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**THE EFFECTS OF DEPENDENT INFANTS ON THE SOCIAL BEHAVIOR
OF MANTLED HOWLER MONKEYS (*ALOUATTA PALLIATE*)**

Keziah Katz

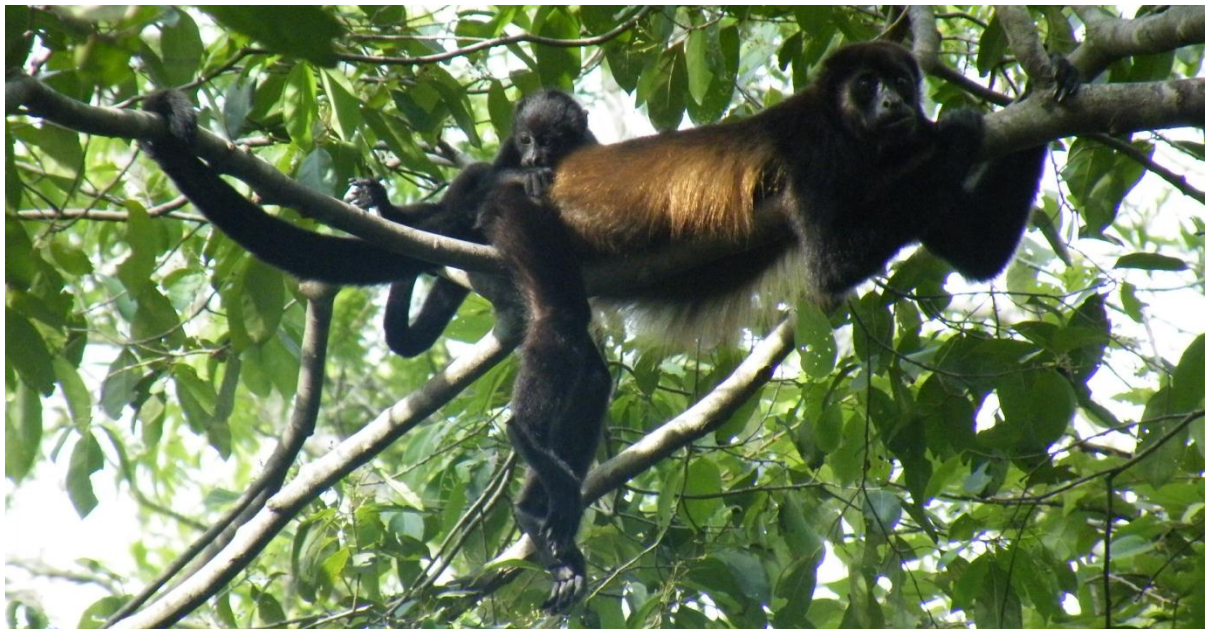


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ABSTRACT

The behavior of eight groups of around 18 adult mantled howler monkeys (*Alouatta palliate*) was observed for six weeks. Resting within one meter of another adult was considered to be a social act of resting in proximity. Males rested in proximity with females significantly more often than would be predicted by chance. This could either be for keeping up a relationship with potential mates or for protecting the young of females with dependent infants. The data was analyzed again with females divided into those with and without dependent infants. Males showed a significant preference for females without infants. This implies that the primary reason for male-female association in mantled howler monkeys is to maintain a relationship with potential mates. The preferences of the females were also analyzed. Females without infants rested significantly less often with females with infants than was expected by random chance. Females with infants did not have a statistically significant preference for proximity partners but they tended away from resting with females without infants. This is thought to be explained by the female with an infant avoiding contact with the lone female to discourage intragroup infanticide (not uncommon in groups of unrelated individuals).

INTRODUCTION

Sociality in Primates

Many animals live in groups in spite of increased resource competition and increased susceptibility to disease. In species that form groups, some combination of advantages outweigh the costs. Some of these advantages are: cooperative foraging, exchange of information, decreased chance of predation and increased defense against

predators and competitors (Rubenstein, 1978). Social groups can be formed by unrelated individuals or individuals with varying degrees of relatedness. Social behavior develops in animals that live in groups. The development of social behaviors increases the advantages of living in a group in the first place. It also provides structure for reproductive competition and has been hypothesized to reduce parasite loads (Alexander, 1974). Motivations for social behavior can be broken into three categories. Reciprocity is when an individual helps another with the hope that the favor will be returned at a later date. Nepotism is when an individual helps a related individual to increase its inclusive fitness. Parental manipulation is when a parent alters the behavior of its offspring in order to increase the parent's reproductive success (Alexander, 1974).

Primates live in many different in social systems including solitude, mating pairs and groups of more than two individuals. The majority of primates fall into this final category which can be broken down into single male groups, single female groups and multimale-multifemale groups (Kappeler and van Schaik 2002). Males disperse from their natal group in the majority of primate species but in some species both sexes will disperse from their natal group and rarely only females will disperse from their natal group (Pusey and Packer, 1987). In cases of single sex dispersal, the non-dispersing sex benefits by living in association with kin and can practice and benefit from nepotism. Thus there are stronger social bonds between members of the non-dispersing sex in primates (Moore, 1991). In cases where both sexes disperse like mantled howler monkey (*Alouatta palliate*), there are no (or few) related adults within each group and the animals cannot practice nepotism (Glander, 1991). This lack of relatedness leads to

an interesting venue to study the nature of social bonds when nepotism cannot play a role.

In complex primate social structures, the animals form bonds with specific conspecifics to help increase their position in the social system. These bonds can be formed through a variety of affiliative social behaviors although grooming is the most common. Similar methods are sometimes used to gain access to reproductive partners (Henzi and Barret, 1999). Grooming is an important social stimulus for most primates. It provides the health benefit of parasite removal but also provides the basis for most primate social bonding. Grooming is so important that some primates devote as much as 20% of their daily activity to performing it (Dunbar, 2010). It is commonly used to assess the social bonds of primate groups.

The mantled howler monkey rarely grooms (Jones, 1979, 1980). This is partly due to the lackadaisical lifestyle of the mantled howler monkey. The majority of their time is spent resting ($63\pm 20\%$) while the remainder is spent feeding ($24\pm 21\%$) and traveling ($9\pm 7\%$) (Cristobel-Azkarate and Arroyo-Rodriguez, 2007). In comparison, mantled howler monkeys only participate in active social activities for about thirty seconds every hour (Estrada *et al*, 1999). Thus active social behaviors cannot be used to assess their social bonds. Howler monkeys spend the majority of their time resting and some of that time is spent in proximity to another adult. Thus resting in proximity (within arm's reach) of another adult was chosen as a measure of social bonds (Crockett and Eisenberg, 1987; Pavelka and Knopff, 2004).

