Ontogeny of the mother-calf relationship in African forest elephants, *Loxodonta africana cyclotis*

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by
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Abstract

African elephants, *Loxodonta africana*, comprise two subspecies which inhabit different environments, which allows us to investigate how differences in ecology influence the expression of social behaviors. Parenting, performed solely by the mother in elephants, is a long-term and psychologically important behavior which may vary between forest elephants, *L. africana cyclotis*, and savanna elephants, *L. africana africana*. Three ecological factors are of particular interest in the rarer and lesser-known forest subspecies: smaller family group size than in savanna elephants; the dispersal of adult females along with adolescent males; and the presence of highly contested mineral pits in forest clearings (bais). Despite the fact that forest elephant calves have few family members present, they do not engage in friendly mother-calf interactions at higher rates than do their savanna counterparts. The fact that both male and female forest elephants disperse may account for a decrease in friendly mother-calf interactions with age, consistent with explanations for an analogous decrease among savanna elephant males (Lee 1986). The rate of maternal aggression increased as forest elephant females aged, likely due to increased competitiveness with the mother for mineral pits, while the rate decreased for more independent males. In examining the dispersal syndrome, it appears that longer separations from the mother do not represent a preparatory behavior, since age of the calf did not significantly affect the duration for either male or female calves. The presence of an older sibling, who may act as an allomother, did, however. This research underscores the importance of mineral pits as an influence on the family dynamics in bais, given that aggression revolved around pits, calves often wandered in order to access pits, and mothers did not frequently initiate reunion with separated calves due to occupation of a pit.
Introduction

Parenting in long-lived, large-brained mammals

Parental care is essential to the lives of mammals, all of whom are at least nutritionally dependent on the mother immediately after birth. The extent and value of parental care beyond this period varies widely among mammals. In certain taxa, parental care has a large impact on the social development of the offspring. Long-lived, large-brained mammals, which include species as distantly related as cetaceans, certain primates, and elephants, tend to have long periods of maternal care (Goodall 1986; Moss 1988) and slow neurological and behavioral ontogeny (Hart et al. 2008). In some cases, offspring gain critical ecological knowledge through imitating their mothers, as in how chimpanzees learn to crack open nuts (Boesch-Ackermann and Boesch 1993). The benefits of social rank are inherited by philopatric offspring in some animals, such as bonobo males (de Waal 1997).

The importance of proper social ontogeny is illustrated in a salient manner by elephants. Exceptionally social animals, elephants are prone to psychiatric disorders and violence if deprived of the doting care received for many years from their families (Foley 2002; Bradshaw et al. 2008). Such behavior is of particular interest because it is highly convergent with that of humans, though apes and elephants are phylogenetically separated by an estimated 103 million years (Murphy et al. 2001). Preserving the elephant’s natural rearing environment is imperative, and necessitates having a thorough understanding of the social behavior of elephant calves. Moreover, geographical variation in parenting due to different habitats elucidates the effect of the environment on the evolution of parental care. The ontogeny of the mother-calf relationship in African forest elephants, Loxodonta africana cyclotis, with respect to mother-calf interactions and separations, is the focus of the current study.
African forest elephants

African forest elephants range widely across Central Africa’s equatorial rainforest and account for 10-33% of the total African elephant population (Turkalo and Fay 2001; Fishlock et al. 2008). They are morphologically and ecologically distinct from the more familiar savanna elephant of east and southern Africa, *Loxodonta africana africana* (Martin 1991; Blake 2002; White et al. 2003), though the forest elephant’s specific classification is still contentious (Roca et al. 2001; Eggert et al. 2002, Debruyn 2005). They spend the majority of their time moving through the rainforest (Blake et al. 2001; Blake 2002), hindering the ability to investigate possible differences in the social behavior between the two subspecies.

