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Patterns of affiliation and agonism in a ringtailed lemur, *Lemur catta*, society: Tests of the socioecological model and other hypotheses

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CHAPTER 1: THE ORGANIZATION OF PRIMATE SOCIAL GROUPS

The diversity of primate social systems has been explained with models that focus on affiliation (cooperation) and aggression (competition) as the primary formative influences. I review these opposing perspectives and their relationship to the popular socioecological model of primate sociality. I then examine the underlying logic of the socioecological model, and review attempts to test the model's predictions across primate taxa. Conflicting reports of the relationship between competition (aggression) over food and social organization suggest that the socioecological model's attention to food-related aggression may have distracted us from considering the influences of inter-individual distance and kinship within groups.

INTRODUCTION:

The evolution of sociality is integrally tied to the costs it imposes and benefits it provides. Social living can only evolve when significant and consistent fitness benefits outweigh the costs of gregariousness (Alexander 1974). At present, group living is a widespread characteristic of diurnal non-human primates (hereafter “primates”). However, there exists a great diversity in primate social systems both between (van Schaik & van Hooff 1983, Strier 2000) and within species (Sterck 1999). Scientists have long attempted to establish the factors that determine this variation. In this pursuit, two extreme views have been developed. In the first, it is argued that social behavior patterns among group members developed from and are maintained by an “automatic mutual dependence among organisms” (Allee 1931: 391), a “basic social instinct” (Alexander 1974: 329), or a “cooperative urge” (Allee in Dugatkin 1997: 8). In the second and more recent view, it is argued that social behavior patterns among group members developed to counteract (de Waal & van Roosmalen 1979, Castles & Whiten 1998, Katsukake & Castles 2001, Aureli *et al.* 2002) and in accordance with (van Schaik 1989) the aggressive and competitive nature of animals (Figure 1). In this literature review, I briefly discuss these two opposing views and then detail how they relate to the foundational assumptions of the socioecological model of primate sociality, which is frequently used to explain the variation in primate social systems. I also review the studies that support and do not support its predictions. In doing so, I aim to examine the strength of the relationship between the characteristics of social organization, and patterns of aggression over food. Social organization is the collective outcome of social interactions and relationships that result among group members.

TWO OPPOSING VIEWS:

In the late 1800's and early 1900's, cooperation was discussed as a fundamental feature influencing social life (Allee 1931, Kropotkin 1972). Mutual support and cooperation among animals was thought to play a much larger role in the evolution and maintenance of life than mutual struggle and competition (Kropotkin 1972, Kessler in Kropotkin 1972). Allee (1938) offered the following findings as evidence of this view, "[1] planarian survived in ultraviolet light as a function of group size; [2] per capita growth rate in bacteria is a function of group size; …[3] amphibians regenerate their tails faster when living in groups; [4] time to fledging in colonial birds is reduced in large colonies; [5] in certain contexts, minnows and goldfish learn tasks faster when living in groups" (as quoted in Dugatkin 1997: 9). Therefore, it was generally accepted that social living and cooperativeness were universally beneficial to all concerned, a view that remained widespread throughout social biology until the 1960's (Alexander 1974).

In stark contrast to Kropotkin's views, Huxley viewed social living as a gladiator show where only the swiftest and smartest lived to fight another day (1888 in Dugatkin 1997). Lorenz (1966) argued that aggression, not cooperation, was a necessary tactic to ensure that the stronger of two individuals of the same species has better reproductive success, to maintain an optimal distribution of individuals, and to prevent overcrowding through forced dispersal. He further stated that aggression "is essential for [a species'] preservation" (Lorenz 1966: 23, 29, 47, 49) and that competition between near relations of the same species is indispensably responsible for driving evolution forward (Lorenz 1966). The idea that animals are inherently aggressive became a central theme in the discussions about human social evolution (de Waal 2000a). However, in contrast to these views, Darwin (1859) acknowledged that the struggle for existence was a metaphorical struggle against the environment. Wallice (1891) further argued that the term did not necessarily imply misery and pain in the animal world.

Alexander (1974) opposed both of these extreme approaches to the evolution of social behavior stating that, "the argument that man is basically cooperative and altruistic is no less instinctivist than its counterpart that he is basically aggressive and competitive" (Alexander 1974: 329). Instead, he stressed that social living evolved because it provides fitness benefits in terms of predator avoidance and ease of accessing and maintaining resources. He went on to argue that social behavior evolves within groups because it functions to maximize the opportunities for increased fitness that social living can potentially provide. For example, grooming, a now widespread behavior of social bonding in animals, initially functioned to control parasites and the spread of disease (Alexander 1974). According to this sequence of events, it was only after the evolution of grooming that this behavior acquired a social role. As a result of this newly acquired function, most social animals groom much more often than is necessary to merely control for parasites (Smuts 1987). However, even if grooming behavior did not evolve as the result of an innate drive to be social, Alexander still recognized the formative role of such behavior in the organization of social groups. For example, grooming had been shown to predict social interactions (Sade 1965) and play a critical role in the reinforcement of social relationships (Sparks 1967).

As a result of Alexander's 1974 influential review and the work of many other scientists, defense against predators became established as one of the major benefits to group living and was often viewed as a driving force in the evolution of social groups (Alexander 1974, Altmann 1974). Wrangham (1980) argued that predator defense did not explain the stability of social groups or the variation in primate social systems. As a result, he believed that feeding competition was a much more appropriate determinant of the evolution and maintenance of social systems (Wrangham 1980). The beginnings of this idea originated from existing socioecological models such as Emlen & Oring's (1977) paper, which attempted to predict the influence of environmental factors, such as those associated with food, on avian mating systems. Wrangham (1980) expanded on this model and developed a formalized socioecological model specifically for primates. Other scientists have elaborated on this basic model (van Schaik 1989, Isbell 1991) and it has gained both great support (Barton *et al.* 1996, Sterck *et al.* 1997, Saj *et al.* 2007) and great criticism (Koenig & Borries 2006, Sussman & Garber 2007, Thierry 2008) in the literature. The model predicts that the variation in the frequency and type of between and within-group competition (as well as some secondary social factors) should underlie the variation in female social relationships (Sterck *et al.* 1997). Therefore, this current socioecological model for primate sociality falls much closer to the intrinsically aggressive ideology of Huxley (1888 in Dugatkin 1997) and Lorenz (1966). This general approach to understanding the variation in primate social systems has been tested in dozens of species and in hundreds of studies over the past 25 years. In the next section, I will review some of this work in order to evaluate how the model stands up under such close scrutiny.

THE SOCIOECOLOGICAL MODEL OF PRIMATE SOCIALITY:

Hypotheses and Predictions:

The hypotheses of the socioecological model are 1) High levels of aggression are primarily the result of contest competition over defensible resources, specifically food (Wrangham 1980, van Schaik 1989, Lu *et al.* 2008). The accompanying prediction is that aggression will frequently occur in the presence of food and food-oriented behavior, especially when food is limited and/or clumped (Wrangham 1980, van Schaik 1989) (Figure 2). 2) Low levels of aggression are the result of scramble competition over less-defensible resources (Wrangham 1980, van Schaik 1989). This predicts that aggression rates will be lower in non-food oriented contexts and when food resources are more abundant and dispersed (Figure 2). 3) Food abundance and distribution and the patterns of food-related agonism that result will influence female social relationships in a predictable and systematic manner (van Schaik 1989, Saj *et al.* 2007). A despotic and nepotistic dominance hierarchy characterized by female philopatry is predicted to result when there is frequent agonistic competition over food (de Waal 1989, Pereira 1995, van

Schaik 1989, Sterck *et al.* 1997). Alternatively, egalitarian and unstable social relationships are predicted to result when there is infrequent agonism over food (Sterck *et al.* 1997) (Figure 2).

Development and Theoretical Background of the Model:

Wrangham (1980) proposed that primate social relationships and the resulting social system reflect the competitive strategy for obtaining fitness-limiting resources. Therefore, he argued that because female reproductive success is primarily limited by access to food resources due to the energetic requirements of pregnancy and lactation (van Schaik 1989), and male reproductive success is limited by access to receptive females (Trivers 1972), it is the behavior of females that determines the social system (Wrangham 1980). Therefore, the characteristics of the primary food resource were argued to be the primary influence on the social organization of primate groups (Wrangham 1980, van Schaik 1989, Sterck *et al.* 1997) (Figure 1). Using this hypothesis, Wrangham (1980) classified primate social groups as either female-bonded or non-female bonded. In 1989, van Schaik incorporated the degree of predation risk and different forms of feeding competition into Wrangham's (1980) model. He also revised Wrangham's (1980) original categories of female-bonded and non-female bonded groups into four categories of social organization; dispersal-egalitarian, resident-egalitarian, resident-nepotistic, and resident-nepotistic-tolerant (van Schaik 1989) (Figure 3). Because of the presumed link between the characteristics of the primary food source and type of feeding competition, primate species are expected to fall into one of these four categories primarily as a function of the types of food they eat (van Schaik 1989, Saj *et* *al*. 2007). For example, when food resources are clumped, of intermediate size, or limited, contest competition will result (Figure 2). Contest competition is an active form of competition in which individuals directly compete for the same resource through agonistic interactions. Contest competition is predicted to generally characterize the competitive regime of frugivorous and omnivorous primate societies. When this form of aggression is strong *within* a social group, the model predicts that it will create frequent, unidirectional aggression, often involving the use of submissive signals, and stable, linear, and nepotistic dominance hierarchies will form (Resident-Nepotistic) (Figure 3) (van Schaik 1989**,** Isbell 1991, Sterck *et al.* 1997, Koenig 2002). Furthermore, female primates are likely to be philopatric and form strong kin bonds to defend resources from non-kin competitors (Saj *et al.* 2007). When contest competition is strong *between* social groups, social relationships will be more egalitarian but are predicted to remain philopatric due to the aid provided by kin in inter-group encounters (Resident-Egalitarian) (Figure 3) (Koenig 2002). If contest competition is strong both within and between groups, a linear, stable dominance hierarchy is predicted but dominant animals are expected to be more tolerant of lower ranking animals. Tolerance is marked by frequent counter-aggression and "reconciliation" (Resident-Nepotistic-Tolerant) (Figure 3) (Sterck *et al.* 1997).

When food is highly dispersed, of low nutritional value, or found in patches that are large relative to the size of the group, scramble competition is predicted to result (Figure 2). Scramble competition is a passive form of competition that occurs when access to a resource is lost because another individual has previously attained it. This form of competition is expected to generally characterize the competitive regime of folivorous primates (Saj et al. 2007). When scramble competition is strong *within* a social group, the model predicts that food-oriented aggression will be infrequent and bidirectional, which will create non-linear, unstable and egalitarian social relationships characterized by weak female bonds (Dispersal-Egalitarian) (Figure 3) (van Schaik 1989, Sterck *et al.* 1997, Koenig 2002). Furthermore, under this type of competition, female dispersal will be favored because resources are not defensible so there is considered to be little benefit to forming kin groups (Wrangham 1980, Sterck *et al.* 1997).

However, food distribution does not consistently explain the variation in primate social systems (Sterck *et al.* 1997, Thierry 2008). As a result, researchers have added additional variables to this model. In 1997, Sterck, Watts, and van Schaik added infanticide avoidance and habitat saturation as potential secondary determinants of primate sociality. This revised model now represents the current socioecological model by which the variation in primate social systems is frequently studied (Thierry 2008). The modern socioecological model retains the prevailing hypothesis that agonistic competition over ecological resources is the most important force shaping the diversity of female social relationships as well as patterns of "reconciliation", coalition formation, nepotism, and dominance (Sterck *et al.* 1997, Saj *et al*. 2007, Lu *et al.* 2008). Therefore, agonistic interactions are considered to be highly influential aspects of the social system (Sterck *et al.* 1997, Wittemyer & Getz 2007).

Hypotheses and Predictions of the "Reconciliation" Hypothesis:

In the socioecological model, aggression is predicted to have the potential to disrupt social bonds, which arguably makes relationship repair mechanisms critical in facilitating continued cooperation and social cohesion (Flack *et al.* 2005). Conflict repair is considered to be especially significant for those groups with high within and between-group contest competition because strong social bonds are important when defending resources from other groups (Sterck *et al.* 1997). Reconciliation, which is when previous combatants affiliate sooner after a fight than when a fight had not occurred (Fuentes 2004), is believed to be an important component of primate social relationships. It is hypothesized that: 1) Group living animals frequently reconcile conflict to restore damaged bonds (de Waal & van Roosmalen 1979). Species that experience high within and between group contest competition are predicted to reconcile more often than those with low frequencies of contest competition due to their reliance on mutual aid during inter-group encounters (Sterck *et al.* 1997). Additionally, there should be a relationship between the intensity of the conflict and the likelihood of reconciliation. 2) An implicit prediction of the "reconciliation hypothesis" is that there is an overall relationship between agonism and affiliation in group living species. The prediction follows that levels of affiliation and agonism between pairs of individuals should be correlated with one another. 3) "Reconciliation" is most likely to occur between individuals with biologically valuable relationships. Individuals who provide the most substantial fitness benefits to their previous opponent will be more likely to reconcile conflict (de Waal & Yoshihara 1983, Aureli *et al.* 2002).

Development and Theoretical Background of the "Reconciliation" Hypothesis:

de Waal and van Roosmalen (1979) observed that previous combatants in the captive chimpanzee group they were studying seemed to participate in affiliation at higher frequencies in the time period immediately following a fight than at other time periods throughout the day. They termed this behavior “reconciliation”, which is argued to be effective at repairing relationships that were damaged by aggression (de Waal & van Roosmalen 1979), reducing future aggression (Castles & Whiten 1998), reducing the stress of previous combatants (Katsukake and Castles 2001) and restoring tolerance in the presence of food (Aureli *et al.* 2002). “Reconciliation” has thus become accepted as a behavioral mechanism that preserves the cohesion of social groups by reducing the negative impacts of conflict (Silk 2002).

However, despite the critical role that post-conflict affiliation is presumed to play in maintaining the integrity of social groups, aggression does not always result in “reconciliation”. Furthermore, when “reconciliation” does occur, its patterns are highly variable (Fuentes 2004). This observation has encouraged research into the conditions under which “reconciliation” is predicted to occur. The “valuable relationship hypothesis” predicts that “reconciliation” is more likely to occur when the relationship between the opponents is biologically valuable (de Waal & Yoshihara 1983, Aureli *et al.* 2002). According to Kutsukake and Castles (2004: 157), the term biologically valuable is “a function of the fitness benefits that can be derived from a relationship.” For example, according to the socioecological model, groups experiencing strong within and between-group contest competition are predicted to reconcile within-group conflicts at high rates because dominant and subordinate animals rely on each other’s support during conflict with other groups (Sterck *et al.* 1997).

In addition to “reconciliation” occurring in the post-conflict period, researchers have also reported increased affiliation between an uninvolved individual and the victim of an aggressive interaction. This triadic post-conflict affiliation has been termed "consolation" and is thought to be an effective conflict management mechanism because it is thought to curtail ongoing aggression (Petit & Thierry 1994). Furthermore, because the consoling third party may be the kin of the opponent, consolation can also function as kin-mediated reconciliation and restore affiliation across genetic lines (Judge 1991, Call *et al.* 2002, Wittig *et al.* 2007). Judge and Mullen (2005) have further argued that quadratic "reconciliation", where bystanders not involved in a fight affiliate with each other in the post-conflict period, can also function to control conflict and restore relationships through the group-wide reduction of tension. While quadratic "reconciliation" has been sparsely studied, "consolation" has been documented in captive chimpanzees (de Waal & van Roosmalen 1979) and stump-tailed macaques (Call *et al.* 2002). However, Arnold and Whiten (2001) and Fuentes *et al.* (2002) did not find this behavior in wild chimpanzees, which lead them to suggest that "consolation" is not a post-conflict behavior of this species in their natural habitat.

Although there seems to be wide acceptance of post-conflict affiliative behaviors functioning to maintain social relationships, Silk (2002: 25) argued that because the term "reconciliation" is a functional label, it is only justified if "we can demonstrate that non aggressive interactions after conflict enable former opponents to settle disputes and restore peace". However, most studies continue to use only the criterion of heightened affiliation after a fight to indicate that a fight has been reconciled (Silk 2002). This practice has lead to the assumption that "behavior that fits the prescribed criteria of operationally defined "reconciliation" does actually function to restore, or at lease improve, the relationship between former opponents after aggressive conflicts" (Cords

1993: 256). In contrast to the proposed relationship repair function indiscriminately attached to post-conflict affiliative behaviors, Silk (2000, 2002) has argued that what we label as “reconciliation” may simply indicate the cessation of violence thereby reducing the uncertainty about the intentions of a previous opponent. She proposes that instead of “reconciliation” behaviors indicating that evolution selected for a mechanism to repair damaged relationships, selection may have simply favored a suite of signals that indicate benign intent. Such signals may allow individuals to obtain short-term objectives without fear of continued aggression (Silk 2000). Therefore, while aggression can have immediate negative impacts, it may not be as universally detrimental to long-term social bonds as is currently thought (Fuentes 2004). Fuentes (2004: 221) argues that the assumption that conflict is so detrimental to social living comes from an “overemphasis on a few short-term, but visibly costly events”. Agonistic behaviors are more dramatic than affiliation and their influence on primate social systems may have been over estimated because of the greater ease of observing and collecting data on conflict (Strier 1994). Furthermore, Getty (1981) argued that the spectacular nature of many aggressive acts is in part responsible for making aggression one of the most studied mechanisms of animal behavior. This is not to suggest that conflicts do not have the potential to disrupt social life, but only that they do not drive it. Furthermore, there is little evidence to suggest that post-conflict behaviors influence lifetime reproductive success and therefore, they may not be the direct result of selection (Fuentes 2004). Therefore, focusing on conflict as selecting for repair behaviors may not offer the best explanation for the post-conflict behavior patterns that have been observed in primate species (Silk 2002, Fuentes 2004).

Silk’s uncertainty reduction hypothesis has become part of the discourse of post-conflict behavior but the primary theme for most post-conflict research continues to focus on the idea that cooperative and affiliative behaviors are adaptations to reduce the costs of aggression (de Waal & Aureli 2000, Silk 2002). In these studies, affiliation and cooperation are treated as a “by-product of tempering aggressive and selfish tendencies” (Beckoff 2004, pg 57). Therefore, although the “reconciliation hypothesis” does emphasize the importance of affiliation in maintaining social living, this emphasis generally occurs in the context of conflict.

Support and Inconsistencies of the Socioecological Model:

Numerous researchers have reported support for the socioecological model. For example, the Peruvian common squirrel monkey, *Saimiri sciureus*, which relies on large fruit trees (i.e. clumped resources), has a linear dominance hierarchy and frequent contests over food while the Costa Rican red-backed squirrel monkey, *Saimiri oerstedi*, which relies on small fruit trees (i.e. dispersed resources), has egalitarian social relationships and does not have frequent food-related agonism (Mitchell *et al.* 1991). In the case of savanna baboons, *Papio cyncephalus*, those living in a habitat with patchy food and abundant predators had linear dominance hierarchies while those living in a habitat with dispersed food had no clear dominance hierarchy (Barton *et al*. 1996). Similarly, Koenig *et al.* (1998) found that the strength of the dominance hierarchy in Hanuman langurs, *Presbytis entellus*, varied with the abundance and the distribution of food. In these cases, the rates of aggression and the resulting dominance hierarchy match the predictions of the socieoecological model (Sterck *et al.* 1997).

Researchers have also reported mismatches between the predictions of the socioecological models and the actual behavior of other primates (Strier 1994, Matsumura 1999, Janson 2000, Koenig 2002, Koenig & Borries 2006, Saj *et al.* 2007, Lu *et al.* 2008). A prediction that frequently does not hold up to empirical testing is the relationship between characteristics of the food resources and agonism patterns. For example, Chancellor and Isbell (2008) found that smaller inter-food distance is not significantly associated with contest competition in rhesus macaques, *Mucaca mulatta*. Furthermore, in contrast to the predictions of the socioecological model, evidence of resource-associated aggression among females is lacking even in species with linear dominance hierarchies (Sussman & Garber 2007). For example, some researchers have found that agonism rates decrease in the presence of clumped food resources (Gore 1993). In baboons, aggression rates are actually lower in the dry season when food is scarce, which suggests the use of an energy-minimizing strategy (Beehner *et al.* 2005), and not behavior patterns structured by resource availability.

In addition to predicting patterns of agonism, the socioecological model posits that the characteristics of the food resource will also predict the overall organization of the social group. For example, folivorous female mantled howler monkeys, *Alouatta palliata*, are expected to have egalitarian or tolerant social systems based on the characteristics of their food resources (see figure 4 for the characteristics of the egalitarian and tolerant social systems) (Koenig 2002). However, Jones (1980) found that females of this species exhibit linear dominance hierarchies and a negative relationship between reproductive success and rank. Similarly, mountain gorillas are expected to have inconsistent dominance relationships (Sterck *et al.* 1997), however, Watts (1994) observed linear dominance hierarchies among females of this species. Additionally, Erhart and Overdorff (2008) found that ringtailed lemurs, *Lemur catta* and Milne-Edward's sifaka, *Propithecus edwardsi*, both of which were predicted to form egalitarian dominance relationships, (Sterck *et al.* 1997) did not fit any of the existing categories explaining female social relationships.

Although I will not review these studies in depth here, the socioecological model also makes tangential predictions regarding the influence of resource competition on the demographic patterns of social group. For example, van Schaik & Hrdy (1991) proposed that resource competition influences birth sex ratios in cercopithecine primates. When resource competition is intense, high ranking females may gain increased benefits from having daughters who will inherit their mother's rank and reproductive success and be able to support them in conflicts. On the other hand, low ranking females who are likely to have low ranking daughters, may not be able to protect their daughters from harassment and thus benefit more by having sons who will eventually emigrate (van Schaik & Hrdy 1991). The opposite pattern is expected when local resource competition is relaxed based on the assumption that sons are more expensive to rear. These hypotheses have not withstood rigorous testing with large sample sizes (Silk & Brown 2004, Silk *et al.* 2005).

Support and Inconsistencies of the "Reconciliation" Hypothesis:

Researchers have documented "reconciliation" in many species of primates (Aureli & de Waal 2000) and other social mammals (Schino 1998, domestic goats, *Capra aegagrus*; Wahaj *et al.* 2001, spotted hyenas, *Crocuta crocuta*). However, there remains a great deal of inconsistency in the types and frequencies of post-conflict “reconciliation” behaviors among primate taxa. For example, recent work on chimpanzees (the frequent reconcilers of de Waal & van Roosmalen’s 1979 flagship study), has indicated that former opponents only reconcile after approximately 20% of their aggressive interactions (Baker & Smuts 1994, Arnold & Whitten 2001, Fuentes *et al*. 2002). There also appears to be great variation in the conciliatory patterns of chimpanzee dyads within a single social group, with some reconciling at high rates, and others not at all (Arnold & Whiten 2001, Fuentes *et al.* 2002, Preuschoft *et al.* 2002). Furthermore, the suites of behaviors used during post-conflict periods are inconsistent between social groups of the same species, which provides unconvincing evidence that there is a specific set of “reconciliation” behaviors in chimpanzees (Fuentes 2004). As a result, it remains unclear if there is a pattern of behaviors that has been selected to repair the damage caused to social relationships by conflict (Silk 2002). Rather, Fuentes (2004) argues that “patterns of association, dyadic histories, individual variation in behavior, and use of space might predict behaviors surrounding conflict better than a focus on the conflict itself or on specific post-conflict behavior sets.” For example, Ray *et al.* (1996 in Fuentes 2004) observed that the post-conflict behavior of female langurs (who affiliated in the post-conflict period at rates identical to their baseline measurements, thus indicating no “reconciliation”), was best predicted by overall patterns of female-female dyadic relationships. Furthermore, Palagi *et al.* (2005) examined post-conflict affiliation in two groups of ringtailed lemurs and found that while the frequency and intensity of agonistic interactions were not significantly different between groups, only one group exhibited “reconciliation”. They posited that the frequency of affiliation within social dyads more accurately predicted the use of conciliatory strategies, with more affiliative dyads being more likely to reconcile (Palagi *et al.* 2005). This pattern has been reported for chimpanzee species, genus *Pan*, as well (Preuschoft *et al.* 2002, Wittig & Boesch 2003). Therefore, competition-induced conflict is not a sufficient explanation for frequencies of affiliative "reconciliation". Instead, it appears that the long-term patterns of dyadic social relationships are a better indicator of post-conflict behaviors.

In addition to the criticism made regarding the findings of these studies and what they imply about the role of conflict management in maintaining sociality, there is also criticism regarding the methods used to document and interpret post conflict behaviors. For example, an assumption of the frequently used PC-MC method is that the MC time period accurately indicates the relationship that would exist between two individuals in the absence of a fight. This assumption is most likely unrealistic because matched-control observations do not necessarily reflect the baseline affiliation of individuals in the absence of a fight (Kappeler & van Schaik 1992, Silk 1997). Furthermore, this method does not take into account the variation in the frequency and type of social interactions that exist through time. For example, because the frequency of affiliation is much greater than agonism in the vast majority of primate social groups (Sussman *et al.* 2005), it is reasonable to expect that a few of these affiliative events will correlate with aggression randomly. Thus, the chance observation of "reconciliation" is most likely for those dyads that affiliate most often because affiliation is simply more likely to occur at all times. In fact, as mentioned above, those dyads with the highest rates of affiliation have been found to "reconcile" the greatest frequency of conflicts (Preuschoft *et al.* 2002, Wittig & Boesch 2003, Palagi *et al.* 2005). These oversights can result in erroneous conclusions about the patterns of "reconciliation" within social groups because the documentation process of the occurrences of this behavior is highly subject to chance events. As a result, Kappeler & van Schaik (1992) proposed the baseline method, which involves conducting several observations of affiliative behavior throughout the study period to get a baseline level of affiliation to which post-conflict behavior can be compared.

Current Status of the Socioecological Model:

Collectively, the studies that provide support for the socioecological model implicate aggression over food as driving the formation of many aspects of a social system: dominance hierarchy, coalitionary patterns, dispersal patterns, strength of social bonds, birth sex ratios, and the behavioral mechanisms that manage conflict. However, despite the predominance of this model in primatology, " relatively few studies have provided a robust test of [its] predictions" (Saj *et al.* 2007). Of those studies that have, some have found support (Mitchell *et al.* 1991, Costa Rican red-backed squirrel monkey, *Saimiri oerstedi*, and Peruvian common squirrel monkey, *Saimiri sciureus*; Barton *et al.* 1996, savannah baboon, *Papio cyncephalus*; Saj *et al.* 2007, Geoffroy's black-and-white colobus monkey, *Colobus vellerosus*) but still others have observed inconsistencies between the predictions of the model and observed behavior patterns of primates, which has sparked great criticism against the validity of a comprehensive model to explain the variation in primate social systems. For example, Sussman and Garber (2007: 642) argued that the discrepancies between the predictions of the socioecological model and the food-oriented behavior of many primates, suggests that "food related agonism among females may not be as important a factor in shaping daily social interactions and individual relationships as is commonly assumed." Additionally, Thierry (2008) and Koenig and Borries (2006) argued that because the predictions of the model are in binary terms (e.g. high/low), empirical data is reduced to qualitative and subjective categories, which make the socioecological model ambiguous and difficult to test.