Mantled howler monkeys spend the majority of their time as a single group that moves, feeds and rests together. Sometimes the group will divide into subgroups during

the day but they usually reunite before resting for the night. These subgroups are usually multimale and multifemale (Mittermeie, 1973). They do not have a strict social hierarchy and all males (or most) will mate with females in estrus within their group. Previous studies have found that both males and females spend more time near females than with males (Wang and Milton, 2003; Zucker and Clark, 1998). This suggests that bonds with females form the central structure of howler monkey social groups.

Role of Infants

Infants are very attractive to conspecifics in primates for both adults and juveniles and especially to females. Conspecifics practice parenting and play with infants (Hrdy, 1976). However in groups of nonrelated females (as in the mantled howler monkey), mothers often resist attempts of practice parenting on her infant as it can lead to harm to the infant (Clarke et al., 1998). In addition primate females with infants are attracted to other females with infants. Interactions between two females with infants benefit both the social development of the infant and occasionally the social status of the mother (Maestriperi, 1994). In some primates, males will capture infants to use as an agonistic buffer against dominate males (Busse Hamilton, 1981)

Infanticide has been documented in many species of primates including the mantled howler monkey (Clarke, 1983). It is a low probability, high risk factor. The benefit of having a male defend its own offspring from infanticide that has been hypothesized to be a major cause of the development of permanent male-female bonds in primates (Schaik and Kappeler, 1997). Female mantled howler monkeys have been shown to be aggressive and even infanticidal towards infants within their own group (Clarke et al., 1998). Females always know who their offspring are but males cannot be

sure in non-monogamous mating system. Male howler monkeys have been shown to commit infanticide against the offspring of females that they did not copulate with near the time of conception. This most commonly occurs during a group take over and it nearly eliminated the chance that a male might accidental kill his own offspring. It is believed that howlers commit infanticide to free up more resources for themselves and their own offspring. This theory is favored in howler monkeys over the hypothesis that infanticide occurs to bring a female into estrus for a number of reasons. Immature males have been observed committing infanticide, infants that were too old to interrupt the mother's estrus have been killed and the female mates with multiple males after losing an infant which leaves a low percent chance that the infanticidal male will sire the next offspring. (Agoramoorthy and Rudan, 1995).

Hypotheses

This study aims to evaluate the social bonds among males, females in general, females with dependent infants and females without dependent infants. This is to determine the effect that the presence of an infant has on the behavior of a female and the behavior of others towards her. It is predicted in each case that the howlers will spend more time resting in proximity to the howlers with which they have the strongest social bonds.

The Role of Sex

In a species where both sexes disperse, there are no bonds of kinship between adult group members. Kinship creates social bonds between members of the non-dispersing sex (Moore, 1992). Without kin bonds, other factors will determine the social order. Previous studies have shown that males prefer to be in proximity with females (Wang and Milton, 2003) and that females also prefer to spend time with females

(Zucker and Clarke, 1998). It is expected that the howlers in this study will behave similarly.

H_♂) Males form stronger social bonds with females for reproductive access

H_♀) Females form stronger social bonds with other females as in past research

The Role of Infant Status

Females without infants have somewhat different priorities than females with infants. Their main priorities are to have enough resource for themselves and any future offspring and to obtain a fit mate to father potential offspring. The hypotheses for proximity partners of females without infants are:

H₁) females without infants form stronger social bonds with males for sexual relations

H₂) females without infants form stronger social bonds with females with infants for allomothering experience

H₃) females without infants spend less time with females with infants because females with infants deny infant-nonmother interactions.

Infants are a valuable resource for a female because their reproductive success is directly link the survival of offspring. Females provide for their offspring and protect them from dangers. A female with a dependent infant faces the risk of infanticide from both outsiders and members of their own group. This implies that females with infants should be cautious about with whom they interact. A common way for primates to reduce infanticide is to keep strong male-female bonds (Schaik and Kappeler, 1997). Males from outside of a howler group have very little chance of being related to infants in that group and present the strongest risk of intergroup infanticide. Most males within a howler group have a chance of being the father of any given infant (as most males

mate with each female in estrus) and thus the males will protect the infants (Schaik and Kappeler, 1997). However, adult females within a howler group also have very little chance of being related to infants they are not the mother of. Females are attracted to infants but these nonrelatives can be careless or malicious and may harm the infant. However, young primates need to play with other young. Female primates with young infants have been known to associate with each other in order to socialize their infants. These conflicting possibilities resulted in the following competing hypotheses:

H₁) females with infants form stronger social bonds with males for protection against infanticide

H₂) females with infants form stronger social bonds with females without infants for allomothering

H₃) females with infants form stronger social bonds with females with infants for infant socialization.

Males should also change their behavior towards females depending upon the infant status of that female. Males need to maintain social bonds with females in order to gain reproductive access but they also must protect infants from infanticide (Schaik and Kappeler, 1997). It is unknown which pressure is strong in mantled howler monkeys. These ideas will be tested with the following hypotheses:

H₁) males form stronger social bonds with females without infants for sexual relations

H₂) males form stronger social bonds with females with infants to protect against infanticide.

METHODS

Study Site

This study was conducted in a v-shaped forest fragment near Cofradia, Honduras on eight groups of mantled howler monkeys. Five of the groups are located in Rancho Manacal in Honduras, a sugar plantation that has chosen to protect the howlers. Across from Rancho Manacal is *Gracias a Dios*, a cooperative water purification plant surrounded by forest. There are three groups of mantled howler monkeys that reside within *Gracias a Dios*. The two properties are separated by a road but connected by a thin strip of forest (Figure 1). There are homes scattered around the edges of the fragment and people visit *Gracias a Dios* daily for water. Because of this, the howlers are habituated to humans.

