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Rhea Marie Esposito

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THE EFFECT OF MATRIARCHS ON GROUP INTERACTIONS, KINSHIP FITNESS,
AND DIFFERENCES IN CHEMOSENSORY BEHAVIOR OF AFRICAN
ELEPHANTS (*LOXODONTA AFRICANA*)

by

RHEA M.M. ESPOSITO

(Under the direction of Bruce A. Schulte)

ABSTRACT

Female African elephants exhibit multiple levels of social organization with the family as the functional social unit. Families consist of related females and the oldest female is the matriarch. Related family groups that frequently fuse are termed kinship groups, led by the grand matriarch. I examined matriarch communication behavior across social context and their role in interactions between families at waterholes in Addo Elephant National Park, South Africa. I analyzed three hypotheses for matriarchal effects on group fitness: a) older matriarchs provide greater access to resources, b) older matriarchs lead more social groups, or c) there is no behavior-fitness relationship and differences in behavior represent behavioral signatures. Matriarch presence in an approaching family significantly increased the likelihood that agonistic interactions or pass away behavior occurred, rather than the most submissive turn back behavior. When more than one kinship group was present, 18 of 24 matriarchs performed chemosensory behaviors compared to 8 of 24 when only their kinship group was present. As the measure of fitness, the kinship calf-to-female ratio increased with grand matriarch age, and was weakly affected by waterhole use but not sociality. Kinship level behavioral signatures also were evident. Matriarchs influenced group interactions and fitness, and their chemosensory behavior increased in more complex social contexts.

INDEX WORDS: Matriarchs, Communication, *Loxodonta africana*, Group interactions, Fitness, Behavioral signatures

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ELEPHANTS (*LOXODONTA AFRICANA*)

by

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B.A., Oberlin College, 2003

A Thesis Submitted to the Graduate Faculty of Georgia Southern University in Partial
Fulfillment of the Requirements for the Degree

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CHAPTER I
MATRIARCHAL FEMALE ROLE IN THE FISSION-FUSION SOCIAL SYSTEM
EXHIBITED BY AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*)

Abstract

Female African elephants (*Loxodonta africana*) exhibit multiple levels of social organization, where the functional unit of fission and fusion is the matriarchal family. Families consist of related females and their offspring, and are led by the oldest female known as the matriarch. Family groups that frequently fuse into larger aggregations and are more closely related are known as kinship groups. This study examined matriarch communication behavior across social context and her facilitative role in common group interactions between elephant family groups. Twenty-five family groups were studied in Addo Elephant National Park from January to July 2007 using focal and behavior sampling with continuous recording. Matriarch presence in approaching family groups significantly increased the likelihood that agonistic interactions or pass away behavior occurred, rather than the most submissive turn back behavior. Eighteen of 24 matriarchs performed chemosensory behaviors when more than one kinship group was present at the waterhole as opposed to eight of 24 when only one kinship group was present. Matriarchs also performed a higher rate of investigatory behaviors than non-matriarchal females. Matriarch presence influenced group interactions and their chemosensory behavior increased in more complex social context. The results from this study advance our understanding of the critical, day-to-day role that matriarchs play in the fission-fusion social structure of African elephants.

Introduction

In highly social animals that spend their adult lives in groups of conspecifics, selective pressure exists to differentiate between group and non-group members, especially in situations where resources are limited or territories are maintained (Goodall 1986, Spong and Creel 2004, Archie et al. 2006a). Interactions between groups vary from agonistic to affiliative based on the specific combination of ecological factors. Resource distribution influences group interactions such that species that use widely distributed resources are likely to display relatively few agonistic interactions in contrast to species that rely on patchily distributed resources (Wrangham 1980, Isbell and Young 2002). In long-lived species where winner and loser effects are high (initial winners/losers tend to continue the same role), agonistic interactions are costly and therefore are rare (Crowley 2001, Wittemyer and Getz 2007). In addition, affiliative group interactions may be beneficial, or even necessary in animal societies (Lazaro-Perea 2001). Hence, group formation is a trade-off between the costs of competing for resources and the benefits of cooperation (Crowley 2001).