These inconsistencies have lead many researchers to question the main prediction of the socioecological model; that aggression and overall social relationships are determined by the characteristics of resource competition. As an alternative, it is possible that agonism rates are a function of other social variables, such as the number and proximity of individuals, which might increase aggression by simply increasing the opportunity for it to occur (Stevenson *et al.* 1998, Vogel & Janson 2007). Sussman and Garber (2007) call this idea the billiard ball phenomena, where the more balls (i.e. group members) on the table at one time, the higher the likelihood that they will interact randomly. Therefore, this hypothesis argues that some agonistic interactions may not be the result of a particular social strategy but of the fact that two individuals cannot occupy the same space simultaneously (Sussman & Garber 2007). However, because individuals themselves are distributed non-randomly in physical space on the basis of their social relationships (McBride 1971, Fairbanks 1976), random social interactions are expected to occur more frequently between some individuals than others as a function of those relationships. There is much evidence indicating the relationship between proximity and social behavior (Altmann 1968, Sade 1965, 1972, Corradino 1990). For example, Fairbanks (1976) found that in hamadryas baboons, *Papio hamadryas*, individuals who maintained the closest proximity were involved in the most agonistic and affiliative interactions. This hypothesis is potentially further supported by the resource dispersion hypothesis, which states that when resources (food and non-food) are heterogeneous (i.e. patchy) in space or time, the cost of group living might be extremely low, even if group living provides few benefits (Johnson *et al.* 2002). This model recognizes the relationship between social behavior and the characteristics of resources but expects this relationship to occur in the opposite direction from that predicted by the socioecological model. Therefore, under this hypothesis, any increase in food-related agonism is not necessarily the result of resource competition, but some other, perhaps proximity-related, factor. However, at present, most of the support for this model comes from mathematical modeling (Bacon 1991).

The potential influence of proximity on social behavior points out the existence of an implicit confound between food distribution and proximity because when food is clumped, individuals are more likely to be clumped as well, which might increase the opportunity for aggression. Therefore, the perceived influence of food characteristics on social behavior might actually be an indirect effect of decreased inter-individual distance. Interestingly, the confound between proximity and food, is actually built into the socioecological model because female gregariousness implies proximity relationships among individuals. However, researchers do not address this confound when collecting or interpreting data.

Regardless of the inconsistencies and recent criticism of the socioecological model, Patton & Kohler (2004: 13) stated that it is “the consensus among Primatologists…that competition over scarce resources is the key to understanding collective actions”. While all primatologists do not agree with this view, it does appear that competition over food is frequently considered to be important in primate social behavior. Alexander (1974: 333) noticed this tendency three decades ago when he argued that "we are often deceived into assigning food a larger role in sociality than it deserves by observing, *a)* species in which individuals are able to parasitize large food finds of others even without the help of evolved signals, and *b)* species in which group-feeding behavior is obvious but the effects of predators actually responsible for grouping are not". He continued on to say that, "the evolution of complex social structure chiefly or solely as a result of feeding advantages is doubtful" (Alexander 1974: 333). Snaith and Chapman (2007: 104) stated that we must "recognize that out focus on feeding competition captures only part of the puzzle" necessary to understand social organization. When considering the natural history of primates, food resources may be even less influential on social behavior than in other taxa because of the behavioral flexibility that characterizes most primate species. Their diversity of diet, ability to quickly shift between seasonal foods, and flexibility of grouping patterns, may limit the conditions under which feeding competition causes significant fitness costs (Sussman & Garber 2007).

There is little doubt that the emphasis on feeding competition has placed increasing emphasis on competition and aggression in primate social groups. de Waal (2000b: 24-25) noted the prevalence of this bias when he wrote that, "the possibility of shared interests was so far from the minds of evolutionary biologists (except with regard to kin) that when it came to accounting for the rarity of lethal violence, rather than assuming a need for cooperation and stable group life, explanations focused exclusively on the physical risk of combat." This overemphasis on clashing individual interests draws attention away from the possibility of shared interests (de Waal 2000b). Thus, over the past two decades, aggression and competition have likely received too much emphasis while affiliation and cooperation have been under examined (Sussman *et al.* 2005) or at least addressed under a misleading framework.

According to Sussman and Garber (2007: 642), it appears that "the socioecological model of primate sociality needs to be reevaluated". However, it is likely that the social relationships of primates are influenced by so many variables that no simple model will be able to explain the diversity in primate societies. As we continue to add these variables into the model, we risk creating a "combinational explosion and render[ing] the model un-testable" (Erhart & Overdorff 2007: 1239). As Thierry (2008) states:

> "It appears at present that the synthetic [Socioecological] model is not repairable. We must give up the dream of a comprehensive model that will encompass all primate societies. There is no single formula for their social relationships, just as there is no single formula for the colors of butterflies or the syntaxes of human languages."
> (Thierry 2008: 96)

OTHER MODELS OF PRIMATE SOCIAL ORGANIZATION:

Not all research on primate social systems is focused on competition and agonism as the primary formative factors in their organization. Rather, many researchers have found that strong social bonds and the elements that control them can be important organizing features of a social group. For example, Kapsalis and Berman (1996) investigated three organizing principles proposed to explain the structure of affiliative relationships in female macaques: 1) Kin-based attractiveness, where females are attracted to and thus develop affiliative relationships with maternal kin, 2) Attraction-to-high-rank, where females are attracted to high ranking females and develop affiliative relationships that represent the competition for such female partners, 3) The similarity principle, where females develop affiliative relationships with those who are most similar to them in terms of age, rank, and relatedness. Kapsalis and Berman (1996) found that, while controlling for the interdependence that exists among these three principles, kin-based attractiveness was likely the primary organizing principle for affiliative relationships in rhesus monkeys, *Mucaca mulatta*. Similar findings indicating the importance of kin relationships have been reported in non-primates species as well. For example, tadpoles of the cascades frog, *Rana cascadae* (Hokit & Blaustein 1997), and the striped chorus frog, *Pseudacris triseriata* Smith 1990), raised in sibling groups had higher survivorships than those reared in mixed groups with both kin and non-kin.

Smuts (1985, olive baboon, *Papio cynocephalus*) and Altmann (1980, yellow baboon, *Papio cynocephalus*) documented the occurrence of strong, stable, social bonds, characterized by high rates of affiliation, between unrelated male and female baboons. Smuts (1985) called this partnership a “friendship”. The preference of females for male partners was not dependent on the rank of the male and higher-ranking males did not have more partners than lower ranking males (Smuts 1985). These bonds have several influences on the social patterns that occur within baboon social groups: 1) They influence mating patterns because strong social bonds during periods of sexual inactivity increased a male’s likelihood of mating with that female when she became receptive (Smuts 1985). 2) They influenced aggression patterns because any threat to a partner or the offspring of a partner frequently resulted in retaliation, regardless of the likelihood that the male was the infant’s father (Smuts 1985). 3) The effectiveness of the male baboon's strategy of using infants as buffers during agonistic attacks was dependent on the pre-existence of a positive relationship between the male and the infant (Altmann 1980). Otherwise, the infant would scream and refuse to cling to the male, thus attracting the attention of females. 4) The bonds between infants and their mother's partners often persisted through adulthood and even positively influenced the weaning of infants (Altmann 1980, Smuts 1985). Similarly, in a 16-year study on baboons, Silk *et al.* (2003), found that females who interacted more frequently with group members had increased infant survival rates and that these values were not correlated with rank or environmental conditions.

Researchers have also found that strong social bonds are a better predictor of "reconciliation" behaviors than is any characteristic of aggression (Arnold & Whiten 2001, chimpanzees; Preuschoft *et al.* 2002, chimpanzees; Wittig & Boesch 2003, chimpanzees; Palagi *et al.* 2005, ringtailed lemurs). Dyads with high affiliation are more likely to exhibit post-conflict affiliation than dyads with low levels of overall affiliation regardless of the nature of the agonistic interaction and the genetic relatedness between combatants. This finding has lead to the conclusion that, whether or not post-conflict affiliation acts to reconcile conflict, post-conflict behaviors are "likely to be dependent on the prevailing social environment" (Arnold & Whiten 2001). Additionally, King *et al.* (2008) found that in chacma baboons, *Papio ursinus,* close follower behavior during times of decision-making was more likely when the social relationships between leaders and followers were strong. This finding allowed the researchers to conclude that, "strong social relationships between leaders and followers [were] necessary for the emergence of despotic group decisions" (King *et al.* 2008: 1836). These findings indicate the importance of affiliative bonds in structuring social interactions. However, they are not alternatives to the socioecological model approach because they address mechanisms of affiliation and not the underlying selective forces that lead to broader patterns of affiliation and agonism.

CONCLUSION:

The socioecological model is far removed from the views of Allee (1931, 1938) and Kropotkin (1972) of which Alexander (1974) was so critical. However, it seems that the emphasis placed on aggression as the primary factor dictating social organization is just as instinctivist an approach as is the oversimplified idea that group-living is maintained because animals are innately social. Furthermore, the inconsistent support of the socioecological model's predictions and the findings regarding the importance of affiliative social bonds indicates that the role of food-induced agonism in social organization is not as important as Wrangham (1980) originally proposed. This is not to say that the characteristics of the primary food resource are useless in understanding social organization. Rather it seems that proximity patterns among individuals are a more direct predictor of social organization and that both extrinsic (food distribution, predation, ect.) and intrinsic (inbreeding avoidance, kin selection, ect.) factors will simultaneously affect these patterns (Figure 5).

FIGURES:

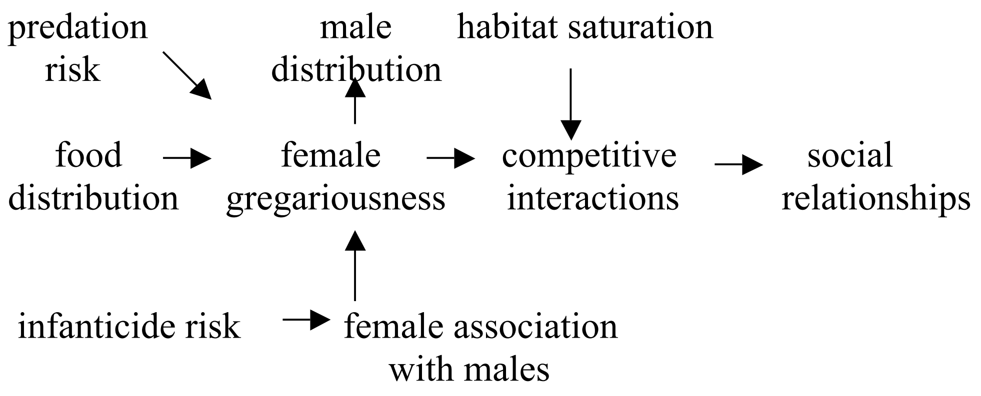
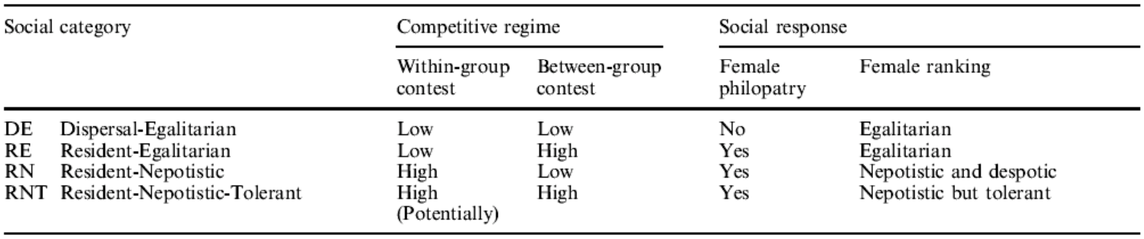


Figure 1: Flow diagram of the proposed socioecological model. Female gregariousness is determined by opposing pressures from predation and/or infanticide risk and from food distribution. The distribution of males depends on a combination of female gregariousness and female choice of protector males. The remainder of the model follows van Schaik (1989): female gregariousness in combination with food distribution determines the type of food competition females experience; this in turn determines female social relationships. Adapted from Sterck *et al.* 1997.

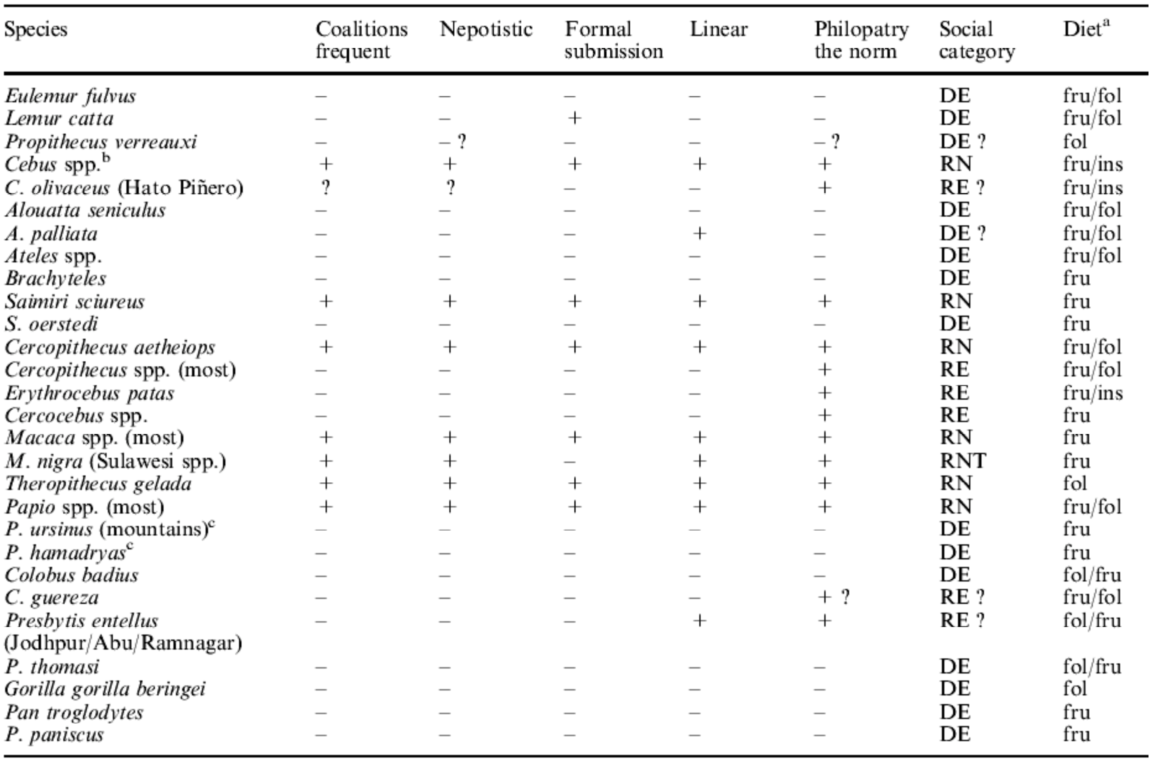
Food qualities	**Type of competition**	**Agonism pattern**	**Social organization**
clumped high quality	Contest	High rate, coalitions, formal submission	Linear, stable hierarchies, strong female bonds
dispersed low quality	Scramble	Low rate, no coalitions, no formal submission	Non-linear, unstable relationships, weak female bonds

Figure 2: Predictions of the socioecological model.



Social category		Competitive regime		Social response	
		Within-group contest	Between-group contest	Female philopatry	Female ranking
DE	Dispersal-Egalitarian	Low	Low	No	Egalitarian
RE	Resident-Egalitarian	Low	High	Yes	Egalitarian
RN	Resident-Nepotistic	High	Low	Yes	Nepotistic and despotic
RNT	Resident-Nepotistic-Tolerant	High (Potentially)	High	Yes	Nepotistic but tolerant

Figure 3: Competitive regime and categories of female social relationships in diurnal gregarious primates. Adapted from Sterck *et al.* 1997.



Species	Coalitions frequent	Nepotistic	Formal submission	Linear	Philopatry the norm	Social category	Diet[a]
Eulemur fulvus	–	–	–	–	–	DE	fru/fol
Lemur catta	–	–	+	–	–	DE	fru/fol
Propithecus verreauxi	–	– ?	–	–	– ?	DE ?	fol
Cebus spp.[b]	+	+	+	+	+	RN	fru/ins
C. olivaceus (Hato Piñero)	?	?	–	–	+	RE ?	fru/ins
Alouatta seniculus	–	–	–	–	–	DE	fru/fol
A. palliata	–	–	–	+	–	DE ?	fru/fol
Ateles spp.	–	–	–	–	–	DE	fru/fol
Brachyteles	–	–	–	–	–	DE	fru
Saimiri sciureus	+	+	+	+	+	RN	fru
S. oerstedi	–	–	–	–	–	DE	fru
Cercopithecus aetheiops	+	+	+	+	+	RN	fru/fol
Cercopithecus spp. (most)	–	–	–	–	+	RE	fru/fol
Erythrocebus patas	–	–	–	–	+	RE	fru/ins
Cercocebus spp.	–	–	–	–	+	RE	fru
Macaca spp. (most)	+	+	+	+	+	RN	fru
M. nigra (Sulawesi spp.)	+	+	–	+	+	RNT	fru
Theropithecus gelada	+	+	+	+	+	RN	fol
Papio spp. (most)	+	+	+	+	+	RN	fru/fol
P. ursinus (mountains)[c]	–	–	–	–	–	DE	fru
P. hamadryas[c]	–	–	–	–	–	DE	fru
Colobus badius	–	–	–	–	–	DE	fol/fru
C. guereza	–	–	–	–	+ ?	RE ?	fru/fol
Presbytis entellus (Jodhpur/Abu/Ramnagar)	–	–	–	+	+	RE ?	fol/fru
P. thomasi	–	–	–	–	–	DE	fol/fru
Gorilla gorilla beringei	–	–	–	–	–	DE	fol
Pan troglodytes	–	–	–	–	–	DE	fru
P. paniscus	–	–	–	–	–	DE	fru

Figure 4: Association between female within-group coalitions, female dominance relationships and female philopatry among non-human primates with multi-female groups. Adapted from Sterck *et al.* 1997. DE = dispersal egalitarian; RN = resident nepotistic; RNT = resident nepotistic tolerant; RE = resident egalitarian. Adapted from Sterck *et al.* 1997.

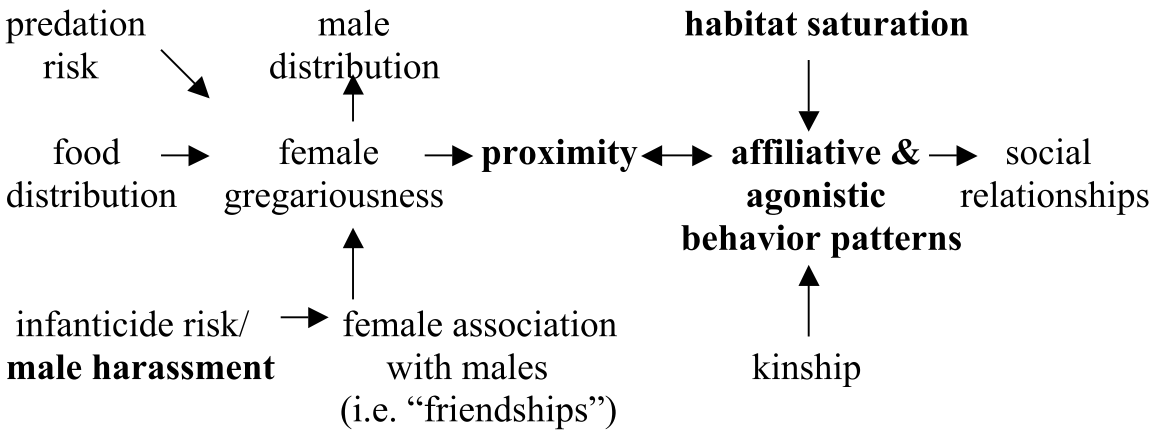


Figure 5: Revised flow diagram of the proposed socioecological model. The bolded words are additions to the model. I added the intrinsic factors of male harassment as potential influencer on female gregariousness. Female gregariousness implies proximity patterns. Proximity then influences and is subsequently influenced by affiliation and agonism (including the competitive regime) patterns (Fairbanks 1976). These patterns of social behavior are also influenced by the intrinsic factor of kinship, which in turn determines social relationships and the social organization of the group.

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CHAPTER 2: AFFECT OF FOOD, PROXIMITY, KINSHIP, AND PREVIOUS AGONISM ON SOCIAL BEHAVIOR IN RINGTAILED LEMURS

Efforts to understand the variation in primate social systems and their underlying interaction patterns have focused on both intrinsic and extrinsic factors. In the socioecological model, food distribution and abundance have been argued to be the primary influences on the social behavior of primate species. I examined the relationship of food resources and three intrinsic factors (kinship, proximity, previous agonism) with patterns of affiliative and agonistic relationships in two semi-free ranging ringtailed lemur, *Lemur catta*, social groups (n=14) at The Duke Lemur Center in Durham, NC. Affiliation and high intensity agonism (although not low intensity agonism) were best explained by kinship. Proximity also explained affiliation but did not explain agonism. Food resources and previous agonism did not convincingly dictate social behavior patterns. Different intensities of agonism have different patterns and should be analyzed individually. These findings indicate that food resources did not dictate social behavior patterns in this study population.

INTRODUCTION:

Group living is a widespread characteristic of diurnal non-human primates (hereafter "primates"). However, there exists a great diversity in primate social systems both between (van Schaik & van Hooff 1983, Strier 2000) and within species (Sterck 1999). A social system is defined by its demographic patterns (i.e. sex ratio, age structure, dispersal behaviors, ect.), mating system, and the social relationships that exist among group members (Kappeler & van Schaik 2002). Many attempts have been made to explain the variation that occurs among primate social systems. In this paper, I discuss four potential factors that have been proposed to specifically explain primate social relationships. Social relationships are composed of the patterns of affiliative and agonistic interactions among individuals. These four factors are: 1) food resources, 2) proximity between individuals, 3) kinship, and 4) previous aggressive interactions. Although this is in no way an exhaustive list of the possible influences, these particular factors are commonly invoked to explain patterns of social interactions. In the next section, I discuss the theoretical background of each factor in more detail.

Food Resources:

A major cost of social living can be increased competition for limited resources. The socioecological model argues that food is the most important resource to primate species and that the characteristics of a species' primary food source will dictate patterns of feeding competition, which in turn shapes female social relationships and patterns of "reconciliation", dispersal, coalition formation, nepotism, and dominance (van Schaik 1989, Sterck *et al.* 1997, Saj *et al*. 2007, Lu *et al.* 2008). Two major hypotheses within the socioecological model are: 1) High levels of agonism are primarily the result of contest competition over defensible resources, specifically food (Wrangham 1980, van Schaik 1989, Lu *et al.* 2008). The prediction follows that agonism will frequently occur in the presence of food and as the result of food-oriented behavior, especially when food is limited and/or clumped (Wrangham 1980, van Schaik 1989). 2) Low levels of agonism are primarily the result of moderate levels of contest competition over less-defensible resources (Wrangham 1980, van Schaik 1989). Based on this hypothesis, researchers predict that agonism rates will be lower in non-food contexts and when food resources are abundant and dispersed through. Savanna baboons, *Papio cynocephalus*, have been found to fit this prediction. For example, those living in a habitat with patchy food have linear dominance hierarchies marked by frequent agonism over food. Conversely, those living in a habitat with dispersed food have no clear dominance hierarchies or coalitions and few agonistic interactions in food contexts (Barton *et al*. 1996).

If agonism patterns in ringtailed lemurs are primarily the result of competition over food resources, I expect the rate of agonistic interactions to be significantly higher in food-oriented contexts as compared to non-food-oriented contexts. I also predict that the rate of agonism will be higher in contexts with clumped, limited, and highly valuable food resources as compared to contexts with dispersed, abundant, and less valuable food resources. Lastly, I predict that agonism will most frequently occur immediately following food-oriented behaviors. See table 1 for a summary of these predictions.

Proximity:

If clumped food sources promote a decrease in inter-individual distance, the correlation between aggression and clumped food may reflect a response to proximity rather than to resource competition. Increased agonism may simply result from the opportunity for it to occur (Stevenson *et al.* 1998, Vogal & Janson 2007). Sussman and Garber (2007) call this influence of proximity on social behavior the billiard ball phenomena, where they argue that some agonistic interactions occur, not as a result of some social strategy, but of the fact that individuals cannot occupy the same space simultaneously. However, because individuals themselves are distributed non-randomly in physical space on the basis of their social relationships (McBride 1971, Fairbanks 1976), random social interactions are expected to occur more frequently between some individuals than others as a function of those relationships. Therefore, the organization of an animal society is though to be reflected in the spatial patterns of its members (Kummer 1968).

These studies suggest that an alternative hypothesis to the socioecological model is that interaction patterns, and thus social relationships, are more directly explained by inter-individual distance than by resource competition. There is much evidence indicating that there is a relationship between proximity and social behavior (Sade 1965, 1972, Altmann 1968, Corradino 1990). For example, Vogel & Janson (2007) found that with all ecological variables held constant, the more white faced capuchin monkeys, *Cebus capucinus*, in a feeding site, the greater the number of aggressive interactions and the higher the intensity of those interactions. Furthermore, Call (1999) found that the tendencies of reconciliation, where individuals make affiliative contact after a fight (in the post conflict time period) sooner than at another time period (the matched control time period), varied as a function of inter-opponent distance during these two periods. Lastly, Fairbanks (1976) found that in hamadryas baboons, *Papio hamadryas*, the social proximity rank (determined by establishing how often each individual was in close proximity to others and ranking them according to that value from lowest to highest time spent in proximity) was positively correlated with both affiliative ($r = 0.68$) and agonistic ($r = 0.59$) behaviors. Thus, individuals who maintained the closest proximity were involved in the most agonistic and affiliative interactions. Dominance rank, on the other hand, was not significantly correlated with the rate of either affiliation ($r = 0.0$) or agonism ($r = -0.07$). if proximity influences patterns of social behavior, I predict that agonism rates will be negatively correlated with the average inter-individual distance (high agonism is related to low inter-individual distance) and positively correlated with the average number of nearby individuals (high agonism is related to a large number of nearby individuals). I further predict that agonism will often follow movement behaviors that occur in close proximity. In light of Fairbanks' (1976) study, it also seems reasonable to predict that affiliation rates will also be negatively correlated with the average inter-individual distance. See table 1 for a summary of these predictions.

Kinship:

Genetic relatedness is widely invoked to explain the interactions of individuals in social groups (Silk *et al.* 1999). Specifically, kin selection theory predicts that individuals would show less agonism and more affiliation towards genetically related kin than non-kin (Hamilton 1964). Kinship has been argued to be a fundamental element of primate sociality (Strier 2004). Some researchers believe that relatedness, especially among females is "the corner stone of sociality" and that female kinship and male response are "the proximate determinant of a social system" (Walker *et al*. 2008: 1361). Furthermore, Gouzoules and Gouzoules (1987) acknowledged kin bias (i.e. the tendency to affiliate disproportionately with kin) to be a central organizational principle of macaque, genus *Macaca* and baboon, genus *Papio*, societies. In ringtailed lemurs, kinship plays a major role in group fission, with it almost always occurring along matrilineal lines (Ichino 2006). Furthermore, some social animals, including ringtailed lemurs (Jolly 1966), live with several generations of kin who have varying degrees of genetic relatedness. Kapsalis & Berman (1996a) found that adult female rhesus macaques, *Macaca mulatta*, affiliate preferentially with close maternal kin ($r \geq 0.125$) (this coefficient of relatedness is only taking into account maternally inherited genes) compared to distant maternal kin ($0.125 \leq r \geq 0.005$), however they do not discriminate between distant maternal kin and non-kin. Similarly, Belisle and Chapais (2001) found that female Japanese macaques, *Macaca fuscata*, tolerated co-feeding behavior, which was characterized by a low rate of agonism, with close maternal kin ($r \geq 0.25$) and showed no discrimination between distant ($0.25 \leq r > 0$) and non-kin ($r = 0$), who received higher levels of agonism. The authors of both papers suggest that their findings indicate the existence of a relatedness threshold that limits nepotism, both in terms of affiliation and agonism, to closely related kin.

If kinship influences patterns of social behavior, individuals are expected to distinguish among degrees of kin and/or between kin and non-kin in their affiliative and agonistic social interactions. I predict that individuals will participate in significantly more affiliation and less agonism with primary kin than either secondary or non-kin. See table 1 for a summary of these predictions.