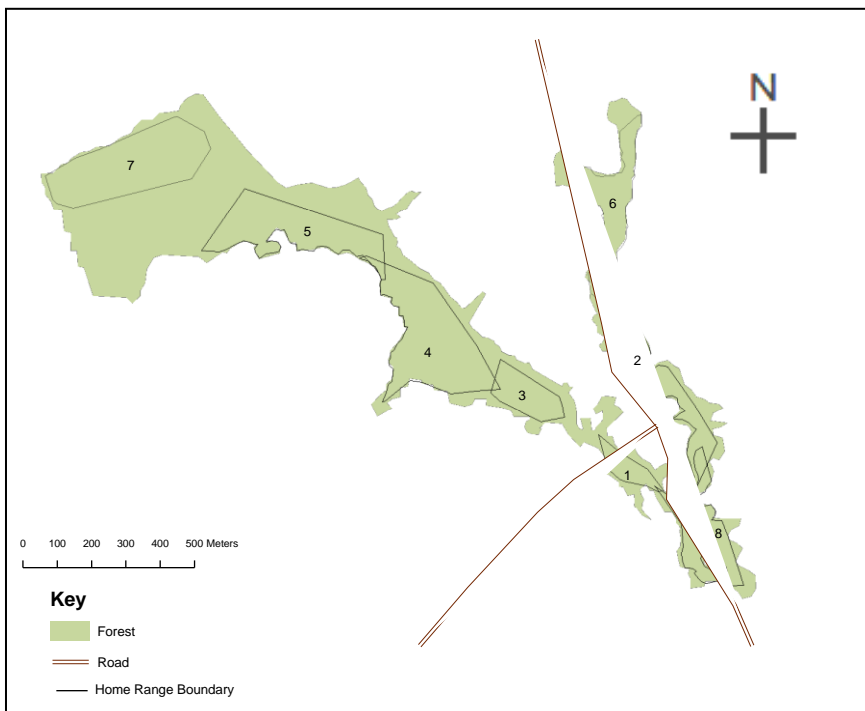


Figure 1: Map of Rancho Manacal and *Gracias a Dios* with the home ranges of the groups of mantled howler monkeys studied (as of August 2009)

Descriptive Data

The number of adult males, adult females, juveniles and infants in each focal group was recorded each day. At the end of the study, the daily compositions of the groups were pooled to determine the minimum number of individuals in each group (Table 1).

Group Number	No. Males	No. Females	No. Juveniles	No. Infants
1	3	10	1	3
2	4	11	2	4
3	4	11	2	3
4	6	14	3	6
5	3	10	1	3
6	11	21	3	10
7	4	10	2	3
8	7	19	3	10

Table 1: The population composition of eight groups of howler monkeys in Rancho Mancal and *Gracias a Dios*

Adult males were identified by a white scrotum, an enlarged throat with a laryngeal sac and a golden mantle. Adult females were identified by their relatively smaller size, a golden mantle and by their lack of laryngeal sac and scrotum. Juveniles were distinguished by an underdeveloped mantle and by moving independently of the mother. Infants were defined as offspring that were still dependent on the mother for food and travel and as the smallest individuals (Glander, 1980).

The home ranges of each group of howlers were mapped by recording the coordinates of all of the locations the group of howlers have been observed at any time. These locations were then mapped and boundaries drawn to include all of the locations (Figure 1).

Behavioral Data

Observations were recorded from June 18th through July 31st for five or six days a week. Two of the howler groups were observed each day from either from 06:00 until 12:00 or 12:00 until 18:00. Four or five morning and afternoon sessions were conducted on each group of howlers. A total of 371 hours of behavior were recorded. Scan sampling (Altman, 1974) was used with a ten-minute interval between scans. Between four and six people were assigned to each group (depending on staff availability); one person was dedicated to physically recoding the data while the others were dedicated to actual observations. Each observer would watch a portion of the howler group and inform the data recorder of the behavior at each scan interval.

Behavioral data was collected on adults and recorded along with the sex and the presence or absence of a dependent infant (or infant status) of each individual. Simple behavioral categories were used to minimize the time spent on each scan and to minimize observer differences (Table 2). If an individual was resting within arm's reach (~1m) of another individual, the two individuals were said to be resting in proximity and the sex and infant status of the proximity partner was recorded. This data recorded for this study were used for a number of studies. The proximity data is the focal data for this study.

Behavior	Definition
Social	Any manipulation of one individual by another (including play behavior)
Feeding	Moving leaves, fruit or flowers towards the body and/or the mastication of leaves, fruit or flowers
Moving	Changing location within or between trees
Out of View	Any monkey not visible during scan
Resting	Inactivity
Vigilant	Stationary position with head raised and alert
Other	Any behavior not mentioned above

Table 2: Ethogram for mantled howler monkeys

Data Analysis

The data were entered into MS Excel 2007 at the end of each day. The data set for each group of howlers was averaged to form a sample size of 8. Chi squared tests were calculated in MS Excel 2007 and paired t-tests were calculated in SPSS Statistics 17.0.

The data were evaluated in two ways: first, separating only by sex and then by sex and infant status. Time spent in proximity with more than one individual was used for calculations of percentage of resting scans spent in proximity but only interactions between two individuals were used when calculating the proximity partner preferences (Table 3).

Preference of....	to rest in proximity to....
Males	Males vs. females(all)
Males	Males vs. females without an infant vs. females with and infant
Females (all)	Males vs. females (all)
Females without an infant	Males vs. females without an infant vs. females with and infant
Females with an infant	Males vs. females without an infant vs. females with and infant

Table 3: Proximity partner preferences tested in this study

By Sex

The percentage of time spent performing each behavior was calculated separately for each sex and the values were compared using paired Student's t-tests. The preference for proximity partner was calculated using a Chi-squared test. The average of the total number of times each type of proximity pairing occurred (♀♂, ♀♀ and ♂♂) in each group was compared to the expected value calculated by the average percentage of the partner sex in each group multiplied by the average number of total proximity scans. An example calculation is shown below:

Observed value for Female Preference for Males: $\frac{\sum \text{♀♂}_i}{8}$

Expected value for Female Preference for Males: $\frac{\sum \text{♂}_i}{8} * \frac{\sum \text{♀}_{pi}}{8}$

♀♂_x: Number of times a male and a female were seen in proximity in group X

♂_x: Number of males in group X

♀_{px}: Total number of time a female was seen in proximity to one adult in group X

By Infant Status

The percentage of time spent performing each behavior was calculated separately for females with an infant (♀♀) and females without an infant (♀) and the values were compared using a paired Student's t-test with the data paired by howler group. The preference for proximity partner was calculated using a Chi-squared test. The average of the total number of times each proximity-pairing (♀♀, ♀♀♀, ♀♀♀♀, ♀♂, ♀♀♂ and ♂♂) for each group was compared to the expected value calculated by the average percentage of the partner class (♀, ♀♀ and ♂) multiplied by the average number of total proximity scans (same method as was used for sex). Residual values $\left(\frac{\text{Observed}-\text{Expected}}{\sqrt{\text{Expected}}}\right)$ were calculated for each statistically significant Chi-squared test to determine which values were significant contributors.

RESULTS

General

The howlers spent more time (65.7%) resting than in any other activity and less than one half of a percent of their time performing any social behavior (Figure 2). 14.5% of the time that the howlers were resting was spent resting in proximity to another adult or 9.7% of their total time.