Many mammals including elephants, chimpanzees, cetaceans, and humans have variable social relationships involving high degrees of cooperative behavior (Douglas-Hamilton 1972, Moss and Poole 1983, Goodall 1986, Christal and Whitehead 2001). These species live in flexible social groups where the size of the group and relatedness of group members vary over time. This structure is referred to as fission-fusion because group structure is dynamic and group interactions are common. In some species, social structure within groups is more rigid than would be predicted by resource availability (Sterck et al. 1997, Archie et al. 2006a, Wittemyer and Getz 2007). A single dominant

individual, termed the leader, has significant influence over group behavior, (Douglas-Hamilton 1972, Christal and Whitehead 2001, Dumont et al. 2005, Fischhoff et al. 2007).

Leader characteristics such as age and size have been shown to influence dominance structures in socially complex species (Robbins et al. 2005, Wittemyer and Getz 2007). These individuals can influence many aspects of sociality including group movement, territory defense and recognition of other groups (McComb et al. 2001, Dumont et al. 2005). For example, the order of individual animals in group movements has been studied in herbivores (Dumont et al. 2005, Fischhoff et al. 2007), focusing on leader identity. Dumont et al. (2005) found one animal dominated the first position in group movements and influenced the actions of the other group members in a group of grazing heifers, acting as the leader. In mammals that exhibit a social structure where dominance hierarchies exist, the position of the most dominant individual in the group can be assessed in differing social situations (Fischhoff et al. 2007). Order of individuals could vary based on social context, and order has the potential to influence group interactions. In species where groups are sexually segregated and consist of related individuals, the female leader is referred to as the matriarch (Douglas-Hamilton, 1972, Krebs and Davies 1997).

African elephant groups exhibit fission-fusion interactions (Archie et al. 2006b) between dynamic social units with varied relatedness (Moss and Poole 1983, Wittemyer et al. 2005). Elephants are polygynous and socially and phenotypically sexually dimorphic. Adult males are generally solitary or live in loosely-associated groups of other males, primarily interacting with females when they are sexually active. Females, in contrast, spend virtually all of their time with other females and their immature offspring

in an intricate social hierarchy. Females remain with the family group for all of their lives, whereas males leave their natal group between 12-15 years of age (Poole 1994). Female elephant social structure has been demarcated into six tiers: mother-calf units (tier 1), families (tier 2), bond/kinship groups (tier 3), clans (tier 4), subpopulations (tier 5), and populations (tier 6) (Wittemyer et al. 2005). The family consists of one or more adult females and their offspring in which the oldest, largest member is the matriarch (Douglas-Hamilton 1972). Bond/kinship groups are made up of families that consistently fuse together into larger aggregations at frequent intervals (Douglas-Hamilton 1972, Dublin 1983, Moss and Poole 1983, McComb et al. 2003). Clans are kinship groups that share the same home range (Moss and Poole 1983).

Kin selection predicts that resource sharing is more likely between relatives or groups of relatives than between non-relatives (Isbell and Young 2002, Spong and Creel 2004). Therefore, groups of more closely related individuals in fission-fusion systems are more likely to fuse and less likely to have agonistic interactions (Griffin and West 2002), though relatedness is not explicit in the fission-fusion model. Families of African elephants almost always consist of closely related individuals and there is also a high degree of relatedness between individuals within kinship groups (Archie et al. 2006b). Relatedness is expected to influence group interactions between families based on their kinship group membership.

The matriarch has an important function in the group as a leader with crucial knowledge of natural resources, as well as facilitating coordination of group defense (Douglas-Hamilton 1972, Dublin 1983, Poole and Moss 1989). The dominance rank of a matriarch affects the ranks of non-matriarchal females in her kinship group (Wittemyer

and Getz 2007) and the patterns of group resource use (Wittemyer et al. 2007). Matriarchs may be aware of the location of other group and non-group members with whom they are traveling (Bates et al. 2008). Additionally, families led by older matriarchs are better able to identify the vocalizations of conspecifics and vary responses based on familiarity (McComb et al. 2001). Group members use distinct rumble vocalizations in the presence of a dominant individual such as a matriarch (Soltis et al. 2005b). Groups with older matriarchs also perform more exploratory behaviors in response to unfamiliar than familiar vocalizations, whereas this is not the case for younger matriarchal groups (McComb et al. 2001). In this sense, matriarchs somehow influence the overall social knowledge of the group, most likely through experience with more individuals. From a preliminary study in Tanzania, the order of the different age and sex classes of elephants in family units was examined during the approach to and departure from a waterhole (M. Groover, unpublished data). Adult females were positioned first or last most frequently. Matriarch identity was not known in this elephant population, but it follows from research on other herbivores that the adult female leading a group may have been the matriarch.

