THE UNIVERSITY OF CALGARY

Effects of Estrous State on Female-Female

Interactions in *Pan paniscus*

by

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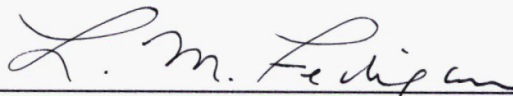
THE UNIVERSITY OF CALGARY

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Effects of Estrous State on Female-Female Interactions in *Pan paniscus*" submitted by Tracy Marie Wyman in partial fulfillment of the requirements for the degree of Master of Arts.

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ABSTRACT

Female sociability has been cited as one of the main factors contributing to the unique social structure of *Pan paniscus*. This study examines the effects of estrous state on female behavior, specifically interactions among females. A total of 244.73 hours of data were collected on four adult females housed at the San Diego Wild Animal Park. Estrous females were observed to spend more time in proximity and to interact more with other adult females than anestrous females. The increase in time spent with other females was correlated with a decrease in time spent with other age/sex classes. Previous research suggests that a long period of estrous in *Pan paniscus* strengthens male-female relationships. The results of this study indicate that a prolonged estrus may also strengthen bonds among females. A combination of low competition and cohesive relationships among females result in the unique social structure of bonobos.

ACKNOWLEDGEMENTS

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CHAPTER ONE - BONOBO FEMALE SOCIABILITY

The Pygmy Chimpanzee

Chimpanzees *(Pan troglodytes)* have been studied since the early 1960's. However, it has only been recognized recently that two separate species of chimpanzees exist. There are three subspecies of *Pan troglodytes* found in: West Africa *(Pan troglodytes verus)*, Central Africa *(Pan troglodytes troglodytes)*, and East Africa *(Pan troglodytes schweinfurthii)*. The other species of chimpanzee known as the pygmy chimpanzee or bonobo *(Pan paniscus)* , is found only south of the Zaire River in central Africa. The Zaire River serves as the dividing line between bonobos and chimpanzees. Unlike the implication of their name, pygmy chimpanzees are not just a smaller version of the common chimpanzee. In fact, data suggests that they are the same weight as the East African subspecies *Pan troglodytes schweinfurthii* (Jungers and Susman, 1984). Bonobos are physically distinguished from chimpanzees by their more gracile build, long hind limbs, short clavicle, and small molars (Johnson, 1981).

The two species were only recognized as separate species by examination of a skull which was initially labeled as a juvenile chimpanzee. In 1929, upon closer examination of the skull held by a Belgian museum, Ernst Schwartz described and reclassified it as a new subspecies of *Pan* (Schwartz, 1929) Later, in 1933, Harold Coolidge described the ape's anatomy in greater detail and officially reclassified it as an entirely new species, *Pan paniscus*. While this discovery occurred in 1933, it was not until 1974 that bonobos were studied in their natural environment.

Since then research has increased steadily, and more is being learned

about the "new" *Pan* species. Although field research has increased, the amount of literature on bonobos is still very small compared to that of the chimpanzee. Long term research on chimpanzees began in the early 1960's by fieldworkers such as Jane Goodall, and Toshisada Nishida. This research, which has continued now for over 30 years (Jane Goodall), has stimulated a great deal of related research as well as its own large body of literature. Unfortunately, bonobo studies are not as common. Habituation of free ranging bonobos requires a long period of time, money, and effort. Only now, after almost two decades, are certain groups of bonobos becoming habituated to the presence of humans. Also, at the present time, political conflict in and around Zaire is preventing some researchers from carrying out further long term research on these unique subjects. Thus, the quantity of bonobo research is relatively small compared to that of the chimpanzee. For this reason, many important aspects of bonobo behavior have been discovered by studying captive individuals.

Bonobos are of particular interest because of their many similarities with chimpanzees, but also because of their striking differences. One area in which the two *Pan* species differ, is in sexual behavior. Since preliminary studies of the bonobo began, the heightened sexual activity of the bonobo has received much emphasis from various researchers. One of the reasons that it has received so much attention is its applicability to models of human evolution. The flexible nature of the bonobos' sociosexual behavior, as well as certain paedomorphic physical features have resulted in the "bonobo model" of human evolution (Zihlman & Cramer, 1978; Zihlman, Cronin, Cramer, & Sarich, 1978). For this reason, there has been a type of "rediscovery" of the bonobo in the 1980's.

In order to fully understand the importance of the differences between chimpanzees and bonobos, a description of general *Pan* society will be · undertaken.

Chimpanzee and Bonobo Society

Pan society

Chimpanzees and bonobos are mainly found in forest habitats. While this is their primary habitat, chimpanzees also inhabit forest-savanna mosaic, woodland, and even dry savanna (Baldwin, McGrew, and Tutin, 1982). On the other hand, bonobos only live in lowland rain forest, and swamp forest (Kano, 1983, 1984). Both chimpanzees and bonobos are diurnal, and omnivorous, with plant foods being the predominant food source (Wrangham, 1977; Kano, 1983; Badrian and Malenky, 1984).

Both bonobos and chimpanzees display a fission-fusion social organization (bonobos: Badrian & Badrian, 1984; White,1988, 1989; chimpanzees: Goodall, 1986; Nishida, 1979). This fission-fusion society is characterized by a number of features: subgroups that move independently of each other, with aggregation into a larger social unit occurring rarely; variance in the size and membership of the subgroups vary; and the occupation of different core areas by individual adults within a range of the entire group or community. Thus, smaller subunits (parties) range over the larger unit's (community) area. The home range is defended from other communities, but there is free mobility within the community range for the various parties within.

Females appear to leave their natal group in early adolescence (Nishida, 1979; Pusey, 1980; Kano, 1982). There is no birth seasonality, with both species displaying a midcycle sexual swelling. Both the chimpanzee and

bonobo display this sexual swelling when in estrus, the middle of their reproductive cycle. Estrus coincides with ovulation. At this time the females become attractive to males, and most mating occurs at this time. There is no evidence for long term relationships between individual mating males and females. Mating occurs mainly during the period of the females' maximal tumescence, and is mostly opportunistic.

Thus, the basic structure of chimpanzee and bonobo society is similar. However, within this basic structure there are striking differences in a number of areas which distinguish the two species, and draw our attention to their differences rather than their similarities. A comparison of chimpanzee and bonobo internal structure, and their individual interactions reveals these differences.

Internal Structure of Chimpanzee Society
ECOLOGY

Chimpanzees are omnivores with their primary food sources being plants. Chimpanzees have been observed to hunt and scavenge vertebrates such as monkeys, and ungulates (Nishida and Uehara, 1983; Hasegawa, Hiraiwa-Hasegawa, and Nishida, 1983). They are also commonly observed to consume ants and termites, often with the aid of tools (Teleki, 1973). In the Ivory Coast, they have also been observed cracking open nuts with stones or wooden clubs and eating them (Boesch and Boesch, 1981).

At both the Gombe and Mahale research sites there are sex differences in animal and plant diets. At these sites, males are observed to consume more meat than females, whereas females consume more insects than males (Gombe: McGrew, 1979; Mahale: Uehara, 1984). In the Ivory Coast, females

appear to be more frequent and efficient nut crackers than males (Boesch and Boesch, 1981).

In chimpanzee communities, the annual range is similar between males and females, however there is a difference in distance traveled per day. Males travel farther per day than females (Nishida, 1979; Wrangham and Smuts, 1980).

SOCIAL ORGANIZATION

Chimpanzee communities can number anywhere from 20 to more than 100 individuals. Most temporary parties are small, composed of six or less individuals (Goodall, 1968; Nishida, 1968; Reynolds & Reynolds, 1965). Any combination of age and sex class can be observed in temporary parties, but there are clear sex differences in grouping patterns. Males spend most of their time with at least one other adult, whereas females spend long continuous periods of time alone (Wrangham and Smuts, 1980). In the majority of communities, females outnumber males (Hiraiwa-Hasegawa, Hasegawa and Nishida, 1984).

SEXUAL BEHAVIOR

All of the sexual relationships between males and females are a type of short term interaction, with the longest exclusive mating relationship between two individuals being for a few days or weeks (Tutin, 1979, 1980). Matings occur only during the period of maximal tumescence (Tutin and McGrew, 1973; McGinnis, 1979; Hasegawa and Hiraiwa-Hasegawa, 1983).

In chimpanzees, cycle length is reported from 31.5 days (Hasegawa and Hiraiwa-Hasegawa, 1983) to 37.3 days (Young and Yerkes, 1943). The

maximum swelling phase has been documented for 10.4 days (Tutin and McGrew, 1973) and 12.5 days (Hasegawa and Hiraiwa-Hasegawa, 1983). Ovulation occurs within one day of detumescence (Graham, 1981).

Possessive matings often occur as the female approaches ovulation (Tutin and McGinnis, 1981; Hasegawa and Hiraiwa-Hasegawa, 1983). The results of competition between males for ovulating females is not completely understood, however, the alpha male appears to achieve a high degree of mating success during this time (Tutin and McGinnis, 1981; Hasegawa and Hiraiwa-Hasegawa, 1983). Matings are mostly initiated by the males, but females have been observed to initiate matings on occasion (Nishida and Hiraiwa-Hasegawa, 1987).

INTERINDIVIDUAL INTERACTIONS

Male-male relationships among chimpanzees are characterized by a high degree of tolerance, with high levels of greeting (Bygott, 1979), grooming (Nishida, 1979), alliance formation (de Waal, 1982), and meat sharing behavior (Teleki, 1973) . Even with this high degree of tolerance, there is also a strong component of competition, as males appear to be continually trying to maintain or raise their dominance rank (Goodall, 1986). However, even with this high degree of competition, adult males are consistently more sociable than female chimpanzees (Goodall, 1986; Nishida, 1968).

Male-female associations are weak. While association between mothers and daughters are quite weak, sons and mothers are often seen traveling together even into adulthood (Pusey, 1983). Other than these mother and son groups, adult females and adult males do not often travel together. Only when females are in estrus do they join up with other adult males (Goodall, 1986;

Nishida, 1979).

Chimpanzee female relationships are characterized by little evidence of mutual attraction (Goodall, 1986; Nishida, 1979). Females rarely engage in long grooming bouts, and aggressive coalitions are uncommon. Although mother-offspring relationships last several years beyond weaning (Goodall, 1986; Pusey, 1983), it is more commonly sons and mothers who maintain ongoing relationships rather than daughters and mothers (Pusey, 1983). Basically, female-female associations are rare. When they occur they are likely to be mother-daughter, and they occur primarily when neither is in estrus (Nishida and Hiraiwa-Hasegawa, 1987).

Internal Structure of Bonobo Society
ECOLOGY

Bonobos are also omnivores with their chief food source being plants. Fibrous foods (shoots, pith and stems of ground plants) are substituted by bonobos more than chimpanzees when fruit is scarce (Kano, 1983; Badrian and Malenky, 1984). Bonobos have not been observed in any group hunting behavior such as that observed in chimpanzees. Nor have they been observed gathering invertebrates by tool use (Badrian and Malenky, 1984; Kano, 1983). Although they do not use tools to gather invertebrates, they eat a wider range of invertebrates than chimpanzees, including earthworms and millipedes (Badrian and Malenky, 1984; Kano, 1983).

SOCIAL ORGANIZATION

The social organization of bonobo society is also classified as a fission-fusion community with temporary parties. However, there are important

differences between the temporary parties of bonobos and chimpanzees. Preliminary studies at Wamba, Zaire suggested that the temporary parties of the bonobos were much larger than those observed in chimpanzees (Kano, 1982). At Wamba, Kano found that parties of 11 or more individuals accounted for 74% of the total parties observed. Compared to the parties of chimpanzees at Gombe with 82% of parties six or less individuals (Goodall, 1968), Kasoge with 50% of parties with five or less individuals, and Budongo with 62% of all parties with six or less individuals (Reynolds & Reynolds, 1965), bonobo parties appear to be much larger. From this, Kano concluded that bonobos were more gregarious than chimpanzees (Kano,1982). However, since this time, further studies indicate that bonobo party size is variable from region to region (Badrian , Badrian, & Susman, 1981; Badrian & Malenky, 1984; Horn, 1980; Kitamura, 1983; Kuroda, 1984; Uehara, 1990; , 1988; White and Wrangham, 1988). While the sizes of parties at Lake Tumba (x= 8.2, Horn 1980), Lomako (x= 7.6, Badrian & Badrian, 1984), and Yolasidi x= 7.9, Kano, 1983) are quite similar, the mean party size at Wamba remains considerably larger (x= 15, Kano, 1984; x= 16.9, Kuroda, 1979). Although the regional differences in party size have yet to be fully understood, the use of provisioning at the Wamba site is often cited as a factor contributing to these differences (White & Wrangham, 1988). Even with this regional variation, it is generally accepted that bonobo party sizes are comparatively large relative to those of the chimpanzee (Nishida & Hiraiwa-Hasegawa, 1987).

With reference to sex, the party composition of bonobos also differs from that of the chimpanzee. Unlike chimpanzees, the predominant composition in bonobo parties is the "mixed group" which consists of adult males, adult females and dependent offspring (Badrian & Badrian, 1984; Furuichi, 1987;

Kano, 1980, 1982; Kitamura, 1983; Kuroda, 1979).

SEXUAL BEHAVIOR

One feature distinguishing bonobos from chimpanzees is a prolonged period of estrus. The maximum swelling phase of chimpanzee females tends to be much shorter than that of the bonobo. While the maximum swelling in the chimpanzee has been documented for 10.4 days (Tutin & McGrew, 1973) and 12.5 days (Hasegawa & Hiraiwa-Hasegawa, 1983), in bonobos the maximum swelling is from 14.6 days (Furuichi, 1987) to 22.4 days (Dahl, 1986). While these values do vary from study to study, it is still clear that in most cases, bonobos demonstrate longer periods of maximal swelling. Results for total cycle length are somewhat clearer (where cycle length is measured from the interval between last days of successive periods of maximal tumescence). The cycle length in bonobos is longer than that of the chimpanzee. Chimpanzees cycle is from 31.5 to 37.3 days (Hasegawa and Hiraiwa-Hasegawa, 1983; Young and Yerkes, 1943) whereas bonobo cycles have been documented for 36 days (Savage-Rumbaugh and Wilkerson, 1978), 42 days (Furuichi, 1987), and 46 days (Dahl, 1986).

One of the features of bonobo sexual behavior which differs from chimpanzee sexual behavior is the use of ventro-ventral copulatory positioning. The earliest studies of bonobo society revealed this unique characteristic (Badrian & Badrian, 1977,1980; Kano, 1980). While they are reported to copulate in ventro-ventral, as well as ventro-dorsal positions, the occurrence of both varies from population to population. The first studies focusing on sexual behavior were in captive situations (Savage & Bakeman, 1978; Patterson, 1979). The studies reported that the majority of copulations in both the San

Diego Zoo group (Patterson, 1979), and the Yerkes Regional Primate Research Center's group (Savage & Bakeman, 1978) copulated ventro-ventrally in the majority of copulations. Since this time, it has been recognized that these figures are most likely the representation of a behavioral extreme. Studies of wild bonobos do not report such high levels of ventro-ventral copulations (Badrian & Badrian, 1984; Furuichi, 1987; Kano, 1989; Thompson-Handler et al., 1984). It has been suggested by some researchers that the ventro-ventral position is preferred by the female partner in relation to the size of her sexual swelling (Savage-Rumbaugh & Wilkerson, 1978). Savage-Rumbaugh & Wilkerson suggest that because the females seem to prefer ventro-ventral copulation when they are not swollen, that this increased flexibility of positioning is linked to the expansion of the females' sexual activity to periods other than their maximal tumescent phase. While this theory is in accordance to earlier studies suggesting that bonobo females were active in sexual behavior throughout their sexual cycle (Badrian & Badrian, 1984; Dahl, 1986; Thompson-Handler, Malenky, and Badrian, 1984; Savage & Bakeman, 1978; Savage-Rumbaugh & Wilkerson, 1978), recent evidence provided by Furuichi (1987) suggests that the females' active participation in sexual behavior is limited more to their maximal tumescence, or peak estrus, than once thought.