The social interactions of forest elephants are most easily observed in seasonally flooded forest clearings called bais (Turkalo and Fay 1996). Elephants visit bais partially in order to drink mineral-rich water, which they access by excavating pits in the soil. The value of mineral water as a nutritional and reproductive resource is illustrated by the heavy competition among elephants for access to pits (Turkalo and Fay 1996) (Figure 1). Bais may also be important as social arenas, since they can attract up to 100 elephants at a time (Turkalo and Fay 1996) and extended families may congregate in them (Fishlock et al. 2008) (Figure 2).

Family groups, which include all adult and subadult females and their dependent offspring whose activities are coordinated to such a degree that they are considered a single behavioral unit (Wittmeyer et al. 2005; Archie et al. 2006), are smaller in forest elephants than in savanna elephants (Turkalo and Fay 2001). Forest elephant family groups at the Dzanga bai, Central African Republic, average 3.2 individuals, with groups up to 11 noted (Turkalo and Fay 2001), though in some other areas groups rarely exceed 5 individuals (Dudley et al. 1992; White et al. 1993). The majority of groups are comprised of a single adult female and one or two calves.
(Turkalo and Fay 1996). By contrast, families of savanna elephants in Amboseli, Kenya, average 9.7 and range from 2 to 35 (Lee 1986; Archie et al. 2006). Forest elephants appear to exhibit a fission-fusien social system similar to that of savanna elephants, in which aggregations of extended, matrilineally related families are occasionally observed (Fishlock et al. 2008; Wittenrezyer et al. 2005; Archie et al. 2006).

Small group size may be advantageous in allowing a family to effectively obtain adequate amounts of their main food source, fruit, and mineral water, both of which are distributed in patches and therefore potentially highly contested (Turkalo and Fay 2001; White et al. 1993; Payne 2003; Fishlock et al. 2008). Relatively low predation by large carnivores and by humans (at least historically) might have played a role as well (Turkalo and Fay 1996; Douglas-Hamilton 1972). Moreover, unlike in the savanna subspecies, both male and female forest elephants disperse from their family group (Fishlock et al. 2008). Juveniles (3-10 years) regularly begin to disassociate from their families when a younger sibling is born (Turkalo and Fay 2001). Males depart at adolescence (10-15 years), as do their savanna counterparts, and remain permanently solitary throughout their lives (Turkalo and Fay 2001; Moss 1988). Females tend to disassociate from their mothers when they are pregnant and birthing for the first time (15-20 years) (Turkalo and Fay 1996).

Comparison of calf-mother interactions between the forest and savanna subspecies

Lee (1986) studied the social interactions of a population of savanna elephant calves of up to ten years old and observed that the social habits of calves reflect the behavioral dimorphism of adults: males leave their family groups to associate with other bulls and seek estrous females while females remain in their family groups to cooperatively travel and raise offspring (Douglas-Hamilton 1972). Using Lee’s (1986) results and functional distinction
between friendly and aggressive interactions, I developed two hypotheses to describe the ontogeny of the forest elephant mother-calf relationship. Both hypotheses are motivated by differences in the family environment and dispersal pattern of forest versus savannah elephants, as well as the unique influence of mineral pits on forest elephant behavior.

**Hypothesis 1:** If relatives are more likely to help a calf and unfamiliar elephants are potentially dangerous, then forest and savanna elephant calves should restrict friendly interactions to elephants in their family group. Play among calves is an exception, since they rarely harm one another (K. Payne, pers. com.) and actively seek unrelated peers as playmates (Lee 1986). Therefore, calves should engage in friendly interactions (excluding play) with group members at higher rates than with unrelated elephants. Since forest elephant family groups are small, I predict that these interactions will overwhelming involve the mother and that the rate of interaction with the mother will exceed that of non-mother group members and extra-group conspecifics. This pattern would differ from that of savanna elephants, whose calves tend to engage in friendly interactions with peers and adolescent females in their family groups at higher rates than with the mother (Lee 1986).