Differentiating between potential interacting groups relies on intra-specific communication between individuals in the groups (Bain 1986). Both male and female African elephants commonly communicate via auditory vocalizations and chemosensory signals (Langbauer 2000, Bagley et al. 2006, Goodwin et al. 2005, 2006). Auditory communication is usually long-distance (McComb et al. 2003, O'Connell-Rodwell et al. 2006), though there is some evidence of short-range vocal communication occurring within elephant groups in captive elephants (Soltis et al. 2005a). Chemosensory

communication, which involves the transmission and reception of chemical signals such as pheromones, occurs over relatively short distances but longer time spans (Karlson and Lüscher 1959, Eisenberg and Kleiman 1972). Groups of African elephants are able to identify potential threats based on olfactory cues (Bates et al. 2007), and regularly use chemosensory behavior to investigate their environment (Rasmussen and Schulte 1998). The rate of common chemosensory behaviors such as sniff, check, place and flehmen (Table 1.1) differs between individual elephants based on numerous life history and contextual characteristics (Bagley et al. 2006, Merte 2006, Meyer et al. 2008), and characteristics such as rank and social context may affect the rate of these behaviors as well. In group interactions, leaders such as matriarchs may be responsible for information exchange within and between groups (McComb et al. 2001, Dumont et al. 2005), and thus may display higher rates of communication behavior when compared with other group members.

Group interactions are common in the fission-fusion social structure of African elephants, yet what mediates which groups are likely to fuse and when groups are likely to separate has not been fully explored. Because agonistic interactions in large, long-lived social mammals can incur heavy costs (Crowley 2001, Archie et al. 2006a, Wittemyer and Getz 2007) and resource value is variable, agonistic interactions should be infrequent. Family groups from the same kinship group are more likely to exhibit resource-sharing, and less likely to behave agonistically towards each other (Archie et al. 2006b, Whitehouse et al. 2001). Group interaction theory predicts that unrelated groups of equal ability are more likely to escalate agonistic interactions, whereas the subordinate group in interactions between unrelated groups of unequal ability will display submissive

behavior (Wrangham 1980). Several alternative hypotheses are presented for what determines competitive quality in elephant groups. Group size may play an important role in determining the ability to defend the resource from an approaching group or to supplant an attendant group. I predicted that larger groups would be more likely to behave agonistically, and smaller groups would be more likely to behave in a submissive manner.

Dominance is also a key factor in many interactions between individuals and groups. Since age of the matriarch has been shown to influence dominance (Wittemyer and Getz 2007), matriarch age is a method of potentially gauging dominance in fission-fusion systems. Position within a group may also be used as a measure of dominance (Dumont et al. 2005). Matriarchs are essential in many facets of elephant society, but their role in common interactions between groups over shared resources has not been examined. It follows from previous research that they may play a crucial role in these interactions (McComb et al. 2001). I tested two hypotheses. In many species, leaders frequently are positioned at the front of the group, so I hypothesized that matriarch position would influence whether approaching groups are likely to interact agonistically or submissively with an attendant group. I predicted that matriarchs would be in the first position for agonistic interactions. However, matriarch presence alone may increase the competitive ability of the group, regardless of her position within the family, since leaders are better able to assess and respond to social situations. Therefore, I predicted that group interactions in which the matriarch was present in the approaching family would be less likely to be submissive and more likely to be agonistic.

Matriarchs may be behaviorally cueing group members about movement and defense (McComb et al. 2001), and they may serve as central points of communication between groups. Group leaders such as matriarchs may be essential in assessing relevant group characteristics including relatedness, group size and dominance rank of groups that fuse and separate frequently. In captive elephants, the behavior of the most dominant individual in the group differs significantly from that of other females (Freeman et al. 2004), and I expected this to be true of wild African elephants as well. Given their leadership role, I hypothesized matriarchs would vary their behavior based on social context indicating an increased awareness of their surroundings. Specifically, I predicted that matriarchs would exhibit a higher rate of exploratory behaviors compared to adult non-matriarchal females. Also, in social situations where an agonistic interaction is more likely to occur (i.e. where families that are not closely related are sharing a resource), I predicted that matriarchs would perform more exploratory behaviors.

Materials and Methods

Study Site and Population

This study was conducted in Addo Elephant National Park (AENP) from January to July of 2007. AENP is 72 km northeast of Port Elizabeth, South Africa. A population of approximately 375 African elephants (*Loxodonta africana*) in six matrilineal groups lives in the fenced main reserve of roughly 103 square km (Whitehouse and Schoeman 2003). A smaller population of some 70 elephants in the Nyathi area was not observed in this study. The vegetation is largely dense thorny thicket with a wide range of shrubs, herbs, grasses, and other plants (Paley and Kerley 1998). There are roads throughout the park,

which provide access to the waterholes and other prime viewing locations for tourists and researchers.