Furuichi studied the sexual swelling, activity, and grouping of females at Wamba in order to provide fundamental data on the sexuality of bonobos. Studies previous to Furuichi recorded the daily appearance of sexual swelling in order to determine periods of maximal tumescence (Savage-Rumbaugh & Wilkerson, 1978; Thompson-Handler et al., 1984), but they graded the sexual swelling on a scale of size only. Furuichi added a second component to the

grading, that of firmness. He used the two measures of size and firmness to determine the parameter of the sexual skin. The results show that the sexual swelling is more adequately measured by its level of firmness, than by its size level. With this information, the author was able to conclude that maximum swelling occurred at maximum firmness, and likewise, that most copulations also occurred during this time (Furuichi, 1987, 1989). Thus, these results counter the conclusion of previous studies that female bonobos copulate irrespective of swelling stage (Savage-Rumbaugh & Wilkerson, 1978; Thompson-Handler et al., 1984).

Other studies have also suggested that age is a factor in ventro-ventral copulations (Badrian & Badrian, 1984; Furuichi, 1987; Kitamura, 1983 as cited in Blount, 1990; Thompson-Handler et al., 1984). All studies reported that either adolescent males and females were more likely to be observed copulating in the ventro-ventral position than were the adults of the same group. For example, Thompson et al. (1984) found that in 10 out of 12 cases of copulation, subadult males used the ventro-ventral position. In Furuichi (1987), the ventro-ventral position was observed more frequently in adolescent females and males than in adults or aged animals. This data also appears to contradict Savage-Rumbaugh & Wilkerson's (1978) study which suggested that the size of sexual swelling influences female sexual activity. They reported that females who were not swollen appeared to prefer ventro-ventral copulation. In adolescent female bonobos, the tumescence-detumescence cycle is irregular. Kano (1989) has reported that the level of tumescence in adolescent females is almost always maintained at the maximum, or near-maximum level. Thus, the findings of adolescent preference for ventro-ventral copulation, and preference for ventro-ventral copulation when swelling size is small are very contradictory.

If females prefer to mate ventro-ventrally when not swollen, it would follow that ventro-ventral copulations would not be observed as often in adolescents who are swollen almost all of the time. Further studies on tumescent-detumescent cycles and their relation to sexual activity are needed in order to clarify the problem.

Other proximate factors have also been suggested for the preference of ventro-ventral mating. Kano (1989) cites individual choice as a factor. He reported that females at Wamba who presented in a ventro-ventral manner, but were responded to by the male mounting dorso-ventrally attempted to separate from the male and re-embrace ventro-ventrally. Kano reported 20 successful attempts by females. Thus, this also sheds light on the female's role in copulatory behaviors. While some authors insist on deemphasizing the female bonobos' role in copulation (Blount, 1990), it is apparent from these findings that in more than a few situations, the female is in control of copulation.

INTERINDIVIDUAL INTERACTIONS

Another of the conspicuous differences between bonobos and chimpanzees is the lower rate of association among male bonobos. Unlike male chimpanzees, male bonobos are found primarily in mixed groups, and rarely in single sex parties (Badrian and Badrian, 1984; Kuroda, 1979). Not only are males rarely observed together in single sex groups, the interactions among males are not as affiliative as those between males and females, or those among females (White, 1989). At the Lomako site, White found that "affiliative interactions involving either two females or a male and a female were common, whereas affiliative interactions between two males were infrequent" (White, 1989:198). Similar results have also been documented by other

researchers (Badrian & Badrian, 1984; Kuroda, 1979, 1980; Uehara, 1988). The dominance relationships of male bonobos do not appear to be as strong as those observed in chimpanzees (Kano, 1980, 1982; Nishida & Hiraiwa-Hasegawa, 1987). The formal "pant-grunts" which serve as greetings in male chimpanzees are not observed in bonobos (de Waal, 1988). This suggests that the dominance hierarchy is weaker than that observed in chimpanzee male relationships. Thus, male-female interactions are much more common in bonobos than in chimpanzees evidenced by the predominance of mixed parties and commonly observed male-female grooming parties, but male-male interactions are less common than in chimpanzees.

Female-female Interactions

One of the most distinct features of interindividual interactions in bonobos is the highly sociable nature of the females. Contrary to the weak female bonds in chimpanzee relationships, bonobo females are well known for their sociability (Furuichi, 1987, 1989; Kano, 1980; Kuroda, 1980; White & Wrangham, 1988). In chimpanzees, females tend to move alone or in small parties whereas the males are observed to stay in large single sex or mixed parties (Goodall, 1986; Nishida, 1979). In bonobos, the females are most often observed as part of large mixed parties (Badrian & Badrian, 1984; Kano, 1982; Kuroda, 1979; White, 1988). Also, unlike female chimpanzees who move alone when anestrus, and join mixed groups when they are in estrus (Goodall, 1986; Nishida, 1979), bonobo females tend to remain in mixed parties regardless of their sexual state (Furuichi, 1987, 1989).

Along with the unique sexual behavior of the bonobo, the sociability of the females is one of the most commonly cited characteristics of the species.

The sociability of females does not appear to be a function of kinship, as bonobo groups are not matrilineal; females are assumed to transfer from their natal group at puberty (Kano, 1982). Thus, sociability of female bonobos is not related to strong kinship ties as in other matrilineal groups displaying strong female-female affiliative relationships.

Instead, a number of factors other than relatedness have been cited as contributing to female sociability. Unlike chimpanzees, bonobo females appear to have a dominance hierarchy similar to that of the males, that is, female bonobos do not rank below male bonobos as they do in chimpanzee relations (Kuroda, 1979, 1980; Furuichi, 1989). While males have not been observed to act submissive to younger females, they have been reported to submit to aged individual females as well as to female aggregations (Kano, 1986; Furuichi, 1989). Another example of female dominance over males is frequently observed at times of feeding. Females have priority of access to feeding areas (Kuroda, 1979). In this respect, the social relations between male and female bonobos do not appear to be differentiated by sex as much as the relations between male and female chimpanzees.

Ecological factors which differ from those of the chimpanzee may also contribute to female sociability. Wrangham (1979) has suggested that the small patches of food that are available to the chimpanzee result in a large amount of competition among females. This high level of competition prohibits female sociability in chimpanzees. In a comparison of chimpanzee and bonobo food patch sizes, White (1989) found that the patches utilized by bonobos are frequently larger than those utilized by chimpanzees. Because the patches are larger, it follows from Wrangham's theory, that bonobos can afford to associate with other females because the competition for resources is not so high (White,

1989). While this explanation seems logical, patch size utilization was only documented at Lomako. In order to substantiate this hypothesis, more comparative data between the various bonobo study sites is needed.

The unique bonobo behavior of "Genito-genital (GG) rubbing " has also been cited as a factor involved in female sociability (Dahl, 1986; Kano, 1980; Kuroda, 1980; Badrian & Malenky, 1984; Thompson-Handler et al., 1984; de Waal, 1986, 1987). GG-rubbing was first described by Kano (1980) as the behavior between two females in which they rapidly rub their genitals together laterally several times while holding each other ventro-ventrally. The function of GG-rubbing is most often described as a type of tension regulation (Kano, 1989; de Waal, 1986, 1987). In a study of captive bonobos at the San Diego Zoo, de Waal (1987) investigated the role of sexual and affiliative behaviors in the regulation of social tensions. De Waal's study illustrated that in situations of increased tension, such as feeding time, or the introduction of a new group member, that the occurrence of GG-rubbing increased. Kano's (1980) observations of wild bonobos suggest similar functions for GG-rubbing. Kano identifies four types of pseudocopulatory behaviors: GG-rubbing, mounting , rump contact, and penis fencing. In the Wamba group studied, Kano found that pseudocopulatory behaviors occurred in the same context as copulatory behaviors. They were both observed most often in the following situations: arrival at a large food source, reunion of a party, and detection of another unit-group. All of these situations result in strong social stimulation. In each , the occurrence of GG-rubbing decreased as the emotional level decreased, suggesting that GG-rubbing was used to ease tensions between individuals. Also, Furuichi (1989) has suggested that GG rubbing is used to help maintain proximity among females. Furuichi recorded the distance between females

before and after GG rubbing. He found that in the majority of cases (77.5%), females remained within close proximity or increased their proximity to the other female. Thus, GG rubbing is a very important factor in female relations. It serves to reduce tensions and helps to maintain proximity among females. Both of these functions lead to high cohesion among females.

This introduction has highlighted a number of the differences between chimpanzee and bonobo social structure. Two factors which seem to be intricately woven into bonobo social structure are the unique female-female relationships, and the prolonged estrus of the females. For this reason it is hypothesized that these two features may be connected. The following section suggests a possible connection between female sociability and estrus in bonobos and chimpanzees.

Estrous State and Female Behavior

While it may seem obvious that these two characteristics of female bonobos are interrelated, as of yet there have not been any investigations into the possible connection. How estrus enters into male-female interactions are often examined in both the chimpanzee and the bonobo. From these studies it has been shown that there is a clear connection between estrous state of the females and subsequent male-female interactions.

Let us return to chimpanzee social relations. As mentioned above, the sexual state of the female chimpanzee affects her interactions with the males of the community. That is, females move among males more easily and more often when in estrus. Indeed, females do not commonly associate with males except when they are in estrus. Thus, sexual state of the female has a profound affect on male-female relationships in chimpanzees. This is also true in

bonobos. The increased sexual activity of bonobos as compared to chimpanzees is attributed to the female bonobos' prolonged period of estrus. Until recently, it was believed that females copulated without regard to sexual state. That is, they copulated even when not at peak estrus. Recent studies suggest that sexual activity is more confined to the females' peak estrus than once thought (Furuichi, 1989). If this is true, the gap is narrowed between chimpanzee and bonobo male-female relations in that both chimpanzees and bonobos confine sexual activity to the females' period of estrus. Therefore, both chimpanzee and bonobo male-female relationships become more cohesive with the onset of estrus.

The effect that female sexual state has on male-female relationships seems clear. However, there is very little known about how sexual state affects female-female relationships in bonobos. Chimpanzee female relations do appear to be affected by their sexual state. Females are rarely observed together except for when they are in estrus. Thus, chimpanzee females associate more often with both males and females when in estrus. Whether this is also true of female bonobos is unknown. However, if it is true that female chimpanzees associate more often with other females when in estrus, the same may also be true of bonobos.

It is known that bonobo females are more sociable than female chimpanzees. A number of factors have been suggested as being involved in these affiliative relationships. Lower competition among females because of larger food patches partially explains the cooperation observed between females, but it cannot explain the occurrence of behaviors such as GG rubbing in the female bonobo. GG rubbing is believed to serve as a mechanism of tension relief, and a proximity maintenance behavior. Both of these functions

increase the likelihood of affiliative interactions among females. Also dominance relations between males and female bonobos are not differentiated as much by sex illustrated by the fact that females do not necessarily rank below males. These factors all appear to be related to female sociability. One factor which has not been investigated is the sexual state of the females.

Because chimpanzee sexual state has such a pronounced effect on both male-female and female-female relationships, it follows that the same may be true of bonobos. Male-female bonds are reaffirmed by the prolonged estrus observed in bonobo females. It is possible then, that like the chimpanzee, the estrous state of the female may also reaffirm bonds among females. For this reason, the effect that female sexual state has on female-female relationships is an important question. A comparison of the social behavior of estrous and nonestrous female bonobos will help to clarify the role of sexual state in female relationships among bonobos.

Research Question

This study will examine female behavior and how it is affected by the females' sexual state in the bonobos at the San Diego Wild Animal Park (Chapter 2). It is hypothesized that female behavior and female-female interactions will differ depending on the estrous state of the females. These hypotheses will be tested and the relationships of the female-female interactions will be explored. These questions are rather broad, encompassing almost all female behavior other than male-female interactions. Therefore the following section will describe the specific objectives of this study.

Objectives

The overall question posed in this study is examined by breaking it down into several components of female behavior. First, female affiliative social interactions are examined (Chapter 3). The hypothesis suggests that female interactions will increase with the onset of estrus. In order to determine if this is is true of affiliative interactions, four specific behaviors are explored. Social grooming, sitting in proximity to, and sitting in contact with other females as well as play among females are examined. Comparisons are made between females in estrus and females who are anestrus. For each of these behaviors, three subtopics are explored. Overall differences between estrous and anestrous females are examined to determine if sexual state affects these affiliative behaviors among all age/sex classes. Next, a comparison is made between estrus and anestrus specifically focussing on female-female interactions. Lastly, each behavior is examined to determine if differences in female-female interactions are similar to differences between other age/sex classes. Also in this chapter, an attempt is made to determine who is responsible for these differences in behavior, the estrous female, or another female. To answer this question, approaches and peering are examined to determine if females differed in the frequency of approaching and/or peering when in estrus.

Chapter 4 discusses the agonistic behavior of estrus and anestrus females. If female social interactions increase during estrus, it is possible that agonistic behavior is affected. Overall differences in agonistic behavior are compared in estrous and anestrous females. Female-female aggression is further examined to determine if the level and cause of aggression are altered when females are in estrus. Agonistic interactions with other age/sex classes

are also examined to determine if the females' sexual state affects the frequency of these interactions.

The last section of results focuses on the unique bonobo behavior of GG rubbing (Chapter 5). Although it is considered an affiliative behavior, it is examined separately from the others for two reasons. First, it is observed only between females, thus an analysis of its occurrence with other age/sex classes is not appropriate. Second, because it is such a unique behavior, it is given special emphasis here. This chapter examines the differences between various aspects of GG rubbing in relation to the females' sexual state. Frequency and context of GG rubbing among estrous and anestrous females are examined to determine if these are affected by the females' sexual state. Solicitors of GG rubbing are examined to determine if sexual state has any effect on initiation of GG rubs. Finally, the pattern of proximity before and after GG rubbing is examined to determine if GG rubbing does in fact serve as a behavior to maintain or increase proximity among females.

By exploring these three aspects of the females' behavior (affiliative interactions, agonistic interactions, and GG rubbing), it is possible to answer the overall question (Chapter 6). Female behavior and estrous state is discussed with respect to competition and cooperation in female bonobos and chimpanzees. Also this topic lends itself to the discussion of the role of female - female bonds in the evolution of hominid society.

CHAPTER 2 - METHODS

The Study Group

The Zoological Society of San Diego houses the largest collection of captive bonobos in North America. At the time of this study, the group consisted of 11 individuals. Seven of these are the result of a very successful breeding program which began at the San Diego Zoo in the early sixties. In 1960 the zoo obtained a feral-born immature male named Kakowet. Two years later they obtained a feral-born female named Linda. This breeding pair produced ten offspring. One reason for the abundance of offspring is the fact that the Zoo in earlier days made it a practice to remove all newborns and hand rear them by human care givers in the zoo nursery. Reintroductions began when the infants were at least one year of age. Since the early 1980s the practice of removing newborns has ceased and every attempt is made by the curatorial staff to allow the mother to raise her own infant. The infants are only removed if the mother has rejected that infant and it appears that it will not be accepted by another bonobo care giver.

There have been a number of changes in group composition with this bonobo collection over the years. In 1989 the collection was transferred from the zoo to its sister organization, the San Diego Wild Animal Park. The move is considered temporary as construction is underway for a new bonobo enclosure at the zoo. The founding pair of Linda and Kakowet are no longer at the zoo. They are now held at Yerkes Regional Primate Research Center in Atlanta, Georgia. At the time of this study, three of the eleven individuals were offspring of Linda and Kakowet. These three individuals are : Louise, Loretta, and Lana. Offspring of these three females also were included in the display groups. Loretta's six year old daughter (Lena), and Lana's three year old daughter

(Laverne) were housed with their mothers. The two offspring of Louise (Lori and Lolita) were also housed at the Wild Animal Park, but were not kept in the same social group as their mother. The remainder of the group consisited of one wild caught adult male (Vernon), and an adult male and an adult female born and raised at Yerkes Regional Primate Research Center (Akili and Lisa). Lisa's two year old offspring who was born at the San Diego Zoo was also present. Table 2.1 lists the individuals according to their group composition.