Lee’s results suggest that the gradual independence that precedes dispersal accounts for a decline in friendly mother-calf interactions (Lee 1986; Moss 1988). In savanna elephants, the rate of friendly maternal interactions varies with the age and sex of the calf, remaining relatively constant for females but declining slightly for males. Lee (1986) notes that this pattern may be influenced by intersexual discrepancies in proximity to the mother, since male savanna elephants spatially disassociate from her as they age, from an average distance of 2 meters at 1 year of age to 10 meters at 6 years. If dispersal in forest elephants is also preceded by gradual social and behavioral independence from the mother, then I predict that the rate of friendly maternal interactions...
interactions should decline with age for both sexes since both disperse. The decline should be more dramatic in males, however, since they disperse earlier (Turkalo and Fay 2001).

**Hypothesis 2:** If forest elephants are aggressive towards conspecifics who threaten their monopoly on a resource (Turkalo and Fay 2001), then mothers should exhibit aggression towards calves that infringe on an occupied or desired pit. Pits are the primary resource available to forest elephants in the bai, while contested resources in the savanna environment include food and water (Moss 1988; Payne 2003). Given the absence of such highly contested resources as mineral pits in the savanna, I predict that forest elephant calves will receive significantly more aggression than their savanna counterparts. Moreover, I expect the rate of maternal aggression to be greater in the forest subspecies due to the high competition over mineral pits in bais (Turkalo and Fay 2001).

In savanna elephants, the rate of maternal aggression increases with age for females, who in remaining in close association with their mothers also compete with her for resources, while males receive a relatively constant rate of maternal aggression with age (Lee 1986). Among forest elephants, calves that try to share pits with their mother should receive aggression from her. Only calves older than two years should be subject to such aggression, since younger calves are nutritionally dependent on the mother and do not need to consume mineral water (Fishlock et al. 2008). I predict that older male and female calves should receive aggression when they attempt to share their mother’s pits, but that overall rates will decrease or remain constant because the calves begin to disassociate from mothers.

*Wandering: unique to forest elephant calves*

Lee (1986) noted that savanna elephant calves of both sexes remain at a mean distance of ten or fewer meters from the mother for the first eight years of life. Forest elephant juveniles (3-
10 years old), however, are often observed separated from their mothers by considerable distances, even entering the bai alone or remaining in the forest when the mother enters the bai (Fishlock et al. 2008; Turkal and Fay 2001). By examining the duration of separations, I tested three hypotheses regarding the function of wandering, the presence of allomothering when infants (1-2 years) wander, and the coordination of reunion at the end of a separation.

**Hypothesis 1:** Reflecting the above assertion that the pattern of interactions by infants and juveniles is shaped by the specifics of their social environment, I hypothesize that wandering is a preparatory behavior related to dispersal. Given that both males and females disperse, older calves of both sexes should spend more time separated from the mother than their respective younger counterparts as part of gradually becoming more spatially and socially independent of the mother. Since males tend to disperse several years earlier than females, however, I predict older males to wander for longer durations on average than their female peers.

**Hypothesis 2:** If allomothering is adaptive, then older sisters should act as allomothers when they and an infant sibling are separated from the mother. Allomothering is potentially adaptive for both older and younger siblings: allomothers gain experience caring for young calves before they have any of their own (a benefit not shared by males, who do not engage in parental care), and incur inclusive fitness benefits from promoting the survival of younger siblings; the younger calves separated from the mother may be safer when accompanied by an older sibling. I predict that infants with older sisters will be found together when both are separated from the mother. I also expect infants with older sisters to wander more frequently, and for longer durations, than peers without older sisters.

**Hypothesis 3:** Since infants are nutritionally dependent on the mother and more vulnerable to harm from conspecifics and other animals (e.g. leopards; see Blake 2004), it is in
the best interest of the mother to monitor the location of infants, while monitoring the location of juveniles is less important. Therefore, mothers should initiate reunion, either vocally or by pursuing the calf, when separated from infants.

