Affiliative interactions between adult male and immature savanna chimpanzees (Pan troglodytes verus)

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Affiliative interactions between adult male and immature savanna chimpanzees
(Pan troglodytes verus)

by

Margaret Ellen Robinson

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

MASTER OF ARTS

Major: Anthropology

Program of Study Committee:
Jill D. Pruetz, Major Professor
Ann L. Jones
W. Sue Fairbanks

Iowa State University
Ames, Iowa
2007

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To my parents-for always encouraging me to chase my dreams even if it meant going to Africa to catch them.
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Abstract

Social interactions between adult male and immature chimpanzees (*Pan troglodytes*) have been understudied compared to those between mothers and their offspring. This study’s aim was to gain a better understanding of such relationships among a population of wild West African chimpanzees (*P. t. verus*). Although overall rates of affiliation between adult males and immatures were low, low-ranking males engaged in such interactions significantly more than higher ranking males. Additionally, males tended to favor the offspring of certain females, although this difference was not statistically significant. It has been suggested that male care in many primate species may serve as a mating strategy. Unlike higher ranking males who engage in displays, low-ranking males may increase their ‘attractiveness’ to females by demonstrating their abilities as care-givers. This hypothesis may explain the findings of the current study; low-ranking chimpanzee males may direct affiliative behavior towards infants and juveniles to gain reproductive benefits.
Chapter One: Introduction

1.1 Background and Significance

Social interactions between adult male and immature chimpanzees (*Pan troglodytes*) have been understudied compared to those between mothers and their offspring (Bloomsmith et al., 2003; Nishida & Turner, 1996; van de Rijt-Plooij & Plooij, 1987; Goodall, 1986; Pusey, 1983). Although there has been some attention given to these relationships (e.g., Goodall, 1986; Nishida, 1983a), few studies have focused exclusively on male-immature interactions (Pruetz & Bloomsmith, 1995). This study aims to gain a better understanding of such relationships within a population of wild West African chimpanzees (*P. t. verus*) living in a savanna environment. The Fongoli community, the study group, is the first group of savanna chimpanzees that has been habituated to human presence to the extent that detailed behavioral data can be collected (J. Pruetz, personal communication).

Although chimpanzees are well-studied in the wild, to date there has been little research conducted on chimpanzees living in a savanna habitat. Several long-term studies (e.g. Tanzania: Goodall’s research at Gombe National Park, Nishida’s research at Mahale Mountain’s National Park; Uganda: Wrangham’s research at Kanyawara, Kibale National Park, Mitani & Watts’ research at Ngogo, Kibale National Park, Reynolds’ research at Budongo Forest Reserve) have considered the behavior and ecology of the subspecies, *P. t. schweinfurthii*. This subspecies lives in mostly wooded or forested habitats (Goodall, 1986). Two long term studies have also considered the behavior of the Western chimpanzee subspecies, *P. t. verus*, living in a forested environment (Sugiyama, 2004; Boesch & Boesch-Achermann, 2000). However, savanna chimpanzees living in Senegal inhabit an extremely hot, dry, and open habitat (McGrew et al., 1981). Furthermore, the Western subspecies is
characterized as bisexually bonded, while other subspecies are considered to be male-bonded (Lehmann & Boesch, 2005). Therefore social relationships between Fongoli chimpanzee community members may differ from those of other subspecies as well. Specifically, males may spend more time in parties with immatures and, as a result, interact with them more frequently.

Given that the social relationships of Western chimpanzees may differ from those of other subspecies and because so little research has considered the social relationships of savanna chimpanzees, this study aims to explore the social relationships between adult male savanna chimpanzees and other members of their community. Moreover, the relationships of adult male and immature chimpanzees have been understudied among all chimpanzee subspecies. As a result, this study will specifically consider how adult males interact with immatures in their community, as well as provide insight about the daily activities of adult males in a savanna habitat.

1.2 Chimpanzee Communities

The basic social structure of chimpanzees is rare among non-human primates. Chimpanzees live in communities, or units groups, which may contain anywhere from fewer than 25 individuals to greater than 140 individuals (as reviewed in Stumpf, 2007; Boesch & Boesch-Achermann, 2000; Tutin et al., 1983). Within these communities, smaller groups or ‘parties’ are formed (Nishida, 1968). Although this fission-fusion community structure is thought to limit competition for resources, party size has been shown to increase as community size decreases (Lehmann & Boesch, 2004). Among unhabituated savanna chimpanzees at Assirik, Senegal, the patterns of party formation appear to differ from those of other chimpanzee communities (Tutin et al., 1983). Among this community, large parties
with adult males were observed more frequently than parties without adult males or solitary individuals (Tutin et al., 1983). Additionally, large parties were formed more frequently to move large distances (Tutin et al., 1983). This was probably a result of several factors, including the limitation of water and food and the threat of predation (Tutin et al., 1983).

The dispersal pattern of chimpanzees is also relatively rare among Catarrhine primates in that males typically remain in their natal communities, while females tend to leave their natal groups and move to other communities (Goodall, 1986; Pusey, 1979). Thus, males are thought to be more closely related to each other than are females (Morin et al., 1994; Goodall, 1986); this hypothesis has been supported by DNA analysis of 15 chimpanzee communities (Goldberg & Wrangham, 1997). Therefore, within the fission-fusion communities of chimpanzees, relationships between group members can be explained, in part, by Hamilton’s (1964) theory of kin selection (Morin et al., 1994; Goodall, 1986).

**1.3 Kin Selection Theory**

Among many animal species, behaviors have been observed that appear to benefit recipients of the behavior but not the actor. In other words, animals have been observed to engage in what appear to be selfless acts that benefit others and may actually be detrimental of the actor. Researchers have long attempted to explain these seemingly altruistic behaviors among animals because such behaviors are often difficult to remedy within the tenets of natural selection.

Kin selection theory has been proposed to explain this seemingly altruistic behavior. This theoretical approach suggests that an individual organism works to maximize its inclusive fitness, or its individual reproductive fitness coupled with the reproductive fitness of its kin (Hamilton, 1964). Put another way, an animal will increase its reproductive success
not only by promoting its own genes directly through reproduction but also by behaving altruistically toward kin and enhancing their reproductive success (Hamilton, 1964).

Kin selection theory has been used to explain relationships among group members in chimpanzee communities (Morin et al., 1984; Goodall, 1986). Because males remain in their natal groups, they are assumed to be more closely related to one another than they are to females (Goldberg & Wrangham, 1997; Goodall, 1986). As a result, males are expected to have more affiliative relationships with other males than with females (Morin et al., 1994; Goodall, 1986). Kin selection theory can also be used to frame male behavior toward immatures. The more certain a male is that he has fathered a particular immature, the more likely he is to invest in that offspring (Higley & Suomi, 1986; Kleiman & Malcolm, 1981; Bales, 1980). However, Goldberg and Wrangham (1997) have found that chimpanzee males are more likely to form alliances with members of their peer group than with maternal kin. Thus, it appears that kin selection theory cannot explain all altruistic relationships among chimpanzees.

1.4 Male-Immature Interactions among Chimpanzees

The nature of the social interactions between immatures and adult males is an area that has not been studied frequently in wild chimpanzee populations of all subspecies. Although some researchers have provided information on these relationships (i.e. Goodall, 1986; Nishida, 1983a), few studies have focused exclusively on male-immature interactions. In order to understand the selection pressures placed on male chimpanzees and how they affect their interactions with immatures, it is necessary to discuss the differences in male and female investment in offspring as they are generally understood.
Parental investment is considered to be any investment in offspring that will improve the likelihood of their survival at the expense of the parent’s ability to invest in other offspring (Trivers, 1972). Paternal investment, then, includes not only the investment of sperm but also parental behaviors (Trivers, 1972). These behaviors may include direct and indirect forms of parental care. In other words, parenting includes not only carrying and provisioning young but also protection from predators, protection from infanticide, and defense of a territory (Trivers, 1972). Trivers (1972) suggests that the level of parental investment can be measured by how much the investment interferes with the parent’s ability to invest in other offspring. Using this definition, a mother chimpanzee with an average interbirth interval of 66 months (Goodall, 1986), would be considered to invest heavily in the development of her offspring.

In mammals, Trivers (1972) suggests that the sex that invests less in its offspring will be the sex that must compete for access to mates. Because males typically invest less in their offspring than females at the time of fertilization (e.g. sperm are smaller than eggs), they are generally the sex that must compete for access to mates (Trivers, 1972). Females, on the other hand, are not expected to compete for access to mates and tend to be more selective when choosing mating partners (Trivers, 1972). In mammals, females continue to carry higher costs after fertilization because they must carry and give birth to their young as well as produce milk to feed them. If a female were to terminate her investment in her offspring at any point after giving birth (since she must carry the fetus after fertilization), she would have wasted a great deal of energy carrying and giving birth to her offspring (Trivers, 1972). Males, however, can leave a fertilized zygote and lose very little since they have only invested the amount of energy required to produce sperm (Trivers, 1972). Thus, while both
sexes can terminate their investment in offspring at any time following birth, females will lose more by doing so. Females, then, are more obligated to continually invest in their offspring than are males (Trivers, 1972). Additionally, males are likely to lose mating opportunities if they invest heavily in their offspring (Trivers, 1972).

Males are thought to maximize their reproductive success by mating with many females (Trivers, 1972). Therefore, males typically have higher reproductive success by mating with multiple females than by mating with one female and investing heavily in the offspring that is/are produced (Trivers, 1972). Following Trivers’ hypotheses, male chimpanzees have been found to invest less in the development of their offspring than females (Goodall, 1986). Additionally, as discussed above, chimpanzees live in multi-male, multi-female groups and males mate with multiple females (Goodall, 1986; Tutin, 1979). To some extent, then, chimpanzees follow the principles proposed by Trivers.

Although Trivers’ predictions regarding differential reproductive strategies between the sexes are one of the main paradigms under which behavioral ecology operates (Tang-Martinez, 2000), there have been critiques of the approach in recent years (Tang-Martinez, 2000; Hrdy, 1986; Dewsbury, 1982; Dawkins & Carlisle, 1976). Dewsbury (1982) notes that although sperm are smaller than eggs, males must produce many more gametes than females. In other words, males must produce millions of sperm to fertilize one egg. Therefore, it is not accurate to compare the size of gametes. Additionally, Dawkins and Carlisle (1976) have noted that parents should invest in their offspring based on future costs, not those costs they have already lost. In other words, females and males are both capable of abandoning their offspring at any time even if they have already invested heavily in them because future costs are more important than sunk costs. The idea that females should choose to mate with the
best male available to them is also questioned (Tang-Martinez, 2000). As reviewed in Tang-Martinez (2000), many female primates mate with multiple males and often solicit copulations. Additionally, females may mate with males even when they are not in estrus (Hrdy, 1986). This behavior may have reproductive advantages for the female, including deceiving males into believing they fathered her offspring. This may, in turn, promote paternal investment and protect a female’s offspring from infanticide (Soltis, 2002; Davies & Boersma 1984). These recent findings suggest that Trivers’ (1972) analysis of parental care may be overly simplistic and may overlook critical components of male and female mating strategies.

Criticisms of Trivers’ generalizations are exemplified among chimpanzees, a species in which females employ a number of mating strategies to confuse male paternity. Females mate with multiple males, thus theoretically decreasing a male’s certainty that he fathered her offspring (Goodall, 1986). It has also been suggested that chimpanzee females living in the Tai Forest, Ivory Coast and in Bossou, Guinea may mate with males outside of their group (Gagneux et al., 1999, 1997; Sugiyama et al., 1993) although the same has not been demonstrated among chimpanzees living at Gombe (Vigilant et al., 2001). Because the chimpanzees at Tai Forest and Bossou are both of the Western subspecies, it is possible that chimpanzees living in Senegal will show similar behaviors. Regardless, paternal certainty among chimpanzees is not high because a male cannot be sure whether he, or another male, sired the offspring of the females with whom he has mated.

Female chimpanzees maintain a large sexual swelling for several days after they ovulate and are at their most fertile point (Deschner et al., 2004). Males, then, cannot be certain that they have enhanced their reproductive success through a single mating. Thus,
following Trivers’ (1972) hypotheses, chimpanzee males attempt to mate with as many
estrous females as possible in order to maximize their reproductive success. Because the
alpha male is generally able to mate with females when they are most fertile (Matsumoto-
Oda, 1999; Takasaki, 1985; Nishida, 1983b), it appears paternity may be biased toward the
dominant male.

It has been suggested that male primates will invest in young if doing so will improve
the likelihood that the immature will survive (which, in turn, increases the father’s
reproductive success). In these cases, investment from both parents should increase the
likelihood of offspring survival when compared with uniparental investment (Clutton-Brock,
1991). Such behavior is often thought to be directly related to paternal certainty (Higley &
Suomi, 1986; Kleiman & Malcolm, 1981; Bales, 1980). Male mammals, unlike females, can
never be sure that they sired a particular offspring because their mates may have had multiple
partners. Therefore, the more certain a male is that he fathered an individual, the more likely
he will be to invest in that individual (Higley & Suomi, 1986; Kleiman & Malcolm, 1981;
Bales, 1980).

As discussed above, male chimpanzees cannot be certain of their paternity of
immatures in their community. This is because chimpanzee females commonly mate with
multiple males, maintain a sexual swelling after ovulation, and possibly mate with males
outside of their community (Deschner, et al. 2004; Constable, 2001; Vigilant et al., 2001;
Goodall, 1986). Thus, male chimpanzees should not show preferential treatment to any
immatures in the community. This hypothesis has been supported in a captive study (Pruetz
& Bloomsmith, 1995), although it has not been studied systematically in the wild. However,
in Pruetz and Bloomsmith’s (1995) study, adult males tended to interact more affiliatively
and less agonistically with their own offspring compared to offspring sired by other males, although the difference was not significant. This suggests that the relationship between adult male and immature chimpanzees may be more complex than was once thought.

There is some evidence that high-ranking males may have greater mating access to females when they are most likely to conceive (Matsumoto-Oda, 1999; Takasaki, 1985; Nishida, 1983). Therefore, it is possible that these males enjoy a greater degree of paternal certainty and, as a result, will more readily invest in immatures in their community. Additionally, male chimpanzees are sometimes able to gain exclusive mating access to receptive females through consortships (Tutin, 1979). During these consortships, a male and a receptive female travel away from the community for a period of days. Males that engage in such mating practices may also have a higher degree of paternal certainty than other males and may invest more readily in the offspring of their consortship partners.

Alternative hypotheses have been presented to counter the paternal certainty hypothesis for paternal care among primates. Another explanation for male investment that has been suggested is that male investment may actually be an attempt to improve mating opportunities (van Schaik & Paul, 1996; Smuts & Gubernick, 1992). Van Schaik and Paul (1996) review the relevant literature and suggest that in many non-human primate species, male interaction with immatures increases the likelihood that females will mate with those males. Such behavior has been well documented among several macaque (Macaca) and baboon species (Papio) (as reviewed in Smuts & Gubernick, 1992). Therefore, if there is preferential treatment toward particular immatures in chimpanzee communities, it may be because males are preferentially caring for the offspring of more ‘attractive’ females with whom they are attempting to mate (van Schaik & Paul, 1996).
Immature chimpanzees have been observed to show differences in behavior based on their sex (Pusey, 1990). Males, who will more than likely remain in their natal group and are more gregarious than females, have much to gain by creating and maintaining social relationships within their community. This may explain why they engage in more social behavior, like grooming adult males, than do their female peers (Pusey, 1990). Additionally, immature males can learn more about their future social roles by interacting with adult males. For example, they may engage in boundary patrols and practice display behaviors (Pusey, 1990). Females, on the other hand, can learn behavior relevant to raising offspring by spending more time in close proximity to their mothers (Pusey, 1990). It seems likely, then, that juvenile males will spend more time interacting socially with adult males than will their female peers.