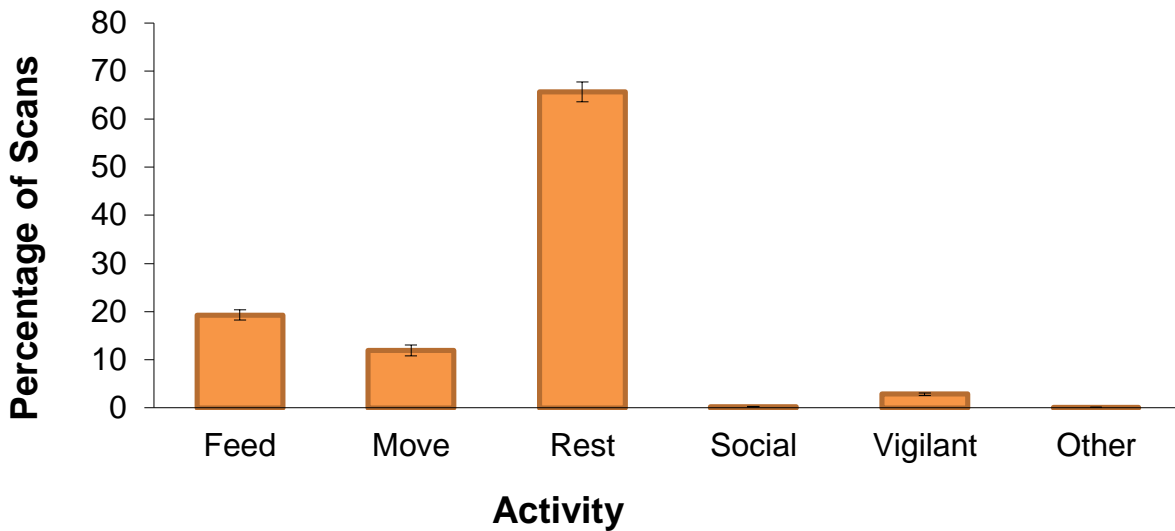


Figure 2: Average percentages of scans for eight groups of mantled howler monkeys that were observed performing each behavior

Differences due to Sex

Females fed more significantly more often than males and males were vigilant significantly more often than females. Males and females showed no significant difference in time spent performing any other behaviors (Figure 3, DF=7; Feed $t = -3.345$, $p = 0.012$; Move $t = 1.45$, $p = 0.19$; Rest $t = 0.200$, $p = 0.847$; Social $t = -0.912$, $p = 0.391$; Vigilant $t = 5.764$, $p = 0.001$; Other $t = 2.035$, $p = 0.081$). Males and females did not spend significantly different amounts of time resting in proximity with another monkey (Figure 4, DF=7, $t = 1.1339$, $p = 0.2942$).

Males significantly preferred to rest in proximity to females and avoided resting in proximity with males (Figure 5, DF=1, $X^2 = 5.2$, $p = 0.02$). Females did not show a preference for proximity partners (Figure 6, DF=1, $X^2 = 1.2$, $p = 0.23$) and rested in proximity to both males and females in proportion to their presence in the group's sex composition.

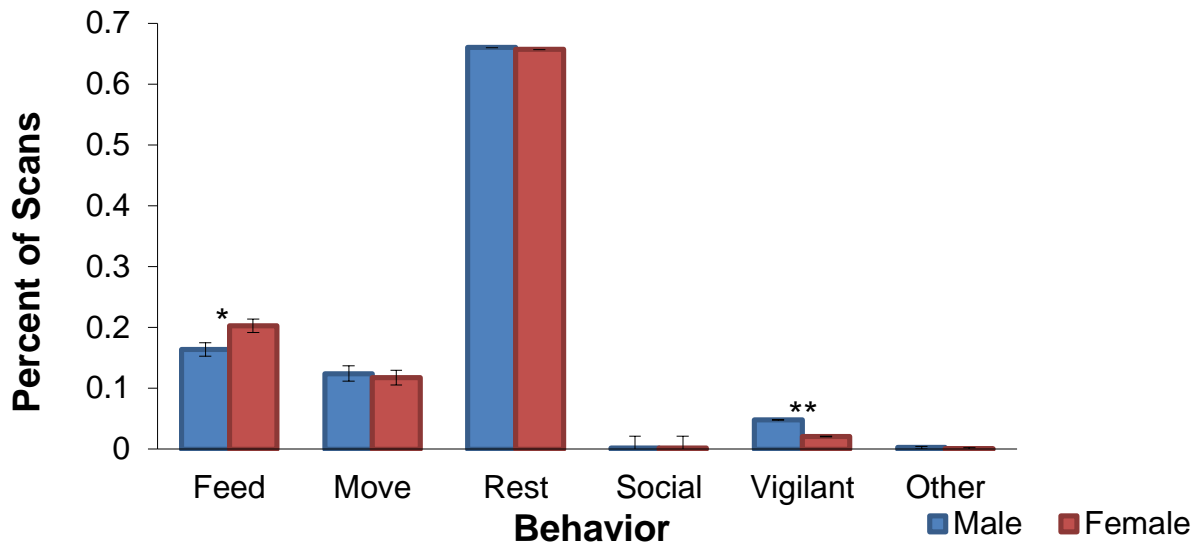


Figure 3: The average percentages of scans for eight groups of mantled howler monkeys performing each behavior were recorded. A significant difference between males and females was found for feeding and vigilance using a paired T-test. (DF=7; Feed $t = -3.345$, $p = 0.012$; Move $t = 1.45$, $p = 0.19$; Rest $t = 0.200$, $p = 0.847$; Social $t = -0.912$, $p = 0.391$; Vigilant $t = 5.764$, $p = 0.001$; Other $t = 2.035$, $p = 0.081$)

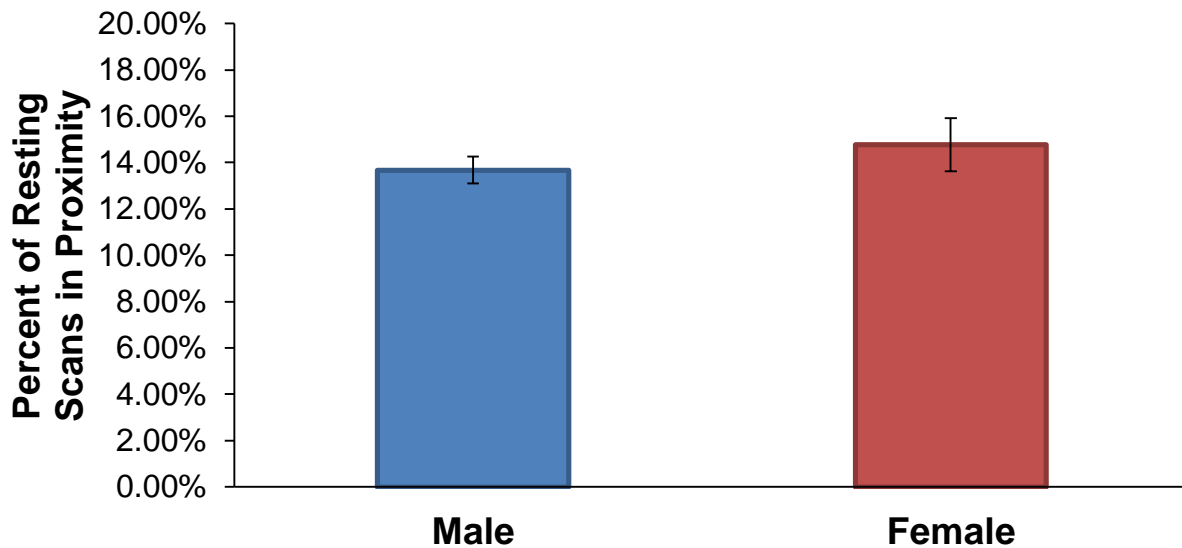


Figure 4: Average percentage of resting scans of eight groups of mantled howler monkeys spent in proximity with a conspecific. No significant difference was found using a paired T-test (DF=7, $t = 1.1339$, $p = 0.2942$)