Conclusion

Investigating the forest elephants’ patterns of mother-calf interactions and separations will elucidate the role of the mother in calf socialization. Adult forest elephants are more independent than their savanna counterparts (Moss 1988), and this difference may be reflected in the social ontogeny of each subspecies’ calves. The hypotheses that I am testing will help to determine how high population density, small group size and scattered, highly contested mineral pits in the bai influence this relationship.

Materials and methods

Study subjects

This study used original video and audio data collected on a population of African forest elephants that frequent a large bai located in the Dzanga-Ndoki National Park of the Central African Republic. Dzanga bai is the largest known bai in Central Africa, measuring 500 x 200 meters and among the most densely populated with forest elephants (Turkalo and Fay 2001). Researcher Andrea Turkalo has been living near the Dzanga bai since 1990 and monitoring the demographics, visitation rate, behavior and social structure of the elephant population (Turkalo and Fay 1996). From a population currently estimated at about 3000 elephants, Turkalo has identified over 3000 individuals and 580 families (Turkalo pers. com.). These data were used to assign sex and age class to each individual used in the analyses. Due to the small size of forest elephant family groups, it is difficult to infer possible matrilineal relationships between adult elephants, and for this study only known family association was assigned.
Video and audio data from the Elephant Listening Project (ELP)

In March 2002, a team of ELP researchers conducted daily 60-minute focal animal samples of the Dzanga elephants. Each focal belonged to a randomly chosen family group. Twenty-three different families were sampled for this study, with one followed on three occasions and two followed twice. The focal elephant was usually the mother, and calves were usually followed simultaneously either by widening the camera view or using an independent camera. While taping the elephants, the researchers also recorded any interactions involving the calves in a notebook.

Using an acoustic array, elephant vocalizations originating within the bai could be assigned to specific individuals (Thompson 2009). Audio data relevant to the sample of focal individual follows had been thoroughly analyzed with regard to the identity and situation of the calling elephant before the beginning of the current study. These data were used in the investigation of calf wandering.

Comparison of maternal interactions: data collection and statistical analyses

In order to draw relevant comparisons with the savanna subspecies, data collection resembled as closely as possible the protocol employed by Lee (1980). For each hour of data, I recorded every interaction involving the focal calf or calves. Relevant interactions fell into two categories, friendly and agonistic, which were the core of Lee’s analyses (1986). I recorded each specific activity, whether the focal calf initiated or received the action, and the identity of each interaction partner. Friendly interactions included greeting (usually accompanied by trunk touch); comforting (rubbing against another’s body and caressing with the trunk); and investigating foods or tasting mineral water by placing the trunk in another elephant’s mouth. Aggressive interactions were more varied, and included stabbing, shoving with the trunk or the body,
kicking, slapping with the trunk, chasing (when initiated by an adult), and displacing from a pit. I recorded whether each aggressive interaction involved a pit. After data collection, I calculated the sum of each calf's friendly and agonistic interactions, respectively; in the case of calves who were followed more than once, I took the average of these values across samples. I set a threshold of five total interactions to be included in the analysis, thereby losing three data points for a final sample size of 20 calves in 17 families.

I used Wilcoxon Paired Signed-Ranks tests to evaluate the frequency of interaction with different classes of partners (e.g. family members and non-family members). Using general linear model (GLM), I evaluated the effect of age and sex as independent variables on the hourly rate of interactions, statistically controlling for the total number of interactions with the mother. I used paired t-tests to compare the mean rates of interactions in forest elephants aged 1-5 years old with comparable results from Lee's study of savanna elephants, pairing the mean rate for all forest elephant calves in a given sex and age class to its counterpart in Lee's study. I did not have any four-year-old forest elephant females in the sample and therefore did not include that age and sex class in the analysis. Data on rates of interaction were natural log transformed for normality (categories that possessed values of 0 were increased by 0.1). All analyses were performed in Minitab 15 (Ryan et al. 2005).

