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Mom's Day Out: Investigating the Proximate Causes of Allomothering in Squirrel Monkeys

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Abstract

Allomothering, which is defined as non-maternal infant care, is a behavior that is found among many animal species. Although it is widely acknowledged in primate species in particular, it is not well understood. Allomaternal behavior is well documented but the proximal causes are not known. Most primate species live in groups and have intense social relations which govern every aspect of their behavior. Allomothering could then be better understood by looking at the social relationships that exist between members of a group. This research tries to better understand what causes certain females to allomother over others by looking at the relationships between mothers, allomothers, and the rest of the colony in Peruvian and Guyanese squirrel monkeys. Observational data was collected on captive groups over a five month period by observing huddling groups, those in proximal contact, and kinship relationships. These factors were thought to affect which individuals participated in allomothering. This research found that huddling groups were not significant indicators of which monkeys would participate in allomothering. Proximal contact had the strongest significant effect on allomaternal behavior while kinship had a weaker, yet significant, effect. However, kinship only had an effect when older siblings carried younger siblings. Although huddling partners were found to be an insignificant factor, this research still suggests that social cliques and kinship do in fact have an effect on allomaternal behavior. One possible reason huddling partners did not have an effect on allomaternal behavior is that because juvenile females do most of the allomothering and females may only huddle with other monkeys that are similar in age. Further research needs to be accomplished on what factors affect this behavior in female squirrel monkeys.

Introduction

The term alloparental care generally refers to males and/or females caring for others' young, while allomothering refers specifically to females caring for non-maternal young. Alloparenting is an integral aspect of many animal communities including primates, carnivores, hoofstock, many bird species, and sea mammals, and overall occurs in nine taxonomic orders and in 120 mammal species (Silk 1999). Although alloparental care is widely documented, the factors leading to a specific individual's alloparental behavior are not well understood.

The young of mammals are unique from other biological Classes due to an extended period of dependency and slower growth rates. While they develop from an infant to a juvenile, they are dependent on parents for food, protection, and basic care. Caring for such helpless young for long periods of time is extremely demanding and exhausting. Alloparental care may be particularly advantageous for mammalian species because it can remove some of the burdens of motherhood. Silk (1999) has discussed four different explanations for the evolution of alloparental care in mammals: inclusive fitness, reciprocal altruism, experience, and reproductive competition. Here, each of these explanations is briefly reviewed.

One explanation of the occurrence of alloparental care is that it enhances the alloparent's inclusive fitness and is thus a form of kin selection. Inclusive fitness (Silk 1999) is a concept derived from evolutionary theory that states that benefits accrued to relatives of an individual are beneficial for that individual since relatives share parts of their genomes. Hence, an apparently altruistic act toward a relative may in fact enhance

the fitness of the individual performing the act by increasing the chances of survival of the relative.

Another explanation for the occurrence of allopaternal care is that it is a form of reciprocal altruism. Silk explains that reciprocal altruism occurs when an alloparent may take care of non-related young while expecting to receive the same assistance when they are a parent. This would provide a possible explanation for why non-kin engage in allopaternal care and complements the inclusive fitness explanation.

Another explanation provided by Silk (1999) is again aimed at explaining why non-kin may engage in alloparenting. It is suggested that natural selection may favor alloparenting because it gives the alloparents experience in raising young. This experience would help to increase the survival of their future offspring.

A final explanation is that it provides the alloparent the opportunity to harm the infant. Harm to an infant by an alloparent does occur at times among certain species such as baboons. This behavior makes alloparenting a form of reproductive competition.

Kin selection, reciprocal altruism, gaining experience, and reproductive competition could each be used to explain the evolution of alloparental care for a specific species or some combination may be most appropriate. One or a combination of these explanations could be potentially applicable to squirrel monkeys. However, other possible explanations that are more species specific to squirrel monkeys will be discussed.

Primate Alloparenting

While alloparenting is observed among mammals due to the importance of providing care to young, primate infants are born even more helpless than other

mammalian species and are dependent for longer periods of time (McKenna 1979). This suggests that alloparenting may be a behavior that is vital for some primate species. Alloparenting is a common primate behavior found among a range of species including squirrel monkeys, baboons, marmosets, tamarins, capuchins, and many others. In primates, alloparental care can range from helping out a small fraction of the time to alloparents helping care for young for up to half of the infancy period as seen among capped langurs. Marmosets and tamarins are unique among primates in that they regularly produce twins twice a year and it has been suggested that this increased reproduction is only possible due to alloparental care (Ventura 2002). Details of primate studies examining alloparental care provide additional insights into this behavior.