1.5 Hypotheses

The goal of this study is to understand the nature of the relationships between adult male savanna chimpanzees and other group members. Specifically, the social relationships between adult males and immatures will be considered. In order to better understand these relationships, the following hypotheses will be tested (the definitions for infants and juveniles will follow Baldwin, 1979, with slight modification following Pruetz & Bertolani, 2007: juveniles are estimated to be between 5-9 years of age and infants are estimated to be younger than 4 years of age):

**Hypothesis 1:** Adult males will engage in affiliative behaviors with infants and juveniles in their community equally.

**Hypothesis 2:** Dominant males in the community will engage in affiliative behaviors with infants and juveniles more often than subordinate males.
Hypothesis 3: Adult males will engage in affiliative interactions with juvenile and infant males more often than with juvenile and infant females.

Hypothesis 4: Adult males will engage in affiliative interactions with juveniles more often than with infants.

The first two hypotheses are framed using the paternal certainty model of male care. Males are expected to invest more in immatures if they enjoy a higher degree of paternal certainty. Because chimpanzee males are thought to be relatively uncertain of their paternity, they are not expected to preferentially care for or affiliate with any of the young in their community. However, several studies suggest that high-ranking males are able to monopolize copulations with females when they are most fertile (Matsumoto-Oda, 1999; Takasaki, 1985; Nishida, 1983b). As a result, these males may have a higher degree of paternal certainty than lower ranking males. Therefore, it is predicted that high-ranking male chimpanzees will affiliate with immatures more often than low-ranking males.

The third and fourth hypotheses consider male-immature interactions from the perspective of juvenile and infant chimpanzees. Immature male chimpanzees remain in their natal community (Goodall, 1986). Therefore, associating with adult males may help them to gain allies in the future. Additionally, immature male chimpanzees must learn social skills that cannot be observed through association with their mothers (Pusey, 1990). Associating with adult males may provide these young males with opportunities for social learning. As a result, adult male chimpanzees are predicted to associate with male immatures more than with female immatures. Additionally, juveniles begin to spend more time away from their mothers than do infants. Therefore, it is predicted that adult males will have greater opportunity to engage in affiliative interactions with juveniles than with infants.
References


Chapter Two: Paternal Care among Non-human Primates

2.1 Introduction

In all mammal species, immatures are cared for by their mothers. Direct paternal care, on the other hand, is observed in less than 5% of mammal species (Clutton-Brock, 1991). Among primates, however, male care is more frequent, occurring in about 40% of primate genera (Kleiman & Malcolm, 1981). This may be partially due to the fact that males and females in most primate species are permanently associated (Smuts et al., 1987). As a result, males and infants have many opportunities to interact. Because of the association of males and infants in primate groups and the high level of male investment seen among primates, they are an interesting group to study when considering the evolution of male investment in immatures.

In an article about sex-biased parental care, Bercovitch (2002) suggests that a single model will not explain the patterns seen in all primate species because, based on their ecology, primate species have different life history strategies. This means that sex-biased parental care strategies will have different advantages for different species. It is likely the same is true for paternal care; no single model of paternal care will explain paternal behavior (or male-immature interactions) for all primate species. In the past, the paternal certainty model was used by most researchers to explain the male-infant interactions observed among primates (as reviewed in van Schaik & Paul, 1996; Whitten, 1987). This, however, does not seem to fully explain the male-infant interactions observed among non-human primates. Instead, it seems males’ investment among primate species could have a variety of evolutionary advantages that are influenced by a number of factors, including paternal certainty, ecology, and reproductive advantages.
Variation regarding the selective pressures influencing male care of offspring is obvious when one considers the range of paternal strategies seen among primates. In some primate species males invest heavily in the development of their offspring while in other species, male care is infrequent or completely absent (Whitten, 1987; Taub 1984). However, as will be discussed below, paternal certainty does not always correlate to the level of male investment in offspring (van Schaik & Paul 1996; Smuts & Gubernick 1992). Because humans and their ancestors are primates, a greater understanding of paternal care among primate species can help to provide insight about the evolution of paternal care in humans. By attempting to identify which factors influence the evolution of the level and types of paternal care seen in non-human primates, possible paternal strategies can be identified for early hominids and a better understanding of the evolution of human male investment can be gained.

2.2 Increased Male Investment

As noted in chapter one, males and females are thought to employ different strategies to maximize their reproductive success. Theoretically, males maximize their reproductive success by investing little in offspring and mating with many females. Females, on the other hand, maximize their reproductive success by investing more in offspring and being choosy in their selection of mating partners (Trivers, 1972). If males and females have such different reproductive strategies and males can easily leave their offspring after fertilization, why would males ever invest in their young following fertilization? There have been several theories proposed to explain male investment in offspring among primates. Some studies have suggested that male primates will invest in young if doing so will improve the likelihood that the immature will survive and thus, increase the father’s reproductive success.
In these cases, investment from both parents should increase the likelihood of offspring survival when compared with uniparental investment (Clutton-Brock, 1991). This dual care is often thought to be directly related to paternal certainty (Higley & Suomi, 1986; Kleiman & Malcolm, 1981; Bales, 1980). Male mammals, unlike females, can never be sure that they sired a particular offspring because their mates may have had multiple partners. Therefore, the more certain a male is that he fathered an individual, the more likely he will be to invest in that individual (Higley & Suomi, 1986; Kleiman & Malcolm, 1981; Bales, 1980). Thus, male investment should be higher in monogamous species than in polyandrous species (Trivers, 1972).

Recently, however, the paternal certainty model has been widely criticized among researchers (Wagner et al., 1998; Kempenaers & Sheldon, 1997; van Schaik & Paul, 1996; Smuts & Gubernick, 1992; Whitten, 1987). Despite these critiques, the paternal certainty hypothesis has long been the model used to explain paternal care in primates (van Schaik & Paul, 1996; Whitten 1987). In order to understand why this model has been critiqued and why it does not hold true for many primate species, it is necessary to review the male-infant interactions seen in various primate species following and elaborating on the discussions in van Schaik and Paul (1996) and Smuts & Gubernick (1992). Primate species will be discussed in relation to their social organization (species that live in multi-male, multi-female groups; species that typically live in one-male units; polyandrous species; pair-bonded species), which is roughly reflective of the degree of paternal certainty. Although this review by no means encompasses all primate species, it does show that the degree of paternal certainty, while sometimes reflective of the amount of male investment among primate
species, does not provide a model that explains the level of male investment seen in all primate species.

2.3 Male Care in Multi-male, Multi-female Groups

Chimpanzees live in multi-male, multi-female groups in which females mate with multiple males in their community (Goodall 1986). Additionally, females employ a variety of strategies that may confuse paternal certainty. Namely, females mate with multiple males within their community while in estrus (Goodall, 1986) and may mate with males outside of their community as well (Vigilant et al., 2001; Sugiyama et al., 1993). As a result, paternal certainty among chimpanzees is relatively low. Thus, following kin selection theory and the paternal certainty hypothesis, males would not be expected to invest heavily in immatures. Among the wild chimpanzees at Gombe, male direct investment in offspring appears to be relatively low (Goodall 1986; reviewed in Whitten 1987). Males do, however, engage in patrols of their territory and drive out, and sometimes kill, males who are not members of their community (Goodall, 1986). This suggests that in this subspecies, at least, there is some investment of males in offspring, following Trivers (1972) inclusion of territory defense as a form of parental investment.

In a captive study of chimpanzees, male-infant interactions were observed often and encompassed behaviors such as play (Davis, 1984). However, the group studied included language-trained apes that had spent a great deal of their time in the presence of humans, so their behavior may not be species-typical. In another captive study, males did not interact more frequently with their offspring than with immatures they did not sire (Pruetz & Bloomsmith, 1995). This is consistent with the behavior that would be expected in groups where paternity is uncertain (Pruetz & Bloomsmith, 1995). Thus, chimpanzees do appear to
support the paternal certainty hypothesis to some extent. However, the same study found that males tended to engage in affiliative interactions with their own offspring more frequently than with young sired by other males, although this difference was not significant (Pruetz & Bloomsmith, 1995). Thus, despite the fact that there is some evidence that chimpanzees support the paternal certainty hypothesis, other factors may be involved in the amount of paternal investment seen among members of this species.

While chimpanzees may support the paternal certainty hypothesis to some degree, the same cannot be said of many baboon and macaque species that also live in multi-male, multi-female groups (Taub, 1984). Among stump-tail macaques (*Macaca arctoides*), for example, male care is observed although paternal certainty should be relatively low (Estrada, 1984). Interestingly, male infants received more attention from adult males than did female infants (Estrada, 1984) which raises additional questions about the evolution of male care and its function in this species. Among yellow baboons (*Papio cynocephalus*), a species that also lives in multi-male, multi-female groups and thus has ambiguous paternity, male care is observed (Stein, 1984a & 1984b). Similar behavior has been observed in six baboon and macaque species living in multi-male, multi-female groups (Smuts & Gubernick, 1992). The evidence suggests that, for these species, the paternal certainty hypothesis does not explain the evolution of increased male investment. There have been several alternative hypotheses (van Schaik & Paul, 1996; Smuts & Gubernick, 1992; Kurland & Gaulin, 1984) proposed to explain the evolutionary benefit of the male-infant behavior seen among macaques and baboons, which will be discussed below.
2.4 Male Care in One-Male Units

Perhaps the best known species living in one-male units are the various gorilla species (*Gorilla beringei* and *Gorilla gorilla*). These groups generally contain one or two silverback (fully adult) males, several females, and their dependent offspring (Fossey, 1983; Harcourt, Stewart, & Fossey 1981). Because there is typically only one male in a group, there is a relatively high degree of paternal certainty (Fossey, 1984). Despite this high level of paternal certainty, males do not frequently interact directly with immatures (Stewart, 2001). This does not mean that gorilla males do not invest in their offspring at all. Gorillas indirectly invest in immatures by protecting them from infanticide and predators, including human poachers (Harcourt and Greenberg, 2001; Watts, 1996; Fossey, 1983).

Additionally, in a captive study it was found that a silverback who sired the juveniles in his group did not direct aggression toward them (Encisco et al., 1999). A male who had not sired the juveniles in his group, however, was observed to behave aggressively toward them (Encisco et al., 1999). Therefore, it appears that juveniles in this case did gain some benefits by associating with a male who was their father. What is interesting, however, is that paternal certainty is higher among gorillas than in multi-male, multi-female groups, yet gorilla males directly invest little in their offspring (Stewart, 2001). The male investment patterns seen in gorillas and chimpanzees both reflect a passive and generally good-natured disinterest in immatures (Higley & Suomi, 1986) despite the fact that gorilla males have high paternal certainty, while chimpanzees do not (Goodall, 1986; Fossey, 1984). This suggests that other factors that have not yet been addressed may influence paternal behavior in gorillas.
Recently, research has shown that one-male units among gorillas may not be as common as was once thought (Kalpers et al., 2003; Robbins, 1995). In gorilla groups with two males, it has been observed that subordinate males are able to gain access to mates, albeit less frequently than dominant males (Robbins, 1999). Perhaps, then, paternal certainty is not as high as was once believed. While this may be true, in most groups with multiple males, the males are thought to be related, typically as father and son (Robbins, 1995; Harcourt et al., 1981). Thus, all immatures in a group would probably be related to both silverbacks in multi-male gorilla groups. According to the theory of kin selection (Hamilton, 1964), silverbacks could improve their reproductive success by providing care to all immatures if they are genetically related to them and the benefits to reproductive success outweigh the costs. Thus, while paternal certainty may not be as high as was once thought in gorillas, the evidence from this species does not seem to support the paternal certainty hypothesis.

Primate species also living in such one-male groups include hamadryas baboons (Papio hamadryas hamadryas) (Zinner et al., 2001). Thus, it is thought that paternity should be fairly certain in this species, although recent research has suggested that extra-group copulations are frequent in captive populations (Smith et al., 1999). If these intergroup copulations are also present in the wild, males may not be aware of them and may enjoy a high, although possibly false, level of paternal certainty. Despite this, there appears to be little paternal investment in offspring (Kummer, 1968) although there is evidence in this species, as in gorillas, that males protect young from predation (Zinner & Peláez, 1999).

The lack of paternal investment among hamadryas baboons raises additional questions about the paternal certainty hypothesis. In fact, in a review of eleven species that live in one-male units, Smuts & Gubernick (1992) found that direct male care was absent in
ten species. It is possible that males of these species gain few fitness benefits through interactions with immatures. In other words, males may be relatively certain of their paternity but gain few benefits by investing in their young. Still, it raises questions about the factors that are thought to shape male-immature interactions.

2.5 Male Care in Polyandrous Species

Among primates, few species exhibit polyandrous mating systems; however, this pattern is frequently seen in the New World monkey family, Callitrichidae, most notably among the species in the genera Saguinus and Leontopithecus (as reviewed in Digby et al., 2007). Among these species, paternal care is the norm with males sharing in all parental duties other than nursing. However, the level of care varies from species to species (as reviewed in Goldizen, 1987 & Whitten, 1987). Because female callitrichids may mate with multiple males, paternal certainty is not particularly high. Therefore, it is surprising that males should invest so heavily in immatures.

Interestingly, callitrichids are considered small relative to other anthropoids and generally give birth to twins (as reviewed in Goldizen, 1987). Therefore, Pook (1984) has suggested that reproduction is extremely energetically draining for females. As a result, and in order for infants to survive, male care is necessary among these primates. In fact, male care may be such an integral part of survival for callitrichids that in some cases polyandry can be tolerated because of the necessity of infant care (Schaffner & French, 2004). These findings indicate that paternal certainty cannot explain male care among the callitrichids. Males in this family often show extensive male care even though paternal certainty is not high (as reviewed in Digby et al., 2007).
2.6 Male Care in Pair-Bonded Species

Gibbons and siamangs, the hylobatids, are characterized as living in pair-bonds that include one adult male and one adult female (as reviewed in Bartlett, 2007). Therefore, males in this family should have a relatively high degree of paternal certainty. However, among all hylobatids other than siamangs, male care is absent (as reviewed in Whitten, 1987), although males of all species do appear to invest in their offspring through territory defense (Leighton, 1987). It is not clear why such a difference in level of male care exists between siamangs and other hylobatids. However, in a captive study, evidence was found indicating that the discrepancy between levels of male care was not as pronounced (Fischer & Geissmann, 1990).

It seems that further research is needed to determine the levels of male care seen in hylobatids. With the present data available, however, only the siamangs appear to support the hypothesis that increased paternal certainty will lead to increased paternal care. Again, it is possible that, in most species, male hylobatids do not invest in immatures because they do not gain extensive benefits by doing so. It is interesting, however, that extensive male care is seen in one species in the genus *Hylobates* and in no others, given that these species live in similar ecological and social environments. It is possible that paternal certainty among hylobatids is not as high as researchers have previously predicted; extra-pair copulations have been documented among both lar gibbons and siamangs (Reichard, 1995; Palombit, 1994). However, males may not be aware of these extra-pair matings and may still enjoy a high, although false, degree of paternal certainty. Therefore, the general lack of male care among the hylobatids raises further questions about the paternal certainty hypothesis.
2.7 Alternatives to the Paternal Certainty Hypothesis

After reviewing various primate species, it seems clear that the paternal certainty hypothesis alone cannot explain the level of male investment seen among primates. This is not to say that the degree of paternal certainty has no influence on the level of male investment. In some species (e.g. chimpanzees and siamangs), the level of paternal certainty may influence the level of male investment. Therefore, it is likely that several factors have influenced the evolution of the degree of male investment among primates. As discussed in the introduction of this chapter, it is unlikely that one model will universally explain any behavior observed among primates because there is such diversity in life history patterns, social structure, and ecology among members of this order (Smuts et al., 1987).