Wandering: data collection and statistical analyses

I classified two elephants as separated when the distance between them exceeded 15 meters for at least 15 seconds (15 m = five body lengths of an average adult female elephant; Thompson 2009). A relatively large threshold for separation ensured that the elephants were not in close visual or olfactory contact. Each wandering calf in the same family was considered an independent separation event, although I noted when they traveled together (when they left or
joined the mother together or were joined for at least thirty seconds when separated from the mother). I considered a separation to be over when the mother and calf were three body lengths apart for at least 15 seconds. The joining threshold was lower than the separation threshold to ensure that the animals were now traveling and acting together.

In order to investigate who initiated reunion, I analyzed both the video data and the audio data. I recorded obvious visual signals on the video that signaled reunion, such as turning toward the other elephant or extending the trunk toward the other elephant. The audio data had already been annotated with the agent and behavioral context of each call corresponding to the hour of a video follow. I recorded any calls attributed to the focal family during a separation, and of particular importance were calls that elicited a behavioral response from a family member: for example, if a mother called and her calf began to approach her. In the analysis, I used the first signal that led the elephants back together to identify the individual who initiated reunion.

I used each wandering event (n = 113) as a data point in the statistical analyses. I used GLM to evaluate the duration of wandering events with the independent variables age and sex. In order to investigate the effect of an older sibling on the duration of infant-mother separations (n = 30), I used ANOVA with the presence of an older sibling as the predictor, and among infants with older siblings I used GLM to investigate how the sex of the older sibling and whether the siblings wandered together affected the duration of wandering events (n = 26). I used chi-square analyses to evaluate whether the mother or calf initiated reunion, with separate analyses for infants (1-2 years; n = 30) and juveniles (3-8 years; n = 86).

Results

Comparison of maternal interactions
Forest elephant calves interacted with their mothers at higher rates than did savanna elephant calves when friendly and agonistic interactions were combined (paired t-test: $t_6 = 2.83, p = 0.022$). When only friendly interactions were examined, forest and savanna elephants show no significant difference in the number of mother-calf contacts per 60-minute sample (paired t: $t_8 = 1.78, p = 0.112$). For forest elephants, there were no significant differences in interaction rate with different partner classes except between intra-group and extra-group individuals (Table 1). The interaction of age and sex had a significant effect on the rate of friendly interactions with the mother (Table 2). Males increase the hourly rate of friendly maternal contacts with age, while females significantly decrease the rate (Figure 3).

Aggressive interactions between mother and calf were always initiated by the mother. Of all aggressive interactions, 84.4% involved a pit. Forest elephant calves received significantly higher rates of aggression from the mother than savanna elephant calves (paired t: $t_6 = 2.58, p = 0.033$). The calf’s age, sex, and total interactiveness with the mother significantly affected the rate of aggression received from the mother (Table 2). Females receive a higher rate of maternal aggression with age, while males receive a lower rate (Figure 4).

**Wandering**

The duration of wandering events was not significantly affected by calf age or sex (GLM: age: $F_{1,27} = 0.05, p = 0.832$; sex: $F_{1,27} = 4.14, p = 0.052$), although the maximum duration for both sexes increased with age (Figure 5).

Infants with older siblings wandered for longer durations than those without siblings (ANOVA: $F_{2,27} = 5.68, p = 0.009$). The sex of the older sibling, as well as whether the calves wandered together, significantly affected the duration of the infant’s wandering (Table 3). As shown in Figure 6, infants with older brothers tended to wander together for longer durations.
than calves with older sisters, and both wandered for longer durations than infants without older siblings.

Both infants (1-2 years) and juveniles (3-8 years) initiated reunion when separated from the mother significantly more than the mother initiated reunion (chi-square: infants: $\chi^2_1 = 5.33, p = 0.019$; juveniles: $\chi^2_1 = 7.86; p = 0.0067$).