Table 2.1 Eleven Display Bonobos at the San Diego Wild Animal Park

Group	Adult	Adolescent/ Juvenile	Sex	Age (Yr)	Parents/Origin
Vernon	Vernon		M	19(Est.)	Wildborn
	Loretta		F	17	Linda/Kakowet
	Lana		F	12	Linda/Kakowet
		Lena	F	6	Loretta/Vernon
		Lori	F	4	Louise/Vernon
		Laverne	F	3	Lana/Vernon
		Lolita	F	2	Louise/Vernon
Akili	Akili		M	11	Bosandjo/Matata (Yerkes)
	Louise		F	19	Linda/Kakowet
	Lisa		F	10	Bosandjo/Laura (Yerkes)
		Lucy	F	2	Lisa/Vernon

Two of the juveniles had recently been reintroduced and had received a great deal of aggression from different members of the group. In order to minimize the aggression, the bonobos were housed in two separate groups.

The two groups were alternately exhibited in an outdoor "island" type of enclosure which originally housed a group of drills *(Mandrillus leucophaeus)*. While one group was outdoors for the day, the other group remained inside their sleeping rooms. The sleeping rooms were designed to provide each group with visual and auditory access to the other group when held indoors for the night. A 15 foot dry moat surrounds the island which was heavily grassed, and sparsely populated with palm trees. Two climbing structures and a wading pool were also available to the bonobos. The sleeping quarters were not accessible to the bonobos on exhibit. However, the entrance was located in the concrete moat, thus allowing for vocal and a minimal amount of visual contact between the display group and the group kept inside. On many occasions the display group became aware of the indoor group's vocalizations, and vocal exchanges would ensue, often occupying the attention of the entire display group.

The display group would be released outdoors after first eating their main meal indoors. They also received another meal when they returned indoors for the evening. Typically, they would be released outdoors between 8- 8:30am and then brought in for the evening before 6pm. Before the group was released into the enclosure, an animal caretaker would scatter small foodstuffs around the enclosure for the bonobos to forage on throughout the day. These food items generally consisted of bananas, oranges, sweet potatoes, apples, sunflower seeds, and raisins. While these items provided the bonobos with nutritional benefits, they were also a source of boredom alleviation. On occasion, the keepers would also provide the group with an afternoon snack which was thrown into the enclosure over the side of the moat.

The San Diego Wild Animal Park attempts to intervene with the animals

as little as possible. In the past, and more specifically, at the zoo, the bonobos were often seen to interact with not only the keepers but also the visiting public. Because the bonobo is a highly intelligent creature and is often given to mimicking, the interactions with the public often got out of hand. Instead of viewing naturalistic bonobo-like behaviors, the public found it more interesting to interact with the animals in a human-like way. Behaviors such as hand clapping, and begging were often brought on by the public, even though they were discouraged by the management. Another result of visitor interactions with the display animals recently became apparent when the two juveniles were reintroduced. The animals became excited by human interactions and unfortunately were observed to displace this excitement by becoming aggressive with the newest members of the group. This is one of the reasons that the bonobos were placed in the enclosure formerly meant for the drills. The enclosure itself can only be viewed by the public from a monorail which passes by every 15 minutes for approximately one minute in duration. The monorail drivers discourage the public from interacting with the bonobos, and if they do not follow their requests, they drive on, leaving the enclosure behind. This management procedure has improved relations within the group, and also has decreased the amounts of human oriented-behaviors, allowing the visiting public the opportunity to see bonobos acting as bonobos.

Subject Animals

Four of the 11 bonobos were included as subject animals in this study (Table 2.2). All four adult females were of reproductive age and had previously given birth to at least one infant. Two females were primiparous (Lana and Lisa), and the other two were multiparous (Louise and Loretta). They ranged in

age from 10 to 19 years of age. The three oldest females were full siblings (offspring of the original breeding pair Linda and Kakowet). The youngest female, Lisa, was unrelated to the other females and was the only subject raised in the nursery at Yerkes Regional Primate Center. All of the subjects were hand reared by human care givers.

Lana and Lisa, the youngest and primiparous females had their only offspring present during the course of the study. The older females had both previously raised at least one offspring successfully. Loretta cared for her two offspring and had parted with the older of the two. The younger offspring remained in her mother's display group during the length of this study. Louise

Table 2.2. Subject Animals

Subject	Group	Year of BirtH	Raised	Offspring/Year	
Louise (LU)	Akili	1972	Nursery (SDWAP)	Lanore Lori Lolita	1982 1987 1989
Loretta (LT)	Vernon	1974	Nursery (SDWAP)	Victor Lena	1983 1985
Lana (LA)	Vernon	1979	Nursery (Yerkes)	Laverne	1988
Lisa (LS)	Akili	1981	Nursery (Yerkes)	Lucy	1989

on the other hand, had successfully cared for her first offspring and this female offspring was removed from the San Diego Zoo collection at the age of six years. Louise has rejected all subsequent offspring. Two of these offspring were raised in the San Diego Zoo Nursery. They were reintroduced into the bonobo group in the year preceding this study. They remained in the other display group for the duration of this study. Louise also had another female infant two months after this study was completed, and once again rejected her. This infant is currently being hand reared by human care givers in the San Diego Wild Animal Park Nursery.

The study lasted from June 13, 1991 till September 13, 1991 for a total of 244.73 hours of focal animal observations. A one week period was set aside at the beginning of the study in order to become familiar with the individuals and their behavior. After this period of familiarization, systematic data collection began. Observations were taken from the edge of the dry moat outside of the enclosure. As the public was confined to the passing monorail, there was very little opportunity for it to disturb the collection of data. However on more than one occasion visiting researchers, keepers, and other grounds people did disrupt data collection. On these occasions the sample was terminated and started anew when they had left, or when the animals did not show any apparent interest in these visitors.

On several occasions the keeper would bring the group a snack. During these times data collection continued, because important features of bonobo behavior (specifically, GG rubbing) were often observed as a result of these interruptions. When this occurred, it was always indicated on the data sheet that a keeper was present, and what he or she was doing.

Data Collection Methods

Ethogram

The ethogram utilized was created for the purpose of this study and is primarily based on that of de Waal (1988). The ethogram consists of 55 behavioral units: 22 states, and 33 events. States are defined as a behavior with a measurable duration. Events are defined as an instantaneous or momentary behavior. In this manner of organization, states are arranged hierarchically, and are mutually exclusive. Most events are mutually exclusive, but their occurrence may coincide with states. The following behavioral units comprise the ethogram used in this study.

States

TERM	DEFINITION
Groom:	careful and systematic cleaning of another individual's body by parting the fur and removing flakes of dry skin, dust, and parasites.
Self-groom:	grooming of the self.
· Nest-build:	the manipulation of nesting materials (leaves, branches, etc.) to form a "nest" around the individual's body.
Manipulate object:	the exploration or handling of an object.
Travel:	locomoting across the ground at a walking speed.
Lope:	traveling at a quick speed using all four limbs.
Group travel:	locomotion of a group of animals who move in the same direction with no apparent leader.
Climb:	moving either up or down an object (generally a tree

or cliff) using both hands and feet.

Feed: mastication and swallowing of any type of food matter.

Forage: active search for food matter.

Rest alone: sitting, reclining, lying, or hanging in a position in which the animal is not exerting itself.

Sit socially: resting within one meter of more than one adult individual.

Sit in proximity: resting within one meter of one other individual.

Follow: an individual travels behind another within one meter at a walking pace.

Social play: any combination of chasing, wrestling, or frolicking with one or more individuals. Often accompanied by a play face and laughing vocalizations.

Beg: an extremity is stretched out in the direction of the recipient of the beg (either another bonobo or a human).

Masturbate: self-manipulation of the genitals.

Monitor: the monitoring of any activity or noise which holds the individual's attention.

Tree play: climbing, swinging, or play involving one or more of the palm trees located in the enclosure.

Water play: play occurring in the water filled pond. Involves stereotypical play behaviors, or swimming and strolling through the water.

Blind man's bluff: an individual travels around its environment with its

eyes covered by either an arm or fingers. A specific
type of play behavior.

Solitary play:
any combination of play behaviors exhibited by a
lone individual.

Events

Approach (direct/receive): initiation of interaction by direct advance of another
individual , or the reduction of social distance
between animals.

Peer (direct/receive):
one individual stares very intensively at another's
mouth or hand while sitting or standing still, usually
within one meter of it.

Embrace (direct/receive):
the arms of one individual are placed around the
body of another individual.

Beg (direct/receive):
arm, hand, or leg and foot stretched out with the
open hand palm facing upward.

Bipedal:
the individual balances on its legs. Can be either
standing or locomoting.

Startle:
a sudden almost involuntary-like movement of the
body upon being surprised by an action or noise in
the environment.

Vomit:
regurgitation of stomach contents, often
accompanied by gagging.

Groom solicitation :
(direct/receive)
an individual presents a portion of its body to
another individual within proximity.

Avoid (direct/receive):
an individual deters physical contact and/or proximity
to another individual by leaning away or

detouring from its direction of travel.

Supplant (direct/receive): an individual displaces another and then remains in the space occupied by that individual.

Retrieve: an individual approaches an infant and carries it away.

Restrain: holding an infant by hand or foot while the infant struggles to free itself.

Handout (direct/receive): arm and hand stretched out toward another individual as a type of aid or reassurance.

Genital inspect: (direct/receive) close inspection and/or manipulation of the genital region by self or others.

Sexual present: (direct/receive) sexual signaling to the partner through exhibition of the genitals by spreading the legs, or presentation of the hindquarters.

Penis present: (direct/receive) upright sitting posture with legs apart exposing erect penis aimed at another individual.

Mount (direct/receive):

    a) ventral-ventral: involves the female (if male-female) lying on her back with her legs wrapped around the the male's waist who is on top of her. If the individuals were both females, the mountee was usually lifted off of the ground during the GG rubbing session.

    b) dorsal-ventral: dorsal-ventral mounts involved the male approaching the female from behind, with the female lying on her ventrum with her abdomen slightly

	raised off of the ground.
Mount attempt:	an individual tries unsuccessfully to mount another individual.
Rejection of sexual present:	the individual who is being solicited refuse to be mounted by either physically moving its body or by ignoring the presenter.
Genito-genital rubbing:	the lateral rubbing of genitals by two females while holding each other ventro-ventrally.
Copulation:	mounting of an individual accompanied with thrusting movements
Chase (direct/receive):	one individual pursues another who is fleeing.
Display (direct/receive):	may be a stationary or traveling behavior in which the individual calls attention to itself. Display behaviors include swaying, slapping ground or walls, object throwing, and often pushing and running with objects.
Charge (direct/receive):	a sudden and vigorous lunge towards another individual often accompanied by pilo-erection. Sometimes aimed at a particular individual.
Poke: (direct/receive):	an individual touches another with an extended finger, often repeatedly.
Push (direct/receive):	an individual uses one or both hands to forcefully move another individual away from itself.
Shove (direct/receive):	an individual uses one or two hands to push another individual away from itself in a sudden and almost

explosive manner.

Hit (direct/receive):	an individual hits another with the flat of its hand.
Punch (direct/receive):	an individual hits another with a clenched fist.
Bite (direct/receive):	an individual seizes another with the teeth.
Swagger:	bipedal walk or run with lateral swing of the upper body, often with pilo-erection.
Hand/arm over (direct/receive):	an individual moves its arm and hand over the entire body of another individual while running past in a threatening manner. Interpreted as a signal of dominance.
Run over (direct/receive):	when running towards another individual the actor does not sway or move away from the crouched over individual, but instead runs directly over its body, sometimes accompanied by a hit on the crouching individual's back. Interpreted as a signal of dominance.

Type of Data Collected

To obtain detailed information on estrous and anestrous behaviors of the bonobos, three types of data were collected. First, focal animal samples (Altmann, 1974) were collected. Focal animal samples are collected by focussing the attention upon a single individual subject for a specific period of time. On each day, one female was randomly selected. After this selection, samples were alternated between the two females available in each display group so that an equivalent number of samples was recorded for each female

throughout the day. Focal sessions were 30 minutes in length. All samples which contained more than 10 minutes of the subject being out of site were aborted, and new samples were undertaken.

The second type of data collected was the grade of sexual swelling. At the beginning of the day, before data collection had begun, and at the beginning of each focal session, the sexual swelling of the subject animal was recorded. The method introduced by Furuichi (1987) was employed. This method grades the size as well as the firmness of the sexual swelling on a three point scale. As outlined by Furuichi:

> "Firmness-1: the sexual skin is greatly wrinkled and sways when walking; Firmness-2: the sexual skin is rather turgid, but small wrinkles are visible on its surface; Firmness-3: the sexual skin seems quite firm, being lustrous without wrinkles. Size-1: the length of the sexual skin is shorter than the distance between the eyes and the mouth of the female; Size-2: the length falls between the eye-mouth and eye-chin distance; Size-3: the length is larger than the eye-chin distance" (1987:311-312).

This method was employed, as it seemed to be the most comprehensive and allowed the researcher to assess the sexual swelling from a distance of more than 10 feet. At the beginning of the study, the keepers were also consulted as to the grading of the sexual swelling of the females.

The third type of data collected was instantaneous or scan samples (Altmann, 1974). Throughout the day, for each fifteen minutes of observation the behavior was recorded for all animals present. For each of the two subject females, proximity data was also collected. It was noted for each whether they were: in contact, within one metre, or within three metres of another individual. The individual(s) who were in proximity were also recorded.

All samples were recorded with pencil and paper on specific focal sheets

created for the the purpose of this study. A digital watch displaying minutes and seconds was used to record the time.

Data Analysis Methods

Grade and Length of Sexual Swelling - Identifying Estrus

As the sexual swelling of each of the subjects was evaluated every day, a clear picture of their sexual cycle can be determined. The system employed graded the size and firmness of the sexual swelling, therefore it is possible to examine both values to determine the estrous state of the female. Theoretically, a female showing full swelling would be graded as a three on both scales of firmness and size. This was not the case for most of the subjects observed in this study. The youngest female (LS) showed no signs of swelling for the entire length of the study. She had given birth just one and a half years previous and was still nursing her dependent offspring. It was assumed that she was experiencing postpartum amenorrhea. Because there could be no division of estrus and anestrus for this female, the data samples collected on her are not included in the analysis. A total of 62.4 hours were collected, but are not included in the analysis.

Each of the other females exhibited different patterns and lengths of swelling. Table 2.3 lists the three females included in the analysis and shows the number of days they were each observed in estrus and anestrus. Louise (LU) never showed a firmness grade of three. Therefore, the days on which she exhibited a size three and grade two are considered to be her full sexual swelling. She showed this full swelling in 19 out of 33 days observed. Thus she was considered to be in estrus 58% of the observed time. One female, Loretta (LT) did show a full swelling which could be graded as a size three and

firmness three during her period of estrus. It was determined that she was in estrous on 12 out of the 35 days observed (34% of days observed). Lana (LA) showed the shortest period of estrus of all three females. Lana also was never observed to exhibit a sexual swelling that could be graded as three on both scales. On days which she was determined to be in estrus, her swelling was graded as two in size and three on the firmness scale. She was observed in estrus for only eight days out of 36, which was only 22% of all observed days. All other combinations of grading were observed for each of the females during their period of pre- and post- maximal swelling.

Although the method employed for grading sexual swelling provided a very detailed description of the females' swelling, the analysis only required a division between estrus, and anestrus. For this reason, "peak estrus" or maximum tumescence was used as the external physical marker of estrus for the subjects in this study. Any other state (ie. less than maximum swelling) is considered anestrus. By using Furuichi's method to grade the sexual swellings of the females, the maximum swelling was discriminated from a less than maximum swelling. Thus, the grading of size and firmness was used as a method to train the observers eye to the subtle differences among various sexual swellings. The data was therefore divided into two categories; estrus (full swelling) and anestrus (any other grade except full swelling). For example, Loretta's full swelling consisited of a grade of three in both size and firmness. On the days that she was recorded as having a grade of three in size and three in firmness, she was considered to be in estrus. Any other grade (eg. size - three, and firmness - two) she was considered to be anestrus.