Previous Agonism:

Early social interactions have the potential to disproportionately influence future interactions (Hinde 1979). As a result, there is a large body of literature that focuses on the relationship between aggressive events and future occurrences of social behavior. The most comprehensive body of work on this subject is the "reconciliation hypothesis" (de Waal & van Roosmalen 1979). "Reconciliation" is operationally defined as a reduced latency or increase in frequency of affiliation between opponents shortly after conflict. Researchers have documented "reconciliation" in many species of primates (Aureli & de Waal 2000) and other social mammals (Schino 1998, domestic goats, *Capra* *aegagrus*; Wahaj *et al.* 2001, spotted hyenas, *Crocuta crocuta*). Therefore it has been proposed that "reconciliation" functions to repair relationships damaged by agonism (de Waal & van Roosmalen 1979), reduce future agonism (Castles & Whiten 1998), reduce the stress of previous combatants (Katsukake and Castles 2001), and restore tolerance in the presence of food (Aureli *et al.* 2002). An implication of this hypothesis is the assumption that "reconciliatory" behaviors evolved as repair mechanisms to counter the unavoidable conflict that is expected to occur in a social group (Fuentes 2004, Sussman *et al*. 2005). "Reconciliation" has thus become accepted as a behavioral mechanism that preserves the cohesion of social groups by reducing the negative impacts of conflict (Silk 2002).

To better understand the "reconciliation" literature, it is important to examine its major hypotheses. These are: 1) Group living animals frequently reconcile after conflict (Sterck *et al.* 1997) although the expected frequency varies by group and species (Cords & Aureli 2000). 2) There is a relationship between the characteristics of the conflict and the probability of "reconciliation" (Fuentes 2004). 3) "Reconciliation" is most likely to occur between individuals with biologically valuable relationships because animals have more at stake when a valuable relationship is damaged by conflict (Cords & Aureli 2000). A biologically valuable relationship is one that provides substantial fitness benefits to one or both parties involved (de Waal & Yoshihara 1983, Aureli *et al.* 2002). However, it is difficult to establish the characteristics that make a relationship valuable (Cords & Aureli 2000).

In addition to serving a "reconciliation" function, post-conflict "conciliatory" behavior has also been suggested to occur between uninvolved bystanders and the victim of an aggressive interaction in several primate species (Judge 1991, pigtail macaques, *Macaca nemestrina*; Petit & Thierry 1994, Tonkean macaques, *Macaca tonkeana*; Call *et al*. 2002, stumptail macaques, *Macaca arctoides*; Wittig *et al.* 2007 hamadryas baboons, *Papio hamadryas ursinus*). This triadic post-conflict affiliation has been termed "consolation" and it is hypothesized to function as a conflict management mechanism because it may curtail future agonism (Petit & Thierry 1994). Furthermore, it also has been suggested that, because the consoling third party may be the kin of the opponent, "consolation" can also function as kin-mediated "reconciliation" and thus restore affiliation across genetic lines (Judge 1991, Call *et al.* 2002, Wittig *et al.* 2007). Arnold and Whiten (2001) and Fuentes *et al.* (2002) did not find evidence of this behavior in wild chimpanzees, *Pan troglodytes schweinfurthii,* which lead them to suggest that "consolation" is not a post-conflict behavior of this species in their natural habitat. Although they are often used as such in the literature (Silk 2002), the terms "reconciliation" and "consolation" do not necessarily indicate purposeful behaviors intended to end conflict. In this study, reconciliation and consolation only referred to the operational definition of the terms (i.e. heightened affiliation after conflict) and did not imply emotional outcomes.

The relationship between a bout of agonism and the reoccurrence of agonism between the same two participants (i.e. renewed agonism) is rarely discussed in the literature, and when it is, it is usually done so in the context of "reconciliation" behaviors. For example, Manson *et al.* (2005) found that prompt "reconciliation" attempts were more likely than delayed attempts to result in renewed agonism. Furthermore, Patzelt *et al.* (2009) found that when an affiliative interaction occurred in the post-conflict period, it was more likely that renewed agonism would occur between the previous combatants than if "reconciliation" had not occurred at all (16% compared with 9% respectively). To my knowledge, there are no published investigations of post-conflict aggression independent of reconciliation.

Unlike prior work on post conflict behaviors, I examined at the relationship between agonism and affiliation as well as between agonism and renewed agonism. Specifically, I predict that if there is a relationship between an aggressive interaction and future occurrences of agonism and/or affiliation, 1) Affiliative and/or agonistic interactions will frequently occur sooner in the post conflict period than at random. 2) Overall dyadic affiliation and agonism frequencies will be correlated with one another. 3) There will be a predictive relationship between the characteristics of the conflict and the probability of "reconciliation" and/or renewed agonism. Without consistent predictors, occurrences of post-conflict affiliation and agonism cannot be shown to be related to the previous aggressive event. In the case of "reconciliation", without predictors of post-conflict affiliation within a species, or at least a social group, it remains unclear if there is a pattern of behaviors that has been selected to repair the damage caused to social relationships by conflict (Silk 2002). 4) There will be a predictive relationship between the probability of "reconciliation" and renewed agonism and the specific category of social relationship between individuals. I have not attempted to weigh the biological value of relationships because valuable relationships can be highly subjective and ambiguous. See table 1 for a summary of these predictions.

METHODOLOGY:

Study Site:

This study was conducted at The Duke Lemur Center (DLC) in Durham, NC. The Duke Lemur Center houses multiple groups of ringtailed lemurs in several semi-free ranging enclosures that are surrounded by a mildly electrified fence. The two groups of ringtailed lemurs observed in this study live in a 14.3-acre and 8.2-acre mixed pine hardwood forest. Several species of wild animals inhabit or visit the naturalistic enclosures and act as potential predators and as competitors for food (Table 2). DLC is one of the four main sites for long-term ringtailed lemur research in the world, the other three being in Madagascar (Sauther *et al.* 1999). See Taylor (1986) and Wright (2008), for a complete description and history of the study site.

Time Frame:

The first field season took place between June 2007 and August 2007 and the second field season between June 2008 and August 2008. Observations were conducted between 7:00 and 16:00, five to six days a week. I controlled for the influence of time of day on behaviors by collecting the same amount of observations in the morning and in the afternoon for each focal animal.

Subjects:

In the summer of 2007, observations were conducted on seven ringtailed lemurs in an established species-typical social group (Table 3). In the summer of 2008, observations were conducted on another seven individuals from a different group (Table

4), for a total sample size of 14. Similar sample sizes are common in other primate studies, including some conducted under completely natural conditions (Table 5). The adult animals in each of the social groups have lived at DLC for at least three years and in most cases, all of their lives. Focal animals represented all gender, age (with the exception of infants), and reproductive classes that were present in each group at the time of the study.

The semi-free ranging animals at DLC are considered to be comparable both behaviorally and physically to wild lemurs. In fact, a study on ringtailed lemurs at St. Catherine's Island, another well-established semi-captive facility in the United States, found that zoo lemurs released into these enclosures eventually resembled wild lemurs in terms of appearance and behavior (Keith-Lucas *et al.* 1999). In the past, six infants and two juveniles have died as the result of predation by the naturally existing predators that also inhabit the enclosures (Table 2). In response to these predators, DLC animals commonly partook in species typical mobbing and vocalization behaviors (Macedonia 1993, *pers. obs.*). The animal's diet was minimally supplemented in quantities that are 50% less than is required by the American Zoological Association for this species when it is maintained in zoos (Table 6). As a result, the animals forage on over 15 species of local flora that grow in the enclosures (Ganzhorn 1986) (Table 7), which takes up much of their feeding time. Furthermore, the average weight, and thus, net caloric intake of the adult lemurs in these study groups are comparable to those of wild ringtailed lemurs (Koyama *et al.* 2007) (Table 8). This similarity suggests that there are comparable levels of feeding competition in these enclosures and in the wild.

Procedure:

Data were collected using focal sampling of the 14 individuals previously noted. All individuals were observed in a random order for between 42 and 50 hours each (660 hours total). Focal behavior and group proximity scans of all visible group members were documented instantaneously at 5-minute intervals. Any occurrence of social behavior (Table 9) was documented continuously from the time of its onset to the time of completion.

I developed the following rubric for documenting behaviors. First, I classified a single social bout to be occurring if the behavior persisted with pauses of no more than 10 seconds. If the behavior ceased for more than 10 seconds, this indicated the end of that behavioral bout. Secondly, whenever an individual joined or left a social bout, subsequent interactions were considered to be a new bout. For example, if focal animal A was being groomed by B and then C moved into contact with A, this behavioral progression was scored as two distinct bouts, the first of which involved grooming by B, and the second of which involved grooming by B and bodily contact with C.

When a social behavior occurred, I documented the identity of relevant individuals, the direction of each interaction, the type of behavior (Table 9), and the context in which the behavior occurred. c) rest, d) travel (directed locomotion with a beginning and end location), e) move (undirected movement), and f) alert. The context of social behaviors was determined based on the context category in which the animal was participating just prior to the initiation of a social behavior. For example, if two animals were foraging and one started to groom the other, this affiliative social behavior was classified as taking place during a foraging context.

For all aggressive behaviors, I document the behaviors that occurred just prior to the aggressive act. This measure was called the behavioral precedent to agonism.

After all data had been collected, I later coded all social behaviors using a combination of the following descriptive categories: *active* or *passive* and *affiliative* or *agonistic* (Table 9). Ambiguous behaviors were coded as *unknown* and left out of all analyses (Table 9). For example, if focal animal A was grooming B, this behavioral unit was coded as *active affiliation* (Table 9). I also coded agonistic behaviors by intensity level. All passive agonism and submissive behaviors were assigned a number on a scale of 1-2 (Table 10). Active agonistic interactions were assigned a number on a scale of 3-7 (Table 10). Those behaviors that were assigned a number between 1-4 were considered to be low intensity agonism and those that were assigned a number between 5-7 were considered to be high intensity agonism. The intensities were assigned based on the presumed likelihood of a behavior resulting in serious physical harm of one or both participants. These classifications are similar to those used by Arnold and Whiten (2001). If an active and passive or high and low intensity behavior occurred simultaneously, the active or high intensity behavior took precedence. For example, if focal animal A was chasing B and B vocalized submissively to A, this event, which contained active (chase) and passive (vocalization) elements, was coded as *active* and *intense agonism.* For each individual, I determined the overall rate per hour of intense vs. mild agonistic behaviors in all contexts. The methods used to collect and code these data are described in further detail in Appendix I.

There were two feeding contexts experienced by the ringtailed lemurs in this study, which were termed as the “provisioned feeding” and the “naturalistic foraging” contexts. In the provisioned feeding context, the lemurs fed on primate chow, which was classified as a highly valuable food source because it is designed to be nutritionally complete for primate species (Mowry & Campbell 1991). The provisioned feeding context was also classified as a clumped resource due to the way in which the food was presented. Lastly, the provisioned feeding context was also classified as containing a limited food resource because the chow was provisioned at quantities that are over 50% less than is required by the American Zoological Association for this species (Table 6) and because both groups of ringtailed lemurs consistently ate the entire ration (69.4g/individual/day) of chow and continued to search for more after it ran out. In the naturalistic foraging context, the lemurs fed on fruits, leaves, bugs, and flowers. This context was classified as containing less valuable food resources that were more plentiful and dispersed through space and time.

Food Resources:

The relationship between food resources and agonism was analyzed by comparing the rate of agonistic interactions in each of six contexts, two of which involve food. This relationship was further examined by comparing the proportion of aggressive interactions that were immediately preceded by a food-oriented behavior. Food-oriented behaviors included feeding, drinking, foraging, and moving towards the water trough. I distinguished between high intensity (HI) and low intensity (LI) agonism for all analyses. To my knowledge, there exists no theoretical basis to suggest that the presence of food resources would influence affiliation because coalition formation is very rare among ringtailed lemurs (Nakamichi & Koyama 1996).

Analysis:

I first compared the two groups to each other using an independent samples t-test and combined all data that were statistically identical for future tests. The rate of agonistic interactions in each context was compared using a repeated measures ANOVA and a post-hoc Bonferroni test. I compared the relative frequency of agonistic interactions that were preceded by food-oriented vs. non-food oriented behaviors using a paired t-test. Because the familywise error rate is high when running many post-hoc comparisons for a repeated measures ANOVA, I limited the post-hoc test to only those comparisons between the provisioned feeding contexts and other contexts. The familywise error rate is the probability of finding at least one comparison in a set of comparisons that is significant by chance alone (Howell 2002). To properly control for the familywise error rate, the critical value of each post-hoc comparison in this test must be $p \leq 0.01$ ($p \leq 0.05$ divided by the number of comparisons, which was 5 in this case) for significance to be reached (Howell 2002).

Proximity:

The relationship between proximity and social behavior was analyzed both within each context and among contexts for both low and high intensity agonism. Using the proximity data collected at each 5-minute interval, I determined the average inter-individual distance of all focal animals to all other members of the group and the average number of individuals within 10 meters of each focal animal. I used 10 meters because Janson (1996) found that dominant brown capuchin monkeys, *Cebus apella nigritus*, only reduced the feeding success of subordiant individuals when within a 10-meter radius.

This finding indicates that for animals of similar size and locomotary capabilities, such as ringtailed lemurs, individuals may be effectively absent from one another's company at distances greater than 10 meters. All animals that were documented as being *out of sight* were given a proximity value of 50 meters. The relationship between proximity and social behavior was further examined by calculating the proportion of agonistic interactions that were immediately preceded by close proximity movement behaviors. This measure does not imply causation but might provide insight into what the fight was over.

Analysis:

I first compared the data sets of the two social groups using an independent samples t-test and combined all data that was statistically identical for all future tests. To determine if the average distance between individuals within a context was related to the average affiliation and agonism frequencies between individuals, I created four matrices for each context. The first matrix indicated the average proximity between pairs of individuals; the other three indicated the average rate of affiliation and high and low intensity agonism between pairs of individuals. I then conducted multiple matrix correlations using a Mantel test with the software MatMan v. 1.1 (Kapsalis & Berman 1996a, Noldas 1998). To determine if the average distance between individuals across contexts was related to the average affiliation and agonism in those context, I conducted a bivariate Pearson's correlation between the average proximity and the rate of social behavior in the five contexts (due to the spontaneous nature of the alert context, I did not use it in these analyses because proximity was likely a product of the context that preceded it). To determine if the average number of individuals within 10 meters was related to average rate of affiliation and agonism within and across contexts, I conducted multiple bivariate Pearson's correlations between these variables. The behavioral precedent to agonism was analyzed using a paired t-test to compare the frequency of close proximity movement behaviors to other behaviors that preceded an agonistic interaction.

Kinship:

Degrees of relatedness were measured using the coefficient of relatedness, *r*, and were determined based on the known pedigree relationships between individuals (Table 2, Table 3). Individuals were categorized as having a coefficient of relatedness of greater than or equal to 0.5, less than 0.5, and 0.0. In this analysis, I used all kin and not just maternal kin, as is commonly done because the two classification methods were entirely equivalent in group 1 and nearly equivalent in group 2. Because dominant male ringtailed lemurs do not monopolize mating opportunities and male residency in any one social group is limited to a few years (Sussman 1992), the majority of kin relationships in wild ringtailed lemurs are likely through the maternal line as well. Additionally, with the recent application of genetic tools, several primate species have been found to be able to recognize paternal kin to varying degrees, although the precise mechanism is still under debate (Alberts 1999, yellow baboon, *Papio cynocephalus*; Widdig *et al.* 2001, rhesus macaques, *Macaca mulatta*; see Widdig 2007 for a review). All individuals used in the analyses have all categories of kin present in their social group. Nepotism was considered to occur when animals showed differential treatment in terms of frequency and type of affiliative and agonistic behaviors toward kin (primary and/or secondary) and non-kin. I analyzed the differences in the amount of affiliation, high intensity agonism, low intensity agonism, and "reconciliation" tendencies (this analysis is presented in the results under *Previous Agonism*) with regards to kinship.

Analysis:

First I compared the data sets of the two groups using an independent samples t-test and combined all data that was statistically identical for future tests. The presence of nepotism was identified using a repeated measures ANOVA to determine if the suite of behaviors observed between primary kin occurred at different frequencies than those observed between secondary kin and non-kin. To make sure that the results of this analyses represented behaviors related to kinship as opposed to rank differences, I conducted a matrix correlation using a Mantel test in the software package MatMan v 1.1 (Noldas 1998) between the pedigree relatedness of pairs of individuals and the differences in dominance rank between pairs of individuals. The dominance relationships in each social group were based on the directions of decided agonistic interactions, which were then used to rank individuals via the software MatMan v. 1.1 (Noldas 1998). These data are presented in chapter 3 of this thesis (Sbeglia 2009).

Previous Agonism:

The relationship between previous agonism and social behavior patterns was analyzed using a framework similar to studies of the "reconciliation hypothesis". "Reconciliation" traditionally has been studied by comparing the affiliation that occurs between previous combatants, in a specified post-conflict time period, with the affiliation that occurs between these individuals during an identical time interval (de Waal & van Roosmalen 1979) and at a similar inter-individual distance (Call 1999) the next day. For example, if a post conflict period occurs at 10:00 while the individuals are 4 meters away from one another, the matched control period would occur at around 10:00 the next day when the individuals are at a similar inter-individual distance. This procedure is called the Post Conflict-Matched Control (PC-MC) method. Most studies using this method specify a 10-minute post conflict time interval because that is when most post-conflict affiliations have been found to occur (Arnold & Whiten 2001, Kutsukake & Castles 2004).

The PC-MC method has been primarily used in captivity and is not entirely appropriate for semi-captive or wild studies due to the subjects increased ability for movement (Arnold & Whiten 2001, Kutsukake & Castles 2004). Therefore, Kutsukake and Castles (2004) refined the method by choosing the MC time interval, a posteriori, from the focal animal sampling data. The MC period was matched with the activity of the focal animal during the PC period and was initiated when the focal animal was within 10 meters from the previous combatant. Because even these conditions are difficult to meet in semi-captive and wild conditions, Arnold & Whiten (2001) relaxed the criteria to allow up to 23 days to pass between the PC and MC time intervals.

An assumption of the PC-MC method is that the MC time period accurately indicates the relationship that would exist between two individuals in the absence of a fight. This assumption is most likely unrealistic because matched-control observations do not necessarily reflect the baseline affiliation of individuals in the absence of a fight

(Kappeler & van Schaik 1992, Silk 1997). Furthermore, this method does not take into account the variation in the frequency and type of social interactions that exist through time. These oversights can result in erroneous conclusions about the patterns of "reconciliation" within social groups because the documentation process of the occurrences of this behavior is highly subject to chance events. As a result, Kappeler & van Schaik (1992) proposed the baseline method, which involves conducting several observations of affiliative behavior throughout the study period to get a baseline level of affiliation to which post-conflict behavior can be compared. I used a similar method in this study except that I compared post-conflict behavior to many random time periods selected post-hoc from the entire data set.

In this study, "reconciliation" was considered to occur when previous opponents made affiliative contact, either active or passive, in the post-conflict time period significantly sooner than at multiple random 10-minute time intervals throughout all observation days. A 10-minute post-conflict interval was initiated in a post-hoc fashion immediately after the secession of an active aggressive interaction. A requirement for all qualifying post-conflict time intervals was that they do not contain an active aggressive interaction. To determine if affiliative behavior occurred sooner in the post-conflict time period than at random time periods, thus indicating "reconciliation", 40 random time intervals were extracted from each focal individual's observation days. The latency to affiliate with the previous opponent in the post conflict period and in each random time periods was calculated. I also calculated the latency of third party affiliation (i.e. "consolation") in the post-conflict time period and the latency of affiliation with all group members in the random time periods. A similar method was used to determine if there was a relationship between previous agonism and future agonism. In this analysis, the latency of an aggressive interaction with a previous combatant was calculated for each post-conflict time period and each random time period. Active agonism was allowed to occur in both the post-conflict time periods and in the random time periods.

Several factors were analyzed as potential predictors of heightened affiliation and/or agonism between previous combatants and third party individuals after a fight. This was done by separating conflicts, and their accompanying post-conflict period, into three categories based on: 1) its intensity, 2) the degree of relatedness of the combatants, 3) overall rates of affiliation between previous combatants and 4) overall rates of agonism between previous combatants.

Analysis:

First, I compared the two groups using an independent samples t-test and combined all data that was statistically identical for future tests. I assessed the relationship between overall dyadic affiliation and dyadic agonism frequencies by conducting a matrix correlation using a Mantel test in the software MatMan.

Heightened affiliation (dyadic or triadic "reconciliation") or agonism in the post-conflict time period was identified through a comparison of the latency times in the post-conflict period and in the random intervals. For each dyad, I created frequency histograms of the latency times in the 40 randomly extracted 10-minute intervals to determine at what latency time fewer than 5% of the random affiliative and aggressive interactions lay. This 5% confidence interval is conceptually equivalent to a p-value of

0.05 and thus represents the latency time at which significance is reached. Because this 5% confidence interval was generated for each dyad individually based on their specific interaction patterns, the variation that existed in the behavior patterns among dyads was controlled. Therefore, the tendency to interact with a specific group member after a fight could be directly compared to the tendencies to interact with that same group member at random time intervals. If the latency in the post-conflict period was less than or equal to latency time that characterized the 5% confidence interval, the social behavior was considered to have occurred significantly earlier after a fight than at random. The proportion of conflicts that had a significant decrease in the latency of affiliation and agonism were determined. The four potential predictors were analyzed using a repeated measures ANOVA and a post-hoc Bonferroni test.

RESULTS:

The per-individual rate of high intensity agonism was 0.92 events per hour in group 1 and 0.19 events per hour in group 2 (Table 11). The per-individual rate of low intensity agonism was 2.18 events per hour in group 1 and 1.81 in group 2. The per individual rate of affiliation was 15.31 events per hour in group 1 and 12.3 events per hour in group 2. Individuals in group 1 spent approximately 0.16% of their overall time in agonism and over 15% of their time in affiliation. Individuals in group 2 spent approximately 0.07% of their time in agonism and over 9% of their time in affiliation (Table 11). See Appendix II for figures of these and other results.

Table 11: Patterns of Affiliation and Agonism per Individual

	Affiliation			High intensity Agonism			Low Intensity Agonism		
	#	Rate/ hr	% time	#	Rate/ hr	% time	#	Rate/ hr	% time
Group 1	719	15.31	10.46	43.71	0.92	0.07	101	2.18	0.091
Group 2	579	12.3	9.26	8.86	0.19	0.008	84.9	1.81	0.065

Food Resources:

There was no significant difference in the rate of agonism in each context (repeated measures ANOV: $n = 14$, $p > 0.05$) (Figure 1). However, when I separated out low intensity agonism, there was a statistically significant difference between the rates of low intensity agonism in the six contexts (repeated measures ANOVA: $n = 14$, $p \leq 0.05$) (Figure 2). These differences were between the feeding context and the foraging context (Bonferroni: $n = 14$, $p \leq 0.01$) and the feeding context and the resting context (Bonferroni: $n = 14$, $p \leq 0.01$). All other contexts had statistically similar rates of low intensity agonism (Bonferroni: $n = 14$, $p > 0.01$).

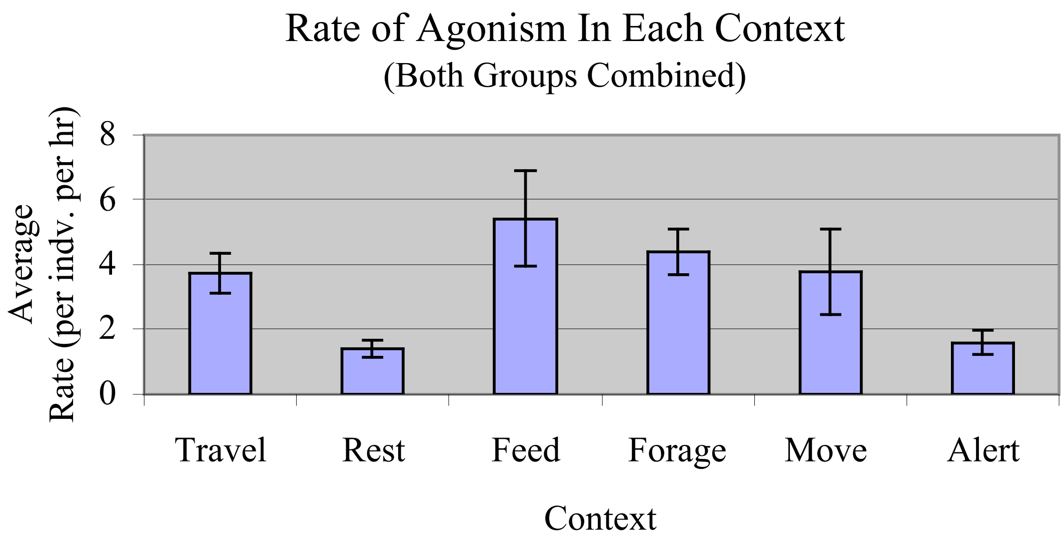


Figure 1 There is no difference in the rate of agonism in each context (repeated measures ANOVA: n = 14, p > 0.05).

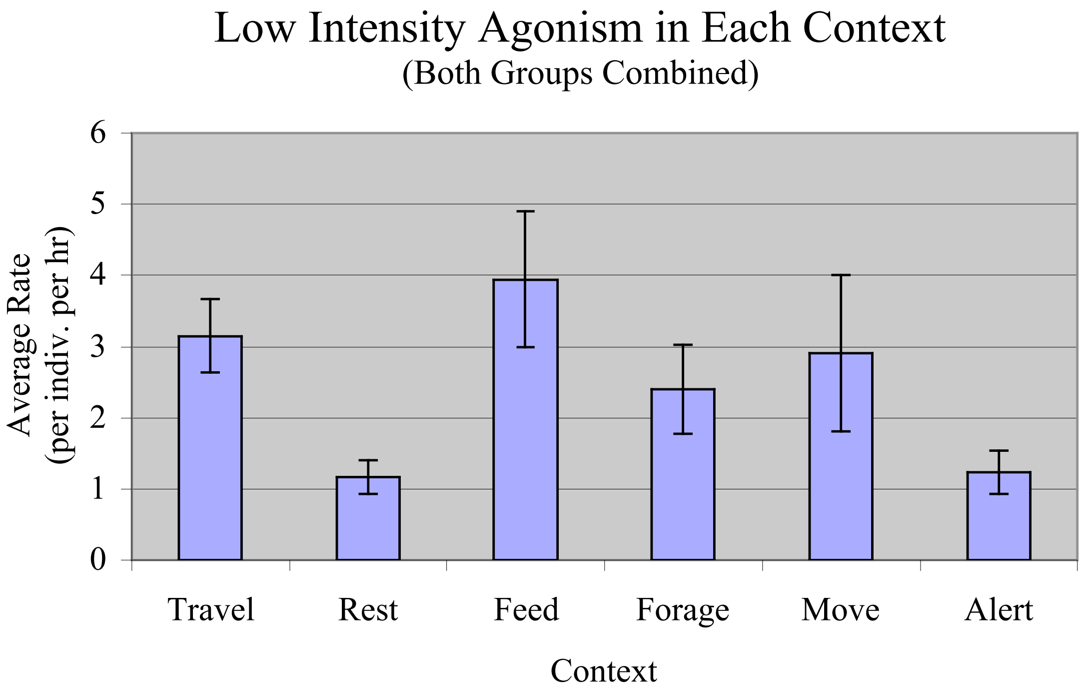


Figure 2. There was a significant difference between the rates of low intensity agonism in the six contexts (repeated measures ANOVA: n = 14, $p \leq 0.05$).