**Discussion**

African forest elephants have a strikingly different ecology and basic group structure compared to the better known African savanna elephant. In forest elephants, family group size averages only a third that of the savannah subspecies, typically including only the mother and one or two dependent calves (Turkalo and Fay 1996). I hypothesized that forest and savanna elephant calves would restrict friendly interactions to familiar conspecifics because they are more likely to get a friendly and safe response than they would from an unfamiliar elephant. Consequently, since the mother is often the only familiar elephant nearby, I predicted that forest elephant calves would engage in friendly interactions with her at higher rates than do savanna elephant calves, which are surrounded by extended family. However, the frequency and character of affiliative mother-calf interaction was surprisingly similar in the two subspecies.

Savanna elephant calves have many family members with whom to interact and, in aggregate, they interact more frequently with non-mothers than with the mother (Lee 1986). Although forest elephant calves are surrounded by fewer familiar individuals, they do not appear to compensate by interacting more with the mother or seeking out unrelated elephants with whom to interact. Indeed, the rate of interaction with the mother is similar to that with all other elephants and with group non-mothers. Only the rate of interactions with the family group exceeds that with extra-group elephants in the forest subspecies. This result supports the
hypothesis that forest elephant calves primarily engage in friendly interactions with familiar conspecifics. Investigating this hypothesis is more difficult in savanna elephants, since it is less common for savanna elephant calves to encounter unfamiliar conspecifics for extended periods.

One factor contributing to the smaller group size observed in forest elephants is that both males and females leave their family groups during adolescence or early adulthood (Turkalo and Fay 2001). In this study, dispersal was preceded by decreased proximity to the mother as calves aged. Savanna elephant males, who disperse at adolescence (10-15 years), also maintain further distances from the mother with age (Lee 1986). I hypothesized that decreased proximity to the mother will lead to fewer friendly mother-calf interactions in forest elephants. Since both males and females disperse, I expected the hourly rate of friendly interactions to decrease with age for both sexes. Females did exhibit a decrease in the rate of friendly mother-calf interactions with age, while males exhibited an unexpected increase (Figure 5). This set of patterns is markedly different from that of savanna elephants, whose females maintained a relatively constant rate of interaction as they aged and males experienced a decrease with age.

For forest elephant males in this study, the results are strongly influenced by a single seven-year-old male who continually tasted the water of his highly tolerant mother and sister (Figure 5). A larger sample of older male juveniles would better illustrate whether this is common (see Payne 2003 for a discussion of individual variation in forest elephants), though the two other seven- and eight-year-old males in the sample were separated from their mothers for most of their respective focal follows. This juvenile’s behavior exemplifies the fixation of forest elephants on mineral water in the bai, which may not correspond with the priorities of elephants in the savanna, where resources are not as limited and highly contested. The resource-based motivation of water-tasting is different from the bond-strengthening motivation of body rubbing.
and trunk caressing. If the analysis for forest elephant males is restricted to only bond-strengthening interactions, then males engage in friendly interactions with the mother significantly less with age (Figure 5), as predicted.

The high level of competition over mineral pits also influences aggressive mother-calf interactions in forest elephants. I hypothesized that forest elephants in bai's are aggressive towards conspecifics that reduce their access to pits, and found that 84.4% of aggressive interactions in my sample involved a pit. Juveniles (3-8 years) may compete with their mothers for pits and thereby receive aggression from her, while infants (1-2 years) obtain the nutrients from their mother's milk and do not need to consume mineral water. Because both males and females disperse, I expected the rate of maternal aggression to decrease or remain constant with age for males for both sexes. The data supported this prediction for males, but females experienced an unexpected increase (Figure 6). Females, becoming independent later than males, evidently become more competitive with mothers over pits as they age. The single six-year-old female in the sample received a relatively low rate of maternal aggression, suggesting that when females reach a certain age they may attempt to share their mother's pits less frequently.

The trend is significant but affected by high levels of individual variation; for example, the mother of a single one-year-old female was dramatically more aggressive towards her than were the mothers of the other three one-year-old females in the sample, thereby weakening the relationship between aggression and calf age. Mothers were also unexpectedly aggressive towards infants. Some would kick and shove infants who were not attempting to enter a pit and may have been more aggressive overall. Moreover, the fact that females experienced an increase in maternal aggression with age renders the basis for a decrease in friendly mother-calf interactions (Figure 3) inconclusive: it may be due to the increase in aggressive interactions, or
due to an increase in social independence preceding dispersal, the latter of which appears to account for the decrease in friendly mother-calf interactions among forest and savanna elephant males (Lee 1986).

