop movement among white-faced capuchins: a second field test. *Behaviour*. 875-901.
- Boinski, S., Campbell, A. F. (1996). The huh vocalization of whitefaced capuchins: a spacing call disguised as a food call? *Ethology*, **102**: 826–840.
- Bugnyar, T., Kijne, M., Kotrschal, K. (2001). Food calling in ravens: are yells referential signals?. *Animal Behaviour*. **61(5)**: 949-958.
- Byrne, R.W., Whiten, A. (1990). Tactical deception in primates: the 1990 database. *Primate Report*. **27**: 1-101.
- Caine, N. G., Addington, R. L., & Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal behaviour*. **50(1)**: 53-60.
- Caine, N. G., Stevens, C. (1990). Evidence for a “Monitoring Call” in red-bellied tamarins. *American Journal of Primatology*. **22**:251–261.
- Cant, J. G. H. (1977). Ecology of spider monkeys (*Ateles geoffroyi*) at Tikal, Guatemala. Paper presented at Ann. l~leet. Amer. Anthropok Ass., Houston.
- Carpenter, C. R., (1935). Behavior of red spider monkey in Panama. *Journal of Mammalogy*. **16**: 171-180.
- Chapman, C. (1990). Association patterns of spider monkeys: the influence of ecology and sex on social organization. *Behavioral Ecology and Sociobiology*. **26**:409-414.
- Chapman, C. A. (1989). Spider monkey sleeping sites: use and availability. *American Journal of Primatology*. **18(1)**: 53-60.
- Chapman, C. A., & Weary, D. M. (1990). Variability in spider monkeys' vocalizations may provide basis for individual recognition. *American Journal of Primatology*. **22(4)**: 279-284.
- Chapman, C. A., Chapman, L. J., & McLaughlin, R. L. (1989). Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologia*. **79(4)**: 506-511.
- Chapman, C. A., Lefebvre, L. (1990). Manipulating foraging group size: spider monkey food calls at fruiting trees. *Anim Behav*. **39**: 891-896.
- Chapman, C. A., Wrangham, R. W., Chapman, L. C. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav Ecol Sociobiol*. **36**: 59-70.
- Charrier, I., Mathevon, N., Jouventin, P. (2003). Fur seal mothers memorize subsequent versions of developing pups' calls: adaptation to long-term recognition or evolutionary by-product?. *Biological Journal of the Linnean Society*. **80(2)**: 305-312.

- Cheney, D. L., & Seyfarth, R. M. (1981). Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour*. 25-61.
- Cheney, D. L., Seyfarth, R. M. (1998). Why monkeys don't have language. In *The Tanner Lectures on Human Values*, ed. G Petersen, **19**:173–210. Salt Lake City: Univ. Utah Press
- Cheney, D. L., Seyfarth, R. M., Palombit, R. (1996). The function and mechanisms underlying baboon 'contact' barks. *Animal Behaviour*. **52**(3): 507-518.
- Cheney, D. L., Seyfarth, R. M., Silk, J. B. (1995). The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Animal Behaviour*, **50**: 249–257.
- Clark, A. P. (1993). Rank differences in production of vocalizations by wild chimpanzees as a function of social context. *American Journal of Primatology*. **31**: 159-179.
- Clark, A. P., Wrangham, R. W. (1994). Chimpanzee arrival panthoots: do they signify food or status?. *International Journal of Primatology*. **15**: 185–205.
- Clay, Z., Smith, C. L., Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: what do these calls really mean?. *Animal Behaviour*. **83**(2): 323-330.
- Coelho Jr, A. M., Bramblett, C. A., Quick, L. B., Bramblett, S. S. (1976). Resource availability and population density in primates: a socio-bioenergetic analysis of the energy budgets of Guatemalan howler and spider monkeys. *Primates*. **17**(1): 63-80.
- Collins, A. C., & Dubach, J. M. (2000). Phylogenetic relationships of spider monkeys (*Ateles*) based on mitochondrial DNA variation. *International Journal of Primatology*. **21**(3): 381-420.
- Davis, W. J. (1986). Acoustic recognition in the Belted Kingfisher: cardiac response to playback vocalizations. *Condor*. 505-512.
- Delgado, R. A. (2006). Sexual selection in the loud calls of male primates: signal content and function. *International Journal of Primatology*. **27**(1): 5-25.
- Di Bitetti, M. S. (2003). Food-associated calls of tufted capuchin monkeys (*Cebus apella nigrinus*) are functionally referential signals. *Behaviour*. **140**(5): 565-592.
- Di Bitetti, M. S. (2005). Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigrinus*. *Animal behaviour*. **69**(4): 911-919.
- Di Fiore, A., Campbell C. (2007). The Atelines: variations in ecology, behavior and social organization. - In: *Primates in Perspective*. (Campbell, C., Fuentes, A., Mackinnon, K., Panger, M., Bearder, S. eds). Oxford, New York: Oxford University Press. p 155-185.
- Di Fiore, A., Link, A., & Campbell, C. (2011). The Atelines: Behavior and socioecological diversity in a New World monkey radiation. In: C. Campbell, A. Fuentes, K. Mackinnon, R.