If the degree of paternal certainty is not the only factor influencing male investment in immatures, what other factors could be involved in the level of male investment seen among primate species? An alternative explanation is that such investment in immatures may actually be an attempt to improve mating opportunities (van Schaik & Paul, 1996; Smuts & Gubernick, 1992). Van Schaik and Paul (1996) review the relevant literature and suggest that in many nonhuman primate species, male interaction with immatures increases the likelihood that females will mate with those males. The authors argue that this suggests that male care may have been a mating strategy during the course of human evolution instead of a byproduct of pair-bonding as other authors have argued.

Kurland and Gaulin (1984) provide a similar, although slightly different argument. These authors suggest that by protecting a group from predators, a behavior that is often labeled as an indirect form of paternal investment (Trivers, 1972), males are actually protecting future mates. Thus, these males are increasing their reproductive success, not by
improving the survival rate of their offspring, but by maintaining their current mate pool. Therefore, the behavior, that is interpreted as male investment may actually be an example of a mating strategy that is unrelated to male care.

2.8 Conclusion and Relevance for this Study

While it is unlikely that a single model will provide an explanation of male investment, additional research can provide insight about which factors influence male investment among primates. By understanding the patterns seen in nonhuman primates, researchers may be able to better understand the evolution of male investment and paternal care in hominids. For example, Smuts & Gubernick (1992) challenge the traditional belief that paternal care arose in hominids when males could be relatively certain that they fathered offspring. Instead, the authors suggest that paternal care may have arisen as a male mating strategy. While this may or may not be true, the authors’ argument highlights the need for additional research concerning male investment in primates.

Although the above discussion illustrates the shortcomings of the paternal certainty hypothesis, chimpanzees appear to fit the model to some degree. As discussed above, these animals have a mating system in which females mate with multiple males (Goodall, 1986), thus, confusing paternal certainty. Because male interaction with immatures in chimpanzee communities is low (Goodall, 1986), chimpanzees may provide some support for the paternal certainty model. Two hypotheses of this study aim to test this model. Specifically, it is hypothesized that males will not preferentially engage in affiliative interactions with any immature in their community because they are relatively uncertain of paternity. Additionally, it is hypothesized that dominant males will interact affiliatively with immatures more frequently than lower-ranking males. This is because higher ranking males are thought
to have greater access to females during their most fertile period and, as a result, may have higher paternal certainty than lower ranking males (Matsumoto-Oda, 1999; Takasaki, 1985; Nishida, 1983b). As discussed above, however, the paternal certainty model has recently been questioned. If the hypotheses are not supported by the data collected, it would provide further support that the paternal certainty model alone cannot explain male-immature interactions among primates.

References


Chapter Three: Methods

Figure 3.1 Map of Senegal. Fongoli is located near Kedougou, in the southeastern part of the country (indicated by circle).

3.1 Study Site

Research was conducted at the Fongoli site in southeastern Senegal (12°55’N 12°02’W), which represents the northern and westernmost region of chimpanzees’ geographical range (Carter et al., 2003). The village of Fongoli is near the town of Kedougou, in the southeastern part of the country (Figure 3.1). The Fongoli chimpanzee (*P. t. verus*) community, the study group, consists of at least 34 identified members and has a range of at least 63 km² (Pruetz, 2006). The Fongoli community has been studied since 2001 under the direction of Dr. Jill D. Pruetz, and certain individuals are now habituated to human presence. The protocol at this site follows health guidelines as discussed by Collins (2003) with some conservative modifications.

The region in which the Fongoli chimpanzees live is considered to be extremely hot, dry, and open (McGrew et al., 1981). It is best described as a mosaic habitat in which the
woodland savanna is broken up by patches of gallery forest and open grassland on laterite plateau (Pruetz, 2006; Hunt and McGrew, 2002; McGrew et al., 1981) (Figure 3.2). This community is the first community of savanna chimpanzees that has been habituated to the presence of researchers (J. Pruetz, personal communication). This community’s range overlaps significantly with that of humans (Pruetz, 2006). Because the Western chimpanzee subspecies is thought to be bisexually-bonded (Lehmann & Boesch, 2005), and savanna chimpanzees have been observed to exhibit larger party sizes than chimpanzees living in more forested environments (Pruetz & Bertolani, 2007; Tutin et al., 1983), it is likely the social behavior of this community will differ from that of chimpanzees at other long-term research sites.

**3.2 Study Animals**

Researchers are able to follow male chimpanzees all day (from nest to nest), but most females are more nervous around humans, and researchers do not follow them as focal subjects. Age classes follow Baldwin (1979), with slight modification (Pruetz & Bertolani,
Adults are estimated to be older than 13 years of age, subadults are estimated to be between 11-12 years of age, adolescents are estimated to be 9-10 years of age, juveniles are estimated to be 5-9 years of age, and infants are estimated to be younger than 4 years of age. Ten adult males, 7 adult females, 2 subadult males, 2 subadult females, 2 adolescent males, 2 adolescent females, 5 juvenile males, 1 juvenile female, 2 infant males, and 2 infant females have been identified at Fongoli (Table 3.1). One infant female, Sonya, was not included as a potential social partner, because her mother was very nervous around researchers and probably avoided joining parties when researchers were present.

The male dominance hierarchy is known based on pant-grunt records (J. Pruetz, unpublished data). During the course of the study Lupin, a subadult male, became integrated into the male dominance hierarchy. At the conclusion of the study he was dominant to Ross, the lowest ranking male. Thus, Lupin is now considered a socially adult male but was not included as a focal subject during the study.
Table 3.1 The chimpanzees of the Fongoli community.

<table>
<thead>
<tr>
<th>Individual</th>
<th>Age/Sex Class</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foudouko (FO)</td>
<td>Adult male</td>
<td>Alpha</td>
</tr>
<tr>
<td>Mamadou (MM)</td>
<td>Adult male</td>
<td>2nd ranking</td>
</tr>
<tr>
<td>Yopogon (YO)</td>
<td>Adult male</td>
<td>3rd ranking</td>
</tr>
<tr>
<td>Killimanjaro (KL)</td>
<td>Adult male</td>
<td>4th ranking</td>
</tr>
<tr>
<td>Diouf (DF)</td>
<td>Adult male</td>
<td>5th ranking</td>
</tr>
<tr>
<td>Bilbo (BI)</td>
<td>Adult male</td>
<td>6th ranking</td>
</tr>
<tr>
<td>Bandit (BN)</td>
<td>Adult male</td>
<td>7th ranking</td>
</tr>
<tr>
<td>Karamoko (KM)</td>
<td>Adult male</td>
<td>8th ranking</td>
</tr>
<tr>
<td>Siberut (SI)</td>
<td>Adult male</td>
<td>9th ranking</td>
</tr>
<tr>
<td>Ross (RS)</td>
<td>Adult male</td>
<td>Lowest ranking; not a focal subject</td>
</tr>
<tr>
<td>Daoulema (DM)</td>
<td>Adult female</td>
<td>Mother of Dawson</td>
</tr>
<tr>
<td>Farafa (FA)</td>
<td>Adult female</td>
<td>Mother of Fanta and Frito; probably David's mother</td>
</tr>
<tr>
<td>LINGUA (LI)</td>
<td>Adult female</td>
<td>Mother of Jino and Jumkin</td>
</tr>
<tr>
<td>Lucille (LU)</td>
<td>Adult female</td>
<td>Mother of Lex and Luthor</td>
</tr>
<tr>
<td>Muso (MU)</td>
<td>Adult female</td>
<td>Mother of Mike</td>
</tr>
<tr>
<td>Natasha (NT)</td>
<td>Adult female</td>
<td>Mother of Sonya</td>
</tr>
<tr>
<td>Nene (NN)</td>
<td>Adult female</td>
<td>Mother of Nellie and Nickel</td>
</tr>
<tr>
<td>Lupin (LN)</td>
<td>Subadult male</td>
<td>Integrating into the male dominance hierarchy; higher ranking than Ross at the conclusion of the study</td>
</tr>
<tr>
<td>Nyegi (NY)</td>
<td>Subadult male</td>
<td>Older than 12 years of age</td>
</tr>
<tr>
<td>Tia (TI)</td>
<td>Subadult female</td>
<td>11-12 years of age</td>
</tr>
<tr>
<td>Tumbo (TU)</td>
<td>Subadult female</td>
<td>Approximately 12 years of age</td>
</tr>
<tr>
<td>Bo (BO)</td>
<td>Adolescent male</td>
<td>Probably the son of Wilema (deceased?); approximately 10 years of age</td>
</tr>
<tr>
<td>David (DA)</td>
<td>Adolescent male</td>
<td>Approximately 10 years of age</td>
</tr>
<tr>
<td>Nickel (NI)</td>
<td>Adolescent female</td>
<td>Older than 10 years of age</td>
</tr>
<tr>
<td>Sissy (SS)</td>
<td>Adolescent female</td>
<td>Older than 10 years of age</td>
</tr>
<tr>
<td>Dawson (DW)</td>
<td>Juvenile male</td>
<td>Approximately 5 years of age</td>
</tr>
<tr>
<td>Frito (FR)</td>
<td>Juvenile male</td>
<td>Older than 5 years of age</td>
</tr>
<tr>
<td>Jumkin (JM)</td>
<td>Juvenile male</td>
<td>Older than 5 years of age</td>
</tr>
<tr>
<td>Luthor (LT)</td>
<td>Juvenile male</td>
<td>Older than 5 years of age</td>
</tr>
<tr>
<td>Mike (MI)</td>
<td>Juvenile male</td>
<td>Older than 5 years of age</td>
</tr>
<tr>
<td>Nellie (NE)</td>
<td>Juvenile female</td>
<td>Estimated to be 4 years of age</td>
</tr>
<tr>
<td>Fanta (FN)</td>
<td>Infant female</td>
<td>Estimated birth date Jan.-May 2005</td>
</tr>
<tr>
<td>Jino (JI)</td>
<td>Infant male</td>
<td>Estimated birth date late 2004</td>
</tr>
<tr>
<td>Sonya (SO)</td>
<td>Infant female</td>
<td>Estimated birth date late 2005; not included as a potential social partner</td>
</tr>
</tbody>
</table>
3.3 Methodology

The study was conducted from May to July, 2006 for a total of eleven weeks. The first ten days in the field were spent becoming familiar with the study animals and their behaviors. Data collection began on 30 May 2006 and concluded 15 July 2006. Behavioral observations were collected four to five days per week with the assistance of Dr. Jill Pruetz and/or a Senegalese field assistant. On days when behavioral observations were collected, a focal male was selected to follow from his morning nest to his evening nest (Altmann, 1974). If the first chimpanzee encountered was a lone male, he was the focal subject. Throughout the study, however, attempts were made to balance the number of hours collected for each male. As a result, the selection of a focal subject was not always random. Males, and not females, were chosen as focal subjects following research protocol that maintains that males may be followed but females may not.

During data collection, a target distance of 10-20 m was maintained between the researcher and the chimpanzees, with a mandatory distance of 10 m kept between the animals and the researcher at all times, following research protocol. If the focal male moved out of sight, efforts were made to locate him visually following this protocol. If, however, the focal moved out of sight and could not be located for more than 15 minutes (three data points), a new focal animal was identified. Chimpanzees were located at the beginning of the day using knowledge of their nests from the previous night or by listening for pant hoots and other noises indicative of chimpanzees.

Once a focal male had been identified, the party size and composition of the party with which he was associated were recorded with the assistance of Dr. Pruetz. The definition
Table 3.2 Behavioral categories and the behaviors recorded.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding</td>
<td>Consuming, foraging for, searching for, or manipulating food.</td>
</tr>
<tr>
<td>Traveling</td>
<td>Locomotion from one place to another, not including traveling during feeding.</td>
</tr>
<tr>
<td>Resting</td>
<td>Not moving: includes sit, lie, and self-groom.</td>
</tr>
<tr>
<td>Social</td>
<td>Engaged in behavior with another individual; includes: play, groom, display, preparation for display, and aggressive behaviors.</td>
</tr>
<tr>
<td>Out of Sight</td>
<td>Any time the focal male cannot be seen or behaviors cannot be identified</td>
</tr>
</tbody>
</table>

for party followed Sakura (1994), which labels a party as the number of individuals present over the course of a day. For the purposes of this study, juveniles and infants were counted as individuals within a party. The focal animal’s behavior was then recorded at 5-minute intervals (Table 3.2; see Appendix for full ethogram). Nonsocial behaviors (e.g., feeding, resting, and traveling) were recorded so that social behaviors (e.g., grooming, copulating, and displaying) could be put in the context of the focal subject’s other activities (Table 3.2).

At 5-minute intervals, individuals in close proximity (within arm’s reach) to the focal male were identified and recorded. Because visibility was sometimes limited, close proximity estimates should be considered a minimum. Additionally, it was not always possible to identify individuals in close proximity individually. If specific identification was not possible, the age and sex class of the individual was recorded.

In addition to the data collected at five minute intervals, the focal male’s interactions with juveniles and infants were recorded on an all-occurrence basis. In other words, all social interactions between the focal male and immatures were recorded whether they occurred at the 5-minute interval or not (Altmann, 1974). When a social interaction did occur, the social partner was identified individually. If this was not possible, the age and sex
Table 3.3 Affiliative vs. aggressive behaviors. For a more detailed description of the behaviors, see the ethogram in Appendix.

<table>
<thead>
<tr>
<th>Behavior Category</th>
<th>Behaviors Included</th>
</tr>
</thead>
<tbody>
<tr>
<td>Affiliative</td>
<td>Play, groom, reassure, affiliative touch, alloparental care</td>
</tr>
<tr>
<td>Aggressive</td>
<td>Threat, attack, chase, display at</td>
</tr>
</tbody>
</table>

class of the social partner was recorded. The type of social interaction was recorded and classified as aggressive or affiliative (Table 3.3). Additionally, play events were recorded on an *ad libitum* basis. In other words, all play events observed were recorded, even if they did not involve the focal male. The data collected by the primary researcher was supplemented by Dr. Pruetz’s *ad libitum* play data collected from 29 May to 2 August 2006.

The goal of this study is to understand the social relationships between adult male chimpanzees and the immatures in their community. In order to do so, the social interactions adult males experience should be put into the larger context of their community and other nonsocial activities. This is why nonsocial behaviors were recorded as well as party demographics. By doing so, the social relationships between adult males and immatures may be put in the context of the males’ daily activities and positions in the community.