The increase in maternal aggression with age for female calves is similar between forest and savanna elephants; however, unlike forest elephants, savanna elephant males receive slightly more aggression from the mother with age, while their forest counterparts receive less. The fact that older male juvenile forest elephant calves often separate from their mothers in the bai and thereby avoid her aggression may account for this difference. Unlike in friendly interactions, the rate of maternal aggression towards calves of both sexes between one and five years old was significantly higher in forest elephants than in savanna elephants, likely due to the presence of the highly contested pits in the habitat of the forest subspecies. Since the rates of friendly mother-calf interactions were similar between the two subspecies, it appears that the mother-daughter relationship in particular is more agonistic in forest elephants than in savanna elephants.

The mineral pits in the bai, which accounted for most of the aggression observed in this study, appear to be the major ecological source of the behavioral difference between the two subspecies of African elephant. The high density of unrelated elephants in the bai and level of competition over pits produce a hyper-social environment that differs from the relaxed environment in which Lee (1986) studied savanna elephant calves. A more congruous comparison might use data on forest elephants collected in the forest, where elephants spend most of their time and may exhibit less aggression, although conducting detailed 60-minute focal animal samples in the rainforest would be difficult and dangerous. An interesting comparison would be to study the behavior of savanna elephant calves in herds, which are temporary seasonal aggregations comprised of up to thousands of elephants (Moss 1988), since the density
of elephants, and perhaps competition for resources, would be more similar to those in the bai. However, the result of this study that forest elephants interact mainly with relatives supports the hypothesis that kinship is an important influence on affiliations in elephants (Archie et al. 2006), suggesting that strong family ties are shared by both subspecies.

The dispersal syndrome in forest elephants led me to examine the duration of events in which calves were separated from their mothers. I hypothesized that calves wander and maintain separations from the mother in preparation for dispersal, and therefore expected both male and female calves to wander for longer durations as they aged. The data did not support this hypothesis. The age and sex of the calves did not significantly affect the duration of wandering events. Figure 5 illustrates that the maximum duration is highest among older calves of both sexes, but the majority of separations across all ages last less than 15 minutes. In many separation events, calves wandered to pits and returned to the mother after a relatively short time. Fifteen minutes separated from the mother may be significantly longer than the average duration of separations in savanna elephants (Moss 1988), however, and may reflect the value of mineral pits.

Separations in forest elephant families with more than one calf were of particular interest, given the propensity for juvenile females (but much less so males) to alloparent their younger siblings in savanna elephants (Lee 1987). One form of alloparenting is ‘babysitting’ an infant (1-2 years) when it is separated from the mother (Bates et al. 2008). I hypothesized that female (but not male) forest elephant juveniles (3-8 years) would babysit their infant siblings when they were both separated from the mother, leading the infant to remain separated for longer durations. However, infant forest elephants with older brothers wandered for significantly longer periods with the brother than they did when either alone or than those with an older sister. Moreover,
infants that had an older sister wandered for roughly equal durations with and without the sister (Figure 8).

The small number of young calves with older brothers likely influenced the result. In this sample, only male infants had older brothers and only female infants had older sisters. The relationship between infants and older siblings of the opposite sex may reveal different trends. However, the dramatically prolonged separations of infants who wander with an older brother suggest that brothers allomother their younger siblings. Though I expected mothers to monitor their vulnerable and dependent infants, they initiated reunion less frequently when separated than did the infants. Adult females in the bai may be too absorbed in obtaining pits and consuming mineral water to be attentive to their offspring, leading infants to wander for short durations when they do not have an older sibling to babysit them.