- Stumpff, & S. Bearder (Eds.), *Primates in perspective*. Oxford: Oxford University Press. (2nd ed.), pp. 155–188.
- Di Fiore, A., Link, A., Schmitt, C. A., Spehar, S. N. (2009). Dispersal patterns in sympatric woolly and spider monkeys: integrating molecular and observational data. *Behaviour*. **146**: 437-470.
- Digweed, S. M., Fedigan, L. M., & Rendall, D. (2007). Who cares who calls? Selective responses to the lost calls of socially dominant group members in the white-faced capuchin (*Cebus Capucinus*). *American journal of primatology*. **69(7)**: 829-835.
- Dittus, W. P. (1984). Toque macaque food calls: semantic communication concerning food distribution in the environment. *Animal Behaviour*. **32(2)**: 470-477.
- Eisenberg, J. P. (1976). Communication mechanisms and social intergration in the black spider monkey, *Ateles fusciceps robustus*, and related species. *Smithsonian Contrib. Zool.* **213**.
- Elgar, M. A. (1986). The establishment of foraging flocks in house sparrows: risk of predation and daily temperature. *Behavioral Ecology and Sociobiology*. **19(6)**: 433-438.
- Elowson, A. M., Tannenbaum, P. L., Snowdon, C. T. (1991). Food-associated calls correlate with food preferences in cotton-top tamarins. *Animal Behaviour*. **42(6)**: 931-937.
- Evans, C. S. (1997). Referential signals. *Perspectives in ethology*. **12**: 99-143.
- Evans, C. S., Evans, L. (1999). Chicken food calls are functionally referential. *Animal Behaviour*. **58(2)**: 307-319.
- Evans, C. S., Evans, L. (2007). Representational signalling in birds. *Biology Letters*. **3(1)**: 8-11.
- Evans, C. S., Marler, P. (1994). Food calling and audience effects in male chickens, *Gallus gallus*: their relationships to food availability, courtship and social facilitation. *Animal Behaviour*. **47(5)**: 1159-1170.
- Fedigan, L. M., Baxter, M. J. (1984). Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*). *Primates*. **25**: 279–294.
- Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*. **56(2)**: 140-148.
- Galdikas, B. M. (1983). The orangutan long call and snag crashing at Tanjung Puting Reserve. *Primates*. **24(3)**: 371-384.
- Gautier, J., Gautier, P. (1977). Communication in Old World monkeys. In: How animals communicate. T. A. Sebeok (ed.). Indiana University press. Bloomington. pp. 890-964.