Table 2.3 Subjects and Number of Days in Estrus

Subject	Days in Estrus Total (%)	Focal Hours Estrus	Focal Hours Anestrus	Total
Louise	19/33 (58%)	27.65	31.36	59.01
Loretta	12/35 (34%)	27.02	38.79	65.81
Lana	8/36 (22%)	14.40	43.11	57.51
Total		69.07	113.26	182.33

Statistical Procedure

In the analysis, no inferential statistical procedures were utilized. Inferential statistics were not used here for a number of reasons. First the sample size was very small. Only three of the four possible subjects are included in the analysis. Second, although the subjects were observed for over 90 days, only one complete estrus was recorded for each of the females included in the analysis. As bonobo cycles have been recorded for up to 46 days, it was assumed that at least two cycles would be observed, this was not the case. Third, one of the objectives of the study was to explore female behavior and how it is affected by estrus. Statistically significant results were not the purpose of the analysis. Instead, trends and patterns were expected to be uncovered if present. As the number of subjects was very small, and there were limited numbers of observations on estrous females, it is not appropriate to use inferential statistics. Instead, the analysis is descriptive in nature. Differences between estrous and anestrous conditions are compared and contrasted on a descriptive level of analysis.

The sample hours for each female and her period of estrus are very different. In order to make comparisons between and among the females the raw data were converted into a different format. When state behaviors are examined, percentage of total observation time per female are analyzed. This allows for a direct comparison between the females to be made. When events are examined, mean rate per ten hours is the format compared. This correction for uneven sample sizes is further explained in Chapter 3 when it is first encountered.

The next three chapters comprise the results section of the study. Results are broken down into three sections; affiliative social interactions, agonistic interactions, and GG rubbing.

CHAPTER 3 - AFFILIATIVE SOCIAL INTERACTIONS

Introduction

This chapter will review the affiliative interactions among the subject females. Affiliative behaviors which are included are: grooming (directed:GD; and received: GR), sitting in proximity (SN), sitting in contact (SC), social play (PL), approaches (AP), and peering (PR). There are a number of behaviors that could also be included in this category, such as; play presents, embracing, and aiding in agonistic interactions. However, these behaviors were not observed and/or scored often enough to be subject to any type of systematic analysis. The first four behaviors (grooming, sitting in proximity, sitting in contact, and social play) are analyzed in a similar manner. First, an overall comparison between estrous and anestrous states will provide a general idea of how sexual state affects the females' interactions with other group members. The second step is to identify who and how often the females were interacting with. Each behavior is broken down into percentage of time spent with each age/sex class (of total time observed in that particular behavior). Then for each behavior, a closer examination of the interactions among adult females will be undertaken to determine what effect sexual state has on these behaviors.

The last two behaviors listed (approaches and peering) are analyzed in a different fashion. Approaches and peers were scored as events, therefore the frequency of their occurrence is examined, not the percent of time spent in these behaviors. This section examines these two behaviors following the same structure as the previous four. Overall behavior, female-female behavior, and then behavior between other age/sex classes are examined. The purpose of this section is to determine who was responsible for the interactions with the females. Specifically, who was responsible for the increased affiliative social

interactions between adult females who were in estrus.

Because the grouping at the San Diego Wild Animal Park included only two adult females in each display group, there are only two possible interacting pairs. Lana and Loretta remained in one group, thus, any adult female interactions observed with Lana could only be with Loretta and vice versa. Similarly, the interacting partner of Louise was always Lisa. As the analysis often involves individual subjects, it is helpful to note the interacting partners: Lana and Loretta, and Louise and Lisa.

In general, the overall differences in state behaviors for the females were not large. The largest difference between estrous and anestrous females was recorded in the category of feeding/foraging. Feeding and foraging behaviors increased for estrous females by 22.57%. The differences in other behaviors were less dramatic. For example the next largest difference was grooming, which was observed 5.34% less for estrous females (discussed in detail below).

Two behaviors that are not discussed further will be mentioned here; resting alone, and resting with a group. Estrous females spent 4.25% more time alone than anestrous females (estrus: 27.91%, anestrus: 23.66%). Complimentary to this result of the females spending more time alone, they also spent less time resting with a group. Anstrous females spent 4.55% of their time resting with a group whereas estrous females only spent 2.65% of their time resting with a group.

Social Grooming
Overall Differences in Grooming - Estrus Vs. Anestrus

Overall differences in grooming between the estrous and anestrous state are broken down into directed grooms (GD) and received grooms (GR).

Anestrous females received almost as many grooms as estrous females with a difference of only .28% (anestrus: 11.18%; estrus: 11.46% of all grooms observed). Grooms directed by females showed more of a difference. When exhibiting maximum swelling, females were observed to groom less often than when anestrus. Anestrous females groomed others 13.59% of all observation time, whereas estrous females only groomed for 8.25%; a difference of 5.34%. Although they were groomed slightly more when in estrus, females groomed others far less when in estrus.

Female-Female Grooming - Estrus Vs. Anestrus

For each female, a profile was constructed for the age/sex classes who she was observed to groom with during periods of anestrus, and estrus. Figure 3.1 graphically represents these grooming profiles. Figure 3.1a represents grooms directed by the estrous female, and Figure 3.1b represents grooms received by the estrous female. The white portion of the columns refers to the time spent in grooming with another adult female. Note that for both Lana and Louise, grooming with another adult female increases in both directed and received grooms during estrus. Loretta did not follow this trend, but instead decreased both the directed (Figure 3.1a) and received grooming with another adult female (Figure 3.1b). However, even with the decrease of female grooming by Loretta, the average of the three females results in an increase in both being groomed by other females and grooming other females. Grooming other females for all three combined subjects increased by an average of 12.69% whereas being groomed only increased by 1.33% (Figure 3.2). Figure 3.2a and 3.2b show that the increase received by adult females in estrus is much smaller than those directed by adult females in estrus. Adult females

Figure 3.1a   Percentage of Time Spent Grooming Others
Broken Down by Age/sex classes -
Estrus Vs. Anestrus
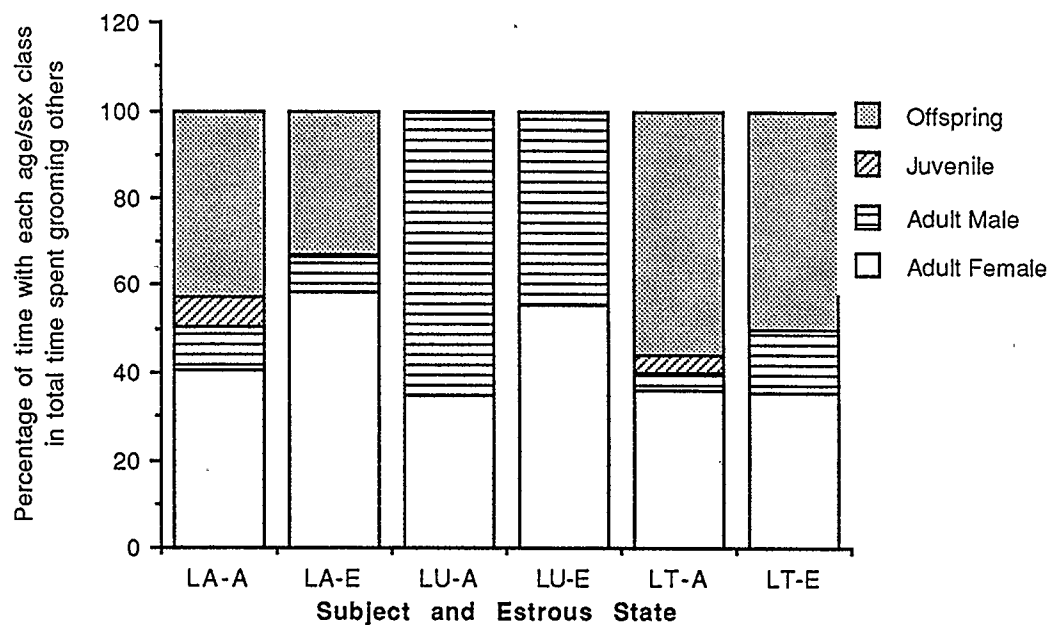
Figure 3.1b   Percentage of Time Spent Receiving Grooms
Broken Down by Age/sex Classes -
Estrus Vs. Anestrus
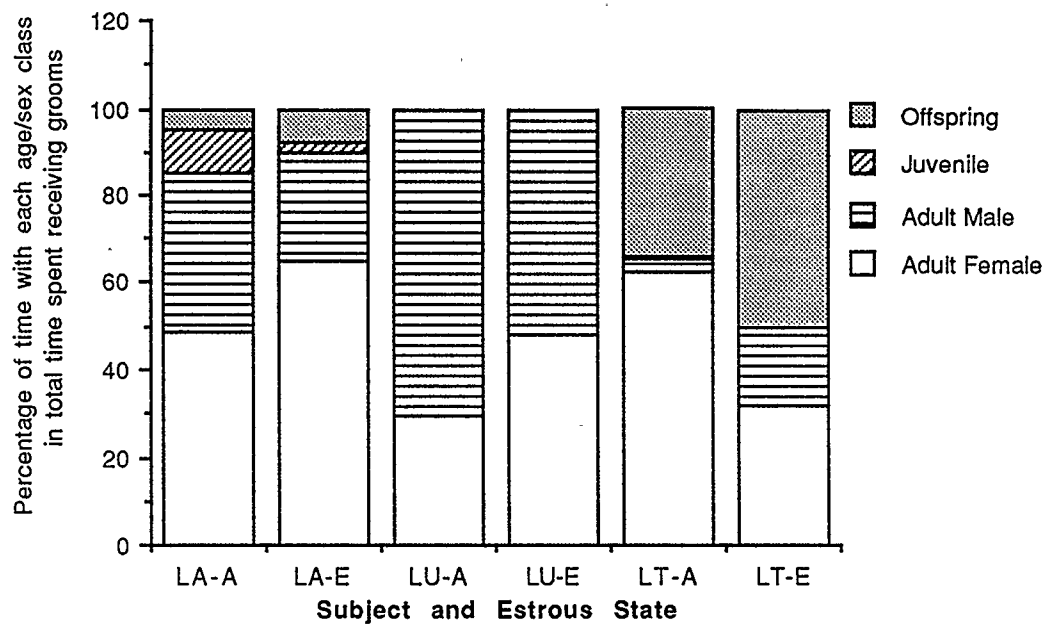
Figure 3.2a Percentage of Time Spent Grooming Other Adult Females-Estrus vs Anestrus

Estrous State of Females
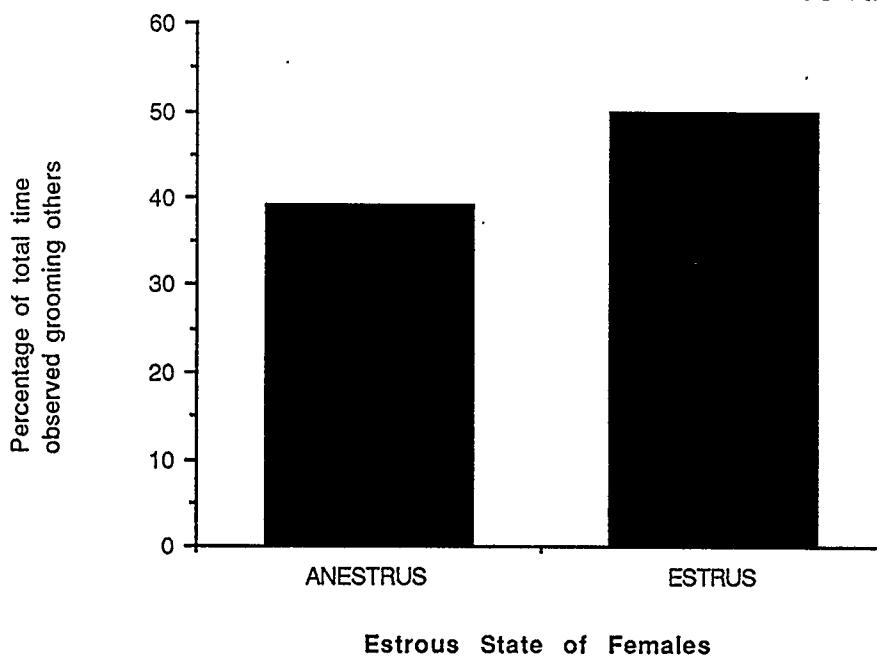
Figure 3.2b Percentage of Time Spent Receiving Grooms From Other Females-Estrus vs Anestrus

Estrous State of Females
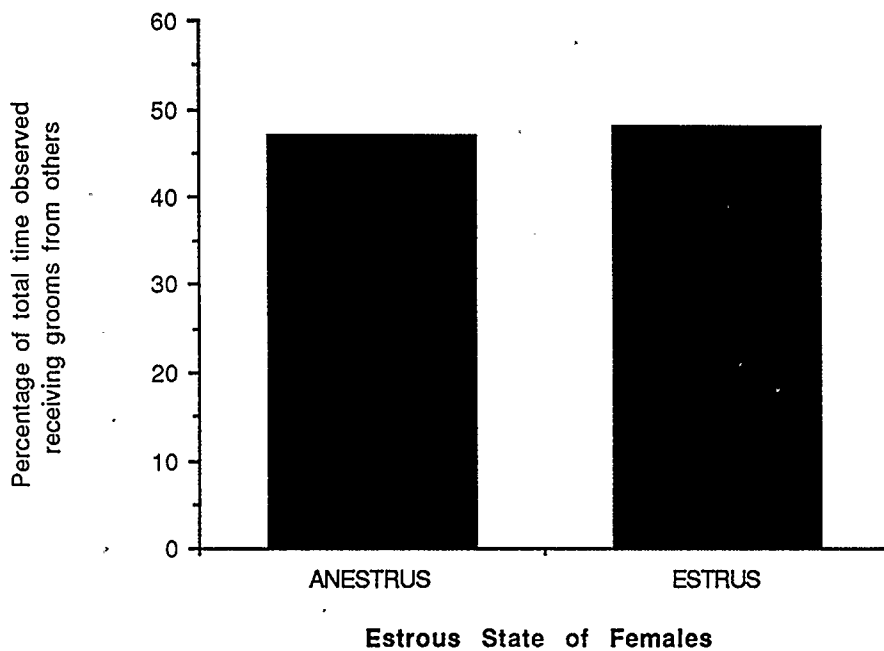
groomed other females 12.69% more when in estrus, but they only received 1.33% more grooms.

Other Age/Sex Classes - Estrus Vs. Anestrus

For both Lana and Louise. the increase of grooming interactions with the female was accompanied by a decrease of grooming interactions with other age/sex classes. The only exception is a slight increase in grooms received by Lana from her offspring (Figure 3.1a-dotted portion of column). Thus, Lana and Louise decreased grooming and being groomed with the adult male, and the juveniles (Louise did not have any grooming interactions with the juvenile in her group, and she did not have any offspring in her group). Loretta did not follow this pattern. Loretta's decrease in female grooming was accompanied by an increase in grooming with the adult male (Figure 3.1a - horizontal lined section). This was an increase in both directed and received grooms. She also received more grooming from her offspring during estrus.

Thus, while Lana and Louise increased grooming interactions with the other female, and decreased grooming with other age/sex classes (both directed and received), Loretta behaved in an opposite manner. She increased grooming with both the male and her offspring, but decreased grooming with the other female during estrus (both directed and received). Even with the decrease of female grooming by Loretta, the average of the three females results in an increase in both being groomed by other females and grooming other females.

Sitting in Proximity

Overall Sitting in Proximity - Estrus Vs. Anestrus

Estrous females were observed in proximity to another individual more often than anestrous females. Sitting near another individual increased 4.25% when females were in estrus (anestrus: 23.66%; estrus: 27.91%).

Females Sitting in Proximity - Estrus Vs. Anestrus

Figure 3.3 represents profiles of the amount of time spent in proximity to other individuals during estrus and anestrus. For all three females, the amount of time spent in proximity to another adult female increased during estrus (white portion of columns). This represents the average, as well as the individual results. Lana demonstrated the largest difference of time spent near another adult female during estrus. In the anestrous state, of the total time spent in proximity to another animal, Lana was in proximity to the adult female 32.34% of the time . When she was estrus, this increased to 50.45%; an increase of 22.11%. Louise and Loretta showed less dramatic increases. Louise sat in proximity to the other female 3.95% more often when in estrus, and Loretta sat near the other female 2.60% more often when she was in estrus. Figure 3.4 shows the average increase in sitting in proximity to another female for all three subjects. The average increase was 8.22% (anestrus: 47.45%; estrus:55.67%).