When I separated out high intensity agonism, there was a significant difference in the rate of high intensity agonism in the six contexts in group 1 (repeated measures ANOVA: $n = 7$, $p \leq 0.05$) (Figure 3). These differences were between the feeding context and the moving context (Bonferroni: $n = 7$, $p < 0.01$). The feeding context and all other contexts reached near significance ($n = 7$, $0.01 \leq p \leq 0.02$) but did not meet the critical p-value of the post-hoc Bonferroni test. The Bonferroni post hoc is a conservative test but it is the appropriate test for these data. In group 2, the rate of high intensity agonism was statistically similar in all contexts (repeated measures ANOVA: $n = 7$, $p > 0.05$). I also compared the rate of high intensity agonism in all food-oriented contexts (provisioned feeding and naturalistic foraging) to that in non-food-oriented contexts (rest, travel, move, alert). In group 1, there was a significantly higher rate of agonism in food-oriented contexts than in non-food-oriented contexts (paired t-test: $n = 7$, $p \leq 0.05$), with an average of 1.96 more agonistic acts per individual per hour occurring around food. Conversely, in group 2, there was no significant difference between the rates of high intensity agonism in food-oriented contexts as compared to non-food-oriented contexts (paired t-test: $n = 7$, $p > 0.05$).

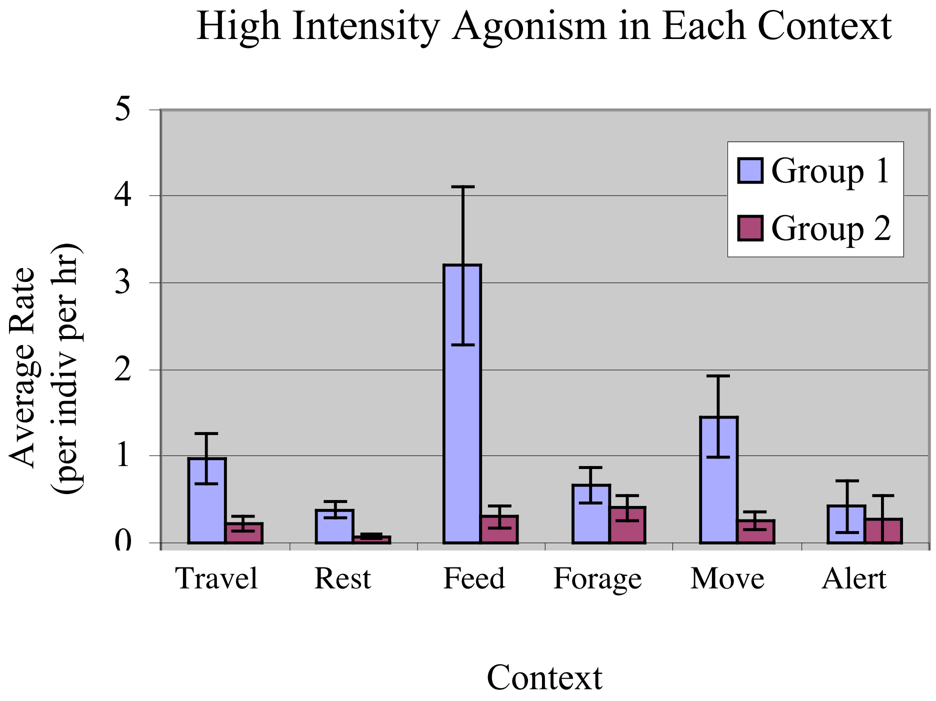


Figure 3: In group 1, there was a significant difference in the rate of high intensity agonism in the six contexts (repeated measures ANOVA: $n = 7$, $p < 0.02$), with the provisioned feeding context having the highest mean rate of agonism. No such pattern existed for group 2 (repeated measures ANOVA: $n = 7$, $p > 0.05$).

When examining at all aggressive interactions regardless of both context and intensity, it was more likely that an aggressive interaction was preceded by a non-food-oriented behavior than by a food-oriented behavior (paired t-test, $n = 14$, $p < 0.02$). This pattern persisted when examining only low intensity agonism (paired t-test, $n = 14$, $p < 0.02$). When examining high intensity agonism, it was no more likely for such aggressive events to be preceded by a food-oriented or a non-food-oriented behaviors (paired t-test, $n = 14$, $p > 0.05$) (Figure 4).

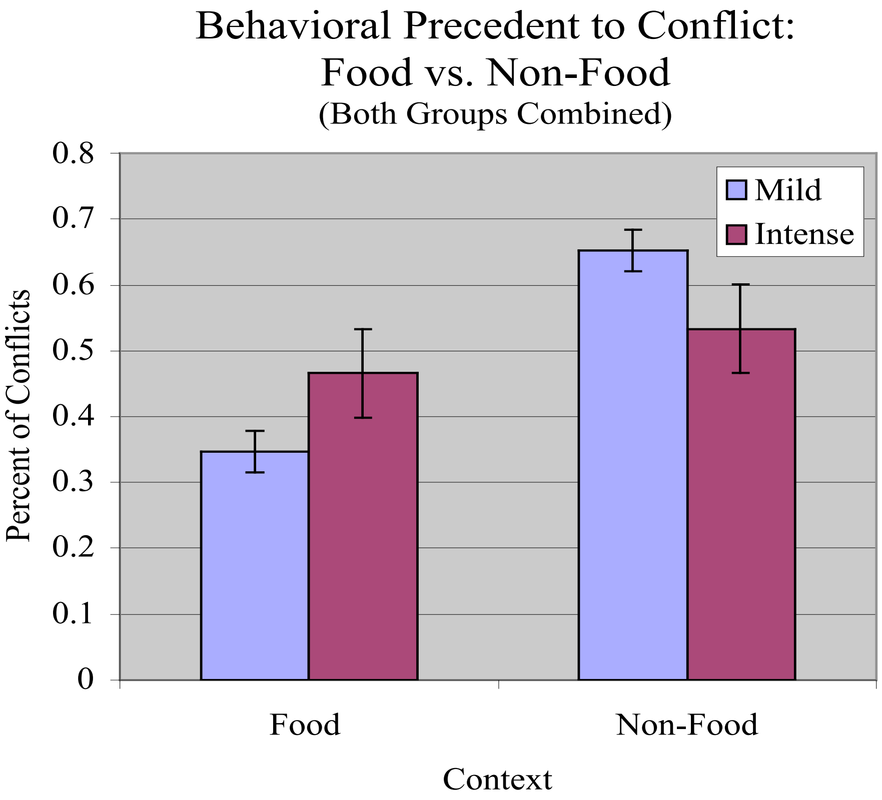


Figure 4. It was no more likely that an intense aggressive event were preceded by a food-oriented behavior than a non-food-oriented behavior in both groups (paired t-test: n = 14, $p > 0.05$). It was more likely that a mild aggressive event was preceded by a non-food-oriented behavior than a food-oriented behavior in both groups (paired t-test: n = 14, $p \leq 0.05$). Therefore, aggressive interactions were not consistently preceded by a food-oriented context regardless of the intensity of the interaction.

Proximity:

There was significantly more agonism in the feeding context as compared to the foraging context (paired t-test: n = 14, $p < 0.01$). There are also significantly more individuals within 10 meters of the focal animal (paired t-test: n = 14, $p < 0.01$) and a significantly smaller inter-individual distance in the feeding as compared to the foraging context (paired t-test: n = 14, $p < 0.02$).

Within each context for group 1, there was no correlation between the average proximity of dyads in non-food contexts and their average rate of agonism in non-food contexts for both low intensity (Pearson's: $n = 7$, $r = 0.03$, $p > 0.05$) and high intensity agonism (Pearson's: $n = 7$, $r = 0.458$, $p > 0.05$). In the provisioned feeding context, there was no correlation between the average proximity of dyads and their rate of *low* intensity agonism (Pearson's: $n = 7$, $r = 0.334$, $r = 0.051$) but there was a significantly positive correlation between proximity and the rate of *high* intensity agonism (Pearson's: $n = 7$, $r = 0.64$, $p < 0.02$). In the naturalistic foraging context, there was no correlation between these variables for high intensity agonism (Pearson's: $n = 7$, $r = 0.032$, $p > 0.05$) but there was a significant negative correlation between these variables for low intensity agonism (Pearson's: $n = 7$, $r = -0.0346$, $p < 0.01$). When examining at all agonism in all contexts, there was no correlation between proximity and agonism for either low (Pearson's: $r = 0.029$, $p > 0.05$) or high intensity agonism (Pearson's: $r = 0.435$, $p > 0.05$). See table 12 for a summary of these data.

There was also no correlation between the average number of individuals within 10 meters of the focal animal and the rate of agonism in any of the contexts (Pearson's: travel, $n = 7$, $r = -0.387$, $p > 0.05$; move, $n = 7$, $r = -0.325$, $p > 0.05$; rest, $n = 7$, $r = 0.281$, $p > 0.05$; feed, $n = 7$, $r = -0.691$, $p > 0.05$; forage, $n = 7$, $r = -0.538$, $p > 0.05$) or overall (Pearson's: $r = 0.0193$, $p > 0.05$). Separating the analysis into high and low intensity agonism did not change these results. See table 12 for a summary of these data.

Group	Correlation Category	Intensity	Proximity Correlations	Individuals w/in 10m Correlations
1	**Non-food contexts**	High	NS	NS
		Low	NS	NS
	Provisioned feeding	High	+	NS
		Low	NS	NS
	Naturalistic foraging context	High	NS	NS
		Low	-	NS
	All contexts	High	NS	NS
		Low	NS	NS
2	**Non-food contexts**	High	-	NS
		Low	-	NS
	Provisioned feeding	High	NS	NS
		Low	NS	NS
	Naturalistic foraging context	High	NS	+
		Low	NS	NS
	All contexts	High	-	NS
		Low	-	NS

Table 12: Correlations between the rate of agonism and average proximity and the rate of agonism and the number of individuals within 10 meters of the focal animal. “NS” = Not significant, “-” Negative correlation, “+” = Positive correlation.

For group two, this same analysis showed that there was a significantly negative correlation between average proximity and the rate of agonism for both low intensity (Pearson’s: $n = 7$, $r = -0.61$, $p < 0.001$) and high intensity agonism (Pearson’s: $n = 7$, $r = -0.407$, $p < 0.02$) in non-food contexts. Conversely, no correlation existed between these variables for high or low intensity agonism in either of the food-oriented contexts (Pearson’s: food_{LI}, $n = 7$, $r = 0.042$, $p > 0.05$; food_{HI}, $n = 7$, $r = 0.244$, $p > 0.05$; forage_{LI}, $n = 7$, $r = 0.029$, $p > 0.05$; forage_{HI}, $n = 7$, $r = 0.022$, $p > 0.05$). However, when examining all agonism in all contexts, there was a significant negative correlation between proximity and agonism for both low intensity (Pearson’s: $r = -0.351$, $p < 0.05$)

and high intensity (Pearson's: $r = -0.28$, $p < 0.01$). See table 12 for a summary of these data.

There was also no correlation between the average number of individuals within 10 meters of the focal animal and the rate of low intensity agonism in any of the contexts (Pearson's: travel, $n = 7$, $r = 0.749$, $p > 0.05$; move, $n = 7$, $r = 0.662$, $p > 0.05$; rest, $n = 7$, $r = 0.253$, $p > 0.05$; feed, $n = 7$, $r = 0.381$, $p > 0.05$; forage, $n = 7$, $r = -0.295$, $p > 0.05$) and high intensity agonism in four of the five contexts (Pearson's: travel, $n = 7$, $r = 0.496$, $p > 0.05$; move, $n = 7$, $r = 0.476$, $p > 0.05$; rest, $n = 7$, $r = -0.04$, $p > 0.05$; feed, $n = 7$, $r = 0.308$, $p > 0.05$). However, there was a significant positive relationship between the average number of individuals within 10 meters of the focal animal and the rate of high intensity agonism in the forage context (Pearson's: $n = 7$, $r = 0.788$, $p \leq 0.05$). There was no overall correlation between the average number of individuals within 10 meters of the focal animal and the total rate of agonism (Pearson's: $r = -0.118$, $p > 0.05$). See table 12 for a summary of these data.

Across contexts, there was no correlation between the average rate of agonism in each of the five contexts and the average proximity in each context (Pearson's: group 1, $n = 5$, $r = 0.159$, $p > 0.05$; group 2, $n = 5$, $r = 0.172$, $p > 0.05$) or the average number of individuals within 10 meters of the focal animal (Pearson's: group 1, $n = 5$, $r = -0.267$, $p > 0.05$; group 2, $n = 5$, $r = -0.444$, $p > 0.05$). Separating the analysis into low and high intensity agonism did not change these results. Furthermore, it was significantly more likely that conflict was preceded by the close proximity movement (CPM) of one of the combatants than by all other behaviors (paired t-test: group 1, $n = 7$, $p \leq 0.05$; group 2, $n = 7$, $p < 0.001$) (Figure 5). When separated out by intensity, low intensity agonism was preceded by CPM significantly more often than other behaviors, while high intensity agonism showed no significant pattern, such that it was just as likely for CPM to precede or nor precede an agonistic interaction (paired t-test: group 1_{HI}, $n = 7$, $p \leq 0.05$, group 1_{LI}, $n = 7$, $p > 0.05$; group 2_{HI}, $n = 7$, $p \leq 0.05$, group 2_{LI}, $n = 7$, $p \leq 0.05$). Overall, close proximity movement preceded a higher proportion of conflicts on average than did food-oriented behaviors (paired t-test: group 1, arithmetic $\text{mean}_{CPM} = 0.54$, arithmetic $\text{mean}_{food} = 0.46$; group 2, arithmetic $\text{mean}_{CPM} = 0.074$, arithmetic $\text{mean}_{food} = 0.36$). However, this was only significant for overall agonism in group 2 (paired t-test: $n = 7$, $p < 0.02$) and for low intensity agonism in both groups (paired t-test: group 1 $n = 7$, $p < 0.001$; group 2, $n = 7$, $p < 0.01$).

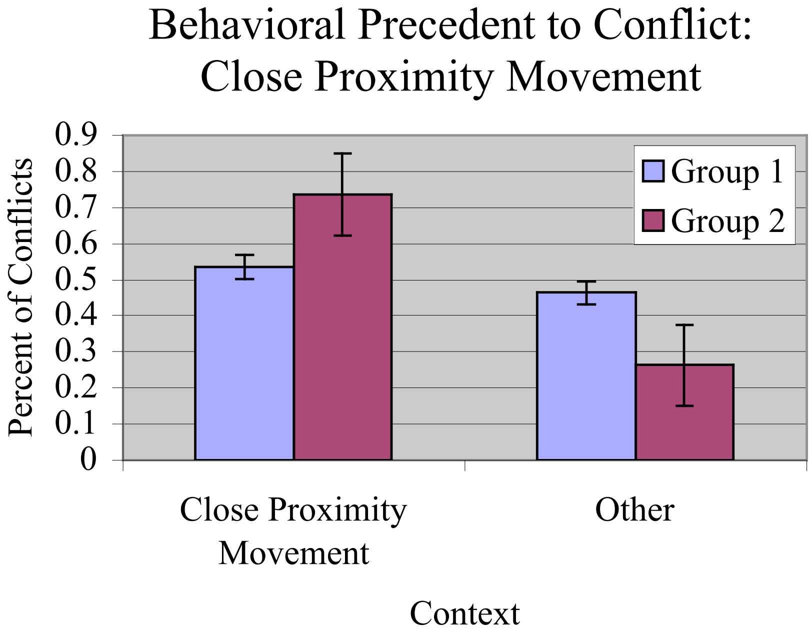


Figure 5: It was significantly more likely that conflict was preceded by the close proximity movement (CPM) of one or both of the combatants than by all other behaviors (paired t-test: group 1, $n = 7$, $p \leq 0.05$; group 2, $n = 7$, $p < 0.001$).

In the case of affiliation for group 1, within contexts, there was a negative correlation between the average proximity between pairs of individuals and the average rate of affiliation in non-food ($n = 7$, $r = -0.67$, $p < 0.001$), feeding ($n = 7$, $r = -0.43$, $p < 0.01$), and foraging ($n = 7$, $r = -0.33$, $p < 0.02$) contexts and overall (Pearson's: $n = 7$, $r = -0.55$, $p < 0.05$). In group 2, there was a significant negative correlation between these variables in the provisioned feeding (Pearson's: $n = 7$, $r = -0.48$, $p \leq 0.05$) and naturalistic foraging context (Pearson's: $n = 7$, $r = -0.36$, $p \leq 0.05$) but no correlation in non-food contexts (Pearson's: $n = 7$, $r = -0.079$, $p > 0.05$) or overall (Pearson's: $n = 7$, $r = -0.214$, $p > 0.05$).

Across contexts, there was no correlation in either group between the average rate of affiliation in each of the 5 contexts and the average proximity in each context (Pearson's: group 1 $n = 5$, $r = -0.414$, $p > 0.05$; group 2, $n = 5$, $r = -0.258$, $p > 0.05$) or the average number of individuals within 10 meters of the focal animal (Pearson's: group 1, $n = 5$ $r = 0.784$, $p > 0.05$; group 2, $n = 5$, $r = 0.262$, $p > 0.05$). See Table 13 for a summary of these data.

Group	**Correlation Category**	**Proximity Correlations**
1	**Non-food contexts**	**-**
	Provisioned feeding	**-**
	Naturalistic foraging context	-
	All contexts	-
2	**Non-food contexts**	NS
	Provisioned feeding	-
	Naturalistic foraging context	-
	All contexts	NS

Table 13: Correlations between the rate of affiliation and average proximity. "NS" = Not significant, "-" = Negative correlation, "+" = Positive correlation.

Kinship:

Overall, there was no significant difference between the proportions of agonistic events occurring between different degrees of kin for group 1 (repeated measures ANOVA: $n = 5$, $p > 0.05$). There was a significant influence of kinship on the proportion of agonistic interactions in group 2 (repeated measures ANOVA: $n = 5$, $p \leq 0.05$) but the difference lay between primary and secondary kin (Bonferroni: $n = 7$, $p \leq 0.016$), implying that primary and non-kin were statistically similar (Bonferroni: $n = 7$, $p > 0.016$) (Figure 6).

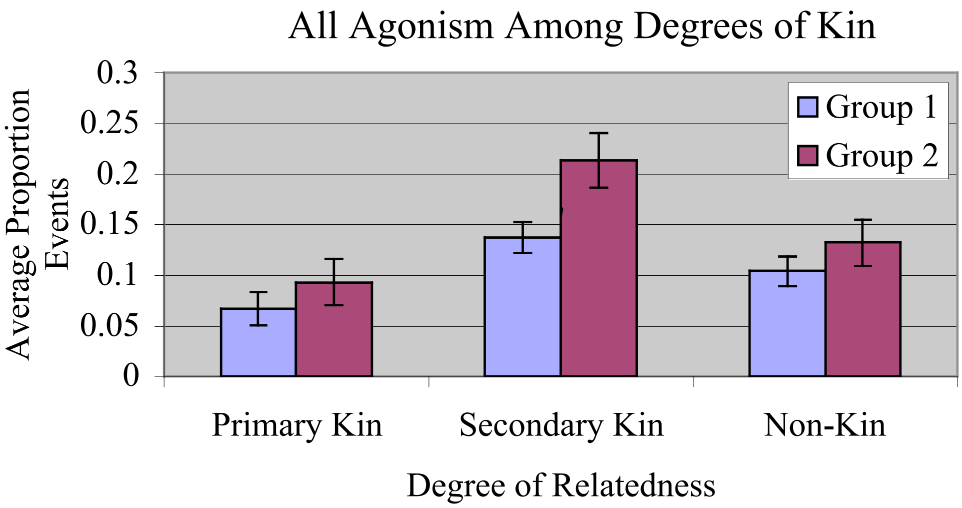


Figure 6: There is no significant difference in the average proportion of agonistic events that occurred between different degrees of kin in group 1 (repeated measures ANOVA, $n = 7$, $p > 0.05$). There is a significant difference between the average proportions of agonistic interactions that occurred between different degrees of kin in group 2 (repeated measures ANOVA, $n = 7$, $p \leq 0.05$). Primary kin are significantly different from secondary kin (Bonferroni: $n = 7$, $p \leq 0.016$).

When separating this analysis out by intensity, there was a significant difference in the average proportion of *high* intensity agonistic events that occurred between different degrees of kin (repeated measures ANOVA: $n = 14$, $p < 0.01$) (Figure 7). The difference lay between primary kin and non-kin only (Bonferroni: $n = 14$, $p \leq 0.016$). There was also a significant difference in the average proportion of *low* intensity aggressive events that occurred among different degrees of kin (repeated measures ANOVA: group 1, $n = 7$, $p < 0.02$; group 2, $n = 7$, $p < 0.02$) (Figure 8). The differences lay between secondary kin and non-kin for group 1 (Bonferroni: $n = 7$, $p \leq 0.016$) and primary and secondary kin for group 2 (Bonferroni: $n = 7$, $p \leq 0.016$). Primary kin and non-kin have statistically similar frequencies of low intensity agonism in both groups (Bonferonni: group 1, $n = 7$, $p > 0.016$; group 2, $n = 7$, $p > 0.016$).

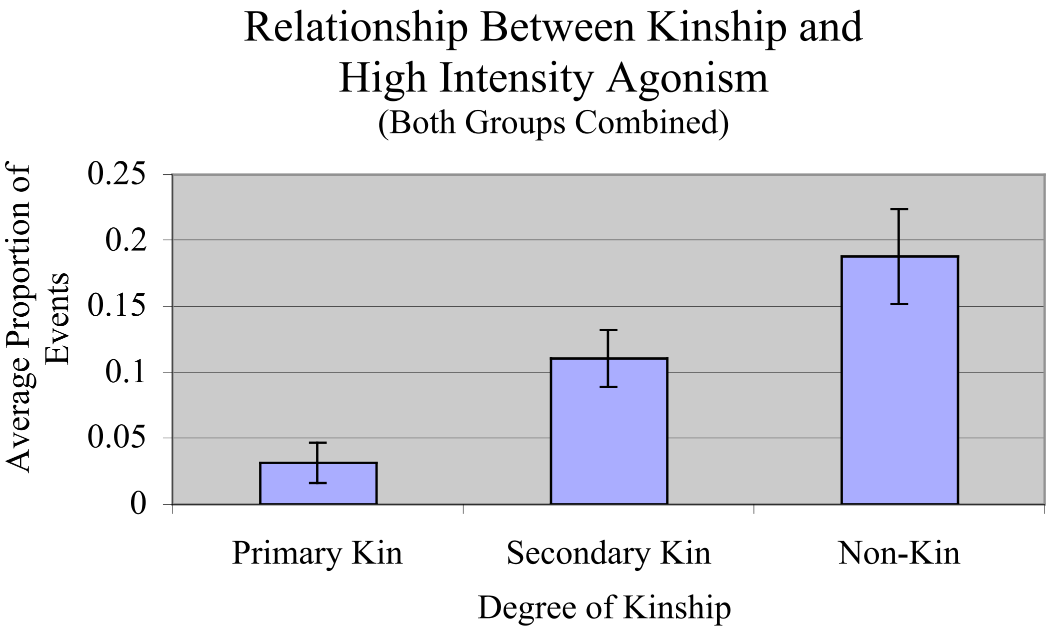


Figure 7: There was a significant difference in the average proportion of aggressive events that occurred between different degrees of kin (repeated measures ANOVA: $n = 14$, $p \leq 0.01$) but only for primary and non-kin ($n = 14$, $p \leq 0.016$) and not between primary and secondary kin ($n = 14$, $p > 0.016$) or secondary and non-kin ($n = 14$, $p > 0.05$).

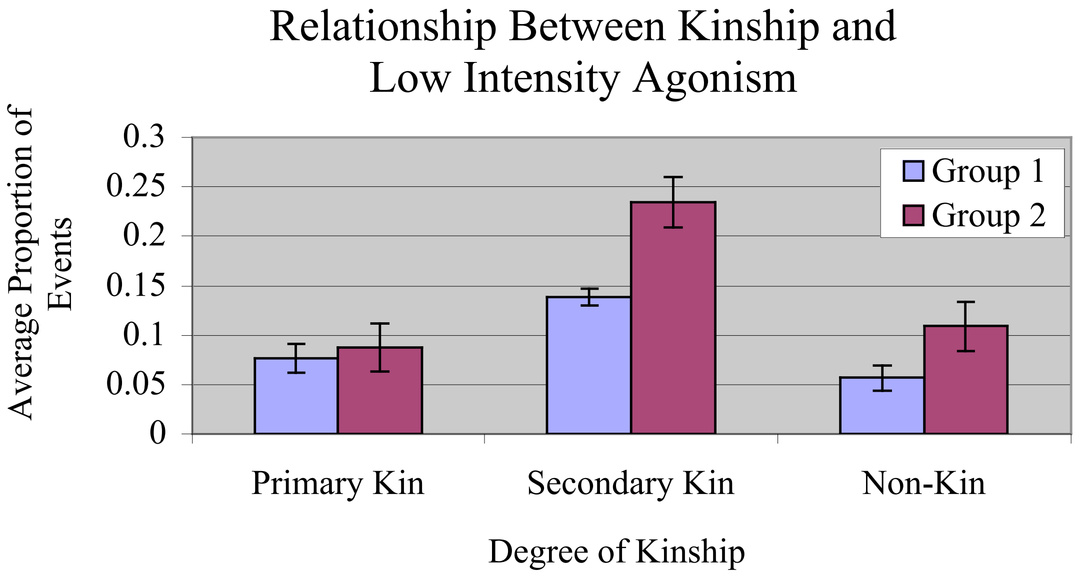


Figure 8: There was a significant difference in the average proportion of low intensity aggressive events that occurred between different degrees of kin (group 1, n = 7, $p < 0.02$; group 2 n = 7, $p < 0.02$) but only between secondary kin ($r < 0.05$) and non-kin ($r = 0$) for group 1 (n = 7, $p \leq 0.016$) and primary ($r \geq 0.5$) and secondary kin for group 2 (n = 7, $p \leq 0.016$).

There was a significant difference in the average proportion of affiliative events that occurred between different degrees of kin (repeated measures ANOVA: n = 10, $p > 0.001$) (Figure 9). Those differences lay between primary and secondary kin (Bonferroni: n = 10, $p \leq 0.016$) and primary and non-kin (n = 10, $p \leq 0.016$). Therefore, individuals in both groups spent a significantly greater proportion of their time affiliating with primary kin than with more distantly related kin and non-kin.

There was no correlation between dominance rank difference and kinship in group 1 (Mantel test: $r = -0.19$, $p > 0.05$) or group 2, the latter of which had no linear dominance hierarchy.

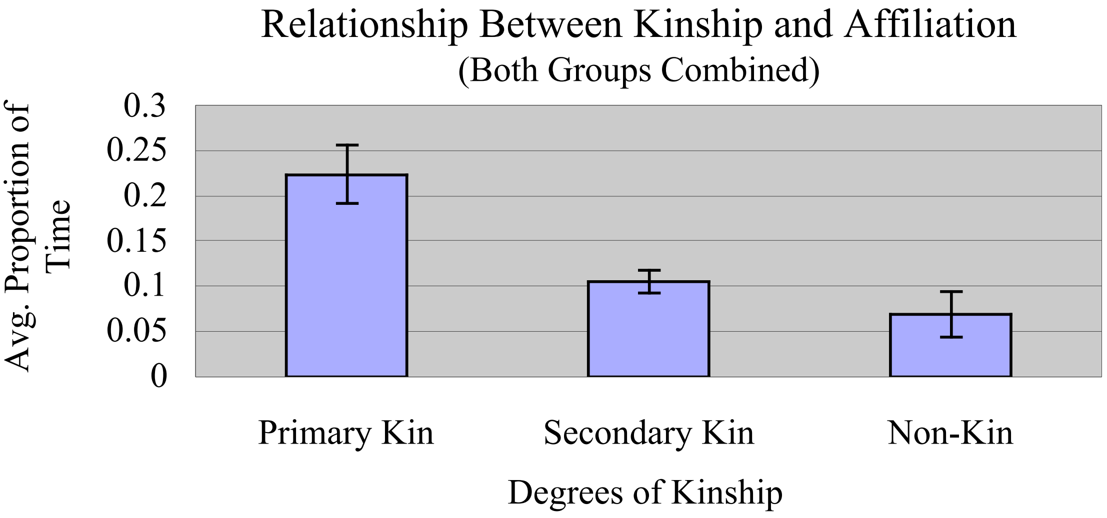


Figure 9: There was a significant difference between the frequency of affiliation based on kinship (repeated measures ANOVA: $n = 10$, $p < 0.001$). The difference lay between primary and secondary kin (Bonferroni: $n = 10$, $p \leq 0.016$) and primary and non-kin (Bonferroni: $n = 10$, $p \leq 0.016$) but not for secondary and non-kin (Bonferroni: $n = 10$, $p > 0.05$).