- Ghiglieri, M. P. (1984). Feeding ecology and sociality of chimpanzees in Kibale Forest, Uganda. *Adaptations for foraging in nonhuman primates*. 161-194.
- Gouzoules, S., Gouzoules, H., Marler, P. (1984). Rhesus monkey (*Macaca mulatta*) screams: Representational signalling in the recruitment of agonistic aid. *Animal Behavior*, **32**: 182–193.
- Green, S. M. (1981). Sex differences and age gradations in vocalizations of Japanese and lion-tailed monkeys (*Macaca fuscata* and *Macaca silenus*). *American Zoologist*. **21**(1): 165-183.
- Gros-Louis, J. (2004). The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller. *Animal Behaviour*, **67**: 431-440.
- Gust, D. A., Gordon, T. P., Hambright, M. K., & Wilson, M. E. (1993). Relationship between Social Factors and Pituitary-Adrenocortical Activity in Female Rhesus Monkeys (*Macaca mulatta*). *Hormones and Behavior*. **27**(3): 318-331.
- Hamilton, W. J. (1982). Baboon sleeping site preferences and relationships to primate grouping patterns. *American Journal of Primatology*. **3**(1-4): 41-53.
- Harcourt, A. H., Stewart, K. J., Hauser, M. (1993). Functions of wild gorilla 'close' calls. I. Repertoire, context, and interspecific comparison. *Behaviour*. 89-122.
- Hartwell, K. (2010). Sexual segregation in spider monkeys in Belize. Masters thesis, University of Calgary.
- Hauser, M. D., Marler, P. (1993). Food-associated calls in rhesus macaques (*Macaca mulatta*): II. Costs and benefits of call production and suppression. *Behavioral Ecology*. **4**(3): 206-212.
- Hauser, M. D., Teixidor, P., Fields, L., & Flaherty, R. (1993). Food-elicited calls in chimpanzees: Effects of food quantity and divisibility. *Animal Behaviour*, **45**(4): 817-819.
- Heinrich, B., Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*. **28**: 13–21.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian journal of statistics*. 65-70.
- Janson, C. H. (1990). Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*. **40**(5): 922-934.
- Jordan, K., Weiss, D., Hauser, M., & McMurray, B. (2004). Antiphonal responses to loud contact calls produced by *Saguinus oedipus*. *International journal of primatology*. **25**(2): 465-475.
- Karakashian, S. J., Gyger, M., & Marler, P. (1988). Audience effects on alarm calling in chickens (*Gallus gallus*). *Journal of Comparative Psychology*. **102**(2): 129.

- Kellogg, R., Goldman, E. A. (1944). Review of the spider monkeys. *Proc. U.S. Nat. Mus.* **96**: 1-45.
- King, B. J., Shanker, S. G. (2003). How can we know the dancer from the dance?: The dynamic nature of African great ape social communication. *Anthropological theory*. **3**(1): 5-26.
- Kitchen, D. M. (2004). Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. *Animal Behaviour*. **67**(1): 125-139.
- Kitchen, D. M., Cheney, D. L., Seyfarth, R. M. (2003b). Female baboons' responses to male loud calls. *Ethology*. **109**(5): 401-412.
- Kitchen, D. M., Seyfarth, R. M., Fischer, J., Cheney, D. L. (2003a). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behav Ecol Sociobiol*. **53**: 374–384.
- Kitzmann, C. D., & Caine, N. G. (2009). Marmoset (*Callithrix geoffroyi*) Food-Associated Calls are Functionally Referential. *Ethology*. **115**(5): 439-448.
- Klein, L. L. (1972). The ecology and social organization of the spider monkey, *Ateles belzebuth*. Ph.D. thesis, University of California, Berkeley.
- Koda, H., Shimooka, Y., Sugiura, H. (2008) Effects of caller activity and habitat visibility on contact call rate of wild Japanese Macaques (*Macaca fuscata*). *American Journal of Primatology*. **70**:1055–1063.
- Kondo, N., Watanabe, S. (2009). Contact calls: Information and social function. *Japanese Psychological Research*, **3**: 197–208.
- Krebs, J. R., & Dawkins, R. (1984). Animal signals: mind-reading and manipulation. *Behavioural Ecology: an evolutionary approach*. **2**: 380-402.
- Krunkelsven, E., Dupain, J., Van Elsacker, L., Verheyen, R. F. (1996). Food calling by captive bonobos (*Pan paniscus*): an experiment. *International journal of primatology*. **17**(2): 207-217.
- Lammers, M. O., Schotten, M., Au, W. W. (2006). The spatial context of free-ranging Hawaiian spinner dolphins (*Stenella longirostris*) producing acoustic signals. *The Journal of the Acoustical Society of America*. **119**: 1244-1250.
- Laporte, M. N. C., Zuberbuhler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behavior*. **80**: 467-473.
- Leighty, K. A., Soltis, J., Wesolek, C. M., Savage, A. (2008). Rumble vocalizations mediate interpartner distance in African elephants, *Loxodonta africana*. *Animal Behaviour*. **76**(5): 1601-1608.