3.4 Data Analysis

Activity Budgets, Social Interaction Rates, and Proximity Data

The number of data points in which males engaged in feeding, resting, traveling and social behavior were tallied and used to calculate the activity budget of each male. The average and standard deviation of these values were calculated using Microsoft Excel. The rate per hour and percent time that males engaged in social behavior with each age/sex class
Table 3.4 Variables and their calculations.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Calculation of Data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Affiliation duration</td>
<td>Affiliative behaviors occurring at the five minute interval were assumed to be representative of the preceding five minute period. Following this assumption, the duration of affiliation was calculated in minutes per hour.</td>
</tr>
<tr>
<td>Affiliation rate</td>
<td>The total number of affiliative events with immatures was tallied for each male. Because the hours of data collected for each focal male differed, these data were converted to events per hour.</td>
</tr>
<tr>
<td>Percent of time in close proximity</td>
<td>The individuals in close proximity, within arm’s length, were recorded at the five minute interval. Following the assumption that these intervals were reflective of the previous five minutes, the percent of time that each age/sex class spent in close proximity to the focal male was calculated.</td>
</tr>
<tr>
<td>Play frequency</td>
<td>Using the all-occurrence play data, the number of play events was tallied for each male. Because these data were collected for all males, on an all-occurrence basis, they were not converted to rates.</td>
</tr>
</tbody>
</table>

were then calculated. The average and standard deviation of these values were also calculated using Microsoft Excel. In addition, the amount of time (as a percent) that males spent in close proximity (within arm’s reach) to each age/sex class was calculated. The average values and standard deviations were calculated for these data as well.

Variables

Data were divided into four variables: affiliation duration, affiliation rate, percent of time in close proximity, and play frequency (Table 3.4). Affiliation duration was calculated using the data collected at five-minute intervals. If affiliative behavior occurred at the interval, it was assumed to be representative of the entire five minute period. Following this assumption, duration of affiliation was calculated in minutes per hour. Affiliation rates were calculated using the all-occurrence data. In other words, all affiliative interactions between the focal male and immatures were tallied and converted to number of affiliative events per hour. Next, the percent of time that a male spent in close proximity to immatures was
calculated using the proximity data collected at five minute intervals. Finally, play counts were tallied using the all-occurrence play data. Because these data involved all males, and not just the focal male, and because all males were generally present on any given day, frequency counts were summed for each male and not converted to rates.

The variables were calculated for each adult male’s interaction with infants and juveniles. They were then accordingly grouped to test each of the study’s four hypotheses. There is some overlap between the different variables. For example, if a male was playing with an immature at the five-minute interval, this play event was used to calculate affiliation duration, affiliation rate, and play frequency.

**Analyses for Hypothesis 1**

*All adult males will engage in affiliative behaviors with infants and juveniles in their community equally.*

This hypothesis could not be tested statistically because of the limited number of interactions observed per male subject (J. Hucket, personal communication). Instead, a qualitative approach was used to consider the patterns of interactions between specific adult males and juveniles and infants in the community.

The variables were calculated regarding each adult male’s interactions with each infant and juvenile in the community. Charts were created to determine whether males preferred certain immatures as social partners. Additionally, Tukey’s Studentized Range (HSD) Tests were carried out using SAS software to determine if certain immatures were favored by males as social partners in general. Because it appeared that the offspring of particular females may have been favored social partners, Tukey’s Studentized Range (HSD) Tests were also carried out to determine if certain females’ offspring were the recipients of
affiliative behavior more frequently that others. Finally, the average sexual swelling score a
female had when her offspring was played with or received affiliation from a male was
calculated. This was done by averaging the known sexual swelling scores of females on days
when their offspring were played with or received affiliation from adult males. (Sexual
swelling scores at Fongoli are recorded daily using a 4 point scale, 0-3, with 3 reflecting
maximum tumescence.)

**Analyses for Hypothesis 2**

*Dominant males in the community will engage in affiliative behaviors with infants and
juveniles more often than subordinate males.*

The four variables discussed above were tabulated for each focal male. These males
were then classified into three dominance categories, high-ranking, mid-ranking, and low-
ranking. Dominance ranks for the Fongoli males are known based on pant-grunt records (J.
Pruetz, unpublished data). Foudouko, Mamadou, and Yopogon (ranks 1, 2, and 3
respectively) were placed in the high-ranking category. Kilimanjaro, Diouf, and Bilbo (ranks
4, 5, and 6 respectively) were placed in the mid-ranking category. Finally, Bandit,
Karamoko, and Siberut (ranks 7, 8, and 9 respectively) were placed in the low-ranking
category. Using SAS software, an analysis of variance was carried out regarding the four
variables. A Tukey’s Studentized Range (HSD) Test was then conducted for each variable to
determine if dominance rank affected the ways in which males engaged in affiliative
interactions with immatures.

**Analyses for Hypothesis 3**

*Adult males will engage in affiliative interactions with juvenile and infant males more often
than with juvenile and infant females.*
The four variables were calculated regarding each adult male’s interactions with juvenile males, juvenile females, infant males, infant females, all males (i.e. both juvenile and infant males) and all females. Because the number of males and females differed (juvenile males: n=5; juvenile female: n=1; infant males: n=3; infant females: n=2 but only 1 was considered a potential social partner), the values were divided by the number of individuals within their corresponding age/sex class. Using SAS software, a t-test was carried out to determine whether the mean difference (between males and females) within the four variables differed significantly from zero. T-tests were done for the differences between juvenile males and females, between infant males and females, and between all males and females.

Analyses for Hypothesis 4

*Adult males will engage in affiliative interactions with juveniles more often than with infants.*

Each of the four variables was calculated regarding each adult male’s interactions with juveniles and infants. Because the number of juveniles and infants at Fongoli is not equal (juveniles: n=6; infants: n=4 but only 3 were included as potential social partners), each value was divided by the number of individuals within its respective age class. Using SAS software, a t-test was carried out to determine whether the mean differences (between juveniles and infants) within the four variables differed significantly from zero.

References


Chapter Four: Results

4.1 Data Collected

Data were collected for a total of twenty days, from 30 May to 15 July 2006. A total of 1533 data points (127.75 hours) were recorded. Attempts were made to balance the amount of data collected for each of the focal males. Additionally, attempts were made to collect data for each male during all parts of the day (i.e. early morning, late morning, early afternoon, late afternoon, and evening). The number of data points collected for each male are given in Table 4.1.

Contact time was defined as the time during which data were collected as well as data intervals when the focal was out of immediate sight but in the vicinity of the observer. If the focal was out of sight for more than three data intervals, the sample was terminated, and contact time ceased until a new focal was selected. The amount of contact time spent with the chimpanzees was 147 hours and 40 minutes. During 239 data intervals, the focal was out of sight; this accounts for 13.5% of the data intervals.

Table 4.1 Number of data points collected for each focal male. Out of sight points are not included.

<table>
<thead>
<tr>
<th>Focal</th>
<th>Number of Data Points</th>
<th>Minutes</th>
</tr>
</thead>
<tbody>
<tr>
<td>FO</td>
<td>140</td>
<td>700</td>
</tr>
<tr>
<td>MM</td>
<td>141</td>
<td>705</td>
</tr>
<tr>
<td>YO</td>
<td>241</td>
<td>1205</td>
</tr>
<tr>
<td>KL</td>
<td>193</td>
<td>965</td>
</tr>
<tr>
<td>DF</td>
<td>136</td>
<td>680</td>
</tr>
<tr>
<td>BI</td>
<td>193</td>
<td>965</td>
</tr>
<tr>
<td>BN</td>
<td>137</td>
<td>685</td>
</tr>
<tr>
<td>KM</td>
<td>120</td>
<td>600</td>
</tr>
<tr>
<td>SI</td>
<td>232</td>
<td>1160</td>
</tr>
<tr>
<td>Total</td>
<td>1533</td>
<td>7665</td>
</tr>
</tbody>
</table>
4.2 Activity Budgets and Time Spent Engaging in Social Behavior

The activity budgets of adult males were divided into four categories: feeding, resting, travel, and social behavior. On average, the adult males spent 19.56% (σ = 9.86) of their time feeding. They spent 60.82% (σ = 8.71) of their time resting and 8.21% (σ = 1.97) of their time traveling. Finally, the males spent, on average, 11.41% (σ = 3.33) of their time engaging in social interactions (Figure 4.1).

The duration (in minutes per hour) of social interaction with each age/sex class was also calculated for each adult male and then averaged (Table 4.2 & Figure 4.2). If the social partner’s age/sex class could not be identified, or if there was no specific social partner (for example, during a display or preparation for a display) the partner was recorded as non-specific. Overall, males engaged in social behavior for an average of 6.85 minutes per hour (σ = 2.00). Males engaged in social interactions with other adult males for an average of

![Figure 4.1](#)

**Figure 4.1** Adult male activity budgets. Average time spent feeding, resting, traveling, and engaging in social behavior by adult males.
Table 4.2 The duration (in minutes per hour) of adult males’ social interactions with each age/sex class. Bandit (BN) simultaneously played with an infant male and juvenile male (italicized values). As a result, his total interaction rate excludes one of these values. If the social partner’s age/sex class could not be identified or if there was no specific social partner, the partner was recorded as non-specific.

<table>
<thead>
<tr>
<th>Age/Sex Class</th>
<th>Amount of Time (Minutes/Hour)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FO</td>
<td>6.43</td>
</tr>
<tr>
<td>MM</td>
<td>8.51</td>
</tr>
<tr>
<td>YO</td>
<td>2.49</td>
</tr>
<tr>
<td>KL</td>
<td>2.18</td>
</tr>
<tr>
<td>DF</td>
<td>6.62</td>
</tr>
<tr>
<td>BI</td>
<td>6.53</td>
</tr>
<tr>
<td>BN</td>
<td>0.88</td>
</tr>
<tr>
<td>KM</td>
<td>0.00</td>
</tr>
<tr>
<td>SI</td>
<td>2.33</td>
</tr>
<tr>
<td>SD</td>
<td>3.03</td>
</tr>
<tr>
<td>Avg.</td>
<td>3.99</td>
</tr>
</tbody>
</table>

Figure 4.2 Average time adult males spent engaging in social interactions with each age/sex class. These data have been corrected for the number of social partners within each age/sex class, where the time spent in social behavior was divided by the number of individuals within each age/sex class. (Sub=subadults, adol=adolescent, juv=juveniles, and inf=infants.)

3.99 minutes per hour ($\sigma = 3.03$) and with adult females for an average of 0.36 minutes per hour ($\sigma = 0.84$). The average time in which males engaged in social interactions with
subadult males and subadult females was 0.32 minutes per hour (σ = 0.86) and 0.23 minutes per hour (σ = 0.62), respectively. The average time spent engaging in interactions with adolescents was 0.39 minutes per hour (σ = 0.86) for males and 0.28 minutes per hours (σ = 0.49) for females. On average, adult males spent 0.41 minutes per hour (σ = 0.83) engaging in social interactions with juvenile males and 0.41 minutes per hour (σ = 0.76) engaging in social behavior with infant males. Males were not observed to engage in social interactions with female juveniles and infants. Adult males spent 0.69 minutes per hour (σ = 0.74) engaging in non-specific social interactions.

4.3 Time Spent in Close Proximity to Community Members

The percent of time that males spent in close proximity (within arm’s length) to each age/sex class was also calculated (Table 4.3 & Figure 4.3). On average, males spent most (19.39%, σ = 6.59) of their time in close proximity to adult males. They spent 2.30% (σ = 2.29) of their time in close proximity to adult females, on average. Males spent an average of 0.65% (σ = 1.41) and 2.36% (σ = 4.52) of their time in close proximity to subadult males and females, respectively. The average amount of time males were in close proximity to

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>FO</td>
<td>28.57</td>
<td>2.14</td>
<td>0.00</td>
<td>2.14</td>
<td>1.43</td>
<td>0.71</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>MM</td>
<td>19.15</td>
<td>0.71</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>YO</td>
<td>14.94</td>
<td>4.56</td>
<td>0.83</td>
<td>1.24</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>3.73</td>
</tr>
<tr>
<td>KL</td>
<td>11.92</td>
<td>0.00</td>
<td>0.00</td>
<td>13.99</td>
<td>0.00</td>
<td>1.04</td>
<td>0.41</td>
<td>0.00</td>
<td>0.00</td>
<td>2.59</td>
</tr>
<tr>
<td>DF</td>
<td>25.19</td>
<td>0.00</td>
<td>0.74</td>
<td>0.00</td>
<td>0.00</td>
<td>1.48</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>BI</td>
<td>28.50</td>
<td>6.22</td>
<td>0.00</td>
<td>0.52</td>
<td>0.52</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>2.07</td>
<td>0.00</td>
</tr>
<tr>
<td>BN</td>
<td>12.41</td>
<td>3.65</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>2.19</td>
<td>5.84</td>
<td>0.00</td>
<td>7.30</td>
<td>0.00</td>
</tr>
<tr>
<td>KM</td>
<td>19.17</td>
<td>0.00</td>
<td>0.00</td>
<td>3.33</td>
<td>4.17</td>
<td>0.00</td>
<td>2.50</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>SI</td>
<td>14.66</td>
<td>3.45</td>
<td>4.31</td>
<td>0.00</td>
<td>1.72</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>3.45</td>
<td>0.00</td>
</tr>
<tr>
<td>SD</td>
<td>6.59</td>
<td>2.29</td>
<td>1.41</td>
<td>4.52</td>
<td>1.41</td>
<td>0.81</td>
<td>2.00</td>
<td>0.00</td>
<td>2.48</td>
<td>0.26</td>
</tr>
<tr>
<td>Avg.</td>
<td>19.39</td>
<td>2.30</td>
<td>0.65</td>
<td>2.36</td>
<td>0.87</td>
<td>0.60</td>
<td>0.97</td>
<td>0.00</td>
<td>2.13</td>
<td>0.13</td>
</tr>
</tbody>
</table>
adolescent males and females was 0.87% ($\sigma = 1.41$) and 0.60% ($\sigma = 0.81$), respectively. Males spent, on average, 0.97% ($\sigma = 2.00$) of their time in close proximity to juvenile males and none of their time in close proximity to juvenile females. Finally, males spent, on average, 2.13% ($\sigma = 2.48$) of their time in close proximity to infant males and 0.13% ($\sigma = 0.26$) of their time in close proximity to infant females.

### 4.4 Affiliative vs. Aggressive Interactions with Immatures

The all-occurrence data suggest that male interactions with immatures were more frequently affiliative than aggressive, although the difference was not statistically significant. On average, males engaged in aggressive interactions with immatures at a rate of 0.08 events per hour. However, they interacted affiliatively with immatures at an average rate of 0.17 events per hour. It is clear that there are individual differences (Figure 4.4); specifically, Bandit interacted affiliatively with immatures significantly more than all other males.
Figure 4.4 Adult males’ rate of affiliative and aggressive interactions with immatures. Males are listed according to their dominance rank, beginning with the highest ranking male on the left.

4.5 Results for Hypothesis 1

All adult males will engage in affiliative behaviors with infants and juveniles in their community equally.

As discussed in chapter three, formal statistical analysis could not be conducted to test this hypothesis. Data will be presented in the form of charts, and the observed patterns will be discussed. Regarding each of the four variables, certain males did prefer certain juveniles and/or infants as social partners. However, there was considerable overlap in preference for particular juveniles and infants. This suggests that factors other than paternal uncertainty may have influenced the ways in which males interacted affiliatively with infants and juveniles. Possible explanations will be explored below.

The amount of time individual males spent engaging in affiliative behavior with each immature varied the least (Figure 4.5). Only three immatures (Jino and Lex, both infants
Figure 4.5 Affiliation duration for each adult male and immature. Males and immatures who did not engage in any affiliative behaviors were not included in the chart.

and Luthor, a juvenile) were included. Two males associated with Lex and Luthor and one male associated with Jino.

Figure 4.6 shows the rate of affiliation (in events/hour) for each adult male with each immature. Again, certain immatures were preferred social partners. Three males interacted with both Jino and Lex; two males interacted with Fanta (female infant) and Mike (juvenile male); and one male interacted with Jumkin and Frito (both juvenile males). Two immatures, Dawson (juvenile male) and Nellie (juvenile female), were not observed to engage in any affiliative behaviors with adult males.