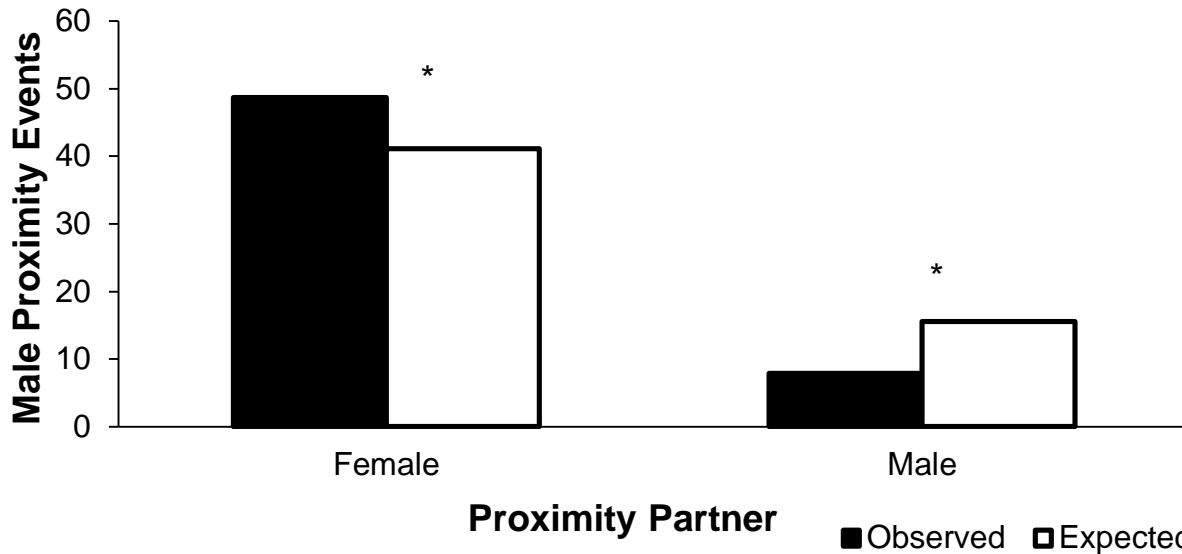


Figure 5: The average number of times a male was resting in proximity to a female vs. a male. Expected values were calculated with the average proportion of each sex in the population. Males significantly preferred to rest with females and significantly avoided resting with other males (DF=1, $X^2=5.2$, $p=0.02$).

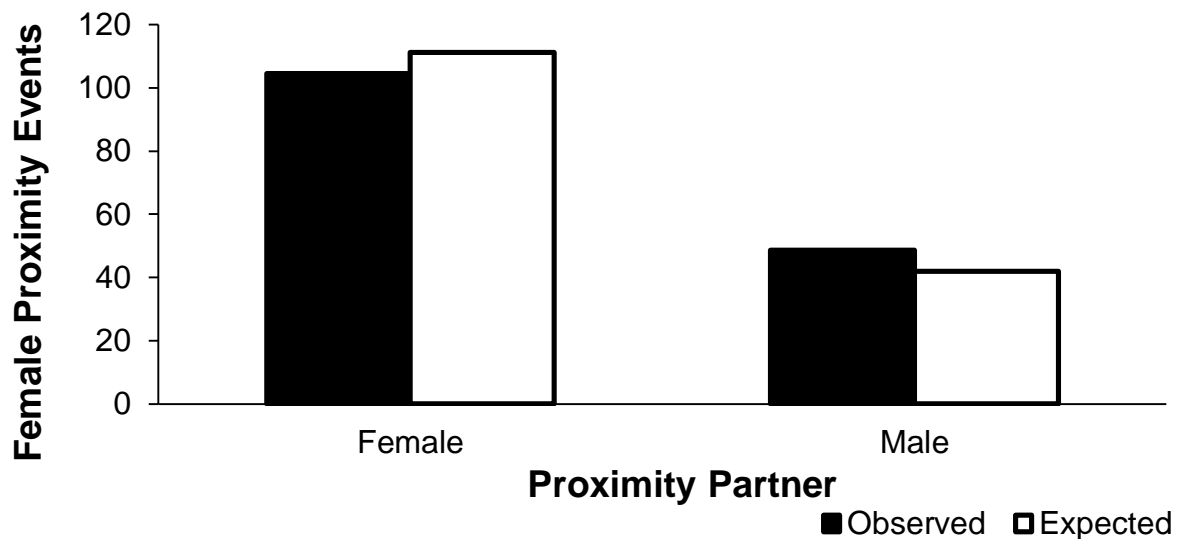


Figure 6: The average number of times a female was resting in proximity to a female vs. a male. Expected values were calculated with the average proportion of each sex in the population. Females showed no significant preference (DF=1, $X^2=1.2$, $p=0.23$)

Differences due to Infant Status

Females with and without infants spent the same percentage of their time performing all behaviors expect for moving. Females without infants spent significantly more time moving than females with infants (Figure 7, DF=7; Feed $t=0.107$, $p=0.918$; Move $t=2.915$, $p=0.022$; Rest $t=-0.596$, $p=0.570$; Social $t=1.232$, $p=0.258$; Vigilant $t=-0.568$, $p=0.57$; Other $t=1.336$, $p=0.223$). Although females with and without infants rested for the same percentage of their time, females without infants spent more time resting in proximity to adults than females with infants did (Figure 8, DF=7, $t=2.568$, $p=0.037$).