- Link, A., Di Fiore, A., (2006). Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. *Journal of Tropical Ecology*. **22**: 235–246.
- Link, A., Di Fiore, A., & Spehar, S. N. (2009). Female-directed aggression and social control in spider monkeys. *Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females*. 157-183.
- Macedonia, J. M. (1986). Individuality in a contact call of the ringtailed lemur (*Lemur catta*). *American Journal of Primatology*. **11**(2): 163-179.
- Macedonia, J. M., & Evans, C. S. (1993). Essay on contemporary issues in ethology: Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*. **93**(3): 177-197.
- Marler, P. (2004). Bird calls. Their potential for behavioral neurobiology. *Annals of the New York Academy of Sciences*, **1016**: 31–44.
- Marler, P., Dufty, A., & Pickert, R. (1986a). Vocal communication in the domestic chicken: I. Does a sender communicate information about the quality of a food referent to a receiver?. *Animal Behaviour*. **34**: 188-193.
- Marler, P., Dufty, A., & Pickert, R. (1986b). Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver?. *Animal Behaviour*. **34**: 194-198.
- Marler, P., Evans, C. S., Hauser, M. D. (1992). Animal signals: motivational, referential, or both. *Nonverbal vocal communication: Comparative and developmental approaches*. 66-86.
- Marler, P., Hobbett, L. (1975). Individuality in a Long-Range Vocalization of Wild Chimpanzees. *Zeitschrift für Tierpsychologie*. **38**(1): 97-109.
- Marler, P., Tenaza, R. (1977) Signaling behavior of apes with special reference to vocalization. In: How animals communicate. T. A. Sebeok (ed.). Indiana University press. Bloomington. pp. 965-1033.
- Mathevon, N. (1997). Individuality of contact calls in the Greater Flamingo *Phoenicopterus ruber* and the problem of background noise in a colony. *Ibis*. **139**(3): 513-517.
- Mendes, F. D., & Ades, C. (2004). Vocal sequential exchanges and intragroup spacing in the Northern Muriqui *Brachyteles arachnoides hypoxanthus*. *Anais da Academia Brasileira de Ciências*. **76**(2): 399-404.
- Miller, D. B. (1979). The acoustic basis of mate recognition by female Zebra finches (*Taeniopygia guttata*). *Animal Behaviour*. **27**: 376-380.
- Mitani, J. C. (1985). Sexual selection and adult male orangutan long calls. *Animal Behaviour*. **33**(1): 272-283.

- Mitani, J. C., Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Anim Behav.* **45**: 735-746.
- Mitani, J. C., & Stuht, J. (1998). The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. *Primates.* **39**(2): 171-182.
- Mitra Setia, T., van Schaik, C. P. (2007). The response of adult orangutans to flanged male long calls: Inferences about their function. *Folia Primatol.* **78**: 215-226.
- Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. *Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge.* 112-124.
- Muller, M. N., & Mitani, J. C. (2005). Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior.* **35**: 275-331.
- Nishimura, A., Fonseca, G. D., Mittermeier, R. A., Young, A. L., Strier, K. B., & Valle, C. M. C. (1988). The miqui, genus *Brachyteles*. *Ecology and behavior of neotropical primates*, 2, 577-610.
- Notman, H., Rendall, D. (2005). Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour.* **70**: 177-190.
- Oppenheimer, J. R. (1977) Communication in New World monkeys. In: How animals communicate. T. A. Sebeok (ed.). Indiana University press. Bloomington. pp. 851-889.
- Owren, M. J., & Rendall, D. (2001). Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology: Issues, News, and Reviews.* **10**(2): 58-71.
- Owren, M. J., Rendall, D., (2003). Salience of caller identity in rhesus monkey (*Macaca mulatta*) coos and screams: perceptual experiments with human (*Homo sapiens*) listeners. *J. Comp. Psychol.* **117**: 380-390.
- Pepper, J. W., Mitani, J. C., Watts, D. P. (1999). General Gregariousness and Specific Social Preferences among Wild Chimpanzees. *International Journal of Primatology.* **20**: 613-632.
- Petter, J. J., Charles-Dominique, P. (1979). Vocal communication in prosimians. *The study of prosimian behavior.* 247-305.
- Pollick, A. S., Gouzoules, H., de Waal, F. (2005). Audience effects on food calls in captive brown capuchin monkeys, *Cebus apella*. *Animal behaviour.* **70**(6): 1273-1281.
- Poole, J. H. (1994). Sex differences in the behaviour of African elephants. *The differences between the sexes.* 331-346.
- Povinelli, D.J. (1993). Reconstructing the evolution of mind. *American Psychologist.* **48**: 493-509.