Figure 4.7 shows the number of times each male played with each immature. Two infants (Jino and Fanta) were play partners of five males; three immatures (Jumkin, Luthor, and Lex) played with three males; and one juvenile (Mike) played with two males. Dawson played with one male, and Nellie and Frito were not observed to play with any adult male.
Figure 4.6 Affiliation rates (in events/hour) for each adult male and immature. Males and immatures who did not engage in affiliative interactions were not included.

Figure 4.7 Play interactions for each adult male and immature. If males or immatures were not observed playing, they were not included in the figure.
Figure 4.8 shows the percent of time each adult male spent in close proximity to each immature. Five males spent time in close proximity to Jino, three with Lex, and two with Fanta. Only one male spent time in close proximity to Frito and Jumkin. Dawson, Nellie, and Mike were not observed in proximity to males.

Tukey’s Studentized Range (HSD) Tests were carried out to determine if, on average, males preferred particular juveniles or infants. For number of play events, Jino was involved significantly more often than Dawson, Frito, or Nellie (Tukey’s: p<0.05 for all three pairs). No other pair-wise comparisons for play were significantly different. No pair-wise comparisons were significant for the other variables (Tukey’s: p>0.05 for all pairs).

However, as Table 4.4 shows, there was a tendency to favor some individuals, namely Jino, Lex, Luthor, and Fanta. This suggests that male chimpanzees do appear to prefer certain

![Figure 4.8](image-url)  
*Figure 4.8* Time each adult male spent in close proximity to each immature. Individuals not observed in close proximity were not included.
Table 4.4 Average adult male interaction rates with each juvenile or infant. Affiliation duration is measured in minutes/hour. Affiliation rate is measure in events/hour.

<table>
<thead>
<tr>
<th></th>
<th>Affiliation Duration</th>
<th>Affiliation Rate</th>
<th>Number of Play Events</th>
<th>Percent Time in Close Proximity</th>
</tr>
</thead>
<tbody>
<tr>
<td>JI</td>
<td>0.055</td>
<td>0.041</td>
<td>1.33</td>
<td>1.334</td>
</tr>
<tr>
<td>LX</td>
<td>0.358</td>
<td>0.5</td>
<td>0.556</td>
<td>0.994</td>
</tr>
<tr>
<td>FN</td>
<td>0</td>
<td>0.021</td>
<td>0.556</td>
<td>0.126</td>
</tr>
<tr>
<td>LT</td>
<td>0.41</td>
<td>0.031</td>
<td>0.444</td>
<td>0.846</td>
</tr>
<tr>
<td>JM</td>
<td>0</td>
<td>0.006</td>
<td>0.333</td>
<td>0.081</td>
</tr>
<tr>
<td>MI</td>
<td>0</td>
<td>0.025</td>
<td>0.222</td>
<td>0</td>
</tr>
<tr>
<td>FR</td>
<td>0</td>
<td>0.019</td>
<td>0</td>
<td>0.046</td>
</tr>
<tr>
<td>DW</td>
<td>0</td>
<td>0</td>
<td>0.111</td>
<td>0</td>
</tr>
<tr>
<td>NE</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

immatures in their community as social partners, countering the paternal certainty hypothesis. Explanations for this preferential association will be explored below.

Although it could not be statistically examined using the data collected, it is possible that certain individuals like Mike, Dawson, and Frito were less likely to interact with the males because they were more nervous than other infants and juveniles around researchers; this is particularly likely for Dawson. Additionally, Frito, a juvenile male, had a bacterial or fungal infection during the time of the study that clearly caused him a great deal of pain. This may have interfered with his level of interactions with adult males.

Another explanation for this apparent pattern of preferred social partners, which could be tested with the data available, is that males preferred the offspring of particular females. Tukey’s Studentized (HSD) Tests were carried out to determine if there were significant differences in males’ interactions with the offspring of certain females. Results showed that males engaged in affiliative behavior (in minutes/hour) significantly more with Lucille’s offspring than Farafa’s (Tukey’s: p<0.05). No other pair-wise comparisons were significant
regarding this variable, nor were any pair-wise comparisons significant regarding any of the other variables (Tukey’s: $p>0.05$). Figure 4.9 shows, however, that there was a tendency for males to prefer the offspring of particular females, namely Lucille, Lingua, and to some extent Farafa. Females’ estrous cycles did not appear to affect whether or not males affiliated with their offspring. In fact, the average sexual swelling score of females whose offspring males played with was 0.07, and the average sexual swelling score of females whose offspring received any affiliative behavior from adult males was 0.21. The sexual swellings of the Fongoli chimpanzees are recorded on a 4 point scale, with 3 reflecting maximum tumescence. This suggests that males were not exclusively affiliating with the offspring of females when the females were in estrus.

Because it could not be tested using formal statistics, hypothesis one could not be rejected or accepted. However, it does appear that males prefer certain immatures as social
partners. Specifically, males may interact more often with the offspring of particular females.

4.6 Results for Hypothesis 2

Dominant males in the community will engage in affiliative behaviors with infants and juveniles more often than subordinate males.

On average, high-ranking males (ranks 1-3) interacted with immatures for 0.167 minutes per hour, mid-ranking (ranks 4-6) males did not interact with immatures, and low-ranking males (ranks 7-9) interacted with immatures for 1.573 minutes per hour (Figure 4.10). Additionally, high-ranking males interacted with immatures at a rate of 0.128 events per hour and low-ranking males interacted with immatures at a rate of 0.394 events per hour (Figure 4.11). During 127.75 hours of observation, the average number of times a high-ranking male was observed playing with an immature was 2.00; the average number of times a mid-ranking male was observed playing with an immature was 1.33; and the average number of times a low-ranking male was observed playing with an immature was 8.67 (Figure 4.12). Finally, on average, high-ranking males spent 1.76% of their time in close proximity to immatures. Mid-ranking males spent, on average, 1.55% of their time in close proximity to immatures. Low-ranking males spent an average of 4.66% of their time in close proximity to immatures (Figure 4.13).

Because low-ranking males consistently interacted more with infants and juveniles than high-ranking males for each of the four variables, hypothesis two was rejected. Dominant males did not spend more time interacting in affiliative interactions with immatures than did subordinate males. ANOVA results indicated that male dominance rank did significantly affect males’ interactions with juveniles and infants for two of the four
Figure 4.10 Average affiliation duration (in minutes/hour) for each male dominance category.

Figure 4.11 Average affiliation rates (in events/hour) for each male dominance category.
**Figure 4.12** Average number of play events for each male dominance category.

**Figure 4.13** Average time spent in close proximity for each male dominance category.
variables (affiliation duration: F=15.86, df\textsubscript{numerator} =2, df\textsubscript{denominator}=6, p=0.004; affiliation rate: F=1.82, df\textsubscript{numerator} =2, df\textsubscript{denominator}=6, p=0.242; play: F=8.38; df\textsubscript{numerator} =2, df\textsubscript{denominator}=6, p=0.018; percent time in close proximity: F=1.63, df\textsubscript{numerator} =2, df\textsubscript{denominator}=6, p=0.272; italicized values significant). As a result, Tukey’s Studentized (HSD) Tests were carried out to determine if low-ranking males interacted with immatures significantly more than higher ranking and mid-ranking males.

Low-ranking males engaged in affiliative behaviors (in minutes/hour) with infants and juveniles significantly more than did high and mid-ranking males (Tukey’s: p<0.05 for both pairs). Low-ranking males also played with infants and juveniles more than did high and mid-ranking males (Tukey’s: p<0.05 for both pairs). Although low-ranking males interacted with immatures at a higher rate (in events per hour) than both mid and high-ranking males, the difference was not statistically significant (Tukey’s: p>0.05 for both pairs). Finally, low-ranking males spent more time in close proximity to infants and juveniles than did both mid and high-ranking males; however, the difference was not statistically significant (Tukey’s: p>0.05 for both pairs).

4.7 Results for Hypothesis 3

Adult males will engage in affiliative interactions with juvenile and infant males more often than with juvenile and infant females.

Adult males interacted affiliatively with juvenile males at an average rate of 0.082 minutes/hour/juvenile male but did not interact affiliatively with the juvenile female. Males interacted affiliatively with infant males at an average rate of 0.207 minutes/hour/infant but did not interact affiliatively with infant females. In total, they interacted with infant and
juvenile males at a rate of 0.082 minutes/hour/male but never with infant and juvenile females (Figure 14.4).

Adult males engaged in affiliative events with juvenile males at an average rate of 0.023 events/hour/juvenile male and were not observed to engage in affiliative behaviors with the juvenile female. They engaged in affiliative events at an average rate of 0.115 events/hour/infant male and with infant females at an average rate of 0.021 events/hour/infant female. Males interacted affiliatively with all immature males at an average rate of 0.021 events/hour/male and with all females at an average rate of 0.010 events/hour/female (Figure 4.15).

Males engaged, on average, in 0.222 play events/juvenile male but were not observed to play with the juvenile female. On average, they engaged in 0.889 play events/infant male and 0.556 play events/infant female. The adult males engaged, on average, in 0.365 play events/male and 0.278 play events/female (Figure 4.16).

On average, adult males spent 0.190% of their time in close proximity to a juvenile male but none of their time in close proximity to the juvenile female. They spent, on average, 1.063% of their time in close proximity to an infant male and 0.125% of their time in close proximity to an infant female. Finally, on average, the adult males spent 0.362% of their time in close proximity to an immature male and 0.063% of their time in close proximity to an immature female (Figure 4.17).

T-tests were conducted to determine if the mean difference between males’ affiliative interaction rates for juvenile males and juvenile females differed significantly from zero. The mean difference did not vary significantly from zero among any of the four variables
Figure 4.14 Average adult male affiliation duration (in minutes/hour) with male and female juveniles and infants.

Figure 4.15 Average adult male affiliation rates (in events/hour) with male and female juveniles and infants.
Figure 4.16 Average number of play events between adult males and male and female juveniles and infants.

Figure 4.17 Average time adult males spent in close proximity to male and female juveniles and infants.
(affiliation duration: $t=1.48$, df=8, $p=0.177$; affiliation rate: $t=1.82$, df=8, $p=0.106$; play events: $t=2.17$, df=8, $p=0.062$; percent time in close proximity: $t=1.46$, df=8, $p=0.183$). T-tests were also carried out to determine if the mean difference between the affiliative interaction rates of infant males and infant females differed significantly from zero. The mean difference did not differ significantly from zero in any of the four variables (affiliation duration: $t=1.64$, df=8, $p=0.140$; affiliation rate: $t=1.46$, df=8, $p=0.183$; play events: $t=1.33$, df=8, $p=0.219$; percent time in close proximity: $t=2.15$, df=8, $p=0.064$). Finally, T-tests were carried out to determine if the mean difference between the affiliative interaction rates of all (juvenile and infant) males and all females differed significantly from zero. The mean difference did not differ significantly from zero for any of the four variables (affiliation duration: $t=2.13$, df=8, $p=0.066$; affiliative rate: $t=1.37$, df=8, $p=0.209$; play events: $t=0.93$, df=8, $p=0.378$; close proximity: $t=2.16$, df=8, $p=0.063$). Although adult males interacted with juvenile and infant males more often than they did with juvenile and infant females, the difference was not significant. Thus, there was no evidence to support the hypothesis. However, this may have been due to small sample size.

4.8 Results for Hypothesis 4

*Adult males will engage in affiliative interactions with juveniles more often than with infants.*

Adult males engaged in affiliative behaviors with juveniles at an average rate of 0.068 minutes/hour/juvenile and they engaged in affiliative behaviors at an average rate of 0.138 minutes/hour/infant. The males engaged in affiliative events with juveniles at an average rate of 0.012 events/hour/juvenile, and with infants at an average rate of 0.041 events/hour/infant. Adult males engaged in an average of 0.481 play events/juvenile and an average of 0.556
Finally, they spent, on average, 0.310% of their time in close proximity to a juvenile and 0.536% of their time in close proximity to an infant (Figure 4.18).

Because infants consistently interacted with adult males more with respect to each of the four variables, there was no evidence to support hypothesis four. T-tests for each of the four data categories were carried out to determine if the levels in which infants engaged in affiliative interactions with adult males were higher than those of juveniles. The mean difference between the rate at which males engaged in affiliative events with infants and juveniles was significantly different from zero ($t = -2.64$, $df = 8$, $p = 0.030$). The mean difference between the interaction rates of juveniles and infants did not differ significantly for the other three variables (affiliation duration: $t = -1.08$, $df = 8$, $p = 0.312$; play events: $t = -0.42$, $df = 8$, $p = 0.68$; percent time in close proximity: $t = -0.92$, $df = 8$, $p = 0.383$).

**Figure 4.18** Average male interaction rates with juveniles and infants.
Chapter Five: Discussion of Results

5.1 Introduction

The results of this study could be interpreted in various ways. Because the lowest-ranking males associated affiliatively with infants and juveniles significantly more often than higher ranking males, it might be interpreted that this affiliative behavior is a mating strategy as suggested by van Schaik and Paul (1996). However, Bandit, the male who associated affiliatively with infants and juveniles most frequently, is thought to have been alpha male before 2005 and may have monopolized copulations at that time (J. Pruetz, personal communication). Since Bandit’s fall from the top rank happened recently, it is possible that he is associating affiliatively with infants and juveniles because he enjoys a high degree of paternal certainty.

Another explanation for low-ranking males affiliating with immatures may be related to the fact that lower ranking males do not spend as much time engaging in displays and other behaviors to assert their dominance as do higher ranking males (Goodall, 1986). As a result, they have more time to interact with infants and juveniles than higher ranking males who must constantly engage in displays to maintain their position in the dominance hierarchy. An alternative explanation may be that males simply have temperamental differences (King & Figueredo, 1997; Buirski et al., 1978) and, as a result, affiliate with infants and juveniles at different rates. However, not all of these explanations are mutually exclusive. For example, it is possible that low-ranking males have more time to associate affiliatively with juveniles and infants and that they also employ these affiliative interactions as a mating strategy. Thus, it is likely that more than one of the proposed explanations could explain the behaviors observed in this study.
5.2 Chimpanzee Mating Systems

Before discussing the possible explanations for the interactions between adult males and infant and juvenile chimpanzees, it is necessary to review the mating system of this species. Specific aspects of the mating system will be discussed in more detail below (section 5.3). Chimpanzees live in multi-male, multi-female groups in which both males and females have multiple sexual partners (Goodall, 1986). Theoretically, this causes males to be uncertain of their paternity. Females exhibit sexual swellings that are thought to act as graded signals because they become increasingly larger as a female nears ovulation and reach their maximum size when a female is ovulating (Deschner et al., 2004).

Among chimpanzees there are four distinct mating patterns. Tutin (1979) outlines the three main patterns: opportunistic mating, possessiveness, and consortships. In opportunistic matings, all males within a community are able to mate with estrous females. During possessive matings, a high-ranking male restricts lower-ranking males’ access to receptive females. Consortships occur when a male of any rank travels alone with an estrous female and her dependent offspring, sometimes for a period of days. During this time, the male maintains exclusive mating access to the female (Tutin, 1979). Finally, recent work has shown that females mate with males outside of their community, although the degree to which this occurs is still widely debated (Vigilant et al., 2001; Gagneaux et al. 1999, 1997; Sugiyama, 1993). Although there are several mating strategies employed by chimpanzees, dominance is thought to affect a male’s reproductive success. This is a topic that will be explored in more detail below.
5.3 Affiliative Interactions as a Mating Strategy

Predictions of this Hypothesis

Van Schaik and Paul (1996) provide three predictions that should be met if primate males are using affiliative interactions with infants and juveniles to gain reproductive benefits. First, they suggest that older males should care for infants more frequently than younger males. This is because these older males are unable to engage in extravagant displays and fighting behaviors that indicate their fitness to females. Despite these limitations, van Schaik and Paul (1996) argue that these males can still gain reproductive benefits through caring for females’ young. Next, the authors suggest that the infants of more ‘attractive’ females should be cared for more frequently than the offspring of less ‘attractive’ females. Finally, they argue that male care should be more prevalent in species where females are better able to choose their mating partners. If females are not able to exert their preference for sexual partners, then the van Schaik and Paul (1996) hypothesis has no value.