Other Age/Sex Classes - Estrus Vs. Anestrus

For all three subjects, the increase in time spent near the adult female was correlated with a decrease in time spent with other age sex classes. Lana, Louise, and Loretta all decreased their time spent near juveniles, and offspring. Only Loretta increased her time spent near the adult male during estrus. In fact

Figure 3.3 Amount of Time Spent in Proximity to Each Age/sex Class

Percentage of time spent in proximity with each age/sex class

Legend:
- Offspring
- Juvenile
- Adult Male
- Adult Female

X-axis labels: LA-A, LA-E, LU-A, LU-E, LT-A, LT-E

Subject and Estrous State
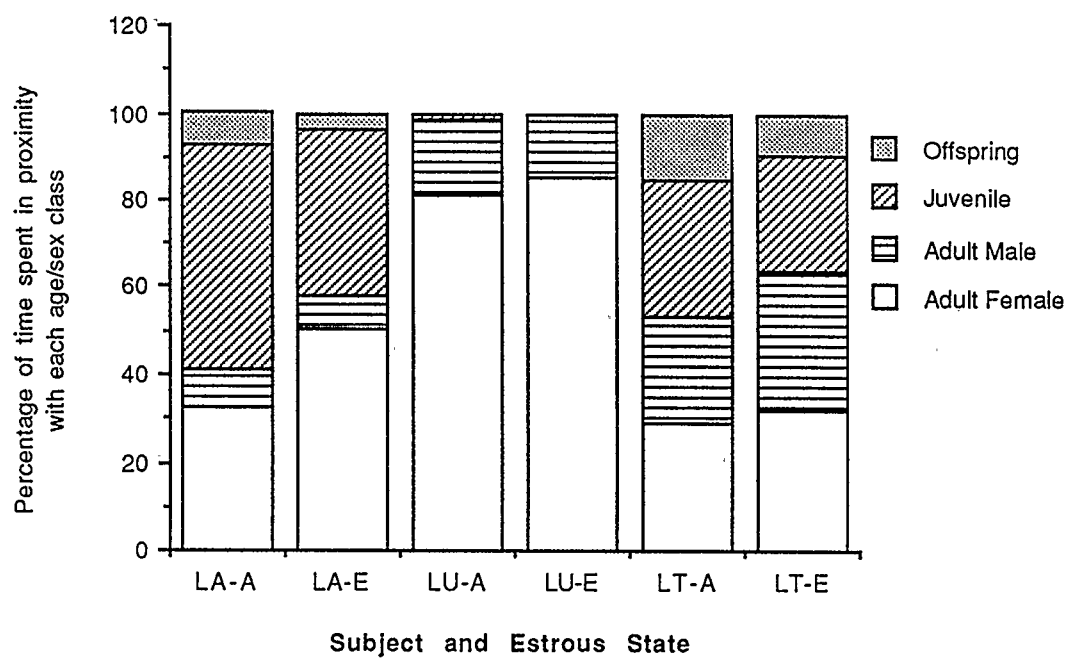
Figure 3.4 Amount of Time Spent Sitting in Proximity to Adult Females - Estrus Vs. Anestrus
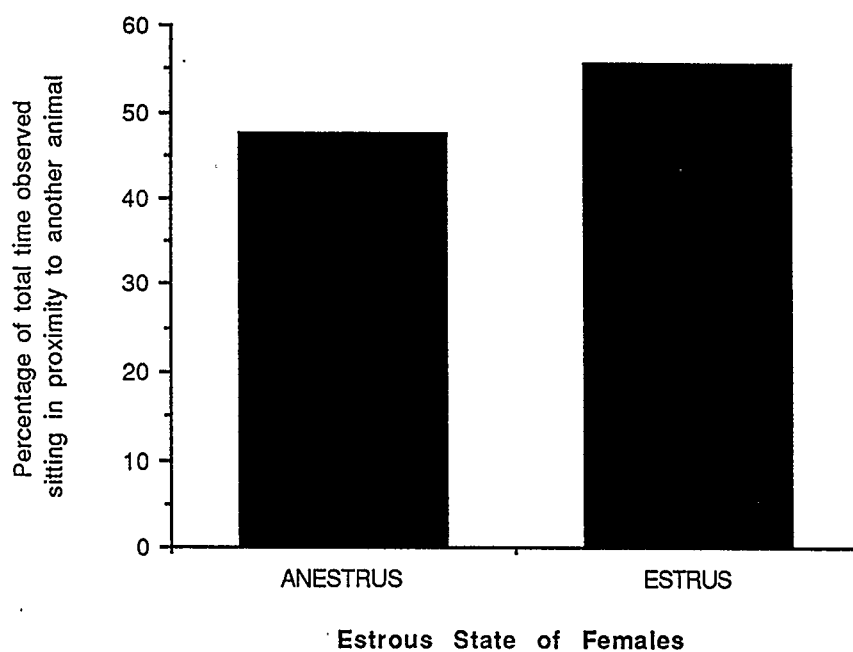
this increased more than the time spent near the adult female; 2.60% for the adult female and 12.12% for time spent near the adult male.

Sitting in Contact

Overall Difference in Contact Behavior - Estrus Vs. Anestrus

Sitting in contact with another individual was not observed very often for estrous or anestrous females. Only 2.54% of all observations involved anestrous females sitting in contact with another individual. This decreased by 0.10% for estrous females.

Female-Female Contact Behavior - Estrus Vs. Anestrus

Once again, a profile was constructed for contact behavior by age/sex class (Figure 3.5). The white portion of the columns indicate the time spent in contact with adult females. These white portions indicate that sitting in contact with another female increased during estrus for all three females. Lana sat in contact with a female 6.81% more often when in estrus (34.77% of all cases) than anestrus (27.96% of all cases). Louise showed a similar increase from 68.00% during anestrus, to 78.16% during estrus; an increase of 18.16%. Loretta sat in contact with a female for 83.33% of all instances of her sitting in contact with others. This is an increase of 11.89% from her period of anestrus (71.49% of all cases). These resulted in an increase in contact with another adult female during estrus of 9.62% (Figure 3.6). When they were anestrus, adult females spent 55.82% of their contact time with adult females, but when they were estrus this increased to 65.44%.

**Figure 3.5   Amount of Time Spent in
Contact with Each Age/sex Class**

Percentage of time spent in contact with each age/sex class

Subject and Estrous State

Offspring

Juvenile

Adult Male
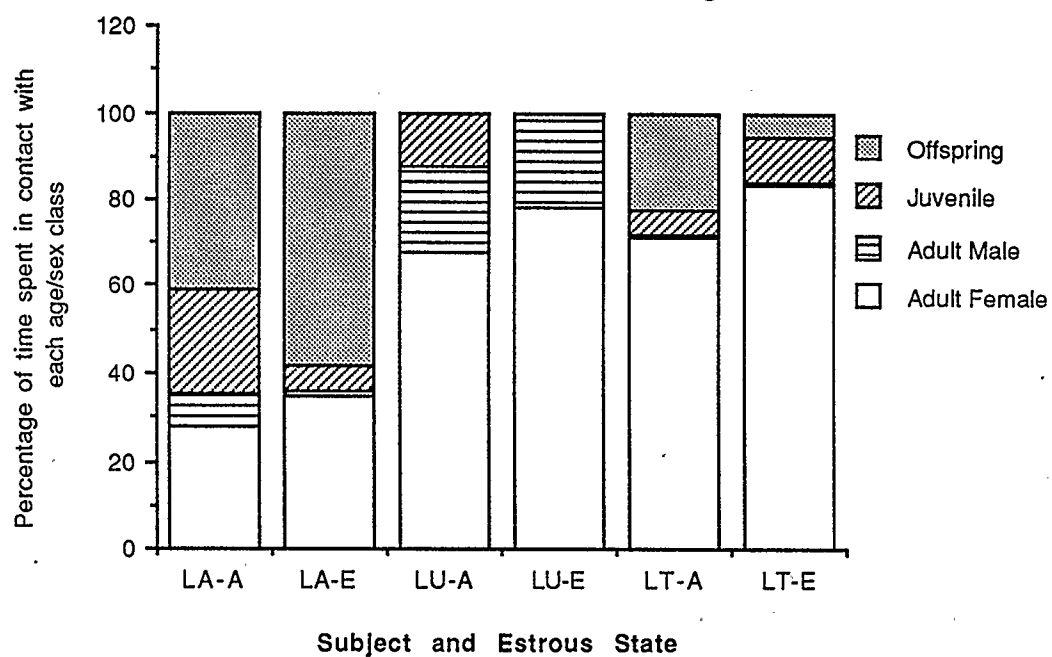
Adult Female

Figure 3.6   Amount of Time Spent Sitting in Contact with
Adult Females - Estrus Vs. Anestrus

Estrous State of Females
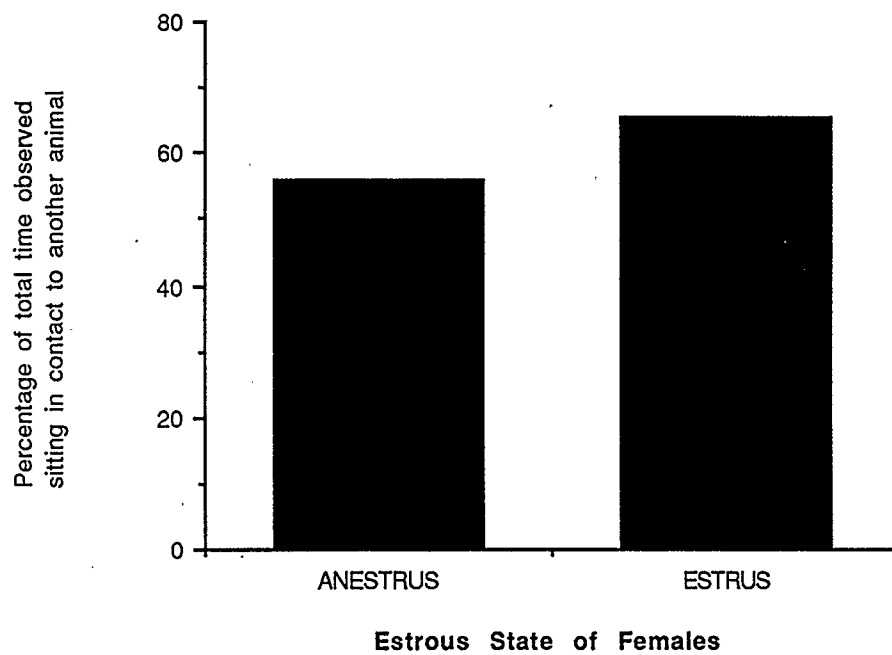
Other Age/Sex Classes - Estrus Vs. Anestrus

The time spent in contact with other age/sex classes varied from female to female. Lana and Louise both decreased the amount of time sitting in contact with a juvenile (Lana, 17.59% decrease; Louise, 10.15% decrease). Conversely, Loretta increased the amount of time spent in contact with a juvenile other than her own offspring by 5.25% (Figure 3.5-diagonal lines). Time spent in contact with offspring also differed for each female. Lana increased the time spent near her offspring by 17.29% while Loretta decreased the time spent in contact with her offspring by 17.11%. Louise did not have any offspring in her social group.

Time spent in contact with the adult male also varied between females. Loretta did not spend any time in contact with the adult male during either anestrus or estrus. Lana was in contact with the adult male 7.62% when anestrous, but only 1.11% when estrus. This is a decrease of 6.51%. Finally, Louise increased time spent in contact by 2.04% with the adult male when estrus.

Contact behavior can be summarized in the following manner: the results are scattered for each age/sex class, except for adult females. The average amount of sitting in contact with another female reflects an increase during estrus.

Social Play

Overall Play Behavior - Estrus Vs. Anestrus

Playing with another individual was also not observed very often for the adult females. The largest amount observed was for anestrous females (2.70% of all observations). Playing decreased to 1.73% for estrous females, a

difference of .97%.

Play Among Females - Estrus Vs. Anestrus

Only one female (Louise) was observed playing with another adult female for more than 1% of all play observations. Figure 3.7 shows that Louise played with the adult female when she was in estrus (white portion of column). Also interesting to note is that during estrus, the adult female was her play partner 53.25% of the time, more than half of her play time.

Other Age/Sex Classes - Estrus Vs. Anestrus

All three females were observed playing mostly with the juveniles of the group (Figure 3.7-diagonal lines). Loretta played only with the juvenile in both estrus and anestrus. Lana and Louise had different play partners during both estrus and anestrus. Of the observed play sessions Lana played with juveniles 61.05%, her offspring 28.24%, and the adult male 10.49 %. Play with all age/sex classes decreased except for play with juveniles which increased by 17.99%. Louise differed from the other two females in that she played with more age/sex classes when in estrus. All of her play in the anestrous state was with the juvenile in her group. However, when she was in estrus, she played with the other adult female (53.25%), the juvenile (40.01%), and even the adult male (6.74%).

Thus, there were no overall trends for the category of social play. Each female seemed to differ in the amount of play, and with whom they played in both the estrous and the anestrous state.

Figure 3.7　Amount of Time Spent Playing with Each Age/sex Class
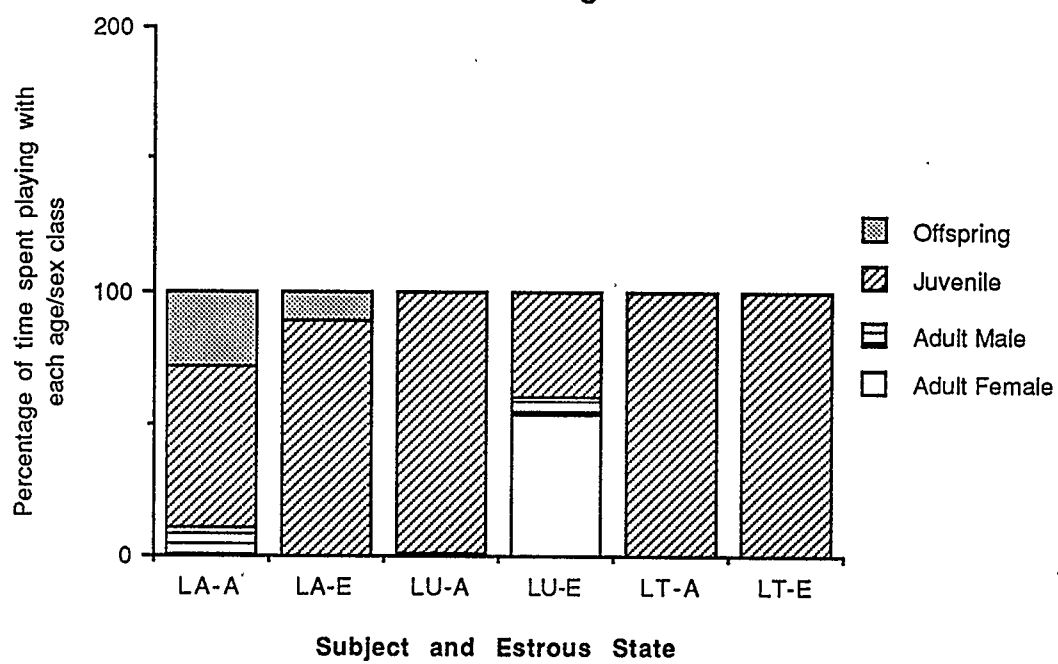
Approaches and Peering

Introduction

The above analysis presented a picture of who, and how much time was spent with each of the age/sex classes in each of the affiliative state behaviors. However an important aspect of the study is to determine (if possible) who was responsible for these increased interactions during estrus. To determine who was initiating the interactions between the adult females, a number of behaviors can be analyzed. An approach, which is defined as: an initiation of interaction by direct advance of another individual , or the reduction of social distance between animals, can indicate who initiates an interaction. Also, but not as obvious perhaps, peering can be a form of initiation. In this study peering is defined as staring very intensively at anothers mouth or hand while sitting or standing still, usually within one meter of it. As Furuichi has suggested (1989), peering appears to serve a broader function than just begging behavior. Because peering never resulted in any foodsharing for the females in his study, he suggested another purpose for peering. Furuichi suggests that peering is a form of self-presentation. This study also treats peering as a form of self presentation, and therefore a type of interaction initiator.