Stanford (1992) looked at the underlying reasons behind allomothering among wild capped langurs. He found that resource distribution affects the social systems of capped langurs such that relationships are regulated by the distribution of resources. Stanford (1992) found that female capped langurs have weak dominance hierarchies and he speculates that this factor allows the prevalence of allomaternal care. Among capped langurs, allomothering is seen as "cooperative alliances" in which allomothering enables mothers to increase their foraging time, increase survivorship of the infants if their mothers died, and increase socialization. It is advantageous for lactating females to increase their feeding time, since it is during this period that they require the most energy. Stanford found that mothers did spend more time feeding while their infants were on allomothers during the first month. Subsequently, allomothers spent less time foraging, while they were taking care of infants. This study could not determine whether allomothers picked a specific infant they wanted to "baby-sit" or if the mother picked the

allomother. He did suggest that allomothering could help to establish bonds with females that have recently moved into a group.

Manson's (1999) research involved infant handling in wild Cebus capuchins, which are very closely related to squirrel monkeys, but have a different social organization. Infant handling is similar to allomothering, but females that participate in infant handling provide little direct care for infants (Silk 1999). The females will gather around the mothers and touch, nuzzle, cuddle, and sniff newborns, but they will not care for or protect them from any danger. Manson hypothesized that infant handling is actually a test used by adult females to examine social bonds. Those with offspring and those without exhibited the same amount of infant handling. Infant handling was not related to dominance hierarchies, however, females did handle the infants of the females who they groomed and with whom they formed strong alliances. That is, certain individuals were allowed to spend more time with infants over others. Infant handling rates were not related to allonursing and females were not documented to swap infants.

Muroyama (1994) and Ventura (2002) found that ultimately, allomothering enables mothers to increase time for foraging as demonstrated in studies of patas monkeys and capped langurs. It is advantageous for the lactating mothers to have extra foraging time since it is such a critical time period and the mothers need extra nutrition.

Further, Muroyama (1994) proposed allomothering in patas monkeys increases the infant's socialization skills. Infants would be more likely to allow a female to carry them during times of rapid flight or danger due to infants being accustomed to riding on other females' backs. An infant's chance of survival would also increase if the mother should die and its care was taken over by others.

Silk (1999) looked at what caused certain females to allomother over others. She found that dominance played a role in infant handling among captive bonnet macaques. When kinship did not play a role in infant handling, higher social status did with higher-ranking females handling infants at higher rates than lower-ranking females.

Stanford (1992) found that kinship played a role in allomaternal care in Japanese macaques because mothers would act more aggressively toward allomothers to which they were less related. Parous females did most of the allomothering so it was thought that they must gain something from it, rather than the younger females needing maternal experience.

While much research has been done on the causes of alloparental care, more investigation is necessary concerning why certain individuals participate in this behavior over others. Stanford (1992) suggests that the causes of alloparental care are very specific to each species. Therefore, research must be done with each species where alloparental care is seen to determine which explanation best fits the data. The proposed research does this by looking at what factors influence those who participate in allomothering among squirrel monkeys.

Squirrel Monkeys

Squirrel monkeys belong to the genus *Saimiri.* They are a member of the Cebidae family and are the smallest member. Five different species have been recognized but the most common is *Saimiri sciureus sciureus*, the common squirrel monkey. Figure 1 shows Peruvian squirrel monkeys at the CNPRR at USA. Squirrel monkeys live in the tropical rain forests of North and Central South America. They are frugivores and insectivores, and their diet consists of foods that are high in protein. They utilize most

layers of the canopy except for the uppermost due to fear of raptor predation. Squirrel monkeys live in multi-male/multi-female groups that usually consist of 20 to 50 individuals. The genus *Saimiri* lacks a number of behaviors, which are a common part of other primate social relationships such as infanticide, habitat saturation, grooming, and reconciliation (Boinski et al. 2002).