I will argue that the results of this study and other research involving chimpanzees support the three criteria put forth by van Schaik and Paul (1996), with slight modification to the first prediction. Additionally, van Schaik and Paul (1996) use the term ‘male care’ to describe the interactions between males and young. They follow Woodroffe et al.’s (1994) definition of care, which maintains that male care includes all behaviors that benefit an immature and would not be carried out in the absence of the immature. Some of the affiliative interactions in this study meet this definition; others, like affiliative touches, may not accrue benefits. Nonetheless, these behaviors may still provide males with greater access to receptive females.
**Dominance Status and Reproductive Success in Chimpanzees**

Van Schaik and Paul (1996) maintain that older males should engage in care behaviors more frequently than younger males because they are less able to engage in behaviors that showcase their health and ‘good’ genes. Because the Fongoli site is a relatively new one, the exact ages of the members of the community are unknown. Although age ranges can be estimated from dentition, muscle mass retention, and pigmentation of the face (J. Pruetz, personal communication), they cannot be determined exactly. Therefore this prediction cannot be tested directly. However, most researchers widely acknowledge that, among chimpanzees, dominant males, and specifically the alpha male, are able to monopolize matings with females during the period of maximum tumescence of their sexual swellings (Boesch et al., 2006; Klinkova et al., 2005; Constable et al., 2001; Houlden et al., 1997; Nishida, 1997). This suggests that dominant males are more ‘attractive’ mates than subordinate males. Van Schaik and Paul maintain that “older males should perform more infant care than younger, dominant males to again increase their attractiveness as mates” (1996: 154). Thus, for the purposes of this study, male rank seems to reflect the same information about status as van Schaik and Paul (1996) argue age will reflect.

As mentioned above, most studies show that dominant male chimpanzees are able to monopolize copulations with females (Matsumoto-Oda, 1999; Takasaki, 1985; Nishida, 1983), and several studies have shown that high-ranking males have higher reproductive success than lower ranking males (Boesch et al., 2006; Klinkova et al., 2005; Constable et al., 2001; Takenaka et al., 1993). As a result, it appears that these males enjoy higher reproductive success than their lower-ranking conspecifics. However, three studies found no relationship between male rank and number of copulations (Meier et al., 2000; Takahata et
However, the Takahata et al. (1996) study did not employ paternity tests to measure reproductive success, thus weakening their claims. Nonetheless, most studies seem to support the argument that more dominant males enjoy higher levels of reproductive success than their subordinates.

If higher ranking chimpanzee males have such high levels of reproductive success, can low-ranking males gain any benefits from associating affiliatively with the young of females? It does appear that these males can gain some reproductive benefits despite the dominant males’ relatively high levels of reproductive success. Several authors have shown that the relationship between male rank and access to cycling females is more complex than a simple linear relationship. In two independent captive studies, Houlden et al. (1997) and Klinkova et al. (2005) found that although the alpha male sired a majority of offspring in the community, other males were also able to father young. Additionally, Constable et al. (2001) found that low-ranking males were able to sire offspring, although they were most successful in doing so when they formed consortships with females. This indicates that although alpha males may have a reproductive advantage, they are not the only males producing offspring in chimpanzee communities.

Nishida (1997) found that alpha male chimpanzees in the wild were able to copulate with females more frequently during the periods when they were most likely to conceive. Interestingly, their allies were also able to mate with females during this time, while their rivals were not. This shows that factors other than an individual’s dominance may impact his access to peri-ovulatory females. If males do use affiliation with young as a mating strategy and they are allies of the alpha male, it is possible that not only will the alpha allow them to mate, but also that females will accept them as sexual partners.
It also appears that within chimpanzee communities the number of males present affects high ranking males’ ability to restrict subordinate males’ mating access to receptive females. The priority of access model maintains that among primate males, access to females is limited not only by dominance but also by the number of males in a population and the number of females cycling at one time (Cowlishaw & Dunbar, 1991; Dunbar, 1988). Following this model, the number of competing males in a chimpanzee community may also impact the reproductive success of alpha males. Boesch et al. (2006) found that when there was a high level of male competition in a wild chimpanzee community (5-9 males present), the reproductive success of the alpha male decreased from 67% to 38%. This is thought to be the result of the alpha male’s limited ability to guard cycling females in larger groups. Boesch et al. (2006) also found evidence that, as more females were simultaneously receptive, the alpha male’s reproductive success decreased. Because the Fongoli chimpanzee community has eleven adult males, it is unlikely that the alpha male will be able to restrict subordinate males’ access to estrous females as easily as he could if the community was smaller. It is likely, then, that subordinate males at Fongoli are able to gain access to cycling females.

Newton-Fisher (2004) found that lower-ranking chimpanzee males at Budongo, Uganda are able to gain more access to receptive females when the dominance hierarchy is unstable. Stumpf and Boesch (2005) found similar results at Tai; they noted that multiple factors influenced males’ reproductive success, among them the stability of the male dominance hierarchy. These authors determined that females preferred younger to older males in the two communities studied. Additionally, they found that both high-ranking and low-ranking males were preferred to mid-ranking males. The low-ranking males eventually
ascended to the position of alpha male so it is likely that females are able to predict such changes in the dominance hierarchy and behave accordingly.

Although it is unlikely that any of the low-ranking males at Fongoli will move up in the dominance hierarchy because of their old age, Stumpf and Boesch’s (2005) study shows that male-female relations among chimpanzees are not reducible to male age and dominance ranks. The authors note that other factors like “male aggression and affiliation, other cycling females, and individual preferences” may affect mating patterns among chimpanzees (Stumpf & Boesch, 2005: 521). In addition, their study shows that female choice is an important factor in the chimpanzee mating system. In other words, high-ranking males are not able to monopolize copulations via dominance rank alone; females have some control as well. This topic will be discussed in more detail below. The studies discussed above suggest that while high-ranking males have a distinct advantage in gaining access to estrous females when they are most likely to conceive, low-ranking males are not completely excluded from the mating pool.

It seems likely that low-ranking chimpanzee males need to engage in unique mating strategies to gain access to receptive females. The findings of the current study suggest that they may do so by engaging in affiliative interactions with the offspring of females, as suggested by van Schaik and Paul (1996). As noted in chapter four, low-ranking males engaged in affiliative interactions with juveniles and infants significantly more than did high-ranking and mid-ranking males. These low-ranking males also played with infants and juveniles significantly more than did higher ranking males. Additionally, they engaged in affiliative behaviors at a higher rate per hour and spent more time in close proximity to infants and juveniles than did higher ranking males, although these differences were not
significant. These findings are consistent with van Schaik and Paul’s (1996) prediction that less ‘attractive’ (e.g. low-ranking) males will engage in affiliative behaviors with young more frequently than more ‘attractive’ males.

Interestingly, mid-ranking males interacted affiliatively with infants and juveniles less frequently than low-ranking males. This is somewhat puzzling because both Houlden et al. (1997) and Klinkova et al. (2005) found that, although high-ranking males had the highest reproductive success, their subordinates’ reproductive success was relatively similar. In other words, mid-ranking and low-ranking males produced young at similar rates. If this is the case, it would be expected that mid-ranking and low-ranking males would interact with infants and juveniles at similar rates. It is possible that mid-ranking males are better able to showcase their ‘good’ genes through displays than are low-ranking males. As a result, low-ranking males may have more to gain through affiliative interactions with immatures. Nonetheless, it appears that the Fongoli chimpanzees meet the first criterion put forth by van Schaik and Paul (1996).

Affiliative interactions with immatures may help low-ranking chimpanzee males gain consortships with females. Tutin (1979) notes that, in theory, low-ranking males could greatly benefit from consortships because they allow males to have exclusive access to receptive females. This has been supported with genetic evidence by Constable et al. (2001) at Gombe. Tutin (1979) also points out that, when data was pooled, females prefer males with whom they spend the most time. Additionally, females prefer males who direct more affiliative behavior towards them (Tutin, 1979). Females may prefer these affiliative males because their infants may gain benefits from future interactions with them (Tutin, 1979). Directing affiliative behavior towards the offspring of females may have similar results.
Therefore, it is possible that low-ranking males may gain opportunities for consortships by directing affiliative behavior toward infants and juveniles.

**Preference for the Offspring of More ‘Attractive’ Females**

Van Schaik and Paul (1996) argue that if males are using affiliation with young to gain access to females, they should spend more time associating with the offspring of more ‘attractive’ females, i.e. those females who are preferred sexual partners. This is an interesting claim because it raises the issue of male choice in mating partners. Bateman (1948) argues that eggs are larger than sperm and therefore more energetically costly to produce. As a result, males and females differ in the ways in which they can optimize their reproductive success. Males, in order to do so, should fertilize many eggs. Therefore male reproductive success is limited by the number of sperm that successfully fertilize eggs. Females, on the other hand, generally do not increase their reproductive success by mating with multiple males. Their reproductive success, then, is limited by their ability to produce eggs and to successfully rear their offspring. As a result, males have long been thought to be less stringent in their choice of mates than females (Trivers, 1972).

Recent work has focused attention on male choice of mating partners and shown that both sexes may be choosy (as reviewed in Manson, 2007; Paul, 2002; Cunningham & Birkhead, 1998; Johnstone et al., 1996). This has been supported among chimpanzees by the recent work of Muller et al. (2006). These authors found that male chimpanzees at Kibale, Uganda solicited more copulations with older females. Additionally, the number of males present in a party was greater when older females were in estrus than when younger ones were. Muller et al. (2006) argue that this indicates that males may be choosy about their mating partners. In addition, it has been suggested that male chimpanzees prefer parous
females, those who have given birth, over nulliparous females, those who have not given birth (Muller et al., 2006; Takahata et al., 1996; Tutin, 1979). This is important to this study for two reasons. First, it provides additional support that male choice is a real phenomenon among chimpanzees. Second, it shows that males will preferentially mate with females who have given birth. Less ‘attractive’ males (e.g. lower-ranking males) should employ strategies to gain copulations with these females. One way in which they may gain access to these females is by interacting with her offspring.

It is, of course, impossible to compare male association with the young of nulliparous and parous females since nulliparous females have no offspring. Still, it raises the issue of male preference among chimpanzees. Pusey et al. (1997) found that dominant females are significantly more reproductively successful than their lower ranking counterparts. It seems likely, then, that males would preferentially mate with these females because the offspring they produce with dominant females are more likely to survive to adulthood. Unfortunately, the female dominance hierarchy is not yet well understood at Fongoli. Still, some females are clearly dominant to others and also more ‘attractive’ to males as mating partners (J. Pruetz, personal communication). Therefore, some estimates of female ‘attractiveness’ can be made for the chimpanzees at this site.

As discussed in chapter four, the offspring of certain females at Fongoli seem to be the focus of male affiliation. In particular, males associated with the offspring of Lucille and Lingua frequently and, to a lesser extent, males engaged in affiliative interactions with Farafa’s offspring. Although it has not yet been quantified, it has been noted that males are particularly interested in Lucille when she is in estrus, compared to other females (J. Pruetz, personal communication). It is also interesting that Lingua, Lucille, and Farafa’s offspring
are the most popular, because these three females have at least two offspring. If females become more ‘attractive’ after having given birth, it is possible that their ‘attractiveness’ rises after multiple births.

Furthermore, Nene’s daughter Nellie was never the recipient of male affiliation. During the course of the study, Nene cycled regularly but attracted little attention from the males in the Fongoli community. The likely explanation for this is that she appears to have some sort of infection. When in estrus, her sexual swelling appears scabbed and irregular. This seems to dramatically decrease her sexual ‘attractiveness’ to the males of the community because no copulations were observed between Nene and males in 2006, although males did copulate with her in 2005 (J. Pruetz, personal communication). If males are using affiliation with females’ offspring as a mating strategy, then it is logical that they would not associate with Nene’s daughter. This provides further support that males are preferentially associating with the offspring of more ‘attractive’ females.

Although they are preliminary, the results of this study appear to meet the second criterion put forth by van Schaik and Paul (1996). Males appeared to prefer the offspring of Lucille, a highly ‘attractive’ female, to the daughter of Nene, a less sexually ‘attractive’ female. As the female dominance hierarchy is better understood and as females’ ‘attractiveness’ is quantified, it is possible that these results will be empirically confirmed.

**Female Choice among Chimpanzees**

The final criterion that van Schaik and Paul (1996) propose is that male care should occur more frequently in species in which females have more freedom to select their mates. Although it was once overlooked, the issue of female choice has become an important part of primate studies (as reviewed in Mason, 2007; Tang-Martinez, 2000). Although the level of
female choice among chimpanzees was not explored in this study, several researchers have recently considered this topic. Their work will be reviewed below.

Recently authors have considered the evolutionary function of the sexual swellings seen in chimpanzees and several other Old World primate species (Deschner et al., 2004; Nunn, 1999; Pagel, 1994). One explanation that has been proposed is that these swellings serve as reliable indicators of the health of the female. In other words, males can gauge the quality of a female’s genes from her sexual swelling (Pagel, 1994). To some extent this hypothesis seems to preclude female choice; males compete for access to females and the females mate with the ‘best’ male. An alternative explanation that has been proposed is the graded-signal hypothesis (Nunn, 1999). This theory maintains that a female’s swelling increases in size as she gets closer to ovulation. It reaches its maximum tumescence when the female is ovulating. This hypothesis allows females greater choice because they are able to mate with multiple males throughout the estrous period. This is because dominant males are most interested in females during times of peak swelling and do not try to monopolize them outside of this time frame (Nunn, 1999).

Deschner et al. (2004) have found compelling evidence to support the graded-signal hypothesis among chimpanzees. The authors found that chimpanzee sexual swellings increase in size the closer a female is to ovulation, and they reach their maximum size when a female is most fertile. Additionally, dominant males are most interested in females when their swellings are largest but do not try to restrict copulations when the swellings are smaller. Thus, it seems that sexual swellings are an indicator of a female’s increasing level of fertility during estrus. Although dominant males were able to secure most of the
copulations with females during times of maximum tumescence, the probability of low-ranking males mating with females was still greater than zero (Deschner et al., 2004).

Matsumoto-Oda (1999) and Stumpf and Boesch (2005) have found evidence that this graded signaling allows females to employ two mating strategies. They are able to mate with multiple males when their swellings are smaller and they are, therefore, less likely to conceive. During times of maximum tumescence, females mate with fewer males. Matsumoto-Oda (1999) found that females at Mahale, Tanzania were most likely to mate with high-ranking males during this period. As discussed above, Stumpf and Boesch (2006) found that females at Tai mated with both high and low-ranking males but resisted mid-ranking males during the period when their swellings were largest. Although these low-ranking males soon ascended to the alpha position, it shows that females do have control over their mating partners. Copulations during times of maximum tumescence are not simply reducible to control by the dominant male. Instead, females are able to accept and resist male sexual advances (Stumpf & Boesch, 2006).