Another type of behavior appropriate for analysis is presenting . For the bonobos, groom presents varied from a simple approach to hand clapping and peering. Therefore, at the time of data collection it was not always obvious that these behaviors were used as a present until grooming had started. Scoring these events as a present after the fact would not be systematic and therefore groom presents could not be included in the analysis. Play presents could be obvious, but the number that was scored was too small for any type of systematic analysis (N=13). Sexual presents did occur often enough to enter

the analysis, however, as they often resulted in genital contact between females, this is examined in the same chapter as GG rubbing (Chapter 5). Thus, two types of behavior are included here: approaches and peering.

As noted in the ethogram, both approaches and peering were scored as events. That is, their occurrence was not timed. Instead of durations, these behaviors are recorded as numbers of occurrences, or frequency. For this reason the analysis takes on a different form for this section of the analysis on affiliative social interactions. For this section of analysis, instead of percentages of observation time, the results will be discussed in terms of mean rate per observation period. For ease of discussion, mean rate per ten hours of observation time is discussed. The rates are calculated by the following method:

$$\frac{\text{frequency of observation}}{\text{hours of observation}} \times 10 \text{ hours}$$

For example, if the behavior occurred 70 times over 70 hours of observation, it would result in the frequency of ten times per ten hours of observation (70/70 x 10 = 10). The data is analyzed in this manner to correct for unequal samples of estrous and anestrous states. By examining the data in this fashion, a direct comparison can be made between estrous states and age/sex classes.

Approaches

Overall Approaching Behavior - Estrus Vs. Anestrus

Figure 3.8 graphically represents the overall approach data for adult females. The dark columns represent approaches directed by the adult females, and the light columns represent approaches received by the adult females. There are three results that merit discussion here. The first interesting

Figure 3.8   Approaches Directed and Received by
Adult Females - Estrus Vs. Anestrus
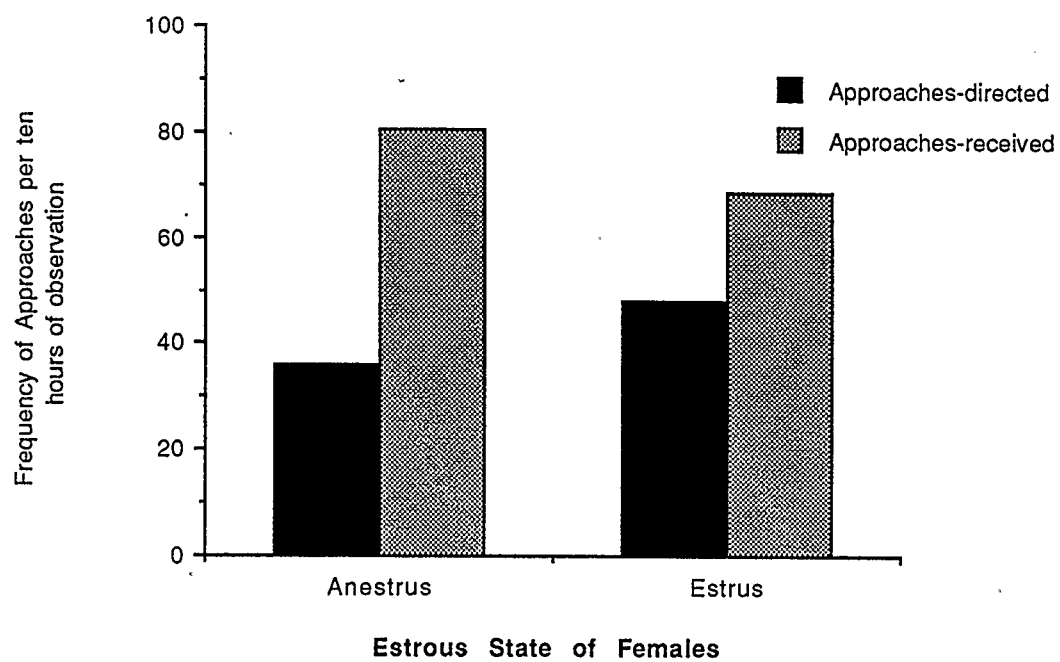
result is the large difference between directed and received approaches in both the estrous and anestrous conditions. Females, regardless of sexual state, received more approaches than they directed towards others. In the anestrous state, they were approached by others twice as often as they approached others.

Second, females approached others at a higher rate during estrus (Figure 3.8 - black columns). Anestrous females approached others 35.8 times per ten hours of observation. Estrous females increased the number of approaches by 12.1 times per ten hours for a total of 47.9 times per ten hours.

The third interesting result is that the subjects received fewer approaches when in estrus. The lighter columns in Figure 3.8 demonstrates the decrease from anestrus to estrus. They were approached by others 80.4 times per ten hours when showing full sexual swelling, but were approached only 68.3 times per ten hours when anestrus. This is a difference of 12.1 times per ten hours.

Female-Female Approaches - Estrus Vs. Anestrus

Approaches between females are presented in Figure 3.9. Once again, there is a difference between directed and received approaches in both the estrous and anestrous conditions. As with the overall approaches, subjects received more approaches from females than they directed. Also similar to the overall results, directed approaches increased when the females were in estrus. Anestrus females approached other females 16.9 times per ten hours. This increased by 3.7 times for estrous females who approached other females 21.6 times per ten hours.

One result did not follow the trend of the overall findings, when only females are considered, estrous females received more approaches than

**Figure 3.9   Appraoches Between Adult Females -
Estrus Vs. anestrus**

Estrous State of Females
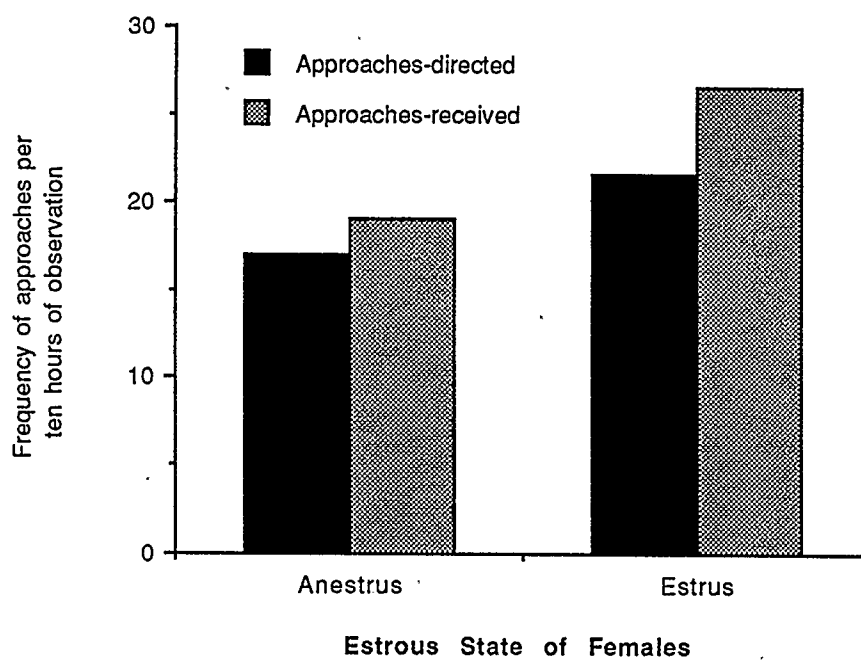
anestrous females. From 18.9 approaches received during the anestrous state, to 26.6 approaches received per ten hours for estrous females. This is a difference of 7.7 approaches per ten hours of observation.

Other Age/Sex Classes - Estrus Vs. Anestrus

Other age/sex classes did not show differences as large as those of adult females. The only other two classes that increased approaches with estrous females were adult males, and offspring. Adult males were approached one time more per ten hours when the females were in estrus (anestrous rate: 11.9 times per ten hours; estrous rate: 12.9 times per ten hours). Offspring of the females approached estrous females 6.9 more times than anestrous females (anestrous rate: 2.3 times per ten hours; estrous rate: 9.2 times per ten hours).

Peering

Overall Peering Behavior - Estrus Vs. Anestrus

Figure 3.10 presents the overall peering between the adult females and other age/sex classes. As with approaches, the black columns represent directed peers and the lighter columns represent received peers. Again, females received many more peers than they directed at others, in both the estrous and anestrous state. The subjects received more than twice as many peers as they directed when anestrus (a difference of 18.8 peers per ten hours) than when estrus (a difference of 6 peers per ten hours).

Peers decreased when the females were in estrus (both directed and received). They directed less than half as many peers when estrus (3.1 peers per ten hours) than when anestrus (11.6 peers per ten hours). An even larger difference was observed in peers received by females. Anestrus females

Figure 3.10 Peers Directed and Received by Adult Females-Estrus Vs. Anestrus

received 30.4 peers per ten hours, but estrous females only received 9.1 peers per ten hours. This is a difference of 21.3 peers per ten hours.

Female-Female Peering - Estrus Vs. Anestrus

The same trends that were revealed for overall peering behavior apply to female-female peering. When females were in estrus, they both directed and received fewer peers from other females. They directed 4.9 peers less per ten hours (Figure 3.11 - black columns), and received 8.7 less per ten hours when in estrus (Figure 3.11 - lighter columns). Also, in both conditions females received more peers from females than they directed towards females.

Other Age/Sex Classes - Estrus Vs. Anestrus

The only group that increased peering with females was the juveniles. Females received 8.3 more peers per ten hours from juveniles when they were in estrus. All other age/sex classes decreased their peering with the adult females when they were in estrus.

Summary of Affiliative Social Interactions

This chapter has reviewed the affiliative social interactions of the subject females. Four affiliative behaviors were examined in order to determine if the females' sexual state had any effect on these behaviors. In the majority of cases, these behaviors decreased between females and other age/sex classes. These are the overall differences, when the analysis concentrates on specific age/sex classes, the trend is very different.

Figure 3.11 Peers Directed and Received among Adult Females - Estrus Vs. Anestrus
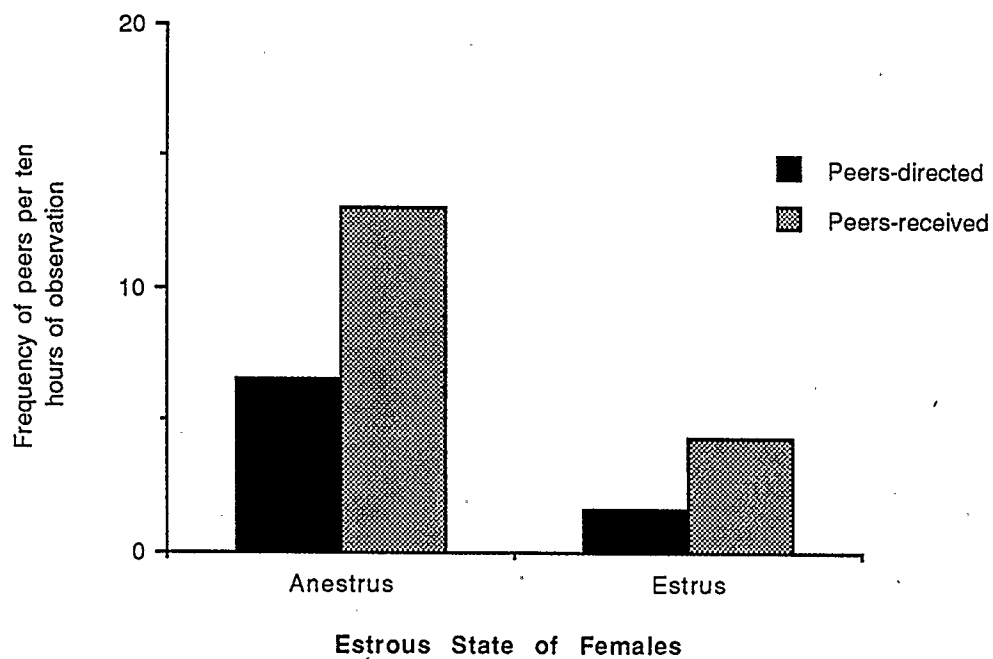
In contrast to the overall results, estrous females were involved in more affiliative interactions with other females than anestrous females. Thus, although females interacted less overall with others when in estrus, they interacted more with the specific age/sex class of adult females when in estrus.

Interactions between other age/sex classes other than adult females varied with each of the behaviors. For these age/sex classes, there was not a detectable trend. Grooming and sitting in proximity decreased with all age/sex classes except for one female with whom it increased. This is also the female for which the average results did not apply. In both grooming and sitting in proximity, her interactions decreased with other females. Sitting in contact, and playing was not observed among the subjects very often. These interactions with other age/sex classes varied for each female, there was no apparent trend for either behavior except for an overall decrease, and an increase between females.

Approaches and peering were examined to determine who was initiating the increased amount of social interactions between the subject females. A number of interesting results were found. In both estrus and anestrus, the females approached others more often than they were approached by them. The differences between approaches received and directed by adult females are in opposition to each other. Approaches were directed at others more often when the females were estrus. But approaches were received by females less often when they were in estrous. These are the overall results. Approaches between females differed in that both received and directed approaches increased for estrous females. The only other age/sex classes that increased approaching behavior with estrous females were adult males and offspring. Adult males were approached by adult females more often, but offspring

approached females more often. All other categories decreased during estrus.

Similar to approaches, females received more peers than they directed in both the estrous, and anestrous condition. Peering results were the same overall and for each specific age/sex class. During estrus, females received and also directed fewer peers towards others. The only exception here was peering between juveniles and adult females; females received more peers from juveniles during estrus.

CHAPTER 4 - AGONISTIC BEHAVIOR

Introduction

As outlined in the introduction (Chapter 1) the third objective involves the examination of agonism and how this is affected by the females' estrous state. This chapter focuses on this question and the results are discussed in the following manner. First, the overall effects of sexual state on agonism is analyzed to determine if there were any major differences between the estrous and anestrous states of the subjects. Second, the results will turn to the aggression observed between females. The differences between estrous and anestrous aggression will be examined by looking at the causes of female aggression . Also the level of aggression is examined to determine if this differs when the females are in estrus. Lastly, the aggression between other age/sex classes will be discussed with respect to the sexual state of the females.

Agonism in the bonobos at the San Diego Wild Animal Park tends to be both infrequent and mild. For the purpose of recording aggressive encounters between individuals, three levels of aggression were scored. Mild aggression consisted of the following or a combination of the following behaviors: threat face with or without vocalization, pushes, shoves and pokes. Medium level aggression could consist of any or a combination of the following behaviors: run past with or without arm extended over the back of the other, run over, or a charge. Aggression was only considered high if the incident involved a hit or a bite by the aggressor.