Figure 1: Two Peruvian mothers with their infants "hanging out"

In squirrel monkeys the males do not participate in alloparental care which means that mothers are the primary caregiver. One such possibility to explain the existence of allomothering is that it relieves the dam of intense parental duties, which provides mothers more time to forage and rest. This is advantageous for a lactating mother, especially if she is the only parent engaged in raising the infant. Additionally, squirrel monkey infants are large when compared to the mother's body weight. An infant monkey makes up about 15-18% of a non-pregnant adult female's body weight (Williams et al. 2002). This places a heavy burden on the mother and allomothering might also help to ease this burden.

Among neotropical primates the genus *Saimiri* is unique because it is the only one that exhibits allomothering and does not live in family or pair groups. Compared to other neotropical primates, squirrel monkeys live in the largest, most cohesive groups. The environment and ecological niche greatly influences and shapes the social systems of squirrel monkeys, which govern their behavior. Just like most primate species, squirrel monkeys have intricate social systems, which play a major role in their actions and behaviors. The environment inhabited by squirrel monkeys and the type of social system they exhibit affect the frequency at which allomothering occurs.

Wrangham (1980) was the first to construct an ecological model that focuses on primate social evolution. This model looks at the importance of female-female bonding and its effect on reproduction and foraging (Boinski et al. 2002). He observed that some females became "female-bonded" and formed cohesive groups. He also noticed that females dispersed according to the distribution of resources, while the males dispersed according to the females in order to increase reproductive success. For example, in Costa

Rica the males and females are egalitarian and the females form weak social bonds. In Peru females are dominant over the males and the females form strong cohesive groups. Alternatively, males are dominant over females in Suriname and the females do not bond or form coalitions. In Costa Rica, food patches are small and widely dispersed while in Peru food patches are large. However, food abundance is low in Suriname (Boinski 2002). Wrangham observed that the females' relationships were predicted by resource distribution.

Boinski et al. (2002) discuss work by Van Schaik and van Hooff who built on Wrangham's ecological model of social evolution, and their model is also centered on sexual selection. One component of the Van Schaik and van Hooff model is that female relationships are dependent upon food competition and are constructed to make the best use of the resources available. For example, direct competition for food is thought to increase the strength and number of social bonds between females. This would have a significant effect on the structure and degree to which dominance hierarchies are used.

In Costa Rica, female bonds are weak, because there are low levels of competition for food. In Peru, female bonds are strong, because there are high levels of competition and a larger area to control. Therefore, it is advantageous for the squirrel monkeys in Peru to form strong groups to maximize foraging opportunities. This evidence also indicates that food distribution affects competition amongst females. This competition is what leads to predictable patterns seen in female relationships.

Boinski (1999) looked at different ecological niches and how each affected the social organization of squirrel monkeys. Although all *Saimiri* species are ecologically similar, they have the most variation in sociality of any neotropical primate that has such

a large geographic spread. They reside in the same habitat, occupy the same position in the canopy, share the same morphology, and prefer the same foods. However, they do not share the same social system, which demonstrates that the environment is related to the social system. Slight differences in the ecology and distribution of food can have significant effects on primate social behavior.

Specific to allomothering, Williams et al. (1994) observed allomaternal behavior in Bolivian squirrel monkeys. They found a number of factors that influence allomaternal care such as the infant's age, maternal ranking, kinship, age and experience of the allomother, and social structure. Williams et al. discussed possible reasons for allomaternal behavior that were suggested by McKenna (1979): 1) establish female-female bonds, which might contribute to group cohesiveness through infant sharing; 2) increase infant survivorship if the biological mother should die; 3) allow young females to learn good maternal skills at an early age; and, 4) encourage infants to attain valuable socialization skills at an early age.

Williams et al. completed two separate studies on mother-infant dyads and their interactions with allomothers by using focal and instantaneous scans from the time the infant was one week to six months old. They found that infant squirrel monkeys spent as much as 30% of their time on allomothers and they start when they are about one to two months old. In this study, 53% of the allomothers were found to be juvenile females between the ages of four and six and only 21% of the allomothers were older (between the ages of seven and nine). In squirrel monkeys, allomaternal care is seen more as a form of babysitting. However, genetic analysis has shown cases where mothers would actually swap and raise the "adopted" infant. Allonursing, when an infant nurses from a

female other than its mother, proved an interesting aspect of the study as it was found that mothers who had lost their infants that year made up 86% of the allonursing events. Parous but infantless females make up a smaller percentage of squirrel monkeys that engage in allomothering. Williams et al. found that kinship did not play a role in allomothering. They found that there were no significant differences in allomothering between kin (first cousins or higher) and non-kin. Williams et al. looked at the age, sex, and reproductive status of allomothers and answered questions regarding the timing and extent of allomothering. However, they suggested more research is needed to examine the proximal causes of allomothering in squirrel monkeys.