Researchers have argued that female chimpanzees may actually mate extensively outside of their community (Gagneux et al., 1999; 1997; Sugiyama et al., 1993). This would suggest that females have even greater freedom of choice than was once perceived; they are not limited to the males within their community. More recent work suggests that the levels of extra-group copulations estimated by Gagneux et al.’s (1999; 1997) are much too high (Vigilant et al., 2001). However, these authors note that some extra-group matings do occur; they are simply not as great as Gagneux et al. (1999; 1997) propose. Thus, it appears that, to some extent, female chimpanzees at some sites are able to choose to mate with males outside of their community.
Recent work makes it clear that female chimpanzees are able exert some control over their choice of mating partners. However, this does not indicate that females factor things like ‘friendship’ into their decision-making process. Nonetheless, other studies have found evidence that females may consider such factors in their selection of mating partners. Hemelrijk et al. (1992) found that in a captive chimpanzee community, females were groomed more often when in estrus. In addition, they were groomed more often by the males with whom they copulated more frequently. The authors argue that this reflects an exchange of grooming for copulations. In a later study, however, Hemelrijk et al. (1999) found no correlation between grooming levels and a male’s reproductive success. They argue, then, that this exchange system is non-existent or that it does not equate to increased male reproductive success.

Stopka et al. (2001) respond to Hemelrijk et al.’s (1999) claims and point out that they do not consider the many factors that affect a female’s choice to copulate. Stopka et al. (2001) argue that no direct, linear relationship will exist between a male’s grooming rates and copulations secured. This is because lower ranking males will have to compensate more. They are not high-ranking and are less ‘attractive.’ Therefore they are expected to groom at higher rates than high-ranking males. Hemelrijk et al. (1999) did not take this into account when conducting their study. Additionally, Stopka et al. (2001) note that males cannot control their overall reproductive success; in other words, they cannot control how many eggs their sperm fertilize. What they are able to manipulate is the number of copulations they secure, thus, increasing the likelihood that they will produce more offspring. They note the importance of this because Hemelrijk et al.’s (1992) earlier study found a correlation
between grooming and number of copulations, suggesting that grooming may be used as a mating strategy (Stopka et al., 2001).

The preceding discussion has shown that among chimpanzees, females are able to exercise some choice in the selection of their mating partners. During the time when they are less likely to conceive, females mate promiscuously with multiple males. When females are more fertile, they are more selective in choosing their mating partners (Stumpf & Boesch, 2006; Deschner et al., 2004; Matsumoto-Oda, 1999). Although dominant males are typically favored during periods of maximum tumescence, low-ranking males are also able to secure some matings (Stumpf & Boesch, 2006; Deschner et al., 2004). Moreover, there is evidence that males may use affiliative behavior to gain mating opportunities with females (Stopka et al., 2001; Hemelrijk et al., 1992).

It seems that the final criterion put forth by van Schaik and Paul (1996) is met to some degree in this study. They argue that more care should be seen in species in which females have greater control over their choice of mates. Because this is not a cross-species study, direct comparisons cannot be made between amount of female choice and level of male care. Nonetheless, it seems that some care should be seen in chimpanzees because females are able to choose their mating partners, to some extent. Moreover, if, as suggested by Hemelrijk et al. (1992) and Stopka et al. (2001), grooming can be exchanged for copulations, it seems likely that affiliative interactions directed at the offspring of females may also incur similar benefits.

**Affiliation with Young as a Mating Strategy?**

This study provides preliminary evidence that chimpanzee males may affiliate with the offspring of females to gain mating opportunities. Most notably, this study,
supplemented by the research of other authors, meets the three predictions put forth by van Schaik and Paul (1996). Less ‘attractive’ (i.e. low-ranking) males interact affiliatively with infants and juveniles more frequently than higher ranking males. Additionally, this study provides preliminary evidence that the offspring of more sexually ‘attractive’ females are favored over those of less ‘attractive’ females. Finally, several studies have shown that female chimpanzees are able to choose their mating partners (Stumpf & Boesch, 2006; Matsumoto-Oda, 1999). Therefore it seems likely that low-ranking males may employ mating strategies to gain access to estrous females.

High-ranking males have been observed to form coalitions with other males to guard estrous females (Watts, 1998). By allowing one or two other males to mate with females, the dominant male may reduce his own reproductive success. However, in large parties males cannot control exclusive access to females. By cooperating with other males, the high-ranking male can increase his own reproductive success by limiting the total number of males who have access to females in estrus (Watts, 1998). Clearly, this strategy cannot be employed by low-ranking males, but it is likely that they have developed their own strategies to gain access to receptive females.

As discussed above, low-ranking males are less likely to mate with estrous females than high-ranking males; however, these low-ranking males are not completely excluded from the mating pool. Because they cannot control the actions of high-ranking males, it seems that low-ranking males should employ mating strategies that rely on aspects that they can control. Theoretically, these males can gain reproductive benefits by engaging in behaviors that label them as good mates. By engaging in affiliative interactions with a female and her young, males may increase the time they spend in close proximity to females.
Additionally, they may ‘prove’ themselves as better mates (van Schaik & Paul, 1996) and, thus, gain reproductive benefits through these behaviors. If males are indeed employing this strategy, it is to gain long-term benefits. In other words, males are not associating with the offspring of females only when the females are in estrus. Instead, it may be a long-term strategy that accrues reproductive benefits over time.

The results of this study are, of course, preliminary. They do raise interesting research questions to be discussed in the next chapter. As noted in the introduction of this chapter, although it seems likely that low-ranking males may associate with females’ offspring to gain reproductive benefits, other factors may explain the affiliative behavior observed. Because the findings of this study are preliminary, it is necessary to explore these alternative explanations below.

**5.4 Affiliation as a Reflection of Paternity**

As discussed in the introduction of this chapter, Bandit was the male most frequently observed to interact affiliatively with infants and juveniles. Bandit was thought to be the dominant male until 2005 before falling from rank and loosing the alpha position to Foudouko. Moreover, it appears that he was able to monopolize copulations with females during this time (Pruetz, personal communication). Additionally, it is likely that most of the infants and juveniles in the community were born or conceived before Bandit’s loss of rank (J. Pruetz, personal communication). Because alpha males are thought to enjoy a high level of reproductive success (Boesch et al., 2006; Klinkova et al., 2005; Constable et al., 2001; Houlden et al., 1997), it is possible that Bandit was associating affiliatively with infants and juveniles because he could be relatively certain of his paternity.
It has been suggested that males may invest in their offspring if doing so will improve their overall reproductive success. Clutton-Brock (1991) notes that in these situations, the likelihood of young surviving should be greater if both parents invest in the offspring than if only one parent does. In order to be considered a form of investment, the parent should accrue a fitness cost to benefit their offspring (Trivers, 1972). Thus, male care should increase with increased paternal certainty (Higley & Suomi, 1986; Kleiman & Malcolm, 1981; Bales, 1980). However, as discussed in chapter two, there are several primate species that do not fit this model.

There is some evidence for male investment in offspring among chimpanzees despite the paternal uncertainty in their social system. For example, chimpanzee males often patrol the boundaries of their territory and ward off males from other communities (Goodall, 1986); Trivers (1972) defines territory defense as a type of paternal investment. However, such behavior has not been observed at Fongoli (J. Pruetz, personal communication). Evidence has also been found that chimpanzees are able to recognize kin (Parr and de Waal, 1999). Therefore it is possible that chimpanzee males are able to recognize their offspring and may invest in them accordingly. Interestingly, Buchan et al. (2003) found evidence that savanna baboon (*Papio cynocephalus*) males are not only able to identify their offspring, they also defend them in agonistic interactions. Because this defense has real benefits for the offspring of the males, these authors argue that they have found an example of true paternal care in a species that lives in multi-male groups. Chimpanzees also live in groups with multiple males (Goodall, 1986), and Buchan et al.’s (2003) study shows that this may not exclude the possibility of direct paternal care.
Although there is evidence that male chimpanzees may know the identity of their offspring and care for them accordingly, other studies provide less support. Pruetz and Bloomsmith (1995) found that captive male chimpanzees did not preferentially associate with any of the young in their group, including their own offspring. The males in their study did, however, engage in more affiliative compared to aggressive interactions with their own offspring compared to the young of other males, although the difference was not statistically significant. Despite these data, Pruetz and Bloomsmith’s (1995) work suggests that, at least in captivity, chimpanzee males do not prefer their own offspring.

Recent work that has explored altruism in chimpanzees has found that kin selection (Hamilton, 1964) is not always the best indicator of altruistic behavior. In Watts’ (1998) study of coalitionary mate guarding in chimpanzees, he found that kin selection may explain some of the coalitions formed, but it could not account for all of them. Some of the coalitions were likely examples of reciprocal altruism. Additionally, it has long been assumed that male chimpanzees in a community associated with one another because they were closely related, given that male chimpanzees remain in their natal communities (Morin et al., 1994; Goodall, 1986). However, Goldberg and Wrangham (1997) found that peer groups were a more accurate predictor of male affiliative dyads than maternal relatedness. These findings suggest that affiliative behavior among chimpanzees cannot always be reduced to kinship. Therefore, even if alpha males can be relatively certain of their paternity, kin selection alone may not explain male relationships with infants and juveniles in their community.

As discussed above, Bandit interacted affiliatively with infants and juveniles more frequently than other males, and he may have a higher degree of paternal certainty than the
other males in the Fongoli community. Stumpf and Boesch (2006) and Newton-Fisher (2004) found that alpha males were less likely to monopolize access to sexually receptive females when the dominance hierarchies were unstable. This may mean that as Foudouko’s ascension in the dominance hierarchy drew nearer, Bandit lost his ability to monopolize matings and, as a result, may have a lower degree of paternal certainty.

Many of the affiliative behaviors observed in this study do not clearly fit the definition of male care. Male care is a behavior that benefits infants and juveniles and would not be carried out in the absence of the infants and juveniles (Woodroffe et al., 1994). Behaviors like affiliative touches may not have extensive benefits for immatures. In addition, males incur little costs by engaging in these behaviors; they simply expend limited energy and time. Because the benefits to infants and juveniles are not great, and because males do not incur significant costs for many of the affiliative behaviors observed, paternal certainty may not be the best model to explain this affiliative behavior.

Although it does not appear that paternal certainty can explain the affiliative behavior observed between adult males and infants and juveniles at Fongoli, it cannot be completely discounted. Because the study site is a relatively new one and because paternity is not known for the juveniles and infants at the site, the explanation of paternal certainty may have merit that has not yet been empirically tested. Still, given the results of this study it appears more likely that males may be affiliating with infants and juveniles as a mating strategy.

5.5 Time Restrictions and Temperamental Differences

It is possible that differences in time constraints placed on low-ranking and high-ranking males may explain the differences in the affiliation rates of these groups. Additionally, temperamental differences and their relationship to dominance may explain the
behaviors observed. Therefore, it is necessary to consider how these two factors differ between high and low-ranking males.

Goodall (1986) observed that high-ranking males displayed more frequently than lower ranking males. Additionally, it has been well documented that high-ranking male chimpanzees must make an active effort to maintain their dominance (Nishida & Hosaka, 1996; Goodall, 1986). The differences between the demands on low-ranking and high-ranking males have been further supported by hormonal analysis (Muehlenbein et al., 2004; Muller & Wrangham, 2004 a,b). Two independent studies have found that higher ranking males have higher levels of testosterone (Muehlenbein et al., 2004; Muller & Wrangham, 2004b). The authors of these studies suggest that this may be a result of the chimpanzee fission-fusion social structure. Because high-ranking males are not always with their competitors, they cannot be sure when their rank will be challenged. As a result, their testosterone levels could be constantly high because these males may have to defend their position at any time.

Klinkova et al. (2004), however, found no relationship between testosterone levels and male rank. However, their study was conducted in a captive setting so it is unlikely that these males experienced the same type or degree of stress as the wild chimpanzees in the aforementioned studies (Muehlenbein et al., 2004; Muller & Wrangham, 2004b). Muller and Wrangham (2004a) also found that higher ranking males had higher levels of cortisol, suggesting they were under more stress than their lower ranking conspecifics. It is likely that these increased cortisol levels among males are a result of increased metabolic stress. In other words, being a dominant male has high energetic demands.
The preceding studies make it clear that dominant males are under a considerable amount of stress and must make an active effort to maintain their dominance status. As a result, they designate a significant amount of their time to maintaining their dominant status (Goodall, 1986). Therefore it is possible that high-ranking males simply do not have the same amount of time to engage in affiliative interactions with juveniles and infants as low-ranking males do. In other words, low-ranking males may interact affiliatively with juveniles and infants more frequently because they have more free time. What is interesting about this explanation is that mid-ranking males interacted with juveniles at lower rates than both low-ranking and high-ranking males. Because chimpanzee males typically only display in the presence of lower-ranking males (Goodall, 1986), it would be expected that mid-ranking males would display more than low-ranking males but less than high-ranking males. If time constraints are the limiting factor in male interactions with infants and juveniles, then mid-ranking males would be expected to interact at a higher rate than high-ranking males. This suggests that while time constraints may affect male-immature interactions, other factors are probably involved as well.

Temperamental differences may also explain the variance in affiliation rates between males. King and Figueredo (1997) found that captive chimpanzees had personality differences similar to that of humans. Moreover, these differences could be identified relatively consistently by the zoo staff that cared for them. Buirski et al. (1978) also found that wild chimpanzee temperaments could be identified consistently by researchers. Furthermore, Buirski et al. (1978) found that certain personality traits were associated with dominance. Among these traits were ‘aggressiveness’ and ‘distrust.’ Low-ranking males were associated with traits such as ‘trust’, ‘timidity’, and ‘impulsiveness’ (Buirski et al.,
This suggests that low-ranking males may have less intimidating temperaments than high-ranking males and, as a result, serve as better social partners for juveniles and infants.

5.6 Sample Size

As discussed in chapter four, the sample size for this study was small given time constraints. This made statistical testing difficult for some hypotheses and prevented statistical analysis of hypothesis one. It also may have affected the testing of hypothesis three, which hypothesized that juvenile and infant males would interact affiliatively with adult males more than juvenile and infant females. Because there was only one infant female who was considered a social partner and one juvenile female in the community, factors other than sex may have affected their interaction rate with males. For example, Fanta, the infant female, is the sister of Frito, a juvenile male with an infection that made walking difficult. Males may not have been able to interact often with Fanta because she and her mother were often separated from the group as they waited for Frito. A longer study may eradicate some of the problems caused by small sample size.

5.7 Benefits to Infants and Juveniles

The preceding discussion has considered how affiliative interactions between adult male chimpanzees and infants and/or juveniles may benefit males. This is not to say, however, that the interactions had no benefit for the immatures. Among mountain gorillas (Gorilla beringei berengei), it has been found that immatures are responsible for creating social situations in which they can interact with the silverback (Stewart, 2001). Stewart (2001) has suggested that increased juvenile interest in adult males comes during the weaning phase, and that immatures may associate with males in order to alleviate the tension created between mother and offspring during weaning. Pusey (1983) has provided evidence
that a similar conflict arises between mother chimpanzees and their offspring during the weaning phase. It is possible, then, that immature chimpanzees may begin to associate more readily with adult males to relieve stress during this difficult period. Although this study did consider weaning effects, this is one benefit that young chimpanzees could theoretically gain through their association with males.

Another benefit to associating with adult males may be that these interactions create situations for social learning. King (1994) has found that active teaching among primates is extremely rare. As a result, immatures are often responsible for creating social situations from which they can learn (King, 1994). Thus, immature chimpanzees may initiate social interactions with males in order to foster an environment for social learning. Such interactions may be especially useful for immature males because adult males can serve as examples as these immatures prepare to fill their future social roles within the community (Pusey, 1990).