Overall Differences in Aggression - Estrus Vs. anestrus

As mentioned above, the total number of aggressive incidents was quite low. Figure 4.1 represents the mean rate of aggressive incidents per ten hours

**Figure 4.1   Aggression Directed and Received by
Females - Estrus Vs. Anestrus**

Estrous State of Females
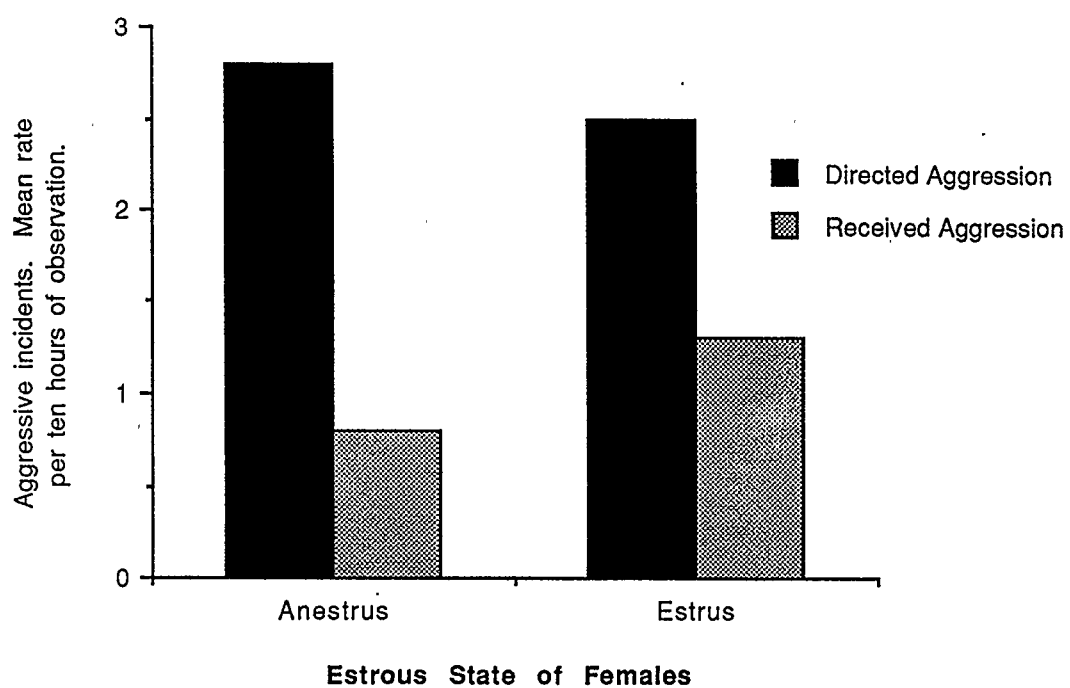
for females during estrus and anestrus. The first two columns are the incidents occurring during anestrus, and the second two columns are the incidents occurring during estrus. The average amount of aggression per ten hours that was directed by anestrous females was 2.8 incidents. This is not very different from the aggression directed by estrous females, 2.5 incidents per ten hours. However, subjects did receive more aggression during estrus. For estrous females, the mean rate is 1.3 per ten hours, but for anestrous females the rate is lower at 0.8 incidents per ten hours.

Aggression was directed by the females more often than it was received, in both the estrus and anestrus condition. During the anestrous state this difference is larger than the estrous state (Figure 4.1 - dark columns). Anestrous females directed aggression 2.8 times per ten hours, but only received aggression 0.8 times per ten hours. The difference between directed and received aggression by estrous females is not as large, but directed aggression was also observed more often (directed: 2.5 per ten hours; received 1.3 per ten hours).

Thus, an overall comparison of aggression between estrous and anestrous females is as follows. Females in either state (estrus or anestrus) directed more aggression than they received. During estrus, females were involved in slightly more aggressive incidents than when anestrus.

Female - Female aggression

A total of 19 aggressive encounters were recorded between the subject females. Table 4.1 lists the level of aggression (mild, medium, and high) and the number of times they were scored for estrous and anestrous females. Generally, aggression between females was considered low. Of the 19

incidents, nine were scored as low level aggression. Next was medium level aggression, which was observed six times. High level aggression was observed on four occasions.

Seven of the aggressive incidents occurred when the subjects were

Table 4.1. Aggression among Females - Estrus Vs. Anestrus

Level	Anestrus	Estrus	Total
Mild	5 (71%)	4 (33%)	9
Medium	0 (0%)	6 (50%)	6
High	2 (29%)	2 (17%)	4
Total	7	12	19

anestrous, the other twelve occurred during their period of estrous. When these amounts are considered relative to the number of hours of data involved, the difference becomes clearer. For ten hours of observation, estrous females were involved in almost three times as many incidents as anestrous females (mean rate per ten hours, anestrus: 0.6; estrus: 1.7).

Level of Aggression - Estrus Vs. Anestrus

Levels of aggression were not equally distributed. Percentage amounts in Table 4.1 represent the amount of aggression observed at mild, medium, or high levels for either of the two sexual states. Most of the aggression involving anestrous females was low level (71%). No medium level aggression was observed when females were anestrous. High level aggression made up 23%

of the anestrous females' incidents. For estrous females, not only the frequency of incidents increased but also, the level of aggression was higher. Low level aggression only made up 33% of all incidents. The remaining aggression was scored as medium level (50%) or high level aggression (17%).

Cause of Aggression

Table 4.2 lists the cause of aggression between females according to when they were recorded; during estrus or anestrus. This table also breaks down the estrous females aggression into directed and received aggression. The cause of the aggression was not apparent in a number of cases. For the females, the only two causes that could be determined were almost equally observed. Aggression caused by having a keeper present (without the presence of food) occurred in five incidents. The other apparent cause was a conflict brought on by the process of nest building. The females were often observed in nest building behavior. A conflict would arise because there was always a very limited amount of nesting material available to the bonobos. Consequently, a struggle for control of the material would sometimes ensue. On six occasions, this led to aggression between the females. In the remainder of incidents (eight cases) the cause of the aggression was undetermined (Table 4.2).

Aggression as a result of the keeper being present was only observed when the subjects were in estrus, and this was the cause for almost half of the aggression between estrous females (five cases). Anestrous subjects were never observed in an aggressive encounter when a keeper was present. An equal amount of aggression was observed between estrous females when the cause was unapparent. Only two cases of aggression were observed as a

result of nestbuilding conflicts between females when the subject was in estrus. Anestrous subjects were never observed in an aggressive encounter when a keeper was present. The causes of anestrous aggression were almost equally divided between nestbuilding conflict and the category of unknown causes

Table 4.2. Aggressive Encounters Between Estrous, and Anestrous Females.

| Cause | Estrus Females | | Anestrous Females |
	Receive	Direct	
Unknown	2	3	3
Keeper	5	0	0
Nestbuild	2	0	4
Total	9	3	7

Aggression with Other Age/Sex Classes - Estrus Vs. Anestrus

The greatest amount of aggression involving the subjects was observed with juveniles. Females directed the most aggression towards juveniles of any age/sex class. There was not a large difference between estrous and anestrous females in these encounters. Estrous females directed aggression at juveniles 1.6 times per ten hours, and 1.7 times when anestrous. Aggression received from juveniles was comparable to the other age/sex classes, which was relatively low.

There were no other distinct differences between estrous and anestrous aggressive interactions with other age/sex classes.

Summary

This chapter has examined the agonistic encounters of the subjects to

determine if estrous state has any effect on the frequency , level, and cause of agonistic behaviors of females. The results suggest that there are differences in agonistic behavior associated with estrous state both among females and between other age/sex classes. Overall, aggression was observed slightly more often when the females were estrus than when they were anestrus. In both states, they directed more aggression than they received.

Aggression between females increased when the subjects were in estrus. Female-female aggression was examined to determine if the level as well as the frequency of aggression was affected by the females' sexual state. Level, or severity of aggression increased when they were in estrus. The cause of aggression was examined and compared between the two states, but the cause of most of the encounters could not be determined. Only two cause were identified, these were conflicts over nestbuilding materials, and aggression as a result of the keeper being present. One difference was observed between estrous and anestrous females. Aggression when the keeper was present was only observed when the female was in estrus.

Aggression with other age/sex classes was also examined to determine if there were differences for estrous females and anestrous females. No major differences were found.

CHAPTER 5 - GENITO-GENITAL RUBBING

Introduction

Genito-genital (GG) rubbing is performed by adult or adolescent females. The behavior involves two females embracing ventro-ventrally while making rapid lateral pelvic thrusts. GG rubbing has been interpreted as a type of tension regulator (Kano, 1980; Kuroda, 1980), and possibly as a mechanism for proximity maintenance (Furuichi, 1989). In situations of strong social stimulation such as encountering a new food patch, or competition over mates, GG rubbing apparently functions to resolve tension between females (Kano, 1980; Kuroda, 1980). Also, recently, Furuichi suggested that GG rubbing helped to maintain proximity between females (1989). This behavior, whether it helps to relieve tensions, or maintain proximity is a unique behavior to the bonobos. There is no similar mechanism practiced by female chimpanzees.

The purpose of examining GG rubbing is to determine if sexual state has any effect on this affiliative social behavior. GG rubbing has been used as an illustration of the sociable nature of female bonobos, therefore any effect that sexual state has on GG rubbing is key to the question posed in the study. A number of aspects will be examined here to see what effect sexual state does have on GG rubbing. The following questions will be addressed:

1) What effect does sexual state of females have on the frequency of GG rubbing ?

2) Does the context of GG rubbing alter with sexual state ?

3) Who initiates GG rubbing more often, estrous or anestrous females ?

4) What function does GG rubbing play in female interactions ?

In this study , one or more occurrences of GG rubbing were scored as

one session if they followed each other within one minute and no other behavior was scored in between. This procedure is to ensure that one GG rub which is interrupted is not scored as two incidents. This method follows that of Furuichi (1989). Often, one of the juveniles would interrupt the GG rubbing by attempting to sit on one of the female's ventrum, or would place a hand or foot between the genitals of the participating females. This occurred in seven samples. None of the sessions were halted by this interference, the females continued GG rubbing without taking notice of the juvenile.

An exception is made in this section by including the noncycling female (Lisa) in the analysis. Because the majority of GG rubbing was observed between Louise and Lisa, the data must include her. All of these GG rubs were recorded when sampling Louise. Although she is discussed in this section, she is separated from the rest of the females by the fact that she was not cycling. For this reason she is not considered estrous or anestrous, and is simply referred to as a non-cycling female.

Frequency of GG rubbing - Estrus Vs. Anestrus

During the focal sessions of the three females included in the analysis, 28 GG rubbing sessions were observed. Of these, five sessions were scored as including more than one GG rub. Of the total 28 sessions, 19 were observed during the focal animals' period of estrus, and nine were during their period of anestrus. Thus, GG rubbing occurred at a mean rate of 0.8 times per ten hours of observation for anestrous females, and 2.7 times per ten hours of observation for estrous females. Thus, GG rubbing occurred three times more often for estrous females than anestrous females.

The number of GG rubbings was also very different for the two sets of

females. Loretta and Lana were observed GG rubbing in only seven of the 28 samples. The remainder of the GG rubbing was performed by Louise and Lisa.

Context of GG rubbing - Estrus Vs. Anestrus

The context associated with each GG rubbing session was noted when it was apparent. However, for the most part, it was not apparent to the observer what the context of the GG rubbing session was. Table 5.1 identifies the four contexts that were scored, as well as a breakdown of the observed GG rubs according to the estrous state of the subject female. Agonism between the participating females was the most often identified context (five of 28). Previous instances of GG rubbing which were not scored as one session were also identified as a context in four instances. Food excitement appeared to be the cause of a GG rubbing session in three instances (see Table 5.1).

Although the frequencies of GG rubbing associated with each context are low, it is interesting to note that the four cases identified as following a

Table 5.1 Context of GG Rubbing Sessions

Context	Estrus Frequency	Anestrus Frequency	Total Frequency
Not apparent to observer	9	7	16
Agonistic encounter	3	2	5
Previous GG rubbing	4	0	4
Food excitement	3	0	3
Total	19	9	28

previous GG rubbing session all occurred when the focal subject was in estrus. Also, it was only during estrus that GG rubbing resulted from food excitement. The only context identified with a GG rubbing female showing less than full sexual swelling was an agonistic encounter (two instances). For the remaining sessions during anestrus, it was not apparent what brought on the GG rubbing (nine cases).

Solicitation of Genital Contact - Estrus Vs. Anestrus

Solicitation for genital contact with another female generally involved the female approaching and presenting her genitals ventrally. Often, this was accompanied by an arm placed on the other female's shoulder or arm. One female (Lisa) was also often observed attempting to ventrally mount the other female without a present. These mount attempts resulted in GG rubbing in 5 out of 21 attempts. The remaining 16 instances did not result in any type of genital contact, instead the female receiving the mount attempt (Louise) completely ignored the soliciting female.

Of the 28 GG rubbing sessions, the solicitor could not be identified in one instance. Table 5.2 is a breakdown of the solicitors and solicitees of the observed GG rubs. Both solicitors and solicitees are divided into estrous and anestrous conditions for further comparison. The one case where the solicitor could not be identified is not included in this table. In 10 of the 27 identified cases, the solicitor was in estrus herself, and in three cases the solicitor was anestrus. The remaining GG rubbings (14) involved the non-cycling female (LS). Although it is impossible to determine if she was cycling irregularly, or not cycling at all, a number of remarks can be made about her participation in GG

rubbing. She was never approached by the other female (Louise) for GG rubbing, she was always the solicitor. Also interesting, is the fact that she approached Louise only half as much when Louise was anestrus, than when she was in estrus. The other females showed the same trend. Solicitors, whether they were in estrus, or anestrus approached and solicited genital contact from estrous females twice as much as anestrous females.

Thus, the most common combination of GG rubs was an estrous female

Table 5.2 Solicitors and Solicitees of GG rubbing Sessions

	Solicitee		
Solicitor	Estrus	Anestrus	Total
Estrus	8	2	10
Anestrus	0	3	3
Non-cycling Female	10	4	14
Total	18	9	27

soliciting genital contact from another estrous female (eight cases). Females were solicited for genital contact from anestrous females and estrous females for approximately the same amount of cases (three and two, respectfully). The only combination not observed was an anestrous female soliciting an estrous female (not including the non-cycling female).

Proximity Preceding and Following GG rubbing - Estrus Vs. Anestrus

Overall Proximity Results

Before and after each session of GG rubbing, the distance between the

participants was recorded. Subjects were either described as within one metre, or outside one metre proximity. In 57.14% of all GG rubbings (16 of 28), females that were within one metre proximity remained so after the GG rubbing session . Another 17.86%(five of 28) that were not within one metre proximity before the GG rubbing remained within one metre after the GG rubbing. An equal amount of females maintained their distance. Of all sessions, five females (17.86%) who were out of one metre proximity moved out of one metre proximity to the GG rubbing individual after the session . The situation observed the least involved a female who was in proximity before the GG rubbing but moved away after; 7.14% or two of 28 sessions.

Proximity - Estrus Vs. Anestrus

There was no difference in the maintenance of proximity between estrous and anestrous females. Out of the 10 GG rubbings initiated by an estrous female, three moved away from the other female after the GG rubbing. In the other seven cases the female was observed within one metre proximity before and after GG rubbing. Similarly, a third of anestrous females moved away from the GG rubbing partner after the GG rubbing session.

<u>Function of GG rubbing</u>

As discussed in the introduction of this chapter, GG rubbing has been interpreted as serving one or two functions for females. This section attempts to determine if this was the case for this study. The two functions suggested in the literature are tension regulation, and maintenance of proximity. Both are supported by the results of this study.

GG rubbing did appear to reduce tension in this study. Of the five GG

rubbings in which agonism was the identified context, all five encounters were terminated with the GG rub. There were no cases that involved a GG rub followed by an agonistic encounter between the two females. Also, in three of the observed sessions where a context was not identified, one of the participating females appeared to be acting somewhat nervous. Nervousness was noted by the females pacing, and constant glancing around. Also, in one situation the female was observed to play with her nipples (recognized by the keepers as a type of nervous behavior). In each of these situations, the nervous female was solicited by the other female for GG rubbing. Similarly, on the three occasions when GG rubs resulted from food excitement, the females remained in proximity after the GG rub. All three of these situations in which a GG rub occurred; after an aggressive encounter, presence of a nervous female, and food excitement, are times of high social stimulation. The GG rubbing apparently served to reduce the tension.

The second identified function of GG rubbing is to help maintain proximity between females. This also was supported by the data. In the majority of cases, after a GG rub, females either maintained proximity (16 of 28), or increased proximity (5 of 28). The cases that showed either increase or maintenance of proximity form the majority of cases observed, 75% (21 of 28). Thus it appears that GG rubbing served as a mechanism to maintain or increase proximity between females.

Summary

GG rubbing was examined in this chapter to determine if and how it is affected by the sexual state of females. Sexual State does appear to have a large effect on GG rubbing. GG rubbing was observed three times more often

for estrous females than anestrous females. Food excitement or a previous GG rub were scored as the context only when females were in estrus. An almost equal amount of GG rubs were scored after an agonistic encounter, or when the context could not be identified.

Solicitation of GG rubbings was also examined to determine if either estrous or anestrous females initiated GG rubbings more often. The results indicate that estrous females did initiate GG rubs more often than anestrous females. The results of this study support the idea that GG rubbing serves two functions, that of tension regulation, and as a mechanism to maintain proximity among females.