Previous Agonism:

Out of 221 qualifying aggressive interactions, only five (2.3%) had affiliation occur significantly sooner in the post-conflict period than at random (thus fulfilling the requirements of "reconciliation"). These five "reconciliation" events were not predicted by the intensity of the fight (repeated measures ANOVA: $n = 14$, $p > 0.05$), the relatedness of the previous combatant (repeated measures ANOVA: $n = 14$, $p > 0.05$), or the overall affiliation (repeated measures ANOVA: $n = 14$, $p > 0.05$) and agonism frequency (repeated measures ANOVA: $n = 14$, $p > 0.05$) between previous combatants. However, though statistically insignificant, there were some interesting patterns. Specifically, when a fight occurred between dyads with medium or high levels of overall affiliation, it was "reconciled" 2.4% and 10% of the time, respectively. However, when a fight occurred between dyads with low or no overall affiliation, they were “reconciled” only 0.8% of the time. Conversely, dyads with high levels of agonism “reconciled” 1% of their fights and those with low levels of agonism “reconciled” 6.7% of their fights. Interestingly, in group 1, only primary kin “reconciled” their conflicts (6.9%) and in group 2, only non-kin “reconciled” conflicts (25%).

Out of 234 qualifying aggressive interactions, 33 (14.1%) of those interactions had third party affiliation occur significantly sooner in the post-conflict time period than at random. These events were not predicted by the intensity of the fight (repeated measures ANOVA: $n = 14$, $p > 0.05$), the relatedness to either of the previous combatants (repeated measures ANOVA: $n = 14$, $p > 0.05$; Friedman: $n = 14$, $p > 0.05$), or the overall affiliation (repeated measures ANOVA $n = 14$, $p > 0.05$) and agonism frequency (repeated measures ANOVA $n = 14$, $p > 0.05$) between previous combatants.

Out of 194 qualifying aggressive interactions, 22 (11.3%) of those interactions had agonism occur significantly sooner in the post-conflict period than at random. These events were not predicted by the intensity of the fight (repeated measures ANOVA: $n = 14$, $p > 0.05$), the relatedness to the previous combatant (repeated measures ANOVA: $n = 14$, $p > 0.05$), or the overall affiliation (repeated measures ANOVA: $n = 14$, $p > 0.05$) and agonism frequency (repeated measures ANOVA: $n = 14$, $p > 0.05$) between previous combatants. Again, though not significant, there were some interesting patterns. Dyads with high affiliation and high relatedness never participated in further agonism after a conflict had occurred. Conversely, dyads with low affiliation and low relatedness participated in further agonism 19.7% and 32.5% of the time, respectively. Dyads with low and medium levels of agonism were more likely to aggress after a fight (18% and 11% of the time, respectively) than dyads with high levels of agonism (5% of the time).

There was no correlation between overall dyadic affiliation and agonism frequencies both when accounting for the direction of the interactions (Mantel test: group 1, $n = 7$, $r = 0.006$, $p > 0.05$; group 2, $n = 7$, $r = -0.136$, $p > 0.05$) and without accounting for the direction of the interactions (Mantel test: group 1, $r = 0.147$, $p > 0.05$; group 2, $r = -0.063$, $p > 0.05$). See table 1 for a summary of these results.

DISCUSSION:

High Intensity Agonism:

High intensity agonism was infrequent for the individuals in both groups, with such events occurring at a rate of less than once per hour. Furthermore, individuals spent very little overall time, much less than 1%, in high intensity agonism.

I predicted that if agonism patterns were best explained by competition over food resources as the socioecological model suggests (Wrangham 1980, van Schaik 1989), the rate of aggressive interactions would be significantly higher in food-oriented contexts as compared to non-food-oriented context. I also predicted that the rate of agonism would be higher in the provisioned feeding context, which represented a clumped, limited, and highly valuable food source as compared to the naturalistic foraging context, which represented a dispersed, abundance, and less valuable food source (van Schaik 1989, Sterck *et al.* 1997, Saj *et al*. 2007, Lu *et al.* 2008). In this study, the provisioned feeding context did have the highest mean rate of overall agonism (5.2 events/hr) as compared to the other five contexts, closely followed by the foraging context (4.2 events/hr). However, these rates are only between 0.5 and 1.5 aggressive events/ individual/ hour greater than those in the moving and travel context. Therefore, although the trends of the data were in the expected direction, there was no statistical difference between the rates of agonism in any of the six contexts, regardless of the presence or absence of food.

When examining high intensity agonism, the individuals in group 1 did participate in a higher mean rate of agonism in the feeding context than in all other contexts. Although statistics revealed that this rate is only significantly higher than some of the non-food contexts, all food-oriented contexts combined had a higher rate of agonism than did the combined rate of all non-food oriented contexts. Furthermore, the rate of high intensity agonism was also higher in the food-oriented context with limited and clumped resources. These findings are mostly consistent with the predictions of the socioecological model. Surprisingly, in group 2, there was no significant difference in the rate of high intensity agonism occurring in food-oriented and non-food-oriented contexts. Furthermore, the rate of food-oriented agonism did not differ as a function of the characteristics of the food resource. These results are inconsistent with the predictions of the socioecological model. Therefore, while high intensity agonism can increase in food-oriented contexts and as a function of food characteristics, as was the case in group 1, it did not necessarily do so, as was the case in group 2. Additionally, these contradictory findings are likely a good reflection of the variation that occurs among social groups within this species. Such stark variation among social groups makes it impossible to conclude that food resources are major factor influencing agonism patterns in a species as a whole. Furthermore, when examining all high intensity agonistic interactions without the filter of context, the majority of agonistic events were not preceded by food-oriented behaviors, suggesting that most conflicts were not over food. Collectively, these findings indicate that heightened levels of agonism are not limited only to those situations that suggest resource competition.

These findings do not convincingly support the predictions of the socioecologcial model. However, it cannot be ignored that the mean rate of agonism was generally higher (though not significantly so) in the feeding context in group 1 than in all other contexts. This increase may be a byproduct of a decrease in inter-individual distance or an increase in the number of near neighbors during feeding and not, as is commonly assumed, of competition over food (Stevenson *et al*. 1998, Vogal & Janson 2007). This hypothesis appears to be likely because the feeding context did have a significantly smaller inter-individual distance and more individuals feeding nearby in both groups. However, in group 1, the rates of high intensity agonism were not consistently correlated in the predicted direction with average proximity or the number of individuals within 10 meters either among or within contexts. Some correlations were positive, some were negative, but overall, there was no significant correlation between agonism and proximity or the number of individuals nearby. Both of these findings are counter to my predictions regarding close proximity as a predictor of agonism.

Conversely, in group 2, the overall proximity and overall rate of high intensity agonism between dyads was negatively correlated. Therefore, high intensity agonism increased as inter-individual distance decreased. This finding supports my predictions. However, when calculating this correlation for each context individually, only non-food-oriented contexts retained a significantly negative correlation (food-oriented contexts showed a non significant correlation). Yet, at the same time, the foraging context was found to have a positive correlation between agonism rate and the number of individuals within 10 meters of the focal animal, suggesting that agonism increased as the number of near neighbors increased in this context. Thus, while these results convincingly indicated that the high intensity agonism in non-food contexts in group 2 was associated with the proximity relationships (in the predicted direction), it was not clear if this same variables could be attributed to high intensity agonism in the provisioned feeding context. This finding provides support for Sussman and Garber's (2007) billiard ball hypothesis. However, because the relationship between proximity and agonism is inconsistent between groups and among contexts, such that no context had the same result in both groups, there appears to be a great deal of variation in the patterns of high intensity agonism in this study population. Thus, even if there is a relationship between proximity and high intensity agonism, it is not a straightforward one that can be easily applied to all social groups in this species.

The factors analyzed so far have provided a mixed bag of results. The most straightforward factor explaining patterns of high intensity agonism in this study population was kinship. As predicted, primary kin had a significantly lower rate of high intensity agonism towards one another than did non-kin. However, primary and secondary kin had statistically similar rates of agonism, suggesting that agonism patterns can only be considered nepotistic between kin and non-kin.

Low Intensity Agonism:

Low intensity agonism occurred more frequently than did high intensity agonism but only at a rate of less than 2.2 events per individual per hour. Furthermore, individuals spent very little overall time, less than 1%, in low intensity agonism.

For both groups, the context with clumped and limited resources (provisioned feeding context) had a significantly higher rate of agonism than the context with relatively dispersed and abundant resources (naturalistic foraging context), as is predicted by the socioecological model. In addition to having a higher rate of agonism than the naturalistic foraging context, the rate of low intensity agonism in the provisioned feeding context was only significantly higher than that in the resting context. Therefore, despite presenting minimal opportunity for resource competition over food, the travel, move, and alert contexts had statistically similar rates of low intensity agonism as did the feeding context. Furthermore, when examining all low intensity agonistic interactions without the filter of context, the majority of agonistic events were preceded by non-food oriented behaviors, which indicates that most agonism was not over food. Similar to those reported for high intensity agonism, these findings also indicate that heightened levels of agonism are not limited only to those situations that suggest resource competition. Again, these findings do not support the predictions of the socioecological model.

In group 1, the rate of low intensity agonism was not correlated in the predicted direction with average proximity or the number of individuals within 10 meters of the focal animal either among or within most contexts. However, there was a negative correlation between average proximity and agonism in the foraging context, suggesting that agonism increased as inter-individual distance decreased in this context. This finding supports my predictions regarding close proximity as a predictor of agonism and might indicate that low intensity agonism in this context is partially caused by two individuals occupying the same space at the same time. In group 2, the overall proximity and overall rate of low intensity agonism between dyads were negatively correlated. Therefore, low intensity agonism increased as inter-individual distance decreased. However, as was the case with high intensity agonism, when calculating this correlation for each context individually, only non-food-oriented contexts retained a significant negative correlation (food-oriented contexts show no significant correlation). Again these results provide some support for Sussman and Garber's (2007) billiard ball hypothesis but only in a single context in group 1 and only overall and in non-food contexts in group 2. Thus, just as is the case for high intensity agonism, because the relationship between proximity and agonism is inconsistent between groups and among contexts, there appears to be a great deal of variation in the patterns of low intensity agonism in this study population. This finding again suggests that the relationship between proximity and high intensity agonism is not a straightforward one and can not be easily applied to all social groups in this species. However, despite the contradictory results of this analysis, when examining the behavioral precedent to all conflict regardless of context, close proximity movement preceded low intensity agonism significantly more often than did any other behavior in both groups, including food-oriented behaviors. This finding perhaps indicates that the relationship between proximity and low intensity agonism is worth further examination.

Low intensity agonism, unlike high intensity agonism, was poorly explained by kinship. Primary and non-kin have nearly identical rates of agonism in both groups while secondary kin have higher rates of agonism than both primary and non-kin. This pattern lacks logical sense if kinship dictates patterns of low intensity agonism. Rather, it seems that there are alternative explanations for the agonism directed at secondary kin that might account for this peak in low intensity agonism. For example, it is possible that there is a decrease in the tolerance for secondary kin without an increase in inter-individual distance that results in a higher then expected frequency of low intensity agonism. This hypothesis is supported by a study on Japanese macaques, *Macaca fuscata*, which found that there was a decrease in tolerated co-feeding as genetic relatedness among individuals decreased (Belisle & Chapais 2001).

All Agonism:

At nearly 0.2% (group 1) and 0.1% (group 2) of overall time, all agonism accounted for a proportion of time similar to that documented by Gould (1994) (0.5%) but less than that documented by Sussman for this species (unpublished in Sussman *et al.* 2005) (1.4%).

In addition to explaining the role of food, proximity, and kinship on agonism patterns, I also tested whether agonism itself can influence future agonism. Out of 194 aggressive interactions, 11.3% involved continued agonism between the previous combatants in the post conflict period, suggesting that agonism can influence patterns of future agonism, although only at a low rate in this study population. In this same species, Kappaler (1993) found that while renewed agonism did occur between the original opponents during the post conflict period, this trend was not significant. He also found that agonism did not significantly affect the rates of agonistic interactions with third party individuals (Kappeler 1993). The low frequency of renewed agonism in this study population, suggests that agonistic interactions do not significantly influence future agonism in ringtailed lemurs. Furthermore, the few incidences of renewed agonism are potentially caused by some other factor, such as the attempted close proximity of a previous combatant.

The potential role of proximity in renewed agonism is anecdotally evidenced by the finding that medium to low levels of overall agonism well predicted post-conflict agonism in this study. While it might seem counter-intuitive that those dyads with low levels of overall agonism would be more likely to participate in agonism during the post-conflict period, I hypothesize that individuals who aggress less overall are less likely to leave the immediate area after a fight, thus making it more likely that they will aggress again within the post-conflict period. This hypothesis is supported by the findings in other studies that attempted or successful acts of "reconciliation" actually made the occurrence of renewed agonism more likely (Manson *et al.* 2005, Patzelt *et al.* 2009). In addition to indicating that the fight had not been reconciled (despite the interaction meeting the traditional definition of "reconciliation"), these studies also support the idea that low inter-individual distance might act to renew agonism, which might account for the incidences of renewed agonism in this study.

Low overall levels of affiliation and low degrees of relatedness also well explained (although not significantly) these incidences of post-conflict agonism. Thus, if proximity did account for the influence of overall agonism on renewed agonism, then the overall affiliation frequency and degree of relatedness are the most direct predictors of post-conflict agonism. Therefore, while agonism can influence a small percent of future agonism in a manner that is consistent with my latter two predictions, it might actually be the affiliative and genetic relationships between dyads that best determine post-conflict agonism tendencies.

Affiliation:

Affiliation occurred at a rate of 15.31 (group 1) and 9.26 (group 2) events per individual per hour and took up approximately 10% of overall time. Therefore, affiliation occurred much more frequently than agonism and took up a much larger proportion of each individual's time regardless of age, gender, or rank.

In group 1, as inter-individual distance decreased in both food and non-food contexts, the rate of affiliation increased. However, there was no across context correlation between the average rate of affiliation and either proximity or the number of individuals within 10 meters of the focal animal. In group 2, as inter-individual distance decreased in food-oriented contexts, affiliation frequency increased. There was also no across context correlation between the average rate of affiliation and either proximity or the number of individuals within 10 meters of the focal animal. As predicted, inter-individual proximity accurately explains affiliative tendencies in group 1 and those occurring in non-food contexts in group 2. Similarly, Smuts (1985) found that in olive baboons, *Papio cynocephalus*, the males with whom a female groomed most were also were most frequently in close proximity. Fairbanks (1976) found that as inter-individual distance decreased, the frequency of both affiliation and agonism increased.

The spatial structure documented in these to social groups is likely both a consequence and a cause of social interactions. A consequence because past interactions may influence spatial relationships and a cause because the non-random distribution of individuals will influence the probability of future social events (Fairbanks 1976). However, Smuts (1985) points out that, although one may argue that females will tend to groom males that happen to be near them, this explanation for the relationship between grooming and proximity was unlikely because 1) females did not always have high grooming scores with males who were frequently near them, thus indicating that proximity was not sufficient to stimulate grooming. 2) Periods of grooming were often preceded by a great deal of movement during which time several individuals were in close proximity but only specific individuals were chosen as grooming partners (Smuts 1985). Therefore, it seems reasonable to deduce that affiliation might act to maintain close proximity in olive baboons and perhaps in ringtailed lemurs as well. Conversely, because close proximity movement preceded the majority of agonistic interactions in my study, it might be the case that most agonistic interactions are disputes related to proximity.

The relationship between proximity and affiliation patterns was most clearly exhibited during food-oriented contexts because both groups had negative correlations between proximity and affiliation during these contexts. Close proximity among individuals is expected to co-occur with the existence of social tolerance (Vervaecke *et al.* 2000, van Schaik 2003). However, close proximity was rarely correlated with low agonism (only in a the provisioned feeding context in group 1), which is one of the indicators of social tolerance (de Waal 1989), thus suggesting that the close proximity during feeding observed in this study population, might simply be an extension of the overall social behavior patterns (including general tolerance) between dyads and does not indicate a tolerance that is specific to incidences of feeding competition.

Kinship was another good predictor of affiliation in this study. Primary kin experienced significantly higher proportions of affiliation than secondary and non-kin; but there was no difference between the proportions of affiliation experienced by secondary and non-kin. These results are consistent with those found by Kapsalis and Berman (1996a) in adult female rhesus macaques and Belisle and Chapais (2001) in Japanese macaques, *Macaca fuscata*. However, in terms of directed agonism, the individuals in my study can and did distinguish between secondary and non-kin and did not distinguish significantly between primary and secondary kin. Thus, patterns of affiliation distinguished the relationship between close and distantly related kin while patterns of agonism only distinguished the relationship between kin and non-kin. This inconsistency indicates that the preferential treatment of primary kin for affiliative behaviors does not result from a behavioral or phylogenetic threshold limiting nepotism (as is argued by Belisle & Chapais 2001 and Kapsalis & Berman 1996a), but rather a legitimate preference for primary kin. Therefore, kinship appears to be more directly related to affiliation than to agonism.

High intensity agonism is likely to be highly costly, which according to kin selection and inclusive fitness theory, leads to the prediction that animals will benefit from low rates of agonism with those individuals with whom the most genes are shared

(Hamilton 1964). However, the results of this study indicate that, although this population of ringtailed lemurs could distinguish between primary and secondary kin, as was the case for affiliation, patterns of agonism were similar among all kin regardless of their degree of relatedness. There are two potential explanations for these surprising patterns. The first is that the same genes that makes individuals related, might also function to make them similar in terms of their needs, which is hypothesized to cause more agonism among closely related kin than is predicted by kin selection theory (West *et al.* 2002). For example, West *et al.* (2001) found that the levels of fighting between non-dispersing male fig wasps (family *Agaonidae*) showed no correlation with relatedness and instead showed a negative correlation with mating opportunities. The second and perhaps more likely explanation of these patterns is that because the rate of agonism was generally low and because most individuals in this population were closely related, distinguishing between primary and secondary kin might provide little or no benefit in terms of inclusive fitness. Therefore, when the rate of agonism is low and the average degree kinship is high, it seems reasonable to hypothesize that affiliation will be more affected by kinship than will agonism for many social animals.

In the analysis of the kinship data, two potential confounding variables must be addressed. 1) Because infant primates highly altricial, and thus reliant on their mothers during early life (Zhao *et al.* 2008), kinship is likely to be highly correlated with maternal effects in most primate species. Ringtailed lemur females carry and suckle their infants for up to five months (Sauther *et al.* 1999), thus offering no reason to believe that this trend is otherwise in this study population. This study did not control for maternal effects and thus, the influence of maternal effects and genetic relatedness should be concurrently attributed to the patterns of affiliation and agonism documented here. 2) Kinship is also often correlated with rank in primate species (Kapsalis & Berman 1996b). Thus, it is possible that the results documented in this study simultaneously indicate the importance of kinship and rank distance on social behavior. However, there was no correlation between rank distance and genetic relatedness in either group, which suggests that rank difference was not confounded by kinship in this study. This pattern is to be expected in ringtailed lemurs because, unlike cercopithecine primates, daughters do not rank immediately below their mothers (Nakamichi & Koyama 1997).

There has been a great deal of work regarding the relationship between agonism and affiliation through the framework of the "reconciliation hypothesis". In this study, affiliation occurred significantly sooner in the post-conflict period than at random in only 2.3% of all qualifying aggressive interactions. These cases of post-conflict affiliation are not significantly predicted by the intensity of the fight, the relatedness to the previous combatant, the overall affiliation frequency, or the overall agonism frequency. The infrequency of post-conflict affiliation suggests that "reconciliation" and "consolation" are not major conflict management mechanisms in this species. Furthermore, dyadic patterns of affiliation and agonism are not correlated with one another, which indicates that it is unlikely that agonism causes affiliation. Kappeler (1993) failed to report any "reconciliation" or "consolation" in this species. This finding is significant because ringtailed lemurs are one of the only primate species with a pronounced dominance hierarchy and kinship structure that does not exhibit significant levels of "reconciliation", a finding that goes against the predictions of the "reconciliation" framework. As a result of this finding, Kappeler (1993) and Kappeler and van Schaik (1992) argued that "reconciliation" is not a pre-requisite for life in permanent social groups. Thus, perhaps agonism is not so detrimental to social bonds as to require conflict-repair mechanisms for social living to evolve and be maintained.

However, if we look closely at the patterns behind these five occurrences of "reconciliation", we see that high affiliation and low agonism best predicted these events, with affiliation being the primary predictor. Therefore, while agonism may have the potential to influence affiliation after a small percentage of fights, it is possible that it was actually high overall affiliation between dyads that best predicted "reconciliation". This finding is not new. Other researchers have found that affiliation is a better predictor of "reconciliation" behaviors than is any aspect of agonism (Arnold & Whiten 2001, Preuschoft *et al.* 2002, Wittig & Boesch 2003, chimpanzees, *Pan troglodytes schweinfurthii*; Palagi *et al.* 2005, ringtailed lemurs, *Lemur catta*). Palagi *et al*. (2005) looked at "reconciliation" in two groups of ringtailed lemurs and found that while the frequency and intensity of agonistic interactions were not significantly different, only one group exhibited "reconciliation". They posited that the frequency of affiliation within social dyads more accurately predicted the use of conciliatory strategies, with more affiliative dyads being more likely to reconcile (Palagi *et al.* 2005). This pattern has been reported for chimpanzee species, genus *Pan*, as well (Preuschoft *et al.* 2002, Wittig & Boesch 2003). Similarly, Patzelt *et al.* (2009) found that in 914 conflicts in Barbary macaques, *Macaca sylvanus*, that rates of "socio-positive interactions and support" were better predictors of post-conflict affiliation than were kinship or rank. Furthermore, Ray *et al.* (1996 in Fuentes 2004) observed that the post-conflict behavior of female langurs (who affiliated in the post-conflict period at rates similar to their baseline measurements, thus indicating no "reconciliation") was also best predicted by overall patterns of female-female dyadic relationships. These results strengthen the conclusion that, affiliative frequencies are the best predictor of "reconciliation" events. However, this finding was not necessarily evidence that individuals with the most "biologically valuable" relationships reconcile most frequently because general affiliation is not synonymous with relationship value (Cords & Aureli 2000).

Most tests of the "reconciliation" hypothesis, especially those that find high rates of "reconciliation", continue to use the highly biased PC-MC method (which compares a post-conflict (PC) time interval with a single matched control (MC) time interval). As a result, the findings of these studies are potentially a byproduct of the fact that a higher baseline affiliation rate among dyads makes it more likely to find post conflict affiliation in those dyads by chance alone. For example, because the frequency of affiliation was much greater than agonism in my study population and in the vast majority of primate species (Sussman *et al*. 2005), it is reasonable to expect that a few of these affiliative events will seem to correlate with aggression randomly and that when they do, they are termed reconciliation. In fact, the finding that individuals that affiliate more overall also "reconcile" the most conflicts, which was reported here and in many other studies over the past few years (Preuschoft *et al.* 2002, Wittig & Boesch 2003, Palagi *et al.* 2005), supports the likelihood that what we currently call "reconciliation" are actually chance affiliative events that do not reflect a strategy to manage conflict. In the method used in this study, I attempted to control for this bias by comparing the latency of affiliation in the post-conflict period to a random distribution of affiliation latencies generated from each focal animal's data set. Therefore, this method presents are more appropriate way to study occurrences of "reconciliation". However, because I only compared the post conflict affiliation latencies to 40 random time intervals, it is still likely that the five reconciliation events reported in this study, are the result of chance alone. Therefore, a statistical method that can create a distribution of 1,000 or more random affiliation latencies would ideally be employed in future tests of the "reconciliation" hypothesis.

Conclusion:

Those factors that most consistently explain patterns of interactions provide insight into the behavioral and/or ecological mechanisms that influence social organization. This is important both affiliation (cooperation) (Allee 1931, 1938, Kropotkin 1972) and aggression (competition) (Lorenz 1966, Wrangham 1980, van Schaik 1989) have been explained to be the primary forces influencing the social organization of group-living animals. The results documented in this study indicate that food resources and previous agonism did not convincingly relate to social behavior patterns. Thus the emphasis placed on competition over food resources in the socioecological model for primate sociality needs to be re-evaluated. Conversely, kinship and/or maternal effects were found to influence both the patterns of affiliation and high intensity agonism in these social groups. Low intensity agonism showed no relationship with this factor. Patterns of affiliation were also well explained by proximity but both high and low intensity agonism were only well explained by this factor in one group. The inconsistent relationship between proximity and agonism in this study indicates that affiliation is more influenced by proximity than is agonism. Therefore, if we agree with Kummer's (1986) statement that the organization of a social group is reflected in the relative spatial arrangement of its members, affiliation is more closely linked to that organization.