Studying Allomothering at the CNPRR

This thesis explores the relationships between mothers and allomothers in two captive squirrel monkey populations (Figure 2) housed at the Center for Neotropical Primate Research and Resources (CNPRR). The CNPRR is the only federally supported laboratory in the United States that is devoted to maintaining self-sustaining colonies and researching captive breeding problems (Williams et al. 2002). This thesis will contribute to the available knowledge of squirrel monkeys and neotropical primates by better understanding the underlying processes of allomaternal care and in determining the proximal causes of non-maternal infant care. This study could serve as a model for examining allomothering in other neotropical primates and other biological Families as well. In addition, this thesis will help to understand the complex breeding and social systems of squirrel monkeys, which will allow scientists the ability to correct breeding problems that often occur in captivity. This will allow scientists the ability to better maintain self-sustaining colonies in captivity.

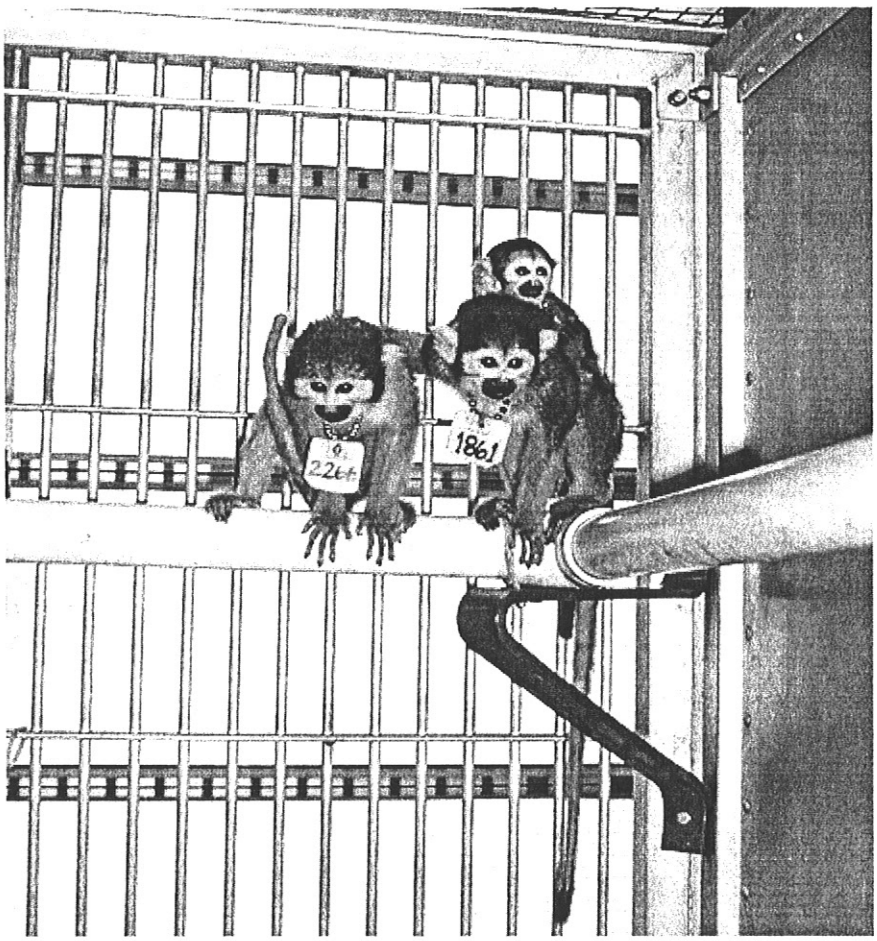

Figure 2: A Peruvian mother and infant within proximal contact of another female friend. They are best buds.