- Printes, R. C., Strier, K. B. (1999). Behavioral correlates of dispersal in female muriquis (*Brachyteles arachnoides*). *International Journal of Primatology*. **20**(6): 941-960.
- Ramos-Fernandez, G. (2005). Vocal communication in a fission-fusion society: do spider monkeys stay in touch with close associates?. *Int J Primatol*. **26**:1077–1092.
- Ramos-Fernandez, G. (2008). Communication in spider monkeys: the function and mechanisms underlying the use of the whinny. - In: *Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles*. (Campbell, C.J., ed). Cambridge University Press, New York, NY, p. 221-235.
- Ramos-Fernandez, G., Boyer, D., Aureli, F., Vick, L. G. (2009). Association networks in spider monkeys (*Ateles geoffroyi*). *Behavioral Ecology and Sociobiology*. **63**(7): 999-1013.
- Rendall, D., Cheney, D. L., Seyfarth, R. M. (2000). Proximate factors mediating "contact" calls in adult female baboons (*Papio cynocephalus ursinus*) and their infants. *Journal of Comparative Psychology*. **114**(1): 36-46.
- Rendall, D., Owren, M. J. (2002). Animal vocal communication: Say what? In: *The cognitive animal*. (M. Bekoff, C. Allen, G. Burghardt. Eds). Cambridge, MA: MIT Press. p 307-313.
- Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean?. *Animal Behaviour*. **78**(2): 233-240.
- Rendall, D., Owren, M. J., Rodman, P. S. (1998). The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations. *The Journal of the Acoustical Society of America*. **103**: 602-614.
- Rendall, D., Rodman, P. S., Emond, R. E. (1996). Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*. **51**(5): 1007-1015.
- Robertson, B. C. (1996). Vocal mate recognition in a monogamous, flock-forming bird, the silvereye, *Zosterops lateralis*. *Animal behaviour*. **51**(2): 303-311.
- Robinson, J. G. (1981). Vocal regulation of inter- and intragroup spacing boundary encounters in the titi monkey, *Callicebus moloch*. *Primates*, **22** (2): 161–172.
- Rylands, A. B., Groves, C. P., Mittermeier, R. A., Cortés-Ortiz, L., & Hines, J. J. (2006). Taxonomy and distributions of Mesoamerican primates. In *New perspectives in the study of Mesoamerican primates* (pp. 29-79). Springer US.
- Schaffner, C. M., & Aureli, F. (2005). Embraces and grooming in captive spider monkeys. *International Journal of Primatology*. **26**(5): 1093-1106.
- Seyfarth, R. M., & Cheney, D. L. (2010). Production, usage, and comprehension in animal vocalizations. *Brain and language*. **115**(1): 92-100.

- Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*. **28**(4): 1070-1094.
- Sharp, S. P., Hatchwell, B. J. (2005). Individuality in the contact calls of cooperatively breeding long-tailed tits (*Aegithalos caudatus*). *Behaviour*. **142**(11): 1559-1576.
- Sherman, P. W. (1977). Nepotism and the evolution of alarm calls. *Science*. **197**(4310): 1246-1253.
- Shimooka, Y. (2005). Sexual differences in ranging of *Ateles belzebuth belzebuth* at La Macarena, Colombia. *International Journal of Primatology*. **26**(2): 385-406.
- Shultz, S., Faurie, C., Noe, R. (2003). Behavioral responses of Diana monkeys to male long-distance calls: changes in ranging, association patterns and activity. *Behav Ecol Sociobiol*. **53**:238-245.
- Shutt, K., MacLarnon, A., Heistermann, M., & Semple, S. (2007). Grooming in Barbary macaques: better to give than to receive?. *Biology Letters*. **3**(3): 231-233.
- Slater, K. Y., Schaffner, C. M., & Aureli, F. (2009). Sex differences in the social behavior of wild spider monkeys (*Ateles geoffroyi yucatanensis*). *American Journal of Primatology*. **71**(1): 21-29.
- Slater, K., Schaffner, C., Aureli, F. (2008). Female-directed Male Aggression in Wild *Ateles geoffroyi yucatanensis*. *International Journal of Primatology*. **29**(6): 1657-1669.
- Slocombe, K. E., & Zuberbühler, K. (2005). Functionally referential communication in a chimpanzee. *Current Biology*. **15**(19): 1779-1784.
- Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., & Zuberbühler, K. (2010). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology*. **64**(12): 1959-1966.
- Smith, W. J. (1977). *The Behavior of Communicating*. Harvard University Press, Cambridge.
- Snowdon, C. T. (1989). Vocal communication in New World monkeys. *Journal of Human Evolution*. **18**(7): 611-633.
- Snowdon, C. T., & Cleveland, J. (1980). Individual recognition of contact calls by pygmy marmosets. *Animal Behaviour*. **28**(3): 717-727.
- Spehar, S. N. A. (2006). The function of the long call in white-bellied spider monkeys (*Ateles belzebuth*) in Yasuni National Park, Ecuador. Dissertation. New York University. New York. NY.

- Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*. **78**(2): 337-347.
- Striedter, G. F., Freibott, L., Hile, A. G., Burley, N. T. (2003). For whom the male calls: an effect of audience on contact call rate and repertoire in budgerigars, *Melopsittacus undulatus*. *Animal behaviour*. **65**(5): 875-882.
- Strier, K. B. (1990). New world primates, new frontiers: Insights from the woolly spider monkey, or muriqui (*Brachyteles arachnoides*). *Int. J. Primatol.* **11**: 7-19.
- Strier, K. B. (1991). Diet in one group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *American Journal of Primatology*. **23**(2): 113-126.
- Strier, K. B., Mendes, F. D. C., Rimoli, J., Rimoli, A. O. (1993). Demography and social structure of one group of Muriquis (*Brachyteles arachnoides*). *International Journal of Primatology*. **14**: 513-526.
- Sugiura, H. (1998). Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. *Animal Behavior*. **55**: p. 673-687.
- Sugiura, H. (2000). Vocal exchange of coo calls in Japanese macaques. In: *Primate origins of human cognition and behavior* (T. Matsuzawa, ed.). Springer-Verlag, Tokyo, p. 135-154.
- Symington, M. M. (1988). Food Competition and Foraging Party Size in the Black Spider Monkey (*Ateles paniscus chamek*). *Behavior*. **105**: 117-134.
- Symington, M. M. (1987). Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. *Behavioral Ecology and Sociobiology*. **20**(6): 421-425.
- Symington, M. M. (1990). Fission-fusion social organisation in *Ateles* and *Pan*. *International journal of primatology*. **11**: 47-61.
- Teixidor, P., Byrne, R.W. (1999). The ‘whinny’ of spider monkeys: individual recognition before situational meaning. *Behavior* **136**: 279–308.
- Townsend, S. W., Deschner, T., Zuberbühler, K. (2008). Female chimpanzees use copulation calls flexibly to prevent social competition. *PloS One*. **3**(6): e2431.
- Trivers, R. L. (1972). Parental investment and sexual selection. – In: *Sexual selection and the descent of man 1871–1971*. (Campbell, B. ed). Chicago: Aldine. p. 136–179.
- Valero, A., Schaffner, C. M., Vick, L. G., Aureli, F., & Ramos-Fernandez, G. (2006). Intragroup lethal aggression in wild spider monkeys. *American journal of primatology*. **68**(7): 732-737.
- Van Roosmalen, M. G. M., & Klein, L. L. (1988). The spider monkeys, genus *Ateles*. *Ecology and behavior of neotropical primates*. **2**: 455-537.