TABLES:

Figure 1: Table of predictions

Factor	Prediction	Affiliation	HI Agonism	LI Agonism
Food	Agonism rates highest in food contexts	NA	✗	✗
	Agonism higher in provisioned feeding context than foraging context	NA	✗	✓
	The majority of agonistic events occurs following food-oriented behavior	NA	✗	✗
Proximity	Affiliation & agonism negatively correlate with inter-individual distance and/or agonism positively correlates with the number of individuals within 10m	✓	✗	✗
	Close proximity movement precedes agonism more often than all other categories of behavior	NA	✗	✓
Kinship	More affiliation and less agonism with primary kin than secondary kin and non-kin	✓	✓	✗
Previous Agonism	Affiliative and/or agonistic interactions frequently occur sooner in the post conflict period than at random	✗	✗	
	Overall dyadic affiliation and agonism frequencies are correlated with one another	✗		
	A predictive relationship exists between the characteristics of conflict and the probability of "reconciliation" or renewed agonism	✗	✗	
	A predictive relationship exists between the probability of "reconciliation" and renewed agonism and the specific category of social relationship between individuals	✗	✗	

"HI" = High intensity, "LI" = Low intensity, "✓" = Prediction fulfilled, "✗" = Prediction unfulfilled, "NA" = Not applicable. The gray coloration indicates the factors that well explained social behavior in this study

Table 2: Potential predators of ringtailed lemurs in captivity and in the wild

Potential North American Predators	**Ecological Equivalent in Madagascar** (the categories, not necessarily individual species, are comparable)
Raptors:	
red-tailed hawk[1] (*Buteo jamaicensis*)	Madagascar harrier hawk[2, 5] (*Polyboroides radiatus*)
red-shouldered hawk[1] (*Buteo lineatus*)	Madagascar buzzard [2, 5] (*Buteo brachypterus*)
great-horned owl[1] (*Bubo viginianus*)	black kite[5] (*Milvus migrans*)
Carnivores:	
gray fox[1] (*Urocyon cineroagenteus*)	fossa[3] (*Cryptoprocta ferox*)
raccoon[1] (*Procyon locor*)	domestic dog[4] (*Canis lupus familiaris*)
weasel[1] (*Mustela sp.*)	domestic cat[5] (*Felis catus*)
Venomous snakes:	
copperhead[1] (*Agkistrodon contortrix*) cottonmouth[1] (*Agkistrodon piscivorus*)	NA
Non-venomous Snakes:	
black rat snake[1] *(Elaphe obsolete*)	Madagascar boa constrictor [3] (*Boa manditra*)

[1]Macedonia (1993), [2]Sauther (1989), [3]Karpanty & Wright (2007), [4]Gould & Sauther (2007), [5]Jolly *et al.* (2006)

Table 3: Composition of social group 1

Name	Gender	Age	Classification	Relatedness
Fern	F	3 mo	Natal infant	Offspring of Cleis and Alexander, half sib of Persephone and Dory, niece of Alena, Tellus, and Niciea
Persephone*	F	2 yrs	Natal juvenile	Offspring of Cleis & Aracus, full sib of Ivy, half sib of Dory, half aunt and half sib of Niciea, Tellus, Alena, and Alex
Alena	F	2 yrs	Natal juvenile	Offspring of Dory & Aracus, grand daughter of Cleis,, full sib to Alex, Niciea, and Tellus, half sib to Berisidies, aunt of Fern, half sib and half nephew of Ivy and Persephone
Niciea*	F	3 yrs	Natal sub-adult	Offspring of Dory & Aracus, grand daughter of Cleis, full sib of Alena, Tellus, and Alexander, aunt to Fern, half sib and half nephew of Ivy and Persephone
Tellus	F	3 yrs	Natal sub-adult	Offspring of Dory & Aracus, grand daughter of Cleis, full sib of Alena, Niciea, and Alexander, aunt to Fern, half sib and half nephew of Ivy and Persephone
Dory*	F	18 yrs	Natal adult	Offspring of Cleis and unrelated male, mother of Tellus, Niciea, Alexander and Alena, half sib of Persephone and Fern, aunt to Berisidies
Cleis*	F	22 yrs	Founder, lactating adult	Offspring of Lethe and Pegasis, mother of Dory, Persephone, Ivy, and Fern, grandmother to Berisidies
Alexander*	M	2 yrs	Natal juvenile, pre-dispersal age	Offspring of Dory & Aracus, grand son of Cleis, father of Fern, full sib of Alena, Niciea, and Tellus
Ivy	M	3 yrs	Natal sub-adult of dispersal age	Offspring of Cleis & Aracus, full sib of Persephone, half sib of Dory, half sib and half uncle(r = 0.375) to Niciea, Tellus, Alena, and Alex
Berisidies*	M	3 yrs	Natal sub-adult of dispersal age	Offspring of Sosiphanes & Aracus, half sib and cousin of Niciea, Tellus, Alena, and Alex, nephew of Dory, grandson of Cleis, half nephew and half sib of Persephone and Ivy
Fritz	M	5 yrs	Transfer adult	Half sib of Cap N’ Lee
Cap N' Lee*	M	7 yrs	Transfer adult	Half sib of Fritz

*Focal animals (no data were collected on interactions with infants, < 1yr)

Table 4: Composition of social group 2

Name	Gender	Age	Classification	Relatedness
Nebe*	F	5 yrs	Natal adult	Offspring of Hector and Katina, mother of Herodotous, half sib of Dorius, half aunt of Justine and Cebes
Dorius*	F	12 yrs	Natal adult	Offspring of Gelon and Katina, mother of Justine and Cebes, half sib of Nebe, half aunt of Hero
Sophia*	F	4 yrs	Natal sub-adult	Offspring of Artemesia and Brennus, half sib of Justine
Justine*	F	3 yrs	Natal sub-adult	Offspring of Dorius and Brennus, half sib of Sophia, half niece of Nebe, half cousin of Herodotus
Chandler*	M	7 yrs	Non-natal adult	Offspring of unrelated individuals, father of Cebes and Herodotous
Cebes*	M	2 yrs	Natal juvenile, pre-dispersal age	Offspring of Dorius and Chandler, half sib and half cousin of Herodotous, half sib of Justine, half nephew of Nebe
Herodotus*	M	2 yrs	Natal juvenile, pre-dispersal age	Offspring of Nebe and Chandler, half sib and half cousin of Cebes, half nephew of Dorieus

*Focal animals

Table 5: Sample sizes of various primate studies in captivity and in the wild

Author(s)	Year	Species	Subject	# of focal indiv.	# hrs of Observation
Gould*	1996	ringtailed lemurs	Affiliative relationships	10	1102
Keith-Lucas *et. al.*	1999	ringtailed lemurs	Changes in behavior after release	6	Not provided
Arnold & Barton	2001	speckled leaf monkeys	Reconciliation/Post conflict behavior	12	165
Sussman *et al.**	2003	ringtailed lemurs	Aggression and affiliation frequencies	4	40
Wittig & Boesch*	2003	chimpanzees	Feeding competition	14	1028
Mallavarapu *et al.*	2006	gorillas	Reconciliation/Post conflict behavior	13	223+
Parga	2006	ringtailed lemurs	Male mate choice	11	Not provided
Wittig *et al.*	2007	baboons	Kin mediated reconciliation	13	Not provided
Palagi *et al.* *	2008	Verreauxi's Sifaka	Reconciliation/Post conflict behavior	16	640

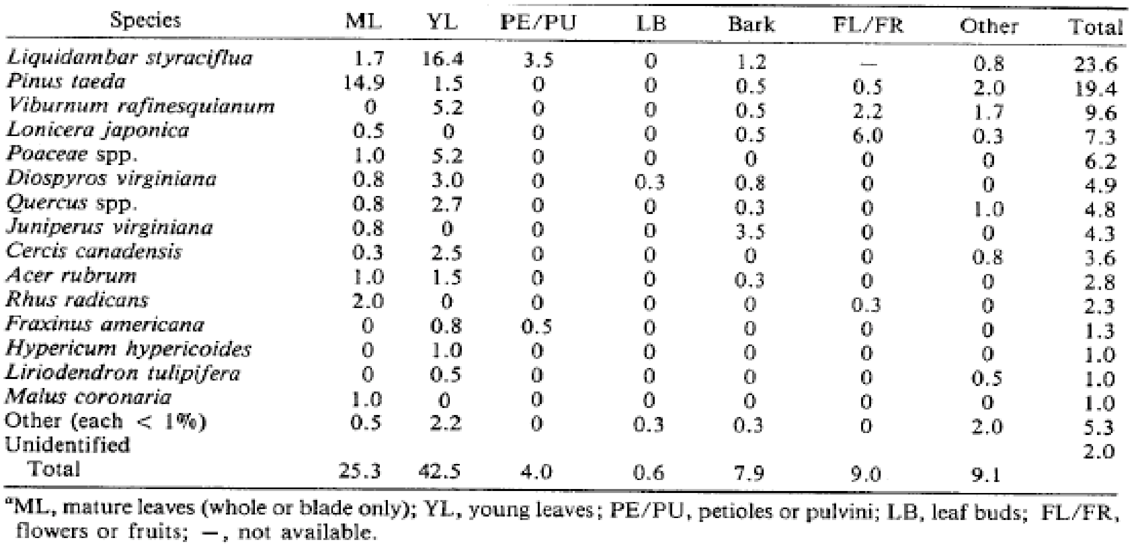
*Studies conducted in the wild

Table 6: Amount of provisioned food

	Chow per indiv. per wk(g)	% of provisioned diet	Fruit & veg. per indiv. per wk(g)	% of provisioned diet	Total food per indv. per wk(g)
Duke Lemur Center[1]	486	56.71%	371	43.29%	857
St. Louis Zoo[2]	588	32%	1260	68%	1848

[1] Duke Lemur Center (2007), [2] St. Louis Zoo (2007)

Table 7: Plant species and plant parts in the diet of *Lemur catta* at Duke Lemur Center. Adapted from Ganzhorn (1986) (N = 402)



Species	ML	YL	PE/PU	LB	Bark	FL/FR	Other	Total
Liquidambar styraciflua	1.7	16.4	3.5	0	1.2	—	0.8	23.6
Pinus taeda	14.9	1.5	0	0	0.5	0.5	2.0	19.4
Viburnum rafinesquianum	0	5.2	0	0	0.5	2.2	1.7	9.6
Lonicera japonica	0.5	0	0	0	0.5	6.0	0.3	7.3
Poaceae spp.	1.0	5.2	0	0	0	0	0	6.2
Diospyros virginiana	0.8	3.0	0	0.3	0.8	0	0	4.9
Quercus spp.	0.8	2.7	0	0	0.3	0	1.0	4.8
Juniperus virginiana	0.8	0	0	0	3.5	0	0	4.3
Cercis canadensis	0.3	2.5	0	0	0	0	0.8	3.6
Acer rubrum	1.0	1.5	0	0	0.3	0	0	2.8
Rhus radicans	2.0	0	0	0	0	0.3	0	2.3
Fraxinus americana	0	0.8	0.5	0	0	0	0	1.3
Hypericum hypericoides	0	1.0	0	0	0	0	0	1.0
Liriodendron tulipifera	0	0.5	0	0	0	0	0.5	1.0
Malus coronaria	1.0	0	0	0	0	0	0	1.0
Other (each < 1%)	0.5	2.2	0	0.3	0.3	0	2.0	5.3
Unidentified								2.0
Total	25.3	42.5	4.0	0.6	7.9	9.0	9.1	

[a]ML, mature leaves (whole or blade only); YL, young leaves; PE/PU, petioles or pulvini; LB, leaf buds; FL/FR, flowers or fruits; —, not available.

Table 8: Average weights of ringtailed lemurs

	Berenty Reserve[1]	Duke Lemur Center[2]	St Louis Zoo[3]	Miami MetroZoo[4]
	Wild	**Semi-free Ranging**	**Captive**	
Adult Female	2.27 kg	2.32 kg	3.52kg	2.73kg
Adult Male	2.22 kg	2.36 kg	2.7kg	4.1kg

[1]Koyama, *et al.* (2007), [2]Duke Lemur Center (2007), [3] St. Louis Zoo (2007), [4]Miami MetroZoo (2007)

Table 9: Categorization of agonistic and affiliative behaviors

Active Affiliation		**Passive Affiliation**	
Groom		Any behavior in contact w/ other individual	
Mutual Groom		Contact vocalizations	
Play		Sniffing others	
High Intensity Agonism		**Low Intensity Agonism**	
Stink fight	Bite	Chase threat	Lunge threat
Hit	Lunge	Food take	Touch
Contact fight	Chase	Mouth to face threat	Squeal*
Grab	Push	Cackle/Deep spat*	Chutter*
		Yip/Spat call*	Displace/Supplant
		Plosive bark*	

* Terms taken from Macedonia (1993)

Table 10: Categorization of agonism by intensity

Behavior Category	Intensity Score	Intensity Level
Submissive and agonistic vocalizations	1	Low
Displace/supplant	2	Low
Mouth to face threat	3	Low
Threats of high intensity agonism (ex. chase threat)	4	Low
Chase, lunge, stink fight* (no contact)	5	High
Unidirectional contact (ex. push, grab, hit)	6	High
Uni- or multidirectional fighting	7	High

*Between males only

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CHAPTER 3: THE RELATIONSHIP BETWEEN FOOD RESOURCES AND SOCIAL ORGANIZATION

Food distribution and abundance have been argued to be the primary influences on the social organization of primate groups. I tested two hypotheses regarding the social organization, defined here by dominance hierarchy, of two semi-free ranging ringtailed lemur, *Lemur catta*, social groups (n=14) at The Duke Lemur Center in Durham, NC: 1) The characteristics of the food resource do not dictate social organization. 2) Social organization is equally or better explained by inter-individual distance than by resource competition. The characteristics of the food source could but did not necessarily influence social organization. Furthermore, close proximity contexts better explained the hierarchical ordering of the overall dominance hierarchy than did food-oriented contexts, suggesting that the apparent influence of food on social organization is potentially an indirect effect resulting from low inter-individual distance. These findings indicate that food resources are not the most direct explanation for the social organization of this study population.

INTRODUCTION:

There are different selective pressures that influence the fitness of male and female animals. For most mammalian species, female reproductive success is primarily limited by access to food resources due to the energetic requirements of pregnancy and lactation (van Schaik 1989), whereas male reproductive success is primarily limited by access to receptive females (Trivers 1972). Wrangham (1980) proposed that primate social relationships and the resulting social system reflect the competitive strategy for obtaining these fitness-limiting resource. Because the male strategy is dependent on females, the selection pressure on the female strategy was expected to determine the characteristics of a social group (Wrangham 1980). Therefore, food distribution (van Schaik 1989) and abundance (Wrangham 1980, Isbell 1991) are argued to be the primary influences on the social organization of a group. Social organization is the pattern of interactions and relationships that result among group members. This general hypothesis is the foundation of the socioecological model for primate sociality. The predictions of the model are that when food resources are clumped, female primates are expected to be philopatric and form kin groups to defend those resources from non-kin competitors (Saj *et al.* 2007). Individuals are also predicted to form linear, stable dominance hierarchies (van Schaik 1989, de Waal 1989, Isbell 1991, Sterck *et al.* 1997). On the other hand, when food is highly dispersed, of low nutritional value, or found in patches that are large relative to the size of the group, the model predicts that female dispersal will be favored, individuals will attain similar amounts of food, and there will be few agonistic interactions over food (Wrangham 1980, Sterck *et al.* 1997). Such a social group is predicted to have non-linear, egalitarian social relationships (van Schaik 1989, Sterck *et al.* 1997, Koenig 2002).

Numerous researchers have reported support for the socioecological model. For example, the Peruvian common squirrel monkey, *Saimiri sciureus*, which relies on large fruit trees (i.e. clumped resources), has a linear dominance hierarchy and frequent contests over food while the Costa Rican red-backed squirrel monkey, *Saimiri oerstedi*, which relies on small fruit trees (i.e. dispersed resources), has egalitarian social relationships and does not have frequent food-related agonism (Mitchell *et al.* 1991). In the case of savanna baboons, *Papio cyncephalus*, those living in a habitat with patchy food and abundant predators had linear dominance hierarchies while those living in a habitat with dispersed food had no clear dominance hierarchy (Barton *et al*. 1996). Similarly, Koenig *et al.* (1998) found that the strength of the dominance hierarchy in Hanuman langurs, *Presbytis entellus*, varied with the abundance and the distribution of food. In these cases, the rates of aggression and the resulting dominance hierarchy match the predictions of the socioecological model (Sterck *et al.* 1997). In this model, the characteristics of the dominance hierarchy are primary variables used to classify the organization of primate social group s.

However, food distribution does not consistently explain the variation in social organizations (Sterck *et al.* 1997, Thierry 2008) and mismatches between the predictions of the socioecological models and the actual behavior of primate species are not uncommon (Strier 1994, Kappeler 1999, Matsumura 1999, Janson 2000, Koenig 2002, Koenig & Borries 2006, Saj *et al.* 2007). A prediction that frequently does not hold up to empirical testing is the presumed relationship between characteristics of the food resources and agonism patterns. For example, in baboons, genus *Papio*, agonism rates are actually lower in the dry season when food is scarce, which suggests the use of an energy minimizing strategy (Beehner *et al.* 2005), and not behavior patterns structured by resource availability. Some researchers have even found that agonism rates decrease in the presence of clumped food resources (Gore 1993). Furthermore, I demonstrated in chapter 2 that the rates of agonism in ringtailed lemur, *Lemur catta*, societies do not consistently vary as a function of food characteristics nor is it highest in food-oriented contexts (Sbeglia 2009).

In addition to predicting patterns of agonism, the socioecological model posits that the characteristics of the food resource will also predict the overall organization of the social group. For example, folivorous female mantled howler monkeys, *Alouatta palliate*, are predicted by the characteristics of their food resources to have egalitarian or tolerant social organizations (Koenig 2002). However, Jones (1980) found that they exhibit linear dominance hierarchies and a negative relationship between reproductive success and rank. Similarly, mountain gorillas are expected to have inconsistent dominance relationships (Sterck *et al.* 1997), however, Watts (1994) observed linear dominance hierarchies among females of this species.

Some species of lemur also present problems when attempting to classify their social system (Erhart & Overdorff 2008). For example, as frugivorous primates, ringtailed lemurs rely primarily on clumped resources and are thus expected to experience frequent aggressive contest competition over food (van Schaik 1989, Koenig 2002), which suggests that this species most closely correspond to Sterck *et al.*'s (1997) category of resident-nepotistic (Erhart & Overdorff 2008). Their linear dominance hierarchies (Jolly 1996, Sauther 1992, Gould 1992) and relatively frequent within and between group agonistic interactions (Overdorff & Erhart 2001), are consistent with this classification. However, because coalition formation is rare in this species (Nakamichi & Koyama 1997) and females do not inherit their mother's rank (Taylor & Sussman 1985), they do not completely fit into any existing category proposed by Sterck *et al. (*1997) (Erhart & Overdorff (2008). The difficulty of categorizing ringtailed lemurs and several other species such as Milne-Edwards' sifaka, *Propithecus edwardsi* (Erhart & Overdorff 2008) has resulted in the subsequent addition of more and more factors into the socioecological model (ex. habitat saturation and infanticide avoidance, Sterck *et al.* 1997).

In this paper, I argue that social interactions involving food resources do not adequately reflect the social organization of ringtailed lemurs. As an alternative, I propose that agonism rates are a function of social variables such as the number and proximity of nearby individuals, which might increase agonism by simply increasing the opportunity for it to occur (Stevenson *et al.* 1998, Vogel & Janson 2007). Because clumped resources promoted a decrease in inter-individual distance in this study population (Sbeglia 2009), inter-individual distance might be a confounding variable influencing the role of food resources in social organization. I tested the following two hypotheses regarding the role of food resources on social organization:

1) The characteristics of the food resource do not necessarily influence the social organization of primates. I predict that if a social group is exposed to two feeding contexts that differ in the abundance, distribution, and nutritional quality of food resources, the linearity of the dominance matrix in each of the contexts will not differ. Conversely, the socioecological model, which hypothesizes that interactions over food resources determine social organization, implicitly predicts that the dominance relationships occurring around clumped resources will result in a linear hierarchy, while the dominance relationships occurring around dispersed resources will be less or non-linear (van Schaik 1989, Sterck *et al.* 1997).
2) Agonism patterns and overall social organization are equally or better reflected by inter-individual distance than by those contexts that suggest resource competition. I predict that the interactions occurring in contexts in which individuals maintain close proximity will similarly or better predict the overall rank ordering of individuals within the dominance hierarchy than will the interactions occurring in food-oriented contexts. This means that there should be fewer inconsistencies in the ranking of individuals between the hierarchy in close-proximity context and

the overall hierarchy than between the hierarchy in food-oriented contexts and the overall hierarchy. If this prediction were supported, it would suggest that the apparent influence of food on social organization is potentially an indirect effect resulting from decreased inter-individual distance. Conversely, the socioecological model implicitly predicts that the interactions occurring in food-oriented contexts will best predict the overall rank ordering of individuals within the hierarchy, such that there should be fewer inconsistencies between the close-proximity hierarchy and the overall hierarchy than between the food-oriented hierarchy and the overall hierarchy.

METHODOLOGY:

Study Site:

This study was conducted at The Duke Lemur Center (DLC) in Durham, NC. The Duke Lemur Center houses multiple groups of ringtailed lemurs in several semi-free ranging enclosures that are surrounded by a mildly electrified fence. The two groups of ringtailed lemurs observed in this study lived in a 14.3-acre and 8.2-acre mixed pine hardwood forest. Several species of wild animals inhabit or visit the naturalistic enclosures and act as potential predators and as competitors for food (Table 1). DLC is considered to be one of the four main sites for long-term ringtailed lemur research (Sauther *et al.* 1999). See Talyor (1986) and Wright (2008), for a complete description and history of the study site.

Time Frame:

The first field season took place between June 2007 and August 2007 and the second field season between June 2008 and August 2008. Observations were conducted between 7:00 and 16:00, five to six days a week. I controlled for the influence of time of day on behaviors by collecting the same amount of observations in the morning and in the afternoon for each focal animal.

Subjects:

In the summer of 2007, observations were conducted on seven ringtailed lemurs in an established species-typical social group (Table 2). In the summer of 2008, observations were conducted on another seven individuals from a different group of similar composition (Table 3) for a total sample size of 14. Similar sample sizes are common in other primate studies, including some conducted under completely natural conditions (Table 4). The adult animals have lived at DLC for at least three years and in most cases, all of their lives. Focal animals represented all gender, age, and reproductive classes that were present in each group.

The semi-free ranging animals at DLC are considered to be comparable both behaviorally and physically to wild lemurs (Sussman *pers. comm.*). In fact, a study on ringtailed lemurs at St. Catherine's Island, another semi-captive facility in the United States, found that zoo animals released in these enclosures eventually resembled wild lemurs in terms of appearance and behavior (Keith-Lucas *et al.* 1999). In the past, six infants and two juveniles have died as the result of predation by the naturally existing predators that also inhabit the enclosures (Table 1). In response to these predators, DLC animals commonly partake in species typical mobbing and vocalization behaviors (Macedonia 1993, *pers. obs*.). The animal's diet was minimally supplemented in quantities that are 50% less than is required by the American Zoological Association for this species when it is maintained in zoos (Table 5). As a result, the animals forage on over 15 species of local flora that grow in the enclosures (Ganzhorn 1986) (Table 6), which takes up much of their feeding time. Furthermore, the average weight, and thus, net caloric intake of all adult lemurs are comparable to those of wild individuals (Koyama *et al.* 2007) (Table 7). This similarity suggests that there are comparable levels of feeding competition in these enclosures and in the wild.

Procedure:

Data were collected using focal sampling of the 14 individuals previously noted. All focal individuals were observed in a random order for between 42 and 50 hours each (660 hours total). Focal behavior and group proximity scans of all visible group members were documented instantaneously at 5-minute intervals. Any occurrence of social behavior (Table 8) was documented continuously from the time of its onset to the time of completion. Count data were documented opportunistically on the agonistic interactions that occurred between two or more non-focal animals.

I developed the following rubric for documenting behaviors. First, I classified a single social bout to be occurring if the behavior persisted with pauses of no more than 10 seconds. If the behavior ceased for more than 10 seconds, this indicated the end of that behavioral bout. Secondly, whenever an individual joined or left a social bout, subsequent interactions were considered to be a new bout. For example, if focal animal

A was being groomed by B and then C moved into contact with A, this behavioral progression was scored as two distinct bout, the first of which involved grooming by B, and the second of which involved grooming by B and bodily contact with C.

When a social behavior occurred, I documented the identity of relevant individuals, the direction of each interaction, the type of behavior (Table 8), and the context in which the behavior occurred. The possible contexts were a) provisioned feeding (occasionally referred to as "feed"), b) naturalistic foraging (occasionally referred to as "forage"), c) rest, d) travel (directed locomotion with a beginning and end location), e) move (undirected movement), and f) alert. The context of social behaviors was determined based on the context category in which the animal was participating just prior to the initiation of a social behavior. For example, if two animals were foraging and one started to groom the other, this affiliative social behavior was considered to be taking place during a foraging context.

After all data had been collected, I later coded all social behaviors using a combination of the following descriptive categories: *active* or *passive* and *affiliative* or *agonistic* (Table 8). Ambiguous behaviors were coded as *unknown* and left out of all analyses (Table 8). For example, if focal animal A was grooming B, this behavioral bout was coded as *active affiliation* (Table 8). I also coded agonistic behaviors by intensity level. All passive agonism and submissive behaviors were assigned a number on a scale of 1-2 (Table 9). Active agonistic interactions were assigned a number on a scale of 3-7 (Table 9). Those behaviors that were assigned a number between 1-4 were considered to be low intensity agonism and those that were assigned a number between 5-7 were considered to be high intensity agonism. The intensities were assigned based on the presumed likelihood of each behavior resulting in physical harm of one or both participants. These classifications are similar to those used by Arnold and Whiten (2001). If an active and passive or high and low intensity behavior occurred simultaneously, the active or high intensity behavior took precedence. For example, if focal animal A was chasing B and B vocalized submissively to A, this bout, which contained active (chase) and passive (vocalization) elements, was coded as *active and intense agonism.* The methods used to collect and code these data are described in further detail in Appendix I.

There were two feeding contexts experienced by the ringtailed lemurs in this study, which were termed as the "provisioned feeding" and the "naturalistic foraging" contexts. In the provisioned feeding context, the lemurs fed on primate chow, which was classified as a highly valuable food source because it is designed to be nutritionally complete for primate species (Mowry & Campbell 1991). The provisioned feeding context was also classified as a clumped resource. A proximity analysis conducted in chapter 2 (Sbeglia 2009) confirmed that the individuals in both groups maintained significantly larger inter-individual distances in the naturalistic foraging context as compared to the provisioned feeding context. Lastly, the provisioned feeding context was also classified as containing a limited food resource because the chow was provisioned at quantities that are over 50% less than is required by the American Zoological Association for this species (Table 5) and because both groups of ringtailed lemurs consistently ate the entire ration (69.4g/individual/day) of chow and continued to search for more after it ran out. In the naturalistic foraging context, the lemurs fed on fruits, leaves, bugs, and flowers. This context was classified as containing less valuable food resources that were more plentiful and dispersed through space and time.

Measures of Resource Competition:

Before conducting any analyses on the social organization of these two groups, I first determined the degree of resource competition that existed in each of the food-oriented contexts according to two well-regarded methodologies. The first methodology suggests measuring resource competition by the amount of agonism that occurs in feeding contexts (Pruetz 2009). This value was determined by generating an average rate of active and passive agonism per individual per hour in each of the two food-oriented contexts. The second methodology suggests measuring resource competition as a function of the encounter rate with food, with lower encounter rates suggesting heightened competition (Sterck *et al.* 1997). This value was calculated using the instantaneous data by determining the proportion of 5-minute intervals during which the focal animal was observed to be feeding. Each measure of resource competition was conducted separately for the feeding and the foraging contexts.

Dominance Hierarchy Analysis:

Interaction patterns among group mates, is a major aspect of social organization, which is characterized as being egalitarian, despotic, or somewhere in between (van Schaik 1989). The degree to which interactions are egalitarian or despotic is measured by the linearity of relationships within a hierarchy (de Vries 1995). The linearity of social interactions measures the degree of transitivity among individuals. A completely transitive, and thus linear set of interactions exist when A is dominant over B and A and

B are both dominant over C, etc. (de Vries 1995). If social interactions occur in a linear manner, the social group is said to have dominance hierarchy and individuals can be ranked according to their agonistic and submissive interactions. In the Socioecological model, the characteristics of the dominance hierarchy are primary variables used to classify the organization of primate social group s. The social interaction patterns in this study population were determined by creating matrices containing frequency information of the winner and loser of all decided agonistic interactions. Decided interactions are conflicts in which one animal exhibits a submissive behavior while the other animal either exhibits or does not exhibit an agonistic behavior (Pereira *et al.* 1990, Nakamicki & Koyama 1997). Those conflicts in which one animal exhibits an agonistic behavior and the other exhibits just an agonistic behavior or both an agonistic and submissive behavior are not considered to be decided agonistic interactions (Nakamicki & Koyama 1997).

The values in each cell were a combination of each dyad's interactions during each of their focal observation days (approximately 100 hours of observation for each dyad). Because high and low intensity agonism exhibited very different patterns in this study population in previous analyses (Chapter 2, Sbeglia 2009), separate matrices were created for high and low intensity behaviors for all analyses (Table 9). Low intensity behaviors included submissive vocalizations, which unlike other agonistic behaviors, are directed away from subordinant individuals and towards dominant individuals. Therefore, I transposed the direction of all submissive behaviors for these analyses. For non-focal animals, matrix values were determined based on that individual's interactions with a focal animal during that focal animal's observation days. The interaction patterns of two non-focal animals were determined using approximately 200 hours of count data that was opportunistically collected during focal observations. This method was only used for active agonistic interactions because passive agonism (Table 8) is often so subtle that it was likely that the interaction patterns indicated by those data would be inaccurate. Therefore, for the low intensity agonism matrices, the interaction patterns of non-focal dyads could not be determined and were treated as having an unknown relationship. Males and females were placed in the same matrix but their interaction patterns were interpreted both independently, as suggested by Jolly (1966), and together. Two dominance hierarchy analyses were conducted in this study, each of which addressed one of the hypotheses posed in the introduction.