This study will build on the research conducted by Williams et al. (1994) by specifically examining the role played by female-female bonds in squirrel monkey allomothering. This study aims to better understand the proximal causes of allomaternal behavior by examining huddling groups, those that are in proximal contact with mothers, and kinship of Peruvian and Guyanese mother-infant dyads. I hypothesize that the monkeys that are in the same social cliques as the mother and those that are closely related to the mother, such as a daughter or a sister, will choose to and be allowed to allomother more than those that are not in the same social cliques and those that are non-

related to the mother. Therefore, I hypothesize that the monkeys that are in proximal contact and huddle with the mothers the most, before and after delivery, will do the majority of the allomothering.

Like most primates, squirrel monkeys have social systems which govern their actions and behaviors. The structure of any social grouping is considered to consist of four integrated levels; individual, dyadic, clique, and inter-clique relations (Tabor, 1986). The first level, the individual, comprises the biological and behavioral characteristics of each member of the group. The second level focuses on the dyadic interactions between individual members. These relationships are defined by characteristics that include strength, stability, and mutuality. The third level looks at the relationships that exist in groups that are made up of more than two individuals and the development of cliques. The fourth level looks at how the social structure is formed through interactions between subgroups. Each successive relationship is dependent on the one before to form a social hierarchy in which each member's position and relationships are developing and changing. These social relationships and cliques regulate with whom they will interact and what role they will play. Thus, social status and social cliques may be important factors in determining why an individual chooses to engage in allomothering and why certain monkeys are allowed to allomother and others are not.

Huddling is a common behavior in which squirrel monkeys will sit or lie together with their tails wrapped over their shoulders. They do this while asleep or at rest, and they have a tendency to huddle with members of their same social status (Williams 2002). Proximal contact is defined as being within one body length of another monkey. I considered monkeys to be in proximal contact if they were within one body length of

each other for 5or more seconds. It is of interest to determine if individuals with whom a pregnant female huddled or were in proximal contact prior to giving birth are more likely to engage in allomothering. As mentioned, huddling and being in proximal contact with one another are related to social cliques so it is critical to consider this factor as well.

The final major factor considered here in relation to allomothering is kinship. Researchers have long suggested a relationship between kinship and allomothering (Williams 1994). Tabor (1986) found that dyadic female relationships were usually those between relatives. Tabor also found that when juvenile females participated in allomothering they carried younger siblings more so than other infants. The CNPRR has kept detailed genealogical data since its inception and these data will be used to determine whether kin are more likely to provide allomothering than non-kin. The author collected the specific data concerning allomothering behavior.

Research Methods

This study is based on observations of individual breeding groups of squirrel monkeys housed at the CNPRR. At the CNPRR, squirrel monkeys are housed in large pens that provide heated air and artificial light. There are translucent vertical doors behind the cages that allow sunlight to enter and the doors are opened when the weather permits. Breeding groups usually have access to two or three pens through circular openings in the walls. The light/dark cycle has been adjusted to coincide with the sunrise and sunset in Mobile, Alabama. Each social group consists of one to two males and up to 30 females (Williams et al. 2002). At the CNPBRR, the birth season occurs mostly from May to August.

Two separate groups of Peruvian squirrel monkeys and two separate groups of Guyanese Squirrel monkeys were studied. A total of 23 subject females were studied. This study is divided into two data collecting stages. First, three scans were collected each week by the author for each pregnant female in June, July, and August 2004. I used a modified instantaneous scan technique. Instantaneous scans (Altman 1973) are used to study an individual's existing activity. It is used to observe an individual's state rather than an event. This technique is used to observe individual behavior separately from a large group. Regular instantaneous scans are those where a specific individual is targeted and that individual's behavior is recorded at that very moment. The modified scans that were completed in this research involved observing a specific individual and then waiting to see which monkey(s) that individual huddled with or with which they came into proximity. While these modified scans allowed me to determine which monkeys huddled together and which monkeys were in proximal contact I do not have accurate frequency data. That is, I am unable to determine the strength of each relationship due to the fact that for a true instantaneous scan I would have recorded no huddling or proximal contact for most individuals, but this would have provided frequency data. Rather, the recorded data concerns who sits next to the mothers and who huddles with the mothers. This did not affect the outcome of the analysis, but for future studies it would be of interest to look at the strength of each relationship through more regular intstantaneous scans. The collected data will be supplemented with genealogical information. Because I did not collect these supplemental data and am unaware of the specifics, my observations were not biased by prior knowledge of kinship relations. The combination

of these huddling, proximity, and kinship data will provide an understanding of the relationships of the adults prior to birth of the infants.