- Wallace, R. (2006). Seasonal variations in black-faced spider monkey (*Ateles chamek*) habitat use and ranging behaviour in a southern Amazonian tropical forest. *American Journal of Primatology*. **68**: 313-332.
- Whitehead, H. (1999). Testing association patterns of social animals. *Anim. Behav.* **57**: 26–29.
- Wilkinson, G. S., Boughman, J. W. (1998). Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour*. **55(2)**: 337-350.
- Wrangham, R. W. (1980). An ecological model of female bonded groups. *Behaviour*. **75**: 262-300.
- Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe national park, Tanzania. *Primate ecology*. 503-538.
- Wrangham, R. W. (1979). On the evolution of ape social systems. *Soc. Sci. Inform.* **18**: 335–368.
- Zuberbühler, K. (2003). Referential signaling in non-human primates: cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior*. **33**: 265-307.
- Zuberbühler, K., Noe, R., Seyfarth, R. M. (1997). Diana monkey long-distance calls: messages for conspecifics and predators. *Anim Behav*. **53**:589–604.

APPENDIX A

SPIDER MONKEY ETHOGRAM Runaway Creek Nature Reserve, Belize (Kayla Hartwell 2011)

SOLITARY BEHAVIOUR		
F	Feed/ Forage	Focal eats or actively searches for food items (also includes smelling fruits). Indicate plant species and plant part consumed.
DK	Drink	Focal consumes water. Indicate where (tree hole, palm, etc.) and how (i.e. dunks hand in water source and drips water into mouth off of knuckles, fingers, wrists or sucks water off fingers, collects water in palm of hand and brings to mouth, brings head to water source and drinks directly).
I	Inactive	Focal sits, lies down or hangs (eyes can be open or closed).
T	Travel	Focal moves (does not include moving around in a tree while foraging for food).
AUG	Auto groom	Focal grooms itself (does not include scratching).
NSP	Non-social play	Solitary play, i.e. swinging from tail, playing with broken branch
PLS	Place sniff/lick	Focal touches nose or tongue to branch/substrate. Usually performed by males directly after a female got up from sitting on a branch/substrate (if known, indicate who was sitting there prior to place sniff). Also indicate if place sniffing/licking urine (rare behaviour).

CR	Chest rub	Focal rubs chest back and forth against substrate/branch (rare behaviour).
GR	Genital rub	Focal sits and rubs ano-genital region back and forth along branch (rare behaviour).
VG	Vigilance	More alert than just scanning an area, usually in response to potential danger, i.e. large raptor flies over (rare behaviour).
SOCIAL BEHAVIOUR (indicate d and r)		
d	Direct	Focal animal initiates action.
r	Receive	Another animal initiates action to focal animal.
SN	Sit Near	Focal is within 2 meters (2 arms reach) of other individual(s). Indicate other individual(s).
SC	Sit Close	Focal is within 1 meter (but not in contact) with other individual(s). Indicate other individual(s).
SIB	Sit in Body Contact	Focal is in physical contact with other individual(s). Indicate other individual(s).
A	Approach	Focal directs (or receives) an approach within 2 meters of other individual (exclude approaches between mother and dependent offspring [=still carried by the mother]). Indicate other individual involved.
L	Leave	Focal directs (or receives) a leave, i.e. one individual distances itself from another individual. Exclude mother-dependent offspring dyads. Indicate other individual involved.
PB	Pass By	Focal directs (or receives) a pass by, i.e. one individual passes within 2 meters of another and keeps on moving without stopping. Indicate other individual involved.

ALG	Allogroom	Focal directs or receives allogroom from other individual (5 sec break between bouts). Indicate other individual involved and d/r.
SG	Solicit Groom	Focal directs (or receives) solicitation to allogroom, i.e. one individual presents body part to another individual for grooming. Indicate other individual involved and d/r.
SP	Social Play	Focal plays with other individual (chasing, wrestling, mock biting and usually accompanied by play vocalization). Indicate individuals involved.
NU	Nurse	Focal nurses their offspring.
PSE	Pectoral Sniff and Embrace	Individual wraps one or two arms around another's shoulder, head or waist and places its nose to the other's neck/chest or arm pit region. Indicate individuals involved and d/r.
WC	Wound Clean	Focal directs or receives cleaning of wound by touching and licking. Indicate individuals involved and d/r (rare behaviour).
GRP	Grapple	Sustained contact (usually minutes) between two individuals that may contain, but is not limited to facial greeting/touching, embracing, tail wrapping, pectoral sniffing, and genital contact. Animals may also move apart, maintaining intense face to face visual contact then move together. Usually accompanied with high pitch whistles, pants, and soft growl vocalizations. Usually