The last three chapters have presented the results of the study in an attempt to answer the question posed; does estrus have an effect on female-female interactions. In each of the sections, there were definite differences in the females behavior towards the group as a whole, and specifically to other females as a result of their sexual state. The last chapter will discuss these results in relation to the current literature on bonobo female relationships.

CHAPTER 6 - DISCUSSION

Estrus and Female Behavior

Strong affiliative female-female bonds exist among bonobos. The results of this study suggest that during their period of estrus, these affiliative tendencies increase for both the estrous female, and the other adult females interacting with her. It is generally accepted that female chimpanzees alter their behavior when in estrus (Nishida, 1979; Wrangham, 1979; Goodall, 1986), but female bonobos do not seem to be as affected (Furuichi, 1987, 1989). In two different studies, Furuichi found that females stayed in mixed parties irrespective of their sexual state. Specifically, he found that "even completely nonreceptive females, in late pregnancy or postpartum amenorrhea, showed an attendance ratio as high as that of cycling females" (Furuichi, 1989: 194). The current study provides evidence suggesting that female bonobos do exhibit differences between estrus and anestrus behaviors. Specifically, the number and quality of interactions with other group members changes. In chimpanzees, the females use their period of estrous as a type of passport to move from one group of males to another. This study suggests that during estrus, bonobo females reaffirm their relationships with the other females of the group by spending more time in proximity with other adult females as well as more time spent in affiliative behaviors with them.

Summary of Results

In order to determine if females' sexual state affects their behavior, three broad categories were examined; affiliative social interactions, agonistic interactions, and GG rubbing. In all three of these behaviors, there were obvious differences between estrous and anestrous behavior of the females

observed.

Affiliative interactions did not increase between all age/sex classes. Instead, there was a noticeable increase in female-female interactions, while the other age/sex classes decreased their interactions during estrus. This result is very interesting because female bonobos appear to associate more with only other adult females. This is different from chimpanzee females who have been observed to associate more with both males and females when in estrus. There was an increase in both directed and received behaviors. The largest increase in affiliative behavior was in the category of grooming. This is interesting as other studies have suggested that female-female grooming is not as commonly observed as once thought (Furuichi, 1989). The other behaviors examined also increased during estrus. Sitting in proximity, sitting in contact, and play behavior were all observed more often when females were in estrus. An important distinction is made here between female-female affiliative behavior, and affiliative behavior with other age/sex classes. While the affiliative interactions with other females increased during estrus, affiliative interactions with other age/sex classes deceased for the most part. Grooming decreased with all age/sex classes except females.

It is also interesting to note here that grooms were directed at a much higher rate toward estrous females than anestrous females. Grooms received from other females did increase during estrus, but the difference is not as large as the grooms directed by estrous females. These averages reflect an increase even with the opposite behavior of one female (Loretta). Loretta was observed to increase her grooming time with the adult male rather than decrease it like the other two females. She also differed in that she did not increase the amount of time spent grooming with another female. This did not alter the average

because the decrease was very small.

Sitting in proximity to another female did increase for all three females. And similar to the results of grooming interactions, sitting in proximity to other age/sex classes decreased. Thus, while females sat in proximity to other females more when in estrus, they sat in proximity less with other age/sex classes. Once again however, Loretta was an exception to this trend. She did sit in proximity to other females more in estrus, but she also was observed sitting near the adult male more often when in estrus.

While she was observed to groom with, and sit near the adult male more often, Loretta did not sit in contact with the adult male more often in estrus. All three females were observed to sit in contact with females more often when in estrus. Contact was decreased with other age sex classes for all three females, except Lana who spent more time in contact with her own offspring during estrus. These results are similar to the grooming results in that the affiliative behavior increased with other adult females, but decreased almost without exception with adult males, juveniles, and offspring.

Results of play behavior between estrous females and other age/sex classes are extremely varied. Although the average play behavior increased for estrous females, this is based on only two females play observations. One subject was never observed to play with the other female. Also, the amount of playing observed by females was very small, 2.70% of all observations.

By examining all of these behaviors it is not apparent to whom the increase can be attributed; the estrous female or the other interacting female. Both directed and received grooms increased, therefore it seems that the estrous female was responsible for some of these interactions. However, because she both groomed and was groomed more in estrus it seems that the

increase in interactions is due to both of the females. The picture does not become much clearer when initiators of interactions are considered. In most cases, the estrous female increased the amount of interactions with the other female by initiating or soliciting affiliative behaviors, but this was also true in the reverse. Estrous females also received more solicitations and initiations from other females.

Three types of data were analyzed to determine which female was responsible for the increased interactions: approaches, peering, and sexual presents. Sexual presents or solicitation for GG rubbing will be discussed with GG rubbing. Approaches were directed and received more by a female in estrus than when she was anestrus.

Unlike approaches, peering was observed less with both the combined age/sex classes, as well as with the females only . Thus, a clear picture of who was responsible for the increased affiliative social interactions between the females can not be determined. The increase appears to be a result of both the estrous female and the other adult female. A combination of both directed and received attention from other females resulted in the increased affiliative interactions between the females when in estrus.

Not only did the females spend more time together when in estrus (as indicated by the increased amounts of sitting in proximity, and sitting in contact), but they also spent qualitatively different amounts of time together. It appears that their interactions became more frequent, and perhaps even more intense.

Although it seems almost contradictory in nature, the results indicate that both the affiliative, and agonistic behaviors increased between females who were in estrus. Agonistic interactions differed by sexual state dramatically only between juveniles and females. Juveniles received a larger amount of

aggression from adult females when the females were in estrus. The same is true for aggressive encounters between females. Estrous females were involved in almost three times as many aggressive encounters than anestrous females. Another interesting finding here was that the level of aggression also increased for estrous females. In the anestrous state females were observed in mostly low and medium level aggressive encounters. Estrous females on the other hand, were involved in more high level aggressive incidents (hitting and biting).

Although the frequency of identified causes of aggression were low, estrous females were involved in aggressive encounters in more situations than anestrous females. Only estrous females were involved in aggressive encounters when the cause was the presence of a keeper. Thus, females were observed in more aggressive encounters which were higher in intensity and brought on by different situations.

Agonistic interactions did appear to be initiated by the other females more often than by the estrous female. This is indicated by the large amounts of aggression received by estrous females compared to that directed by them to other females. Unlike the category of affiliative social behaviors where the increase could not be attributed to one or the other females, aggression appeared to be initiated by anestrous females more than by estrous females. This result lends itself well to a framework of competition between females (discussed below).

As mentioned above, all affiliative behaviors increased. GG rubbing, which is also considered to be a highly affiliative behavior as well as a type of tension regulator was examined separately from the other affiliative social behaviors . This also increased during estrus. Estrous subjects were involved

in GG rubbing three times as much as anestrous subjects.

Similar to the results of agonistic encounters, GG rubbing was observed in more situations when the subject was in estrus than when the subject was anestrus. GG rubbing was only observed in contexts of food excitement, and following a previous GG rub when the subject was in estrus. So, like agonistic encounters, GG rubbing was observed more often and in more situations when the subject was in estrus.

Solicitation of GG rubbing was observed the most by estrous females, and towards estrous females. Of all possible solicitors and solicitees, the most commonly observed situation was an estrous female soliciting another estrous female for genital contact. The noncycling females' participation in GG rubbing also compliments this trend. Lisa (the noncycling female) solicited genital contact from the other female (Louise) twice as often when Louise was in estrus. Thus, it appeared that estrous state had a very dramatic effect upon GG rubbing.

The occurance of GG rubbing was very much biased by individual participation. Louise and Lana were observed GG rubbing in the majority of cases. In fact, Loretta and Lana were only observed to GG rub in seven of 28 cases. One explanation for this result may be due to kinship effects. Sexual behavior between opposite sex individuals is often avoided. It may also be true that sexual behavior is avoided among same sex individuals who are closely related. This could explain the few GG rubbings observed between Loretta and Lana who are full siblings. The other two females, Louise and Lisa, were not related and were observed to GG rub more often. Thus, avoidence of closely related partners in sexual relations may also be involved in GG rubbing. While this concept is offered as a possible explanation, unfortunately, these effects

could not be examined in this study.

This can be interpreted on two levels. First, because it is understood to be an affiliative behavior between females, it seems to follow the general trend of increasing frequency during estrus. Second, as a type of tension regulator it was a necessary increase as the levels of aggression also increased for females who were in estrus. Tension regulation was one of the functions of GG rubbing that was examined in the study. The results showed that GG rubbing did serve as a type of tension regulator. Another function of GG rubbing was also suggested. Furuichi suggested that GG rubbing serves as a mechanism that helps to maintain proximity between females (Furuichi, 1989). This did appear to be the case in this study. After the majority of GG rubbing, proximity either remained the same, or increased. This was the case in 75 % of all GG rubs.

Although GG rubbing did appear to serve these two functions in a number of situations, they do not completely explain the occurance of all GG rubbing. On a number of occasions there was no apparent cause for GG rubbing, and neither tension regulation nor a maintenance of proximity could explain its occurance. One possibility for these GG rubbings may simply be proximate satisfaction. Bononos are highly sexual animals. Genital contact between females may serve as a form of sexual gratification. Unfortunately, this study could not asses this hypothesis, and so it is only mentioned as a possibility. Further research examining this possibility would be very interesting.

As a concluding remark to this summary of the results, it must be emphasized that these results are based on limited observations. The results do suggest some very interesting patterns. However, the methodological

limitations of this study group which are abundant: captive animals, small sample sizes, unnatural social structure, and limited time span. Thus, the study itself should be explored further if possible on wild bonobos. Although the patterns are confined within a limited study, there are very interesting trends which lend themselves well to a discussion of female bonds among bonobos, chimpanzees, and hominid social evolution. The following discussion is an elaboration of these topics.

Competition and Cooperation among Female Bonobos and Chimpanzees

Competition between bonobos does not appear to exert as much pressure as it does on chimpanzees. One interpretation of this lower pressure has been offered by some researchers (White, 1989; White and Wrangham, 1988; Wrangham, 1977). They suggest that one result of the high feeding competition among chimpanzee females is their unique social structure. Female chimpanzees spend more time alone, foraging with their dependent offspring in their core feeding areas and generally only join larger parties when in estrus. Wrangham suggests that this is due to the small food patches that are available to chimpanzees. Patch utilization studies by White (1988, 1989) and White and Wrangham (1988) found that the bonobo food patches did appear to be larger than the chimpanzees'. It follows from this data that competition for resources is not as high among female bonobos. While this does appear to be the case, larger patches do not result in a total absence of competition.

A number of factors indicate that competition among female bonobos does indeed exist. Agonistic encounters were noted to be the most severe (although they were not the most frequent) among females than among any

other type of dyad at Wamba (Furuichi, 1989). In the current study, where competition for resources should be relatively low due to the constant provisioning, agonistic interactions among females were the most frequently observed, as well as the most severe in nature of any possible dyad. Male-female agonism occurred almost half as much as female-female agonistic encounters (male-female, 11; female-female, 21). The severity of male-female aggression never reached a high level. All incidents between males and females were scored as either low, or medium level aggression. Also notable was the fact that aggression increased among females when one or both females were in estrus. Specifically, estrous females received three times as much aggression as they directed aggression towards other females. This indicates that it may be competition that brings on aggression among estrous females.

This result may not be as pronounced in a free-ranging group of . bonobos, since estrous females are always present in a mixed party. Thus, competition for estrous females would be lower in wild bonobos, than in this captive group where the cycling female displaying full sexual swelling was not as common as in the free ranging population. This may be the reason why aggression between females was so high in this study. With only one adult male and two adult females in each display group, the structure of the bonobo group at the Wild Animal Park did not approximate the composition of a free ranging group of bonobos in the wild. It follows that the agonistic interactions between the subject females would be higher in frequency and severity than in a free ranging group with more individuals and a larger range area.

Thus, while competition among bonobo females is much lower than that observed among female chimpanzees, some degree of competition does exist.

Differing levels of competition combined with a longer period of estrus for the bonobo results in opposing strategies for chimpanzee and bonobo females. Because competition between bonobo females is low to begin with, due possibly to larger food patches, they can afford to associate with other females more intensively and more often. Competition between males for mates is also lower than in chimpanzees due to the females' prolonged period of estrus. The combination of low female-female competition and low male-male competition results in a very different social strategy for female bonobos as compared to female chimpanzees. Instead of avoiding other females (as is the case for chimpanzees), female bonobos appear to strengthen their relationships by spending more time with other females. The most competitive time between females is when either the resources were low, or when they themselves were the objects of competition by the males. This appeared to be the case in this study as agonistic interactions between females increased when females were in estrus. However, becoming more affiliative towards other females, the estrous female can maintain her proximity to these females and therefore, her proximity to the resources. When there are estrous females present, there are usually males present as well. Thus by increasing affiliative behaviors towards other females, estrous females maintain proximity with both males and females. This essentially results in greater cohesion among all group members, male and female.

By examining the relationships among females a great deal of understanding is reached regarding group cohesion, and interindividual relationships as well as the resulting social structure. Other researchers have begun to take notice of the importance of the females' position in groups of bonobos, and the resulting group cohesion. For example, a study by Furuichi

(1989) in which the social life history of females was explored uncovered the important role that females play in bonobo society. Furuichi noted that females, and especially the old adult females, were considered the foci of social associations. He suggests that the close associations of female bonobos with their high dominant status (among females and males) allows them to form a close association in the center of the party. In this manner, unrelated females form the cohesive center of the group. For this and other reasons, bonobos seem to provide a viable model for hominid social evolution.

Female-Female Bonds in the Evolution of Hominid Society

The effects of estrus have often been discussed in terms of male-female bonds. In chimpanzees, the foremost effect of sexual state has been discussed in terms of the female's ability to move among the males (Goodall, 1986; Nishida, 1979). Only as a consequence of these male-female interactions, does the female-female bond result. At least this is how it is generally discussed. Similarly, in bonobos, up until recently, female-female bonds were not discussed as the primary bonds. Instead comparisons have been made between male-female relationships (Blount, 1990; Kano, 1980; Savage-Rumbaugh and Wilkerson, 1978; de Waal, 1987), and male-male relationships (Nishida and Hiraiwa-Hasegawa, 1987) in chimpanzees and bonobos.

This study suggests that in bonobos, estrous state of the female influences her bonds with other females as well as with males. This is particularly relevant to early models of human evolution as the bonobo appears to be the best model for hominid social evolution (Furuichi, 1989; Kano, 1986). The nonfemale bonded society of bonobos appears to be held together in a cohesive fashion by strong nonkin related bonds of the females. This is unique

among the pongidae. A patrilineal, multimale-multifemale group, which is also very cohesive, approaches the model of the basic society from which early hominid society may have evolved.

Because bonobo, and possibly early hominid societies, are nonfemale bonded, and kinship does not necessarily hold females together, the bonds among females are very important and deserve further attention. Factors that affect the bonds among females are therefore of primary importance. This study has suggested that the estrous state of the female influences the formation and maintenance of bonds among females. Not only do these results, and those of others (Furuichi, 1987, 1989) explain a great deal in the understanding of social interactions and social structure among bonobos, but it also has applications to the understanding of female sexuality in social life in general.

Directions for Future Study

As mentioned previously, this study was very limited in a number of areas. The size of the study group was very small, three individuals. Also the group composition did not allow for interactions between more than two adult females at one time. An ideal study would also encompass more than one menstrual cycle for each female, as well as record the interactions among many females. Thus, there are countless options for future studies on this important topic.

A long term study of wild bonobos would be the ideal situation for this type of study. A large number of identified females could be monitored over several cycles. From results of this type, factors such as individual attributes, age, and rank could also be included in the analysis. The possibilities for studies of this type are endless. Although a study of wild bonobos is ideal, this

area would also benefit from more captive studies dealing with female relationships and estrous state.

In this study it has been suggested that the two factors of estrous state, and female-female sociability are intricately woven into bonobo society, and social structure. The results not only apply to bonobos and chimpanzees, but it has also been suggested that understanding female-female relationships can shed some light in our understanding of bonds between females in early hominid society.

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