After delivery, ten-minute focal observations were conducted on each mother-infant dyad (Figure 3). Focal observations (Altman 1973) consist of recording all specified activities or interactions in which the subject animals may participate. These focal observations were used to determine with whom they huddled, with whom they were in proximal contact, and who is doing the allomothering. The mother-infant dyads were observed for approximately 10 weeks or until the infants spent most of their time on their own and off their mothers.

Figure 3: Collecting data at the CNPRR is fun times!

Next, the data collected on those that were in proximal contact and those that huddled with the mothers before delivery were analyzed. Subjects were divided into two

groups, those that associated together and those that did not. This allowed a test of whether allomothering was based on association or if some other factor was the cause. Finally, the kinship data that had been previously collected were analyzed to see if this factor had an effect on allomaternal care as well. These data were analyzed using a Chi-square goodness of fit test and other categories were compared as well. Kin were compared to those that were in proximal contact with the mothers before delivery and those that huddled with the mothers before delivery. Kin were also compared to those that were in proximal contact with the mothers after delivery and those that huddled with the mothers after delivery. Then, those that were in proximal contact with the mothers before delivery were compared to those that were in proximal contact with the mothers after delivery. Those that huddled with the mothers before delivery were also compared to those that huddled with the mothers after delivery. Phi coefficients were computed to test the significance of these comparisons.

Results

The Chi-square test was used to compare allomaternal care and proximal contact before delivery. The analysis showed that allomaternal care and proximal contact before delivery was significant at the .001 level (Table 1.1). This means that allomaternal care is not random and those monkeys that came into proximal contact with the mothers before delivery were more likely to allomother than those monkeys that did not. The Chi-square test was also used to compare allomaternal care and huddling before delivery, which was not significant (Table 1.2). This means that huddling groups do not indicate those that will engage in allomothering. The Chi-square test was used to compare allomaternal care and kinship as well. This compared allomothers and mothers,

daughters, and sisters. This showed that allomaternal care by kin was significant at the .001 level (Table 1.3). However, there are differences between the kin. For example, 24 % of the allomothering was done by older daughters of the mother, while only 3.2% of the allomothering by sisters and 1.6 % by mothers. The Chi square test took the number of non-kin females and kin females into account so that 24% is a significant number. When allomothering and kin were compared the observed number of older daughters participating in allomothering is significantly above the expected number. When comparing kin and allomaternal care, most of the allomothers were siblings of the infants being allomothered.

Based on this study kinship is a good indicator of who will participate in allomothering and the kin are older sisters. There was no correlation between kin and those that were in proximal contact with the mothers before or after delivery. There was also no correlation between kin and those that huddled with the mothers before or after delivery. However, there was a significant correlation between those that were in proximal contact to the mothers before and after delivery and those that huddled with the mothers before and after delivery. This means that those that associate with the mothers before delivery are the same monkeys that associate with the mothers after delivery.

Discussion

This research has investigated three main factors that were thought to influence allomaternal care. The first factor was if proximal contact with the mothers before delivery was a good indication of which females would participate in allomothering. Proximal contact was found to be significant and a good indication of who would allomother. Those that remain in proximity to one another are assumed to exist in the

same social cliques. This research shows that those that are in the same social cliques will most likely participate in allomaternal care.

The second factor that was examined was huddling partners. Those that huddle together are also assumed to be in the same social cliques. The results showed that huddling groups were not significant in terms of who participated in allomaternal care. This is somewhat unexpected given the proximity results, since huddling groups inicate social clique membership and it did not influence those who participated in allomothering.