		observed between subadult and adult males. Indicate individuals involved and d/r if obvious (rare behaviour).
ALC	Allocarry	An individual (not the mother) carries an infant/juvenile while moving (rare behaviour).
IH	Infant Handle	An individual (not the mother) sits and handles an infant, letting infant climb on them and/or cling to them (rare behaviour).
SIH	Solicit Infant Handle	Individual (not the mother) presents chest/stomach area to infant for it to climb on (rare behaviour).
CP	Copulation	Self explanatory, indicate individuals involved (rare behaviour).
KF	Kissy-Face	Focal gazes in direction of other and purses lips outward in a wide kiss-like gesture, usually accompanied with a guttural whinny vocalization. Indicate other individual (rare behaviour).
GT	Genital Touch	Focal touches/sniffs anogenital region of another individual. Indicate other individual and d/r (rare behaviour).
FS	Finger sniff	Focal touches the genitals of another individual and sniffs their fingers. Indicate other individual and d/r (rare behaviour).
SCO	Solicit copulation	One individual invites other to copulate (copulation may or may not follow) (rare behaviour).
OS	Out of Site	Focal is out of view.

AGGRESSION		
AGG	Aggression	<p>Indicate d/r, individuals involved if a coalition, and the scale of intensity 1-4:</p> <p>1=lunge, open mouth threat, vocalizations (growling, screams), short in duration</p> <p>2= same as above, but continued chase with no physical contact</p> <p>3= same as above with physical contact (slaps, hits, grabs, bites) but no serious injury</p> <p>4= same as above with noticeable injury (wounds, bleeding, limping)</p>
TD	Threat display	Focal threatens observer, potential predator (or nothing obvious) by growling and/or shaking/breaking branches.
PBT	Piggy Back Threat	2+ individuals pile on top of each other in a threat display
DP	Displacement	Individual displaces another. Indicate other individual involved (rare behaviour).
AV	Avoid	Individual moves out of the way when another individual approaches. Indicate other individual involved (rare behaviour).
VOCALIZATIONS		
WHV	Whinny	most common vocalization, wavelike frequency modulation that varies in length tone and harshness
THV	Tee-Hee	similar sound to a whinny but a shorter 2 note call
OBV	Ook-Bark	Alarm call, harsh short notes varying in intensity.

SCV	Scream	given when individual is under attack or physical threat
GRV	Growl	Harsh noisy sound vocalized during threat display or aggression and rough physical contact play.
LCV	Long Call	Very loud and long call given in an attempt to re-establish contact with other sub-groups.
PLV	Play Vocalizations	Light or heavy panting and growling used during social play. Can vary in intensity
CHV	Chirps	High pitch short notes given repeatedly, usually during threat display or aggression.
TSV	Tschook	Similar to a long call but less intense, harsh gurgle in the throat.
HPWV	High-Pitch Whistle	a flat high pitch vocalization held for 2-3 seconds and usually repeated – kind of like a whine

APPENDIX B

Results from three GEE models with the sex of a subject, and the number of adults (Group size model 1) females (Group size model 2), or males (Group size model 3) in a subject's subgroup as the independent variables. The dependant variable was the presence/absence of a whinny vocalization emitted by a focal animal.

Model	Effect	β	p
Group size 1	Sex of subject	0.901	0.140
	Number of adults in subjects subgroup	0.143	0.555
	Sex of subject* Number of adults in subjects subgroup	-0.152	0.566
Group size 2	Sex of subject	-0.080	0.666
	Number of females in subjects subgroup	0.059	0.828
	Sex of subject* Number of females in subjects subgroup	-0.074	0.808
Group size 3	Sex of subject	0.845	0.074
	Number of males in subjects subgroup	0.225	0.360
	Sex of subject* Number of males in subjects subgroup	-0.90	0.521