Males preferred to rest with females without infants, avoided resting with males but showed no preference for females with infants (Figure 9, DF=2, $X^2=6.9$, $p=0.031$; Residuals: $\sigma=-1.9$, $\sigma=1.8$, $\sigma\sigma=-0.3$). Females without infants rested with females with infants less often was expected but showed no preference for resting with males or other females without infants (Figure 10, DF=2, $X^2=11.3$, $p=0.004$; Residuals: $\sigma=0.9$, $\sigma=1.5$, $\sigma\sigma=-2.9$). Females with infants did not show any preference for proximity partners but did tend towards resting with other females with infants and away from females without infants (Figure 11, DF=2, $X^2=4.6$, $p=0.099$; Residuals: $\sigma=0.4$, $\sigma=-1.5$, $\sigma\sigma=1.5$)

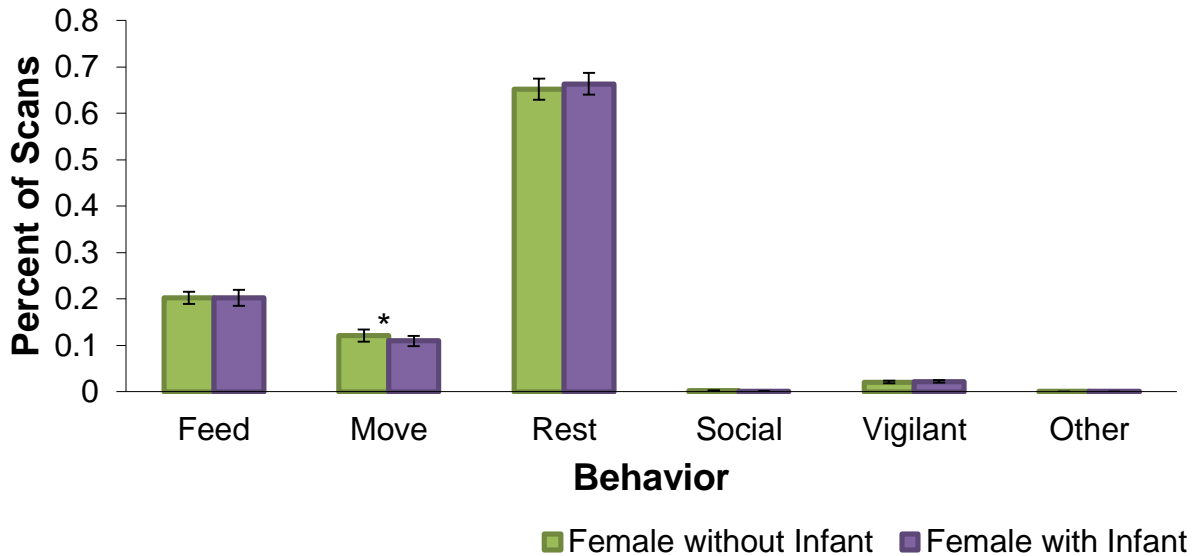


Figure 7: The average percentages of scans for females with and without dependent infants from eight groups of mantled howler monkeys performing each behavior. Females without infants moved significantly more often than females without infants using a pair T-test. No other significant differences were found (DF=7; Feed $t=0.107$, $p=0.918$; Move $t=2.915$, $p=0.022$; Rest $t=-0.596$, $p=0.570$; Social $t=1.232$, $p=0.258$; Vigilant $t=-0.568$, $p=0.57$; Other $t=1.336$, $p=0.223$)

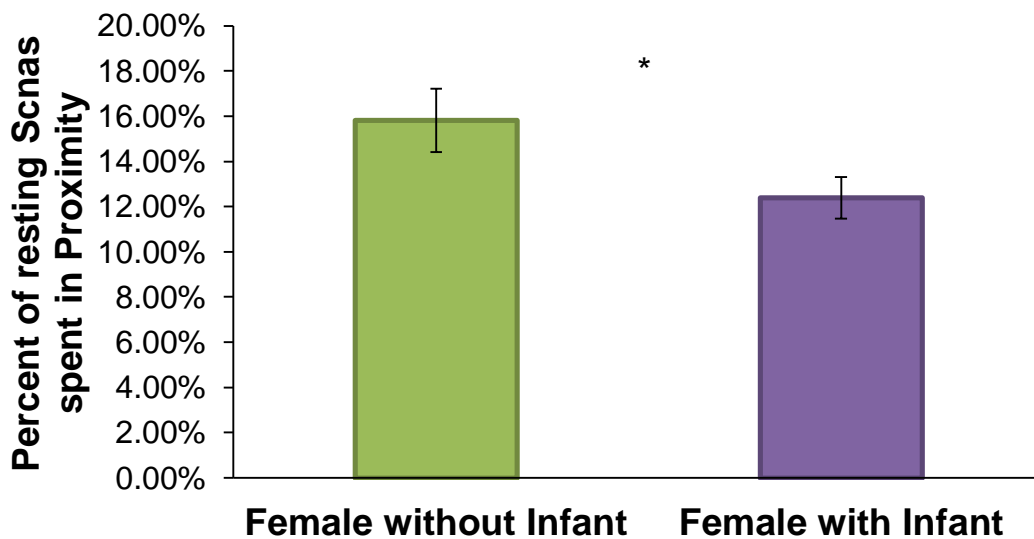


Figure 8: Average percentage of resting scans of eight groups of mantled howler monkeys spent in proximity with a conspecific. A paired T-test found that females without infants rested in proximity significantly more often than females with infants (DF=7, $t=2.568$, $p=0.037$)

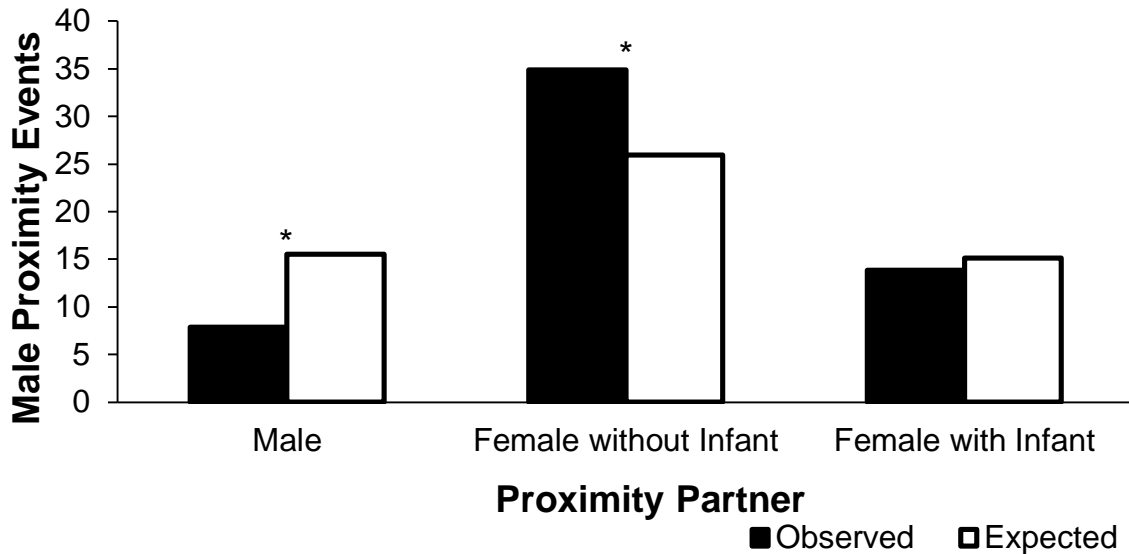


Figure 9: The average number of times a male was resting in proximity to a male vs. a female without an infant vs. a female with an infant. Expected values were calculated with the average proportion of each class in the population. Males significantly preferred to rest with females without an infant and significantly avoided resting with other males. Males showed no significant preference for females with an infant (DF=2, $X^2=6.9$, $p=0.031$; Residuals: ♂=-1.9, ♀=1.8, ♀♀=-0.3)