The results presented here do correspond to the research conducted by Williams et al. (1994). They found that most of the allomothers were juvenile females between the ages of four and six. While conducting my observations, I noticed that most of the females that did the allomothering were juvenile females as well. Also, I found that before delivery pregnant females usually only huddled with other pregnant females, this is likely the reason why huddling and allomothering were not related. After delivery the mothers usually huddled with other mothers and adult females. More analysis is needed to examine the relationships between age and huddling partners. If it was found that age was a factor, and most allomothering is done by juveniles, then it would make sense that huddling partners did not influence allomothering. I think it would be of interest to examine whether the juvenile daughters of the females that huddle with the mothers participate in allomaternal care more than expected for random chance. This is because my observations suggest that huddling groups are a strong indication of the intense social relationships that are found among squirrel monkeys. It is these relationships that govern their behavior and their social interactions (Tabor 1986).

The third factor that was examined was kinship. The question was if whether kin participated in allomothering more than non-kin. Kinship was found to be a significant factor that influenced allomothering. However, it was mostly the previous daughters of the mothers that were found to allomother their siblings. This differs from what Williams et al. (1994) found. They found that allomaternal care was not based on kinship. However, Williams et al. studied Bolivian (*Saimiri boliviensis boliviensis*) squirrel monkeys and this study focused on Peruvian (*Saimiri boliviensis peruviensis*) and Guyanese (*Saimiri sciureus sciureus*) squirrel monkeys. It is possible that different subspecies or species could exhibit differences in allomaternal care, but more research needs to be undertaken on whether kinship influences allomothering and if different subspecies and species behave differently when allomaternal behavior is concerned.

Patterns in these data were used to examine the various hypotheses put forward to explain the evolution of alloparenting. As previously discussed Williams et al. (1994) and McKenna reviewed different explanations for the evolution of allomothering. If establishing female-female bonds and enhancing social solidarity is a reason for infant sharing, then allomothers would most likely already be in the same social group of the mothers they are helping or they may become members of the same social group through allomothering. This study showed that those that were in proximal contact with the mothers before and after delivery were the most likely to participate in allomothering. Although huddling partners before delivery were not found to influence allomothering those that allomother and were found to be in proximity to the mothers before delivery indicate that a reason allomothering may exist is to enhance the existing bonds between females. It would be of interest to determine if individuals became new members of

social cliques through allomothering. The data showed that those that were in proximal contact and huddled with the mothers before delivery were also in proximal contact and huddled with the mothers after delivery. However, it would be of interest to look at who is in proximity to and huddling with the mothers 10 weeks after delivery to see if the relationships stayed the same. Instantaneous scans have been collected for weeks 11-16 after delivery. This data has not been analyzed yet but may offer some future insight into how allomothering affects the relationships between squirrel monkeys. The explanation that allomaternal care may increase infant survivorship can not be tested in this study because data are being collected only from a single season and none of the infants that were studied have died. Another possible explanation for the evolution of allomothering among squirrel monkeys is that they gain important experience from this behavior. If this explanation is applicable to squirrel monkeys, then it would be expected that allomothering would be most often provided by younger females, whether related or not, who have not been mothers in the past. Williams et al. have already provided some support for this explanation since they found that 53% of allomothers were between the ages of four and six. Age has not yet been analyzed and compared to those who participated in allomaternal care but based on my observations most of the females that did allomother were juveniles. This suggests that allomothering may also have evolved to increase juvenile female's experience with caring for infants. Another study of interest would be to look at females that either drop their infants or have infants that die young and see if they had any allomothering experience. One could also look at mothers that did not drop their infants and had healthy infants and see if they had any allomothering experience. The final explanation, that allomothering causes infants to gain valuable

socialization skills, cannot be tested in this study. Future research should also be conducted on this area.

This thesis looked at some of the possible proximate causes of allomaternal behavior in squirrel monkeys. Further research needs to be completed to more precisely determine why allomothering exists in squirrel monkeys and what has driven its evolution.

Table 1.1 - 1.3 Chi-square results

1.1 Allomaternal Care by Proximal Contact Before Delivery

	O	E	Chi ²
No- Prox	19	36.58	8.45
Prox	43	17.63	36.15

Chi ² = 44.95 $p < 0.001$

1.2 Allomaternal Care by Huddling Before Delivery

	O	E	Chi ²
No Huddle	56	57.14	0.022
Huddle	6	4.86	0.267

Chi ² = 0.289 p = not significant

1.3 Allomaternal Care by Kin

	O	E	Chi ²
Non-Kin	44	55.8	2.49
Kin	18	6.2	22.45

Chi ² = 24.94 $p < 0.001$

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