If immatures are learning through their interactions with adult males, it is likely that males will gain more through these interactions than females (Pusey, 1990). This is because males will remain in their communities while females are likely to disperse. Additionally, male immatures will learn more about their future roles within the community through observing males than will immature females (Pusey, 1990). In a similar vein, the affiliative behavior that was observed most frequently between adult males and infants and/or juveniles was play. Walters (1987) notes that play may be a way for immatures to practice skills that they will use later in life. In particular, immatures may use play to practice behaviors that are too dangerous to carry out in their appropriate context. Therefore, juveniles can learn motor skills that are to be used later in life through play.
Among chimpanzees, males are more likely to need skills that are involved in fighting and intimidation because they must frequently display to maintain their dominance status (Goodall, 1986). Because these skills can be learned through play, it is likely that males will engage in this behavior more than females. Maestripieri and Ross (2004) have found distinct sex differences in play among gorillas; males engage in play more often than females. While chimpanzee males do not defend their groups in the same way as gorillas do, chimpanzees must defend their home ranges and may engage in fights with other males; therefore, it is likely that chimpanzees will exhibit similar patterns of play. As discussed in chapter four, male infants and juveniles engaged in affiliative interactions with adult males more than infant and juvenile females, although this difference was not significant. It is possible, then, that these sex differences were due to the fact that male immatures will benefit more from interactions with adult males than will immature females. It should be noted, however, that the sample size of females in this study was very small (n=2) and this may have affected the results.

It is clear that affiliative interactions with adult males have potential benefits for infants and juveniles. Although it is likely that males gain reproductive benefits through their associations with immatures, immatures may also gain social skills through these interactions. While the benefits to infants and juveniles were not explored extensively in this study, they provide an interesting direction for future research.

5.8 Relevance of the Study for Understanding Early Hominid Behavior

Because behaviors do not fossilize, it is extremely difficult to draw conclusions about the social structures that characterized our earliest hominid ancestors. As a result, the degrees of body size and canine size sexual dimorphism found in a species are often used as
indicators of social structure and mating systems. However, several researchers have argued that specific determinations of social structure and mating systems cannot be inferred in this manner (Plavcan, 2001; Plavcan, 2000; Plavcan & van Schaik, 1997; Frayer & Wolpoff, 1985). Recent studies have compared dimorphism levels of extant species and the mating and social patterns of these species (Plavcan, 2001; Plavcan, 2000; Plavcan & van Schaik, 1997; Frayer & Wolpoff, 1985). They have all found minimal evidence that correlations exist between body mass dimorphism and distinct mating patterns (Plavcan, 2001; Plavcan, 2000; Plavcan & van Schaik, 1997; Frayer & Wolpoff, 1985). It does seem, however, that polgyny or intense male-male competition for access to mates can be interpreted in cases where there is significant body or canine size sexual dimorphism (Plavcan, 2001; Plavcan, 2000; Plavcan & van Schaik, 1997).

* *Australopithecus afarensis,* an early example of a hominid and a likely ancestor of modern humans, showed significant levels of body size sexual dimorphism, probably similar to that of extant gorillas and orangutans (Lockwood et al., 1996). As discussed above, this suggests that this species exhibited a mating system in which males competed for access to females and mated with multiple females. Both chimpanzees and gorillas exhibit such mating systems, although chimpanzees show far less body size dimorphism than gorillas (Goodall, 1986; Harcourt et al., 1981). Therefore, both species may be able to provide us with insight about the social behavior of our earliest ancestors.

Van Schaik and Paul (1996) argue that male care may have evolved partially through its benefit as a mating strategy. This study has provided preliminary evidence that this may be the case for extant chimpanzees. Although gorillas were once thought to live primarily in groups with one adult male and multiple females, recent research has shown that two males
may live in a group with multiple females (Kalpers et al., 2003; Robbins, 1995). In these multi-male groups, the dominant male has greater access to sexually receptive females than the subordinate male but the lower ranking male is not completely excluded from the mating pool (Robbins, 1999). Although it has not empirically tested, it is possible that these low-ranking gorillas may interact with immatures in their group as a mating strategy. If this is the case and additional research supports the findings of this study, then such a mating strategy may be an ancestral ape behavior. In other words, if chimpanzees and gorillas exhibit the behavior, than early hominids may have as well. Again, this is only a hypothesized mating strategy for early hominids, but it raises interesting questions for future research.

5.9 Conclusion

The findings of this study provide preliminary evidence that low-ranking adult male chimpanzees may interact affiliatively with infants and juveniles to gain mating access to their mothers. This is supported by the fact that low-ranking males interact affiliatively with infants and juveniles significantly more than high-ranking males. In addition, the offspring of more ‘attractive’ females seem to be the preferred affiliative partners. Finally, chimpanzees live in a social structure in which females are able to choose their mates. Together, these factors indicate that affiliation may be a male mating strategy among chimpanzees.

This study also provides support for the hypothesis that early hominids may have employed a similar mating strategy. In addition, it provides direction for future research investigating the benefits of such interactions for immatures. Because this was a short study with a small sample size, more extensive research is needed to confirm its findings. These new directions for research will be explored in the following chapter. Nonetheless, this study
provides an intriguing perspective about the mating strategies of low-ranking male chimpanzees.

References


Chapter Six: Conclusion

6.1 Findings of the Study

The current study provides preliminary evidence that male chimpanzees may interact affiliatively with immatures as a mating strategy. Specifically, low-ranking males seem to prefer the offspring of more ‘attractive’ females as their social partners. Additionally, following the predictions put forth by van Schaik and Paul (1996) regarding this hypothesis, chimpanzee females are able to choose their mating partners (Stumpf & Boesch, 2006; Matsumoto-Oda, 1999). Although chimpanzees live in multi-male, multi-female groups in which males are able to mate with multiple females (Goodall, 1986), high ranking males typically secure a majority of the copulations (Matsumoto-Oda, 1999; Takasaki, 1985; Nishida, 1983) and tend to have higher reproductive success than low-ranking males (Boesch et al., 2006; Klinkova et al., 2005; Constable et al., 2001; Takenaka et al., 1993). Because they tend to display when in the presence of lower ranking males and not higher ranking males (Goodall, 1986), low-ranking males have limited opportunities to showcase themselves as mates in this way. Alternatively, they may gain mating benefits by behaving affiliatively with the offspring of females, demonstrating to females that they are helpful mates (van Schaik & Paul, 1996).

Tutin (1979) has suggested that low-ranking males should benefit the most from engaging in consortships because this mating pattern gives them exclusive access to receptive females. Additionally, she suggests that females may prefer males who direct affiliative behavior towards them. This hypothesis has been empirically tested and supported within a captive group of chimpanzees (Hemelrijk et al., 1992). Additionally, Boesch et al. (2006) found that the reproductive success of high-ranking males at Tai dramatically decreased as
the number of males in a party with an estrous female increased. High-ranking males were less able to guard receptive females when there were many males present. The Fongoli community has eleven adult male chimpanzees, so it is unlikely that high-ranking males will be able to maintain exclusive access to females.

Previous research on chimpanzees suggests that low-ranking males at Fongoli may be able to gain access to females in a number of ways. They may be able to obtain consortships with females, allowing them to travel with a female for several days while she is sexually receptive. Alternatively, they may be able to secure opportunistic matings when part of a larger party because high-ranking males are limited in their abilities to restrict access to receptive females. By directing affiliative behavior toward a female and her offspring, these low-ranking males may increase the likelihood that females will accept, and not reject, their sexual solicitations in both situations.

As was discussed in chapter five, there are several alternative explanations that could be used to explain the findings of this study. High-ranking male chimpanzees must display frequently in order to maintain their position in the dominance hierarchy (Goodall, 1986). Furthermore, they must constantly be prepared to defend their position in the dominance hierarchy; they can never be sure when another male is going to challenge their rank (Muehlenbein et al., 2004; Muller & Wrangham, 2004 a,b). This may limit the amount of time that they have to interact with immatures. Low-ranking males, on the other hand, do not have the same time constraints as high-ranking males. These males, then, may simply have more time to affiliate with infants and juveniles.

It has also been shown that chimpanzees have temperamental differences similar to that of humans; these temperaments can be consistently recorded by researchers that work
with the animals (King & Figueredo, 1997; Buirski et al., 1978). Buirski et al. (1978) found that certain temperamental traits like ‘trust’ and ‘timidity’ were displayed in low-ranking males, while high-ranking males were associated with traits like ‘aggression’ and ‘distrust.’ Therefore it is possible that low-ranking males are less intimidating to immatures than high-ranking males, and this is why low-ranking males interact affiliatively with immatures more frequently than higher ranking males.

These explanations are not necessarily mutually exclusive. Presumably, high-ranking males are able to gain their position in the dominance hierarchy, at least in part, because of their temperaments. Moreover, they are able to monopolize copulations with receptive females by chasing away other males (Tutin, 1979) and may even form coalitions to do so (Watts, 1998). It is logical to assume that low-ranking males have developed unique mating strategies that fit with their positions in the dominance hierarchy, and possibly with their temperaments. In other words, it is likely that chimpanzee mating strategies are dependent upon a variety of factors including social status and individual variability. This study provides preliminary support that low-ranking males affiliate with immatures as a way to gain mating access to their mothers.

6.2 Directions for Future Research

Because of the short duration of this study and because the Fongoli site is a relatively new one, the findings of this study are preliminary. Additional research is needed to test the hypothesis that low-ranking chimpanzee males associate affiliatively with immatures as a mating strategy. Alternatively, males may preferentially care for their own offspring, following the tenets of kin selection (Hamilton, 1964). Therefore, a long-term study should be developed to test both hypotheses.
Future research should use DNA analysis to determine paternity within a chimpanzee community. Several recent studies have shown that this is possible through fecal and hair analysis (Boesch et al., 2006; Constable et al., 2001; Vigilant et al., 2001). Determinations of paternity also allow for estimations of reproductive success to be made. Moreover, knowing paternity will allow researchers to determine if males are more likely to produce offspring with females when they direct affiliative behavior toward the females’ young. Because a male cannot control his reproductive success, only the number of copulations he gains (Stopka et al., 2001), males’ copulations rates should also be considered. Do males copulate more frequently with the females whose offspring they affiliate with? Are they able to secure more consortships with these females?

Additionally, a more detailed assessment of the females whose offspring are preferred should be conducted. Quantitative research should be done to consider whether certain females in the community elicit a greater response from males when cycling. Do males in the community sexually solicit particular females more often than others? Does the number of males in a party increase when particular females are maximally swollen? Dominance ranks among females should also be determined. Do males prefer to mate with more dominant females? Do males prefer the offspring of more dominant females? As noted in chapter five, Muller et al. (2006) found that older female chimpanzees at Kibale, Uganda were preferred mates. Correspondingly, do males prefer the offspring of older females? Another issue that should be explored is whether the offspring of ‘unattractive’ females receive any male affiliation.

Future research should also consider how male affiliation benefits immatures. Do the offspring gain fitness benefits through their affiliative interactions with males? Do these
encounters provide an atmosphere conducive to social learning? Furthermore, future studies should consider whether the sex differences observed in this project are reflective of larger patterns. As discussed in the previous chapter, male immatures were more often the recipients of male affiliation than females. However, the difference was not significant and may be the result of small sample size. However, Pusey (1990) did observe sex differences in behavior among immature chimpanzees at Gombe. Do male immatures benefit more from their interactions with adult males than females?

It is also possible that early hominids may have employed affiliation with immatures as a mating strategy. To test this possibility, comparative studies with both bonobos (Pan paniscus) and gorillas should be carried out. Such studies will suggest whether the behavior is a candidate for an ancestral trait of the African apes. If this is the case, then it is likely that the common ancestor of apes and humans demonstrated this trait and, correspondingly, it is likely that early hominids may have shown the behavior as well. Thus, further research may provide insight about the evolution of male care in hominids and humans.

6.3 Affiliation as a Mating Strategy?

In conclusion, this study provides preliminary evidence that low-ranking male chimpanzees may affiliate with immatures in their community in an effort to gain mating access to the immatures’ mothers. A much longer and detailed study is needed to test this hypothesis further. Specifically, this study raises many interesting questions that should be explored utilizing molecular technology and between-species comparisons. Still, the results of the study indicate that low-ranking male chimpanzees interact with immatures more often than their higher ranking conspecifics. These findings raise intriguing questions about the evolutionary reasons for these differences. Additionally, this study sparks questions about
the benefits not only to adult males and immatures but also the benefits to the mothers of the immatures. Future research on this topic will provide additional insights into the mating system of chimpanzees and possibly into the evolution of male care in humans.

References


Appendix: Ethogram

Ethogram adapted from Nishida et al. (1999).

**Agonistic Behavior**

*Aggressive behavior:* attack or threatening another group member. Behaviors include: attack, display, and threaten.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>attack</td>
<td>physical contact that is aggressive between two or more group members; includes: push, kick, hit, grab, slap, bite, drag, charge, stamp, pinch, and scratch</td>
</tr>
<tr>
<td>display</td>
<td>patterns include: throw, drag branch, sway branch, slap, stamp, flail, drum, rake, and occasionally beat chest, hair piloerection, compressed lips and face or pant hoots; when nonvocal is often directed toward another individual and is often used in male dominance rivalry</td>
</tr>
<tr>
<td>threaten</td>
<td>a precursor to physical aggression; includes: head tip, arm wave, hit toward, throw at, branch wave, stamp, slap, charge, charging display, hunch, fixed stare, soft bark, waa bark, wraa call, compressed lip and scream with full open grin</td>
</tr>
</tbody>
</table>

**Sexual Behavior**

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>consort</td>
<td>male takes a female to the periphery of the community range to allow for an exclusive sexual relationship</td>
</tr>
<tr>
<td>copulate</td>
<td>sexual intercourse (includes intromission) between a male and an estrous female</td>
</tr>
<tr>
<td>interfere copulate</td>
<td>an immature interferes with copulation of male and female</td>
</tr>
</tbody>
</table>
**Other Social Behavior**

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>approach</td>
<td>move toward another group member</td>
</tr>
<tr>
<td>alloparental care</td>
<td>care directed at an immature; similar to maternal care but is performed by a chimpanzee other than the immature's mother; includes: hug, groom, transport, mouth, pat, touch, protection hold, scratch, food share, restrictive hold, and play with</td>
</tr>
<tr>
<td>groom mutually</td>
<td>groom simultaneously</td>
</tr>
<tr>
<td>patrol</td>
<td>a party of males moving along the periphery of the community's boundary; among this community may include: vocalizations, stare, piloerection, male-male reassurance behaviors (J. Pruetz, pers. comm.)</td>
</tr>
</tbody>
</table>

**Other Behavior**

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>depart</td>
<td>begin to move away from party or feeding site</td>
</tr>
<tr>
<td>feeding/foraging</td>
<td>consuming food or locating and processing food</td>
</tr>
<tr>
<td>observer related</td>
<td>behavior in response to the researcher; includes: approach, display, piloerection, avoid</td>
</tr>
<tr>
<td>other</td>
<td>behavior other than those included in the ethogram</td>
</tr>
<tr>
<td>out of sight</td>
<td>focal subject cannot be visually located by researcher or activity is unclear</td>
</tr>
<tr>
<td>rest</td>
<td>not moving; includes: sit or lie</td>
</tr>
<tr>
<td>travel/move</td>
<td>locomotion from one place to another, does not include movement while feeding</td>
</tr>
</tbody>
</table>

**Reference**