1) Influence of Provisioned Feeding vs. Naturalistic Foraging on Social Organization:

The simultaneous occurrence of two feeding contexts with different distributions, quantities, and nutritional quality of food, allowed me to indirectly manipulate the impact of these three characteristics on social interactions. In this way, I was able to document the influence of a proposed independent variable that is predicted by the socioecological models to determine the competitive regime. Sterck *et al.* (1997) consider such a manipulation to be a viable method of indirectly testing the relationship between the characteristics of the food source and the competitive and aggressive behaviors of primates. This method is further valid because it is possible for the same group of animals to have a dominance hierarchy that is evident in some contexts but absent or undetectable in others (Pruetz 2009).

For both groups, I created a separate high and low intensity agonism matrix for the provisioned feeding and the naturalistic foraging context (four matrices total). This analysis tested whether the characteristics of the food resource in each context influenced the linearity in those contexts. My methodology was consistent with that of Pruetz (2009), who compared the dominance hierarchy of a single group of vervet monkeys, *Chlorocebus pygerythrus*, in two environments, one with high and one with low food density.

2) Does Proximity or Food Provide a Better Explanation of the Overall Dominance Hierarchy?

I created a low and high intensity agonism matrix for each context individually (I did not use the alert context because it was so infrequent and it contained too few interactions to confidently create a hierarchy) (10 matrices total). Then, I combined appropriate matrices into four non-mutually exclusive categories; food-oriented and non food-oriented and close proximity and distant proximity. The provisioned feeding and the naturalistic foraging contexts were considered to be food-oriented contexts and all other contexts are considered to be non-food-oriented. The average proximity for each focal animal in each context was calculated in chapter 2 (Sbeglia 2009) and is displayed in table 9. Close proximity contexts were those that had an average inter-individual distance of less than seven meters. By this definition, the provisioned feeding and the resting contexts were considered to be close proximity contexts. I then compared the linearity and rank ordering of individuals within the matrices of each of these four categories (food-oriented and non food-oriented and close proximity and distant proximity) to the overall matrix. The rank ordering of individuals within a matrix was compared using the number of inconsistencies that existed between two given matrices.

The number of inconsistencies was determined based on the number of order changes that would be required for the rank ordering of individuals to match that of the overall matrix. A matrix of dyadic interactions could only be classified as a hierarchy within which individuals have a specific rank order if the matrix was found to be significantly linear (Noldas 1998, de Vries 1998). Therefore, while the linearity among matrices could still be compared if the matrix was non-linear, the analysis of the rank ordering of individuals within a hierarchy could only be carried out if a matrix was first found to be significantly linear. Therefore, I will discuss all matrices but will only visually present in this paper those matrices that were significantly linear. This analysis allowed me to determine which categorization of interactions, food-oriented, non-food-oriented, close proximity, or distant proximity, best explained the overall hierarchy.

Analysis:

The linearity of each matrix was determined using the software package MatMan v. 1.1 (Noldas 1998, de Vries *et al.* 1993). MatMan is the standard software by which dominance matrices are currently analyzed. MatMan uses Landau's index (h) to determine the linearity of a matrix on a scale of 0 to 1 (de Vries 1995). If the matrix is significantly linear, MatMan uses the "I (inconsistency) & SI (strength of inconsistency) linear ordering procedure", detailed in de Vries (1998), to rank individuals into the most appropriate linear hierarchy. MatMan deals with unknown relationships by conducting an "improved test for linearity", which randomly assigns dominance relationships to each unknown cell 10,000 times (de Vries 1995). The average of all the resulting linearity values (h) is the corrected linearity index (h^1). The hierarchy is considered linear when

>95% of the random matrices have a smaller linearity index (*h*) than the corrected linearity index (h^1) (Wittig & Boesch 2003). Because MatMan automatically converts raw numbers into overall scores that represent dominant and subordinate individuals within dyads ("1" if the row individual is dominant, "-1" if the row individual is subordinate, "0.5" if the row individual and the column individual are tied, and "0" if there is no interaction between the dyad), the actual number of interactions does not influence the analysis. Therefore, the different raw number of interactions that appeared in each matrix did not bias the comparison of the individual context matrices to the overall matrix. The number of inconsistencies between hierarchies was determined using the *Reorder rows* function in MatMan.

RESULTS:

Measures of Resource Competition:

Method 1: The average rate of agonism in the provisioned feeding context was 5.41 agonistic interactions per individual per hour and the rate of agonism in the naturalistic foraging context was 2.94 agonistic interactions per individual per hour. In both groups, there was a significantly higher rate of agonism in the provisioned feeding context as compared to the naturalistic foraging context (paired t-test: $n = 14$, $p \leq 0.05$).

Method 2: On average, each individual was involved in an encounter with food 50.9% of the time in the provisioned feeding context and 27.62% of the time in the naturalistic foraging context. This difference was significant (paired-t-test: $n = 14$, $p < 0.001$).

Overall Hierarchy:

Group 1:

The overall matrices for high intensity agonism (*h'*= 0.81, p < 0.001) (Table 11) and low intensity agonism (*h'*= 0.77, p < 0.001) (Table 12) were significantly linear. There were 2 inconsistencies in the ordering of the female hierarchy and 6 inconsistencies in the ordering of the male hierarchy between the two matrices. See table 13 for a summary of these results. The letters M and F in these and all subsequent matrices represent the gender of the individual and the number represents that individual's within-gender hierarchical ordering in the overall hierarchy. Those individuals at the top of each hierarchy are the highest in rank, such that all females are ranked above all males in both hierarchies. The letter-number combination to which each individual was assigned differed between the two hierarchies because some individuals held different ranks in the low intensity and high intensity hierarchies. The rank order of individuals in each of these hierarchies represented an overall ordering to which all subsequent matrices (food-oriented, non-food-oriented, close proximity, distant proximity matrices) were compared. Therefore, the number assigned to each individual remained consistent in the subsequent analysis of the low and high intensity agonism matrices even if the rank order of individuals differed from the overall matrix. See table14 for a list of these number-letter combinations for each individual in both the low and high intensity hierarchies.

Group 2:

The overall matrix for high intensity (*h'*= 0.71, $p > 0.05$) and low intensity agonism were non-linear (*h'*= 0.64, $p > 0.05$). It was thus inappropriate to create a rank ordering of individuals for these matrices (Noldas 1998, de Vries 1998). See table 14 for a summary of these results.

1) Influence of Provisioned Feeding vs. Naturalistic Foraging on Social Organization:

Group 1:

For high intensity agonism, the provisioned feeding matrix was significantly linear (*h'*= 0.76, $p < 0.0001$) (Table 15) and the naturalistic foraging matrix was non-linear (*h'*= 0.25, $p > 0.05$). For low intensity agonism, the provisioned feeding matrix was linear (*h'*= 0.59, $p < 0.05$) (Table 16) and naturalistic foraging matrix was non-linear (*h'*= 0.3, $p > 0.05$). See tables 17 and 18 for a summary of these results.

Group 2:

For high intensity agonism, the provisioned feeding matrix (*h'*= 0.41, $p > 0.05$) and naturalistic foraging matrix (*h'*= 0.57, $p > 0.05$) were non-linear. Similarly, for low intensity agonism, the provisioned feeding matrix (*h'*= 0.59, $p > 0.05$) and the naturalistic foraging matrix (*h'*= 0.46, $p > 0.05$) were non-linear. See tables 17 and18 for a summary of these results.

2) Does Proximity or Food Provide a Better Explanation of the Overall Dominance Hierarchy?

Group 1: High Intensity Agonism

Both the food-oriented matrix (*h'*= 0.76, $p < 0.05$) (Table 19) and the non-food-oriented matrix (*h'*= 0.74, $p < 0.05$) (Table 20) were significantly linear for high intensity agonism. There were zero inconsistencies in the ordering of the female hierarchy and four inconsistencies in the ordering of the male hierarchy between the food-oriented matrix (Table 19) and the overall matrix (Table11). There were six inconsistencies for both genders combined (0[females]+4[males]+2[between genders]). There were four inconsistencies in the ordering of the female hierarchy and three inconsistencies in the ordering of the male hierarchy between the non-food-oriented matrix (Table 20) and the overall matrix (Table 11). There were seven inconsistencies for both genders combined (4[females]+3[males]+ 0[between genders]). See tables 21 and 22 for a summary of these results.

Both the close proximity matrix (*h'* = 0.85, $p < 0.0001$) (Table 23) and the distant proximity matrix (*h'* = 0.57, $p < 0.01$) (Table 26) were significantly linear for high intensity agonism. There were zero inconsistencies in the ordering of the female hierarchy and four inconsistencies in the ordering of the male hierarchy in the close proximity matrix (Table 23) as compared to the overall high intensity agonism matrix (Table 11). There were four inconsistencies for both genders combined (0[females]+4[males]+0[between genders]). There were three inconsistencies in the ordering of the female hierarchy and four inconsistencies in the ordering of the male hierarchy in the distant proximity matrix (Table 24) as compared to the overall high intensity agonism matrix (Table 11). There were 11 inconsistencies for both genders combined (3[females]+4[males]+5[between genders]). See tables 21 and 22 for a summary of these results.

Group 1: Low Intensity Agonism

The food-oriented matrix ($h' = 0.76$, $p \leq 0.05$) (Table 25) and the non-food-oriented matrix ($h' = 0.71$, $p \leq 0.05$) (Table 26) were significantly linear. There were two inconsistencies in the ordering of the female hierarchy and three inconsistencies in the ordering of the male hierarchy in the food-oriented matrix (Table 25) as compared to the overall low intensity agonism matrix (Table 12). There were seven inconsistencies for both genders combined (2[females]+3[males]+2[between genders]). There were two inconsistencies in the ordering of the female hierarchy and zero inconsistencies in the ordering of the male hierarchy in the non-food-oriented matrix (Table 26) as compared to the overall low intensity agonism matrix (Table 12). There were four inconsistencies for both genders combined (2[females]+0[males]+2[between genders]). See tables 21 and 22 for a summary of these results.

Both the close proximity ($h' = 0.59$, $p < 0.001$) (Table 27) and distant proximity ($h' = 0.69$, $p < 0.01$) (Table 28) matrices were significantly linear. There were zero inconsistencies in the ordering of the female hierarchy and two inconsistencies in the ordering of the male hierarchy in the close proximity matrix (Table 27) as compared to the overall low intensity agonism matrix (Table 12). There were two inconsistencies for both genders combined (0[females]+2[males]+0[between genders]). There were three inconsistencies in the ordering of the female hierarchy and two inconsistencies in the ordering of the male hierarchy in the distant proximity matrix (Table 28) as compared to the overall low intensity agonism matrix (Table 12). There were seven inconsistencies with both genders combined (3[females]+2[males]+2[between genders]). See tables 21 and 22 for a summary of these results

Group 2: High and Low Intensity Agonism

The food-oriented matrices were non-linear for both high intensity agonism ($h' = 0.61$, $p > 0.5$) and low intensity agonism ($h' = 0.57$, $p > 0.05$). The non-food-oriented matrices were non-linear for high intensity agonism ($h' = 0.73$, $p > 0.05$) and linear for low intensity agonism ($h'=0.84$, $p \leq 0.05$) (Table 29). However, because the overall low intensity agonism hierarchy was non-linear for this group, the inconsistencies in rank ordering of individuals between the two matrices could not be established. See tables 21 and 22 for a summary of these results.

The close proximity matrices were non-linear for high intensity agonism ($h'= 0.5$, $p > 0.05$) and low intensity agonism ($h'= 0.68$, $p > 0.05$). The distant proximity matrices were non-linear for high intensity agonism ($h'= 0.64$, $p > 0.05$) and linear for low intensity agonism ($h' = 0.75$, $p \leq 0.05$) (Table 30). Again, because the overall low intensity agonism hierarchy was non-linear, the inconsistencies in rank ordering of individuals between the two matrices could not be established. See tables 21 and 22 for a summary of these results.

DISCUSSION:

Measures of Resource Competition:

There was significantly more agonism in the provisioned feeding as compared to the foraging context, which according to the first methodology used to measure resource competition suggests that there was more competition during provisioned feeding than during naturalistic foraging (Pruetz 2009). However, these same individuals, on average, encountered more food per unit time in the provisioned feeding context than in the naturalistic foraging context, which, according to the second methodology used to measures resource competition, suggests that there was higher competition during naturalistic foraging (Sterck *et al.* 1997). Therefore, the "agonism during feeding" method and the "encounter rate with food" method offered opposing conclusions as to which context contained more competition over resources. Consequently, I could not conclusively identify which context had the most feeding competition. Therefore, at least one of these measures of feeding competition needs to be re-evaluated.

1) Influence of Provisioned Feeding vs. Naturalistic Foraging on Social Organization:

In group 1, the high intensity agonism matrix was significantly linear in the provisioned feeding context, where food is clumped, and non-linear in the naturalistic foraging context, where food is dispersed. The low intensity matrices in both contexts were non-linear. Therefore, there is a difference in the organization of social interactions in the high intensity agonistic interaction is these two contexts. Similarly, Nakagawa (2008) found that two populations of patas monkeys, *Ethrocebus patas*, exhibited linear dominance hierarchies where food resources were clumped and non-linear relationships when resources were dispersed. This finding supports the predictions of the socioecological model because the characteristics of the food resource appear to influence the dominance hierarchy, such that clumped food resources result in a more linear hierarchy than dispersed resources (van Schaik 1989, de Waal 1989, Isbell 1991, Sterck *et al.* 1997). However in group 2, the low and high intensity agonism matrices in both contexts were non-linear. This finding was counter to the predictions of the socioecological model because the characteristics of the food resource did not influence the dominance hierarchy. Therefore, these latter patterns of social behavior did not provide convincing evidence that the characteristics of the food resources dictated social organization in group 2.

These results indicated that while it is possible for the characteristics of food resources to reflect the patterns of social organization, as was the case for high intensity agonism in group 1, this is not necessarily true across all social groups of this species, as was demonstrated in group 2. Pruetz (2009) studied a single group of vervet monkeys, *Chlorocebus pygerythrus*, who regularly switched between two habitats, one with clumped resources and the other dispersed resources. Upon an examination of their dominance relationships, she found that although the vervets had significantly linear hierarchies overall, the contests over clumped food resources were non-linear and thus, did not account for that linearity. These findings, as well as the results reported in this study, do not support the predictions of the socioecological model (Wrangham 1980, van Schaik 1989) and are consistent with the alternative hypothesis that the characteristics of food resources do not necessarily account for social organization.

2) Does Proximity or Food Provide a Better Explanation of the Overall Dominance Hierarchy?

Group 1: High Intensity Agonism

In group 1, the food-oriented hierarchy better explained (i.e. fewer inconsistencies) the overall female hierarchy for high intensity agonism than did the non-food-oriented hierarchy. Conversely, the non-food-oriented hierarchy slightly better explained the overall male hierarchy for high intensity agonism than did the food-oriented hierarchy. This pattern is consistent with the socioecological model, which predicts that female social organization is primarily influenced by the distribution (van Schaik 1989) and abundance (Wrangham 1980, Isbell 1991) of resources. Although the non-food-oriented hierarchy best predicted the overall male dominance hierarchy, there were still three inconsistencies between them, which indicated that neither categorization adequately predicted male social interaction patterns. Thus, the mechanisms responsible for male social interactions remain to be identified.

When using close and distant proximity as categories, I found that the male high intensity agonism hierarchy was poorly explained by both close and distant proximity. The female close proximity hierarchy explained the overall hierarchy as well as did the food-oriented hierarchy. However, the close proximity hierarchy better explained the overall hierarchy for high intensity agonism than did food-oriented behaviors. This is because the overall hierarchy placed all females at the top of the rank order, such that all females were dominant to all males. The close proximity hierarchy mirrored this dominance pattern, while the food-oriented hierarchy failed to do so. Female dominance is the typical dominance pattern documented in the literature for this species (Pereira *et al.* 1990, Kappeler 1990a, b, Sauther 1992). Therefore it appears that it was the aggressive behaviors that occurred while individuals were in close proximity that most influenced the collective social relationships of females in this group. Conversely, the agnostic behaviors that occurred while food was absent best predicted the male hierarchy. But, with three within-gender inconsistencies, the mechanisms responsible for the male high intensity agonism hierarchy remain to be convincingly identified.

Group 1: Low Intensity Agonism

The low intensity female hierarchy was equally well explained by both the food-oriented and non-food-oriented hierarchies. However, the non-food-oriented hierarchy better explained the low intensity male hierarchy than did the food-oriented hierarchy. It has been suggested that male lemurs might confer female feeding priority through the mechanism of spatial deference (Jolly 1984), which might have some carryover affect on the interactions among males as well. This is a possible explanation as to why the male overall hierarchy is best explained by those interactions that occur in the absence of food. However, there existed a total of seven inconsistencies in the food-oriented hierarchy and four in the non-food-oriented when they were compared to the overall low intensity agonism hierarchy, which indicates that the mechanisms responsible for the male low intensity agonism hierarchy remain to be convincingly identified.

The close proximity hierarchy, with no inconsistencies, better explained the overall low intensity female hierarchy than did the food-oriented hierarchy with two inconsistencies. Furthermore, only the close proximity hierarchy distinguished the dominance relationships between the two genders (i.e. all females ranked higher than all males), which, is the observed pattern in the overall low intensity hierarchy. The male's overall low intensity hierarchy was poorly predicted by both distant and close proximity. As was the case for the high intensity hierarchy, the female's overall low intensity hierarchy was best explained by close proximity and the male's hierarchy is best explained by those contexts that do not involve food.

Group 2: High Intensity Agonism

All hierarchies for high intensity agonism were non-linear. The non-food-oriented hierarchy had a linearity index that was closest to that of the overall hierarchy, with the distant proximity hierarchy being the second closest. Therefore, it terms of degree of linearity, the interactions in the food-oriented hierarchy do not offer the best explanation of the overall high intensity agonism hierarchy.

Group 2: Low Intensity Agonism

The overall, food-oriented, and close proximity hierarchies were non-linear but the non-food-oriented and distant proximity hierarchies were significantly linear. Therefore, it appears that the interactions in the food-oriented or close proximity hierarchy are most likely responsible for the non-linearity of the overall hierarchy. Furthermore, because the close proximity hierarchy has a linearity index closest to that of the overall hierarchy, I argue that the interactions that occur while individuals are in close proximity may best account for the overall index of linearity in this study population. Thus, because both food and proximity could be used to explain the non-linear social organization of this study group, this finding is counter to the predictions of the socioecological model.

Conclusion:

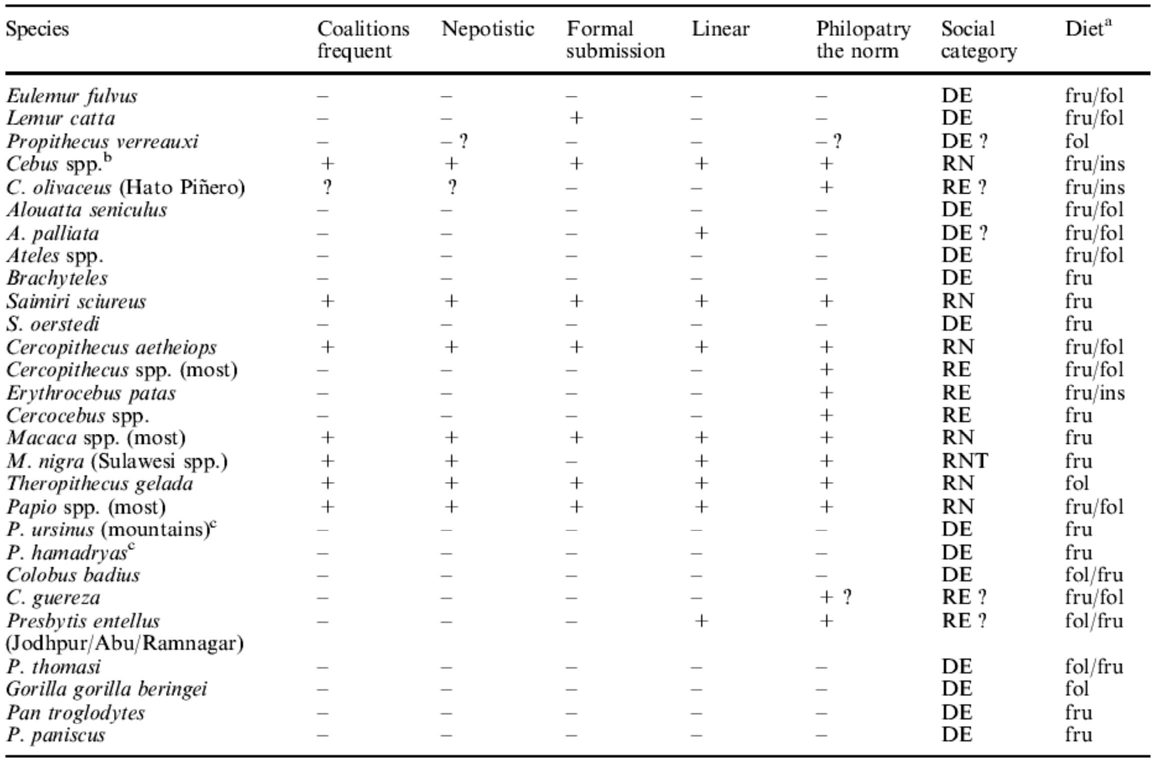
The most important finding in this paper is that the proximity between individuals, and not the characteristics related to food resources, most directly explained the social organization with respect to dominance in this study population. Therefore, the fact that group 1 had a significantly linear hierarchy in a context with clumped, limited, and highly valuable food resources and a non-linear hierarchy in a context with dispersed, abundant, and less valuable food, may not indicate that the characteristics of food resources influence patterns of social organization. Rather, this apparent influence of food on social organization was potentially an indirect effect resulting from the different proximity patterns in each context. However, given these results regarding the importance of proximity in structuring the dominance hierarchy, it would be inappropriate to conclude that food resources are irrelevant to social organization. This is especially true because in the methodology used in this study, the close proximity matrix included the behaviors in the provisioned feeding context, where food is clumped, and the distant proximity matrix included the behaviors in the naturalistic foraging context, where food is dispersed. Therefore, there is an implicit confound between proximity and food distribution because when food is clumped, individuals are likely to be clumped as well (Sbeglia 2009), which might increase the opportunity for agonism. As a result, it is likely that the characteristics of the food resource indirectly and in part influence the social organization of females, however close proximity appears to be a more direct mechanism responsible for the social relationships that occurred within the dominance hierarchy. This finding does not support the socioecological model and instead supports the alternative predictions posed in this paper. Interestingly, the confound between proximity and food distribution, is actually built into the socioecological model because female gregariousness implies proximity relationships among individuals. However, researchers do not address this confound when collecting or interpreting data.

Despite the influence of proximity on social organization shown in this paper, I reported in chapter 2 (Sbeglia 2009) that agonism rates among the ringtailed lemurs in this same population were not consistently correlated with proximity. This contradiction might suggest that while the actual number of aggressive interactions was not necessarily related to proximity, the ***consistency*** in the direction of those interactions was. It has been previously documented that the number of interactions and the consistency in the direction of interactions can offer differing results. For example, scientists have observed that while the consistency in the direction of interactions is used to create dominance hierarchies, the sheer number of agonistic interactions is not necessarily related to dominance rank. Altmann (1980) reported that dominance ranks among female yellow baboon mothers showed no relationship with their rates of agonism. Additionally, because close proximity best explained dominance relationships and only affiliation was influenced by proximity in these social groups (chapter 2, Sbeglia 2009), it is also possible that affiliation is a more significant contributor to the formation of social relationships than is agonism.

The results of this study also indicate that for high intensity agonism, the male hierarchy is much more variable than the female hierarchy and not as convincingly affected by either food or proximity. This variability between context categories suggests that the cumulative outcomes of dyadic interaction did not necessarily reflect identical dominance relationships in all contexts (Strier 1994). For example, Popp and DeVore (1979) found that male great apes might submit during feeding but win contests over access to receptive females. In ringtailed lemurs, Gould (1997) suggested that the instability in male rank could result from the fact that higher-ranking males do not offer benefits to low ranking males and/or because male dispersal constantly alters male membership in the group. Therefore, as is predicted by the socioecological model, there appears to be different factors influencing male and the female dominance patterns within a social group in this species (Wrangham 1980). However, as was indicated by Gould (1997), the social behavior patterns of males may be related to the natural history of the species and not to resource competition. Therefore, at this time, it is not clear that male social organization is predominantly dependent on female competition over food, as the socioecological model suggests.

Overall, the dominance patterns in the two groups of ringtailed lemurs observed in this study 1) do not fit the predications of the socioecological model and 2) show a great deal of variation between groups and among contexts. In fact, there has been mounting evidence of the vast variation in social systems that can occur within single species (Kappeler 2000, Pochron & Wright 2003, sifaka, *Propithecus diadema*; Chapman *et al.* 2002, red colobus monkeys, *Procolobus badius*; Sinha 2005, bonnet macaques, *Macaca radiata*; see Chapman & Rothman 2009 for a review) and even within a single social group (patas monkeys, *Erthrocebus patas*, Nakagawa 2008). Thus, elucidating an overarching model (like the socioecological model) that attempts to explain social relationships in primate species, either proximity-based or resource-based, seems unrealistic.

FIGURES:



Species	Coalitions frequent	Nepotistic	Formal submission	Linear	Philopatry the norm	Social category	Diet[a]
Eulemur fulvus	–	–	–	–	–	DE	fru/fol
Lemur catta	–	–	+	–	–	DE	fru/fol
Propithecus verreauxi	–	– ?	–	–	– ?	DE ?	fol
Cebus spp.[b]	+	+	+	+	+	RN	fru/ins
C. olivaceus (Hato Piñero)	?	?	–	–	+	RE ?	fru/ins
Alouatta seniculus	–	–	–	–	–	DE	fru/fol
A. palliata	–	–	–	+	–	DE ?	fru/fol
Ateles spp.	–	–	–	–	–	DE	fru/fol
Brachyteles	–	–	–	–	–	DE	fru
Saimiri sciureus	+	+	+	+	+	RN	fru
S. oerstedi	–	–	–	–	–	DE	fru
Cercopithecus aetheiops	+	+	+	+	+	RN	fru/fol
Cercopithecus spp. (most)	–	–	–	–	+	RE	fru/fol
Erythrocebus patas	–	–	–	–	+	RE	fru/ins
Cercocebus spp.	–	–	–	–	+	RE	fru
Macaca spp. (most)	+	+	+	+	+	RN	fru
M. nigra (Sulawesi spp.)	+	+	–	+	+	RNT	fru
Theropithecus gelada	+	+	+	+	+	RN	fol
Papio spp. (most)	+	+	+	+	+	RN	fru/fol
P. ursinus (mountains)[c]	–	–	–	–	–	DE	fru
P. hamadryas[c]	–	–	–	–	–	DE	fru
Colobus badius	–	–	–	–	–	DE	fol/fru
C. guereza	–	–	–	–	+ ?	RE ?	fru/fol
Presbytis entellus (Jodhpur/Abu/Ramnagar)	–	–	–	+	+	RE ?	fol/fru
P. thomasi	–	–	–	–	–	DE	fol/fru
Gorilla gorilla beringei	–	–	–	–	–	DE	fol
Pan troglodytes	–	–	–	–	–	DE	fru
P. paniscus	–	–	–	–	–	DE	fru

Figure 1: Association between female within-group coalitions, female dominance relationships and female philopatry among non-human primates with multi-female groups. Adapted from Sterck *et al.* 1997. DE = dispersal egalitarian; RN = resident nepotistic; RNT = resident nepotistic tolerant; RE = resident egalitarian. Adapted from Sterck *et al.* 1997.