Future research characterizing female associations would be fruitful, since the largely agonistic relationship of older female juveniles and their mothers belies the temporary affiliations observed between mothers and adult daughters (Turkalo and Fay 2001). The ontogeny of the mother-daughter relationship as the daughter reaches adolescence, sub-adulthood, and independence may illuminate what interactions are the most important influences on this relationship. The value of proper social ontogeny in elephants is evident in the violence and asociality of elephants who were raised isolated in captivity or whose families had been poached or hunted (Foley 2002; Bradshaw et al. 2005). Elephant mothers offer social support and discipline that may have significant consequences on the behavior of their offspring, which in turn potentially affects everything around them; therefore, understanding and preserving this relationship is of utmost importance.
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Literature Cited


Table 1. Comparison of calf interactiveness across classes of interaction partners using paired Wilcoxon tests

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<th>Comparison</th>
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* Denotes statistical significance at alpha = 0.05

Table 2. The effect of age, sex, and on the hourly rate of friendly and agonistic interactions with the mother (natural log transformed) using GLM. The total number of interactions with the mother (natural log transformed) is used as a leveler

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<td>1,15</td>
<td>2.56</td>
<td>0.131</td>
</tr>
<tr>
<td>Aggressive</td>
<td>Age</td>
<td>-0.0375</td>
<td>1,15</td>
<td>0.06</td>
<td>0.816</td>
</tr>
<tr>
<td>interactions</td>
<td>Sex</td>
<td>n/a</td>
<td>1,15</td>
<td>7.57</td>
<td>0.015*</td>
</tr>
<tr>
<td></td>
<td>Age x sex</td>
<td>0.5545</td>
<td>1,15</td>
<td>12.23</td>
<td>0.003*</td>
</tr>
<tr>
<td></td>
<td>Total interactions with mother</td>
<td>1,1357</td>
<td>1,15</td>
<td>12.66</td>
<td>0.003*</td>
</tr>
</tbody>
</table>

* Denotes statistical significance at alpha = 0.05

Friendly interactions: $R^2 = 13.03\%$
Aggressive interactions: $R^2 = 33.42\%$

Table 3. Effect of older sibling on duration of infant (1-2 years) wandering events using GLM

<table>
<thead>
<tr>
<th>Source</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex of sibling</td>
<td>7.81</td>
<td>0.011*</td>
</tr>
<tr>
<td>Siblings wander together</td>
<td>6.15</td>
<td>0.021*</td>
</tr>
<tr>
<td>Sex of sibling x siblings wander together</td>
<td>22.36</td>
<td>0.000*</td>
</tr>
</tbody>
</table>

* Denotes statistical significance at alpha = 0.05

$R^2 = 45.28\%$
Figure 1. Two adult male forest elephants in a contest for a mineral pit in the Dzanga bai, Central African Republic (photo © Andrea Turkalo).
Figure 2. Forest elephants drinking mineral water in Dzanga bai (Photo © Andea Turkalo).
Figure 3. The rate of friendly interactions with the mother in relation to age and sex of the calf.

A) When all friendly interactions are included, the interaction of age and sex is significant ($p = 0.043$; GLM: $R^2 = 13.03\%$); males increase the rate of friendly interactions with age, while females decrease the rate. B) When water tasting is excluded, the rate decreases with age for both males and females.
Figure 4. The rate of aggressive interactions from the mother in relation to the age and sex of the calf (GLM: $R^2 = 33.42\%$). The interaction of age and sex is significant ($p = 0.022$); the number increases for females with age and decreases for males.
Figure 5. Duration of wandering events in relation to the age and sex of the calf (GLM: $R^2 = 6.92\%$). Males exhibit a non-significant tendency to wander longer with age, while females do not.
Figure 6. Mean ± SE duration of wandering events of infants calves (1-2 years) based on whether they have an older sibling and whether the siblings wander together. Numbers above bars indicate the number of associated wandering events. Infants with siblings wandered for longer durations than those without, and those with older brothers wandered for significantly longer durations than when alone and than those with older sisters or no siblings.