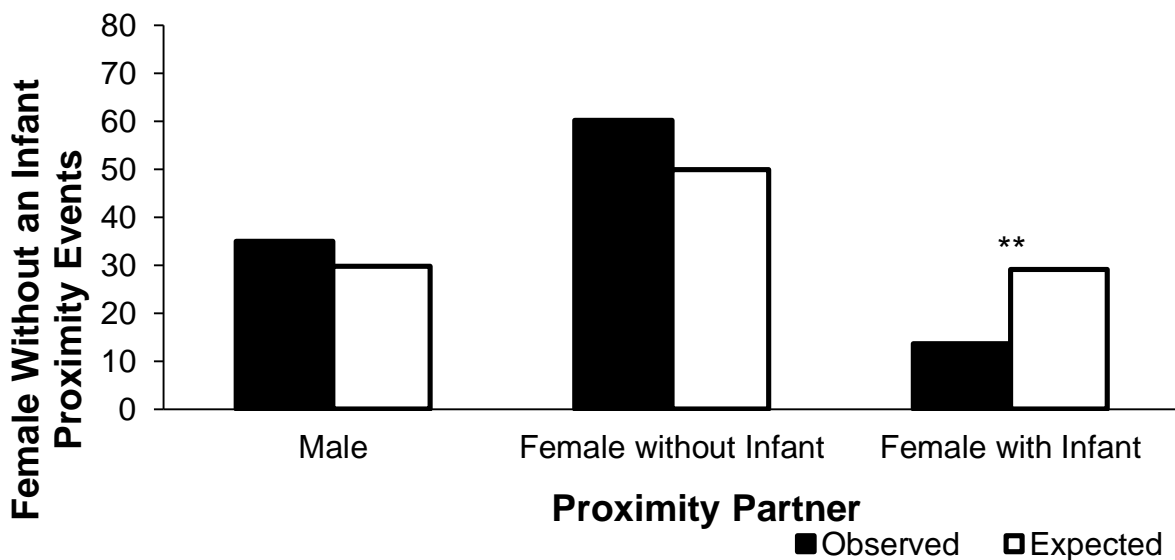


Figure 10: The average number of times a female without an infant was resting in proximity to a male vs. a female without an infant vs. a female with an infant. Expected values were calculated with the average proportion of each class in the population. Females without an infant rested significantly less often with females with an infant. Females without an infant rested without major preference with males and other females without an infant. (DF=2, $X^2=11.3$, $p=0.004$; Residuals: ♂=0.9, ♀=1.5, ♀♀=-2.9)

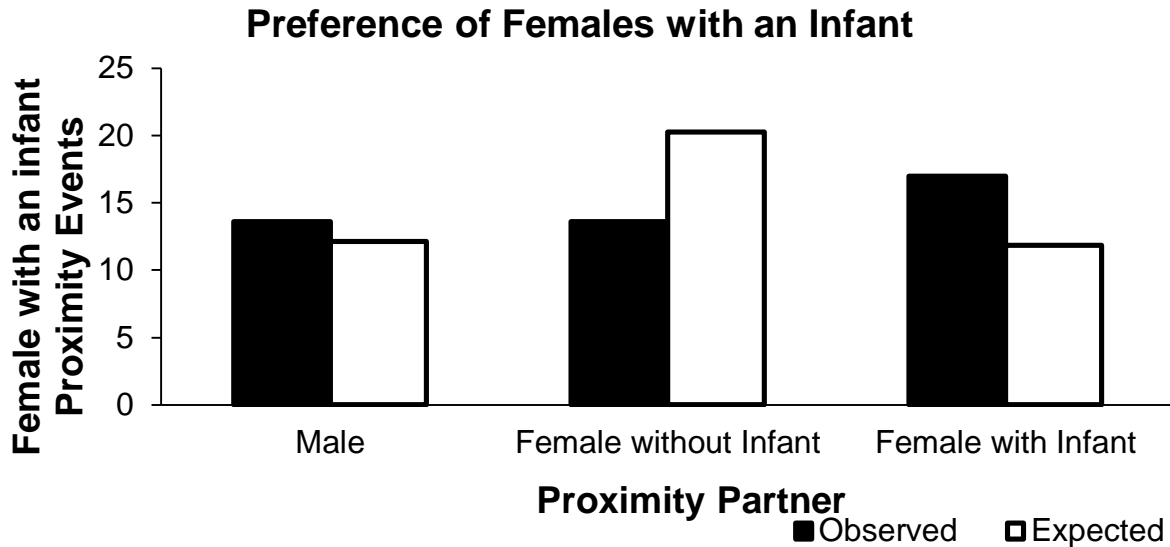


Figure 11: The average number of times a female with an infant was resting in proximity to a male vs. a female without an infant vs. a female with an infant. Expected values were calculated with the average proportion of each class in the population. Females with infants showed no significant preference (DF=2, $X^2=4.6$, $p=0.099$; Residuals: ♂=0.4, ♀=-1.5, ♀♀=1.5)

DISCUSSION

General

The howler monkeys in this study spent their time in a similar manner to those in other studies. The vast majority of their time was spent resting and overt social behaviors were rarely observed (Pavelka and Knopff, 2004). All overt social behaviors were recorded under a single category in the ethogram. The social behaviors that were observed include: playing, embracing, biting, hair pulling, striking, grooming, reproduction and chasing. The howlers spent nearly 100x more time resting in proximity than they spent in other social activities.

Occasionally a resting howler would react negatively to a second howler attempting to rest in proximity. The reaction was sometimes as simple as leaving the

area soon after the second howler sat too close. However, instances of aggression from a howler already resting to a newcomer were observed. In one such instance a male howler was struck by another resting howler when it attempted to rest near the first howler. Since overt social behaviors are too rare to study the method of measuring resting proximity is a better method for determining social bonds in howler monkeys. Social proximity has been shown to correlate well with overt social activities in chimpanzees (Mitani and Amstler, 2003) and has been used in numerous studies of howler monkey social behavior (as in Crockett and Eisenberg, 1987).