TABLES:

Table 1: Potential predators of ringtailed lemurs in captivity and in the wild

Potential North American Predators	**Ecological Equivalent in Madagascar** (the categories, not necessarily individual species, are comparable)
Raptors:	
red-tailed hawk[1] (*Buteo jamaicensis*) red-shouldered hawk[1] (*Buteo lineatus*) great-horned owl[1] (*Bubo viginianus*)	Madagascar harrier hawk[2, 5] (*Polyboroides radiatus*) Madagascar buzzard [2, 5] (*Buteo brachypterus*) black kite[5] (*Milvus migrans*)
Carnivores:	
gray fox[1] (*Urocyon cineroagenteus*) raccoon[1] (*Procyon locor*) weasel[1] (*Mustela sp.*)	fossa[3] (*Cryptoprocta ferox*) domestic dog [4] (*Canis lupus familiaris*) domestic cat[5] (*Felis catus*)
Venomous snakes:	
copperhead[1] (*Agkistrodon contortrix*) cottonmouth[1] (*Agkistrodon piscivorus*)	NA
Non-venomous Snakes:	
black rat snake[1] *(Elaphe obsolete*)	Madagascar boa constrictor [3] (*Boa manditra*)

[1]Macedonia (1993), [2] Sauther (1989), [3]Karpanty & Wright (2007), [4]Gould & Sauther (2007), [5]Jolly *et al.* (2006)

Table 2: Composition of social group 1.

Name	Gender	Age	Classification	Relatedness
Fern	F	3 mo	Natal infant	Offspring of Cleis and Alexander, half sib of Persephone and Dory, niece of Alena, Tellus, and Niciea
Persephone*	F	2 yrs	Natal juvenile	Offspring of Cleis & Aracus, full sib of Ivy, half sib of Dory, half aunt and half sib of Niciea, Tellus, Alena, and Alex
Alena	F	2 yrs	Natal juvenile	Offspring of Dory & Aracus, grand daughter of Cleis,, full sib to Alex, Niciea, and Tellus, half sib to Berisidies, aunt of Fern, half sib and half nephew of Ivy and Persephone
Niciea*	F	3 yrs	Natal sub-adult	Offspring of Dory & Aracus, grand daughter of Cleis, full sib of Alena, Tellus, and Alexander, aunt to Fern, half sib and half nephew of Ivy and Persephone
Tellus	F	3 yrs	Natal sub-adult	Offspring of Dory & Aracus, grand daughter of Cleis, full sib of Alena, Niciea, and Alexander, aunt to Fern, half sib and half nephew of Ivy and Persephone
Dory*	F	18 yrs	Natal adult	Offspring of Cleis and unrelated male, mother of Tellus, Niciea, Alexander and Alena, half sib of Persephone and Fern, aunt to Berisidies
Cleis*	F	22 yrs	Founder, lactating adult	Offspring of Lethe and Pegasis, mother of Dory, Persephone, Ivy, and Fern, grandmother to Berisidies
Alexander*	M	2 yrs	Natal juvenile, pre-dispersal age	Offspring of Dory & Aracus, grand son of Cleis, father of Fern, full sib of Alena, Niciea, and Tellus
Ivy	M	3 yrs	Natal sub-adult of dispersal age	Offspring of Cleis & Aracus, full sib of Persephone, half sib of Dory, half sib and half uncle to Niciea, Tellus, Alena, and Alex
Berisidies*	M	3 yrs	Natal sub-adult of dispersal age	Offspring of Sosiphanes & Aracus, half sib and cousin of Niciea, Tellus, Alena, and Alex, nephew of Dory, grandson of Cleis, half nephew and half sib of Persephone and Ivy
Fritz	M	5 yrs	Non-natal adult	Half sib of Cap N' Lee
Cap N' Lee*	M	7 yrs	Non-natal adult	Half sib of Fritz

*Focal animals (no data were collected on interactions with infants, <1yr)

Table 3: Composition of social group 2.

Name	Gender	Age	Classification	Relatedness
Nebe*	F	5 yrs	Natal adult	Offspring of Hector and Katina, mother of Herodotous, half sib of Dorius, half aunt of Justine and half aunt of Cebes
Dorius*	F	12 yrs	Natal adult	Offspring of Gelon and Katina, mother of Justine and Cebes, half sib of Nebe, half aunt of Hero
Sophia*	F	4 yrs	Natal sub-adult	Offspring of Artemesia and Brennus, half sib of Justine
Justine*	F	3 yrs	Natal sub-adult	Offspring of Dorius and Brennus, half sib of Sophia, half niece of Nebe, half cousin of Herodotus
Chandler*	M	7 yrs	Non-natal adult	Offspring of unrelated individuals, father of Cebes and Herodotous
Cebes*	M	2 yrs	Natal juvenile, pre-dispersal age	Offspring of Dorius and Chandler, half sib and half cousin of Herodotous, half sib of Justine, half nephew of Nebe
Herodotus*	M	2 yrs	Natal juvenile, pre-dispersal age	Offspring of Nebe and Chandler, half sib and half cousin of Cebes, half nephew of Dorieus

*Focal animals

Table 4: Sample sizes of various primate studies in captivity and in the wild

Author(s)	Year	Species	Subject	# of focal individuals	# hrs of Observation
Gould*	1996	ringtailed lemurs	Affiliative relationships	10	1102
Keith-Lucas *et. al.*	1999	ringtailed lemurs	Changes in behavior after release	6	Not provided
Arnold & Barton	2001	speckled leaf monkeys	Reconciliation/Post conflict behavior	12	165
Sussman *et al.**	2003	ringtailed lemurs	Aggression and affiliation frequencies	4	40
Wittig & Boesch*	2003	chimpanzees	Feeding competition	14	1028
Mallavarapu *et al.*	2006	gorillas	Reconciliation/Post conflict behavior	13	223+
Parga	2006	ringtailed lemurs	Male mate choice	11	Not provided
Wittig *et al.*	2007	baboons	Kin mediated reconciliation	13	Not provided
Palagi *et al.* *	2008	Verreauxi's Sifaka	Reconciliation/Post conflict behavior	16	640

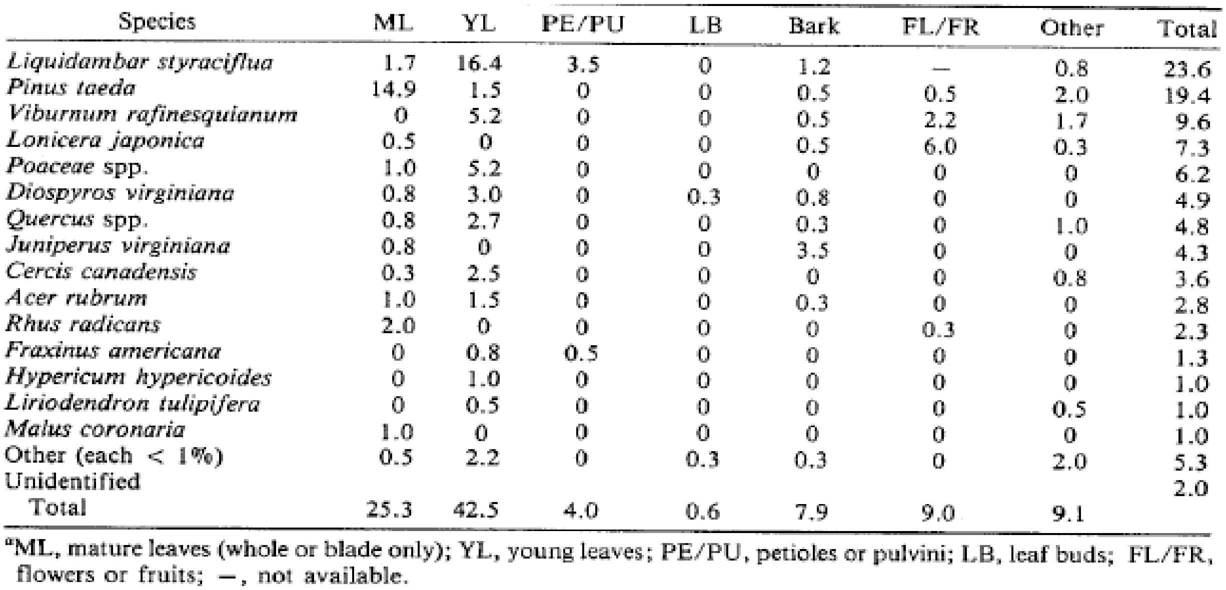
*Studies conducted in the wild

Table 5: Amount of provisioned food

	Chow per indiv per wk(g)	% of provisioned diet	Fruit & veg per indiv per wk(g)	% of provisioned diet	Total food per indv per wk(g)
Duke Lemur Center[1]	486	56.71%	371	43.29%	857
St. Louis Zoo[2]	588	32%	1260	68%	1848

[1] Duke Lemur Center (2007), [2] St. Louis Zoo (2007)

Table 6: Plant species and plant parts in the diet of *Lemur catta* at Duke Lemur Center. Adapted from Ganzhorn (1986) (N = 402)



Species	ML	YL	PE/PU	LB	Bark	FL/FR	Other	Total
Liquidambar styraciflua	1.7	16.4	3.5	0	1.2	—	0.8	23.6
Pinus taeda	14.9	1.5	0	0	0.5	0.5	2.0	19.4
Viburnum rafinesquianum	0	5.2	0	0	0.5	2.2	1.7	9.6
Lonicera japonica	0.5	0	0	0	0.5	6.0	0.3	7.3
Poaceae spp.	1.0	5.2	0	0	0	0	0	6.2
Diospyros virginiana	0.8	3.0	0	0.3	0.8	0	0	4.9
Quercus spp.	0.8	2.7	0	0	0.3	0	1.0	4.8
Juniperus virginiana	0.8	0	0	0	3.5	0	0	4.3
Cercis canadensis	0.3	2.5	0	0	0	0	0.8	3.6
Acer rubrum	1.0	1.5	0	0	0.3	0	0	2.8
Rhus radicans	2.0	0	0	0	0	0.3	0	2.3
Fraxinus americana	0	0.8	0.5	0	0	0	0	1.3
Hypericum hypericoides	0	1.0	0	0	0	0	0	1.0
Liriodendron tulipifera	0	0.5	0	0	0	0	0.5	1.0
Malus coronaria	1.0	0	0	0	0	0	0	1.0
Other (each < 1%)	0.5	2.2	0	0.3	0.3	0	2.0	5.3
Unidentified								2.0
Total	25.3	42.5	4.0	0.6	7.9	9.0	9.1	

[a]ML, mature leaves (whole or blade only); YL, young leaves; PE/PU, petioles or pulvini; LB, leaf buds; FL/FR, flowers or fruits; —, not available.

Table 7: Average weights of ringtailed lemurs

	Berenty Reserve[1]	Duke Lemur Center[2]	St Louis Zoo[3]	Miami MetroZoo[4]
	Wild	Semi-free Ranging	Captive	
Adult Female	2.27 kg	2.32 kg	3.52kg	2.73kg
Adult Male	2.22 kg	2.36 kg	2.7kg	4.1kg

[1]Koyama, *et. al* (2007), [2] Duke Lemur Center (2007), [3] St. Louis Zoo (2007), [4] Miami MetroZoo (2007)

Table 8: Categorization of behaviors.

Active Agonism:	**Passive Agonism:**
Chase Chase threat Bite Lunge Lunge threat Hit Mouth to face threat Touch Grab Push Food take Fight/Wrestle Stink fight[1]	Displace Chutter/Deep spat* Plosive Bark*
Passive Aggression, Submissive:	**Unknown:**
Yip/Spat call* Flee and Squeal*	Stink fight[1] Food share/take [2] Cackle*[3]

*Terms taken from Macedonia (1993)

[1] A stink fight can represent both an aggressive and a sexual interaction depending on the individual to whom the behavior is directed. Therefore, a stink fight behavior is considered to be *active aggression* when it is directed at a male and *unknown* when directed at a female.

[2] It is difficult to tell whether individuals are actively sharing food or behaving submissively.

[3] This behavior is thought to be a defensive vocalization indicating a willingness to become aggressive if pressed (Macedonia 1993). Therefore, it is unclear as to whether it is submissive or aggressive.

Table 9: Categorization of agonism by intensity.

Behavior Category	Intensity Score	Intensity Level
Submissive and agonistic vocalizations	1	Low
Displace/supplant	2	Low
Mouth to face threat	3	Low
Threats of high intensity agonism (ex. chase threat)	4	Low
Chase, lunge, stink fight*	5	High
High intensity contact (ex. push, grab, hit)	6	High
Uni- or multidirectional fighting (ex. wrestle)	7	High

*Between males only

Table 10: Average inter-individual distance between animals during different contexts (based on data from chapter 2, Sbeglia 2009).

	Feed (m)	**Forage (m)**	**Move (m)**	**Travel (m)**	**Rest (m)**
Group 1	6.06	7.21	13.57	8.3	6.62
Group 2	5.46	8.45	7.63	8.03	5.5

Table 11: Group 1's overall linear dominance hierarchy for high intensity agonism. The bolded and underlined numbers represent ordering inconsistencies within the matrix.

	F1	**F2**	**F3**	**F4**	**F5**	**F6**	**M1**	**M2**	**M3**	**M4**	**M5**
F1	*	30	2	1	12	3	5	4	42	6	20
F2	0	*	2	0	4	4	3	11	21	2	9
F3	0	1	*	1	13	8	6	5	17	2	24
F4	0	0	0	*	3	4	2	7	11	0	5
F5	0	4	0	0	*	0	4	0	28	0	28
F6	0	0	0	0	0	*	0	0	3	0	2
M1	0	0	0	0	0	0	*	2	1	***0***	0
M2	0	0	1	0	0	0	0	*	6	0	1
M3	0	1	0	1	0	0	0	3	*	1	0
M4	0	0	0	0	0	0	***1***	0	0	*	1
M5	0	0	0	0	1	0	0	0	0	0	*

Table 12: Group 1's overall linear dominance hierarchy for low intensity agonism. The bolded and underlined numbers represent ordering inconsistencies within the matrix.

	F1	**F2**	**F3**	**F4**	**F5**	**F6**	**M1**	**M2**	**M3**	**M4**	**M5**
F1	*	20	7	0	7	16	8	9	14	23	18
F2	1	*	4	1	10	35	26	5	7	33	5
F3	3	1	*	17	9	16	12	3	1	19	5
F4	0	1	16	*	1	38	4	1	1	12	8
F5	1	1	6	0	*	6	1	0	0	10	1
F6	0	5	11	2	3	*	2	2	3	19	1
M1	1	1	1	2	1	1	*	0	2	7	7
M2	0	0	1	0	0	0	0	*	1	***3***	3
M3	0	0	1	0	0	0	0	0	*	39	4
M4	0	1	4	0	0	2	1	***4***	14	*	4
M5	0	2	1	0	1	1	1	1	0	2	*

Table 13: Dominance analysis for overall high and low intensity agonism

Group	Matrix Category	Linearity
1	High Intensity	0.81*
2	High Intensity	0.71*
1	Low Intensity	0.77*
2	Low Intensity	0.64

*Significant at the 0.05 level

Table 14: Rank order of each individual in group 1 in the high and low intensity hierarchy.

Individual	High Intensity Agonism	Low Intensity Agonism
Dory	F1	F1
Persephone	F2	F2
Alena	F3	F4
Cleis	F4	F3
Niciea	F5	F6
Tellus	F6	F5
Berisidies	M1	M5
Alex	M2	M1
Cap N' Lee	M3	M4
Ivy	M4	M2
Fritz	M5	M3

Table 15: Group 1's linear dominance hierarchy for high intensity agonism in the provisioned feeding context.

	F1	F2	F3	F4	F5	M2	M4	F6	M1	M5	M3
F1	*	15	1	1	6	1	3	2	4	10	23
F2	0	*	1	0	1	4	0	1	1	3	7
F3	0	0	*	1	5	2	2	4	4	8	6
F4	0	0	0	*	2	2	0	1	1	0	7
F5	0	0	0	0	*	0	0	0	1	6	15
M2	0	0	0	0	0	*	0	0	0	1	2
M4	0	0	0	0	0	0	*	0	0	0	0
F6	0	0	0	0	0	0	0	*	0	0	2
M1	0	0	0	0	0	0	0	0	*	0	0
M5	0	0	0	0	0	0	0	0	0	*	0
M3	0	0	0	0	0	1	0	0	0	0	*

Table 16: Group 1's linear dominance hierarchy for low intensity agonism in the provisioned feeding context. The bolded and underlined numbers represent ordering inconsistencies within the hierarchy.

	F1	**F2**	**F5**	**F3**	**F4**	**M3**	**M2**	**F6**	**M1**	**M4**	**M5**
F1	*	9	1	5	0	3	5	8	4	8	9
F2	1	*	0	2	1	2	1	4	13	4	0
F5	1	0	*	1	0	0	0	2	1	0	***0***
F3	2	0	0	*	5	0	2	4	4	3	4
F4	0	0	0	0	*	1	1	13	0	5	1
M3	0	0	0	0	0	*	0	0	0	10	2
M2	0	0	0	1	0	0	*	0	0	1	1
F6	0	2	0	0	0	0	0	*	1	9	0
M1	0	0	0	0	0	0	0	0	*	3	1
M4	0	0	0	1	0	1	0	1	1	*	2
M5	0	0	***1***	1	0	0	0	0	0	0	*

Table 17: Dominance analyses for high intensity agonism: Provisioned feeding vs. naturalistic foraging

Group	**Matrix Category**	**Linearity**
1	Provisioned Feeding	.76*
1	Naturalistic Foraging	.25
2	Provisioned Feeding	.41
2	Naturalistic Foraging	.57

*Significant at the 0.05 level

Table 18: Dominance analyses for low intensity agonism: Provisioned feeding vs. naturalistic foraging.

Group	**Matrix Category**	**Linearity**
1	Provisioned Feeding	.59
1	Naturalistic Foraging	.3
2	Provisioned Feeding	.59
2	Naturalistic Foraging	.46

*Significant at the 0.05 level

Table 19: Group 1's linear dominance hierarchy for high intensity agonism in food-oriented contexts.

	F1	**F2**	**F3**	**F4**	**F5**	**M2**	**M4**	**M6**	**M1**	**M5**	**M3**
F1	*	17	1	1	7	1	3	2	4	11	23
F2	0	*	1	0	1	6	0	1	1	3	7
F3	0	0	*	1	5	2	2	4	5	10	6
F4	0	0	0	*	2	2	0	1	1	0	7
F5	0	0	0	0	*	0	0	0	2	7	17
M2	0	0	0	0	0	*	0	0	0	1	2
M4	0	0	0	0	0	0	*	0	0	0	0
F6	0	0	0	0	0	0	0	*	0	0	2
M1	0	0	0	0	0	0	0	0	*	0	0
M5	0	0	0	0	1	0	0	0	0	*	0
M3	0	0	0	0	0	1	0	0	0	0	*

Table 20: Group 1's linear dominance hierarchy for high intensity agonism in non-food-oriented contexts. The bolded and underlined numbers represent ordering inconsistencies within the hierarchy.

	F1	**F4**	**F3**	**F5**	**F2**	**F6**	**M4**	**M1**	**M2**	**M3**	**M5**
F1	*	0	1	4	13	1	3	1	3	17	8
F4	0	*	0	1	0	3	0	1	5	4	5
F3	0	0	*	8	1	4	0	1	3	11	14
F5	0	0	0	*	4	0	0	2	0	11	21
F2	0	0	1	3	*	3	2	2	5	14	6
F6	0	0	0	0	0	*	0	0	0	1	2
M4	0	0	0	0	0	0	*	1	0	***0***	1
M1	0	0	0	0	0	0	0	*	2	1	0
M2	0	0	1	0	0	0	0	0	*	4	0
M3	0	1	0	0	1	0	***1***	0	2	*	0
M5	0	0	0	0	0	0	0	0	0	0	*

Table 21: Dominance analyses for high intensity agonism: Does Proximity or Food Provide a Better Explanation of the Overall Dominance Hierarchy?

Group	**Matrix Category**	**Linearity**	**Inconsistencies w/ overall matrix**
1	Food-Oriented	0.76*	0 female, 4 males, 6 total
1	Non-Food-Oriented	0.74*	4 females, 3 males, 7 total
1	Close Proximity	0.85*	0 female, 4 male, 4 total
1	Distant Proximity	0.57*	3 female, 4 male, 11 total
2	Food-Oriented	0.61	NA
2	Non-Food-Oriented	0.73	NA
2	Close Proximity	0.50	NA
2	Distant Proximity	0.64	NA

*Significant at the 0.05 level

Table 22: Dominance analyses for low intensity agonism: Does Proximity or Food Provide a Better Explanation of the Overall Dominance Hierarchy?

Group	**Matrix Category**	**Linearity**	**Inconsistencies w/ overall matrix**
1	Food-Oriented	0.76*	2 female, 3 male, 7 total
1	Non-Food-Oriented	0.71*	2 female, 0 males, 4 total
1	Close Proximity	0.59*	0 females, 2 males, 2 total
1	Distant Proximity	0.69*	3 females, 2 males, 7 total
2	Food-Oriented	0.57	NA
2	Non-Food-Oriented	0.84*	No hierarchy to compare to
2	Close Proximity	0.68	NA
2	Distant Proximity	0.75*	No hierarchy to compare to

*Significant at the 0.05 level

Figure 23: Group 1's linear dominance hierarchy for high intensity agonism in close proximity contexts. The bolded and underlined numbers represent ordering inconsistencies within the matrix.

	F1	**F2**	**F3**	**F4**	**F5**	**F6**	**M2**	**M4**	**M1**	**M5**	**M3**
F1	*	21	1	1	8	3	1	5	4	15	32
F2	0	*	1	0	4	3	7	1	3	6	16
F3	0	0	*	1	7	6	4	2	4	15	10
F4	0	0	0	*	3	1	4	0	1	4	11
F5	0	3	0	0	*	0	0	0	1	20	24
F6	0	0	0	0	0	*	0	0	0	1	3
M2	0	0	1	0	0	0	*	0	0	1	5
M4	0	0	0	0	0	0	0	*	0	0	0
M1	0	0	0	0	0	0	0	0	*	0	0
M5	0	0	0	0	0	0	0	0	0	*	0
M3	0	1	0	0	0	0	1	0	0	0	*

Figure 24: Group 1's linear dominance hierarchy for high intensity agonism in distant proximity contexts. The bolded and underlined numbers represent ordering inconsistencies within the matrix.

	F1	**F3**	**F5**	**F2**	**M3**	**F4**	**M4**	**M1**	**F6**	**M2**	**M5**
F1	*	1	3	9	8	0	1	1	0	3	4
F3	0	*	6	1	7	0	0	2	2	1	9
F5	0	0	*	1	4	0	0	3	0	0	8
F2	0	1	0	*	5	0	1	0	1	4	3
M3	0	0	0	0	*	1	1	***0***	0	2	0
F4	0	0	0	0	0	*	0	1	3	3	1
M4	0	0	0	0	0	0	*	1	0	0	1
M1	0	0	0	0	***1***	0	0	*	0	2	0
F6	0	0	0	0	0	0	0	0	*	0	1
M2	0	0	0	0	1	0	0	0	0	*	0
M5	0	0	1	0	0	0	0	0	0	0	*

Figure 25: Group 1's linear dominance hierarchy for low intensity agonism in food-oriented contexts. The bolded and underlined numbers represent ordering inconsistencies within the matrix.

	F1	**F2**	**F5**	**F3**	**F4**	**M3**	**M2**	**F6**	**M1**	**M4**	**M5**
F1	*	13	2	5	0	3	5	11	5	8	10
F2	1	*	1	3	1	2	1	6	14	4	1
F5	1	0	*	2	0	0	0	4	1	1	1
F3	3	0	0	*	5	0	2	4	7	3	4
F4	0	0	0	2	*	1	1	16	2	5	1
M3	0	0	0	0	0	*	0	0	0	21	2
M2	0	0	0	1	0	0	*	0	0	1	1
F6	0	2	2	0	0	0	0	*	2	10	***0***
M1	0	0	1	0	0	0	0	0	*	3	2
M4	0	0	0	2	0	3	0	1	1	*	2
M5	0	0	1	1	0	0	0	***1***	0	0	*

Figure 26: Group 1's linear dominance hierarchy for low intensity agonism in non-food-oriented contexts. The bolded and underlined numbers represent ordering inconsistencies within the matrix.

	F1	**F4**	**F2**	**F3**	**M1**	**F5**	**F6**	**M2**	**M3**	**M4**	**M5**
F1	*	0	7	2	3	5	4	4	10	13	8
F4	0	*	1	14	2	1	22	0	0	7	7
F2	0	0	*	1	12	9	29	4	5	29	4
F3	0	12	1	*	5	9	12	1	1	16	1
M1	1	2	1	1	*	0	1	0	2	4	5
F5	0	0	1	4	0	*	2	0	0	9	0
F6	0	2	3	11	0	1	*	2	3	9	1
M2	0	0	0	0	0	0	0	*	1	***2***	2
M3	0	0	0	1	0	0	0	0	*	18	2
M4	0	0	1	2	0	0	1	***4***	11	*	2
M5	0	0	2	0	1	0	0	1	0	2	*

Figure 27: Group 1's linear dominance hierarchy for low intensity agonism in close proximity contexts. The bolded and underlined numbers represent ordering inconsistencies within the matrix.

	F1	**F2**	**F3**	**F4**	**F5**	**F6**	**M3**	**M1**	**M2**	**M4**	**M5**
F1	*	11	6	0	2	9	9	4	7	14	15
F2	1	*	3	1	4	21	5	20	3	21	***0***
F3	2	1	*	16	4	13	***0***	6	2	9	5
F4	0	0	12	*	0	25	1	1	1	8	5
F5	1	1	4	0	*	4	0	1	0	6	***0***
F6	0	3	11	1	0	*	2	1	0	15	1
M3	0	0	***1***	0	0	0	*	0	0	20	4
M1	0	1	1	1	0	0	0	*	0	4	2
M2	0	0	1	0	0	0	0	0	*	3	1
M4	0	1	2	0	0	2	9	1	2	*	3
M5	0	***1***	1	0	***1***	0	0	0	1	2	*

Figure 28: Group 1's linear dominance hierarchy for low intensity agonism in distant proximity contexts. The bolded and underlined numbers represent ordering inconsistencies within the matrix.

	F1	**F4**	**F2**	**F3**	**M1**	**F6**	**F5**	**M3**	**M4**	**M2**	**M5**
F1	*	0	9	1	4	6	5	4	7	2	3
F4	0	*	1	4	3	13	1	0	4	0	3
F2	0	0	*	1	6	14	6	2	12	2	5
F3	1	1	0	*	6	3	5	1	10	1	0
M1	1	1	0	0	*	1	1	2	3	0	5
F6	0	1	2	0	1	*	3	1	4	2	***0***
F5	0	0	0	2	0	2	*	0	4	0	1
M3	0	0	0	0	0	0	0	*	19	***0***	0
M4	0	0	0	2	0	0	0	5	*	2	1
M2	0	0	0	0	0	0	0	***1***	0	*	2
M5	0	0	1	0	1	***1***	0	0	0	0	*

Table 29: Group 2’s linear dominance hierarchy for low intensity agonism in non-food oriented contexts.

	F1	**F2**	**F3**	**M1**	**M2**	**F4**	**M3**
F1	*	33	40	7	12	71	5
F2	0	*	9	7	3	13	0
F3	2	2	*	12	2	7	6
M1	1	0	0	*	7	14	5
M2	1	1	0	6	*	3	10
F4	1	0	4	2	3	*	2
M3	1	0	1	1	2	0	*

Table 30: Group 2’s linear dominance hierarchy for low intensity agonism in distant proximity contexts.

	F1	**F2**	**F3**	**M2**	**M1**	**M3**	**F4**
F1	*	39	36	16	6	12	93
F2	1	*	6	0	5	0	7
F3	2	2	*	1	9	16	5
M2	1	0	0	*	8	10	3
M1	0	0	2	6	*	12	15
M3	1	0	1	2	1	*	2
F4	2	0	5	1	2	1	*

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