Effects of Sex

Males and females spent their days slightly differently. Males were vigilant more often and females fed more often. Males were more vigilant because the vigilance behavior includes howling which males perform often than females due to intergroup communication. Females may have fed more due to the added nutritional requirements of lactation or pregnancy. The dissimilar activities did not affect the percentage of time spent performing the focal behaviors of this study (resting and social). Males and females spent the same percentage of their resting time in proximity with another adult. This indicates that neither males nor females dedicate more of their time to forming social bonds.

Males preferred to rest in proximity to females and rested with males less often than they would have due to random association. However, females showed no preference for resting with either males or females. This indicates that males are maintaining the social connection with the females while the females are more passive, resting with neighbors without concern for the sex of the partner. The presence of male-

female bonds is necessary in order to gain mating access in a multimale social group. It seems that it is up to the males to maintain this contact in howlers.

Effects of Infant Status

The presence of a dependent infant has only a minor influence on the activity budget of a female howler monkey. Females without infants moved more frequently than females with infants because a dependent infant may impair the ease of movement of the mother. This difference did not affect the focal behaviors of this study (resting and social). Females with infants and females without infants spent the same percentage of their time resting but females without infants spent more time resting in proximity than the females with infants. This is likely due to the risk of infanticide that females with infants face. Although rare, intragroup infanticide does occur and any interactions with other adults can increase the risk of infanticide occurring (Clarke et al., 1998). It is safer for the infants if the female with infant minimizes her interactions with even her own group members. However, it would not be advantageous to completely cut social bonds because those bonds will protect against intergroup infanticide and will be needed in order to obtain the next mate (Schaik and Kappeler, 1997).

Males showed a preference for resting with females without infants, did not show a preference for resting with females with infants and showed an aversion for resting with males. One purpose of permanent male-female association is to assure the amiability of potential mates. In a multimale group, males need to keep up relations with females in order to be able to mate with them. Thus the males' preference for females that are more likely to be sexual active is advantageous. However, it is not ideal for the males to completely ignore the females with infants. First, ignoring the female with infant

would leave them vulnerable to infanticide (Schaik and Kappeler, 1997). Second, the female may have an infant at the present but will be sexual active again after the infant is weaned.

Females without infants did not display any preference towards males or females without infants but rested less often with females with infants. Evenly potentially sexually active females are passively accepting male attentions rather than purposely strengthening the bonds. The lack of interaction between females without infants and females with infants is more likely due to the actions of the females with infants than the females without. Females tend to be interested in infants but they are also the most likely to commit intragroup infanticide (Clarke et al., 1998). This risk of infanticide could discourage females with infants from resting near females without infants. This could have lead to females without infants resting less with females with infants.

Females with infants did not show any significant preference for resting partners. However there was a trend ($p=0.099$). Females with infants tended to rest with females with infants more often and rested with females without infants less often than is expected by random chance. They were neutral towards resting with males. Females with infants were the smallest group and thus the least amount of data was collected on them. The small sample size may have contributed to the lack of statistically significant results.

It is healthy for young primates to interact with each other to learn social behaviors and play (Baldwin and Baldwin 1978). This may contribute to the preference of females with infants to spend more time with other females with infants. The trend of females with infants avoiding resting with females without infants is consistent with the

significant preference of females without infants avoiding resting with females with infants. This can thus also be explained by the risk of intragroup females committing infanticide (Clarke et al., 1998).

CONCLUSION

Hypotheses

This study examined hypotheses about the social bonding of adult howler monkeys. Bonding between males and females was examined first. The hypotheses were that proximity with females would be preferred by both male and females. This was confirmed by the preference of males but females showed no preference for partners. Thus males prefer the company of females but females have no preference for males or for females. The male preference is consistent with previous research (Wang and Milton, 2003). This likely occurs because males within howler groups must compete with each other for mating opportunities. There seems to be no benefit for having strong social bonds with other males but females provide reproductive opportunities. The lack of a female preference neither confirms nor refutes previous research claiming that females form the strongest bonds with other females (Zucker and Clarke, 1998).

Next the effects of dependent infants were explored. Two competing hypotheses were suggested for male behavior: H₁) males form stronger social bonds with females without infants for sexual relations and H₂) males form stronger social bonds with females with infants to protect against infanticide. The first hypothesis was given support by this study; males spent significantly more time resting in proximity with females without infants. This implies that maintaining close bonds with potential sexual

partners is more important to males than protecting existing potentially related young. This minimal interest in the defense of infants likely stems from the uncertain paternity of infants within the group. The time males spend with sexually receptive females is most likely a primitive form of primate courtship to encourage sexual relations when the female is in estrus (Manson, 1997)

There were three hypotheses for the behavior of females without infants: H₁) females without infants form stronger social bonds with males for sexual relations, H₂) females without infants form stronger social bonds with females with infants for allomothering and H₃) females without infants spend less time with females with infants due to the females with infants denying infant-nonmother interactions. The third hypothesis was supported; females without infants spent significantly less time resting in proximity to females with infants. Allomothering is common in other primate species but these primate groups generally consist of related individuals where it could harm the inclusive fitness of an individual to harm another female's infant. When social groups are a mix of related and nonrelated individuals as in langurs only related individuals are allowed to allomother (Stanford, 1992). Monkeys that are raised without ever socializing with other young do not form proper social understanding of their own species and do not even mate successfully (Harlow et al, 1966)

The last three hypotheses were for the behavior of females with infants: H₁) females with infants form stronger social bonds with males to reduce infanticide, H₂) females with infants form stronger social bonds with females without infants for allomothering, H₃) females with infants form stronger social bonds with females with infants for infant socialization. Females with infants showed no significant preference for

proximity partners but did tend toward resting with females with infants and tend away from resting with females without infants. Avoiding resting with females without infants would support the behavior of females without infants seen in this study and is consistent with interactions of nonrelated howler monkeys (Clarke et al, 1997)

Future Research

This study examined a larger population of howler monkeys than many previous studies but had a much shorter duration (Zucker and Clarke, 1998; Wang and Milton 2003). With a longer period of study, more data would be able to be collected on females with infants and then the true effects that infants have on social behavior of the mother would be clearer. This type of study (involving multiple groups) is necessary to achieve a good sample size of females with infants.

Future studies could also include patterns of sub-grouping to determine the preferences for larger scale social grouping. Examining the sex ratios compared to the number of infants in subgroups could provide some interesting results.

Importance

This type of study and others like it are essential for the conservation and understanding of howler monkeys and similar primates. The howler monkeys' ability to survive in very fragmented habitat makes them the last primates to exist in damaged habitats. The damages that these animals have suffered are nearly all due to human interference (Horwich, 1998). Studying howler monkeys also can act as a model for the formation of social bonds of primates in the absence of kinship bonds.

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