The AENP population was established in 1931, following a near-extinction of the regional population from hunting. Eleven elephants were placed on a reserve in an effort to preserve the elephant population at the southern end of its range (Whitehouse and Hall-Martin 2000). The park was later fenced in 1954, and the current population is derived almost entirely from the original eleven individuals. From in-depth studies and an analysis of data since the park's creation in 1931, reliable matrilineages have been determined, and these matrilineages are less closely related than would be expected from such an extreme bottleneck event (Whitehouse et al. 2001). These six matrilineages form six kinship groups and two clans. Kinship groups served as the basis for categorizing group membership and the six grand matriarchs were the oldest females in each of the kinship groups (Table 1.1). Twenty-five family associations with identifiable matriarchs are known within these kinship groups (Loizi 2004, Bagley 2004, Gough & Kerley 2006, Merte 2006, Meyer 2006), which were confirmed during the current study.

Behavioral Methods

Observations focused on family units interacting at the waterholes. Elephants are habituated to vehicles in close proximity, so all observations were made from a vehicle located near elephants partaking in natural activities. Using behavior sampling with continuous recording (Martin and Bateson 1993), potential interaction bouts between families were observed; measurements were started when the approaching group was approximately 30 m from the waterhole and continued for 10 min or until the group interaction ended. Group type, group number, group identification (ID) and arrival order

(age/sex/ID of first and last elephant) were recorded for every family group. A group was defined as any assemblage of two or more elephants in which every individual was within 3 body lengths of its nearest neighbor. Groups containing more adult males than females were not included in the analysis. Group ID was determined by identifying the matriarch and at least two of the adult (>20 y) or pubescent (10-20 y) females in the group. The ID of the oldest female in the group served as the group ID if the matriarch was not present. During my study, 387 family group entries were observed for a total of 34 hours of observation. Of these 387 group entries, 240 resulted in a group interaction between two family groups. Additionally, two 10-min focal observations were recorded for 24 of 25 matriarchs in the population, and one 10-min focal observation was recorded for 19 of the 37 adult female non-matriarchs in the population. I recorded 12.6 total hours of focal animal observations with continuous recording (Martin and Bateson 1993). Matriarch focal observations were conducted in different social contexts; one when she was at a waterhole with only members of her kinship group and males, and one when other kinship groups were present. All behavior measures were made based on the definitions given in Tables 1.2 and 1.3 and in Appendices A.1 and A.2.

Data Analysis

Data were analyzed using the JMP4 statistical program (SAS Institute, Cary, NC). Group interactions were defined into three categories (agonistic, avoidance, non-threatening) and seven interaction types (Table 1.3, Fig. 1.1). For the comparisons of interactions within and between kinship groups, agonistic and avoidance categories were combined, since which group initiated the agonistic interaction was not considered. These broader categories also were used to examine seasonal and time of day trends. For other

analyses, all seven interaction types were represented unless noted. All descriptive statistics are reported as mean \pm SE. Analyses compared distributions using contingency tables and Chi-square tests, as well as comparing variation using repeated measures ANOVA analysis. Non-normal data or data with unequal variances were analyzed using a Wilcoxon matched-pairs comparison or Kruskal-Wallis analysis of ranks.

The assumptions that interactions did not vary based on seasonal or daily abiotic factors were tested to assure consistency across the sampling period. The likelihood of agonistic, avoidance and non-threatening interactions did not vary by time of year ($F=0.52$, $df=2,198$, $p=0.59$) or time of day ($F=1.22$, $df=2,197$, $p=0.30$). Group size ranged from 2-60 individuals and showed no relationship to date ($R^2=0.001$, $F=0.71$, $df=1,368$, $p=0.40$). Group size on entering a waterhole area averaged 8.5 ± 0.5 elephants (Fig. 1.2a). This is consistent with previous research on wild elephant families (Laursen and Bekoff 1978, Moss and Poole 1983).

Results

Matriarchal Effects on Group Interactions

The majority of group interactions were non-agonistic (157/240, 65% of all observed group interactions, Fig. 1.3). Mix, defined as approaching and attendant groups becoming visually indistinguishable from each other (Fig. 1.1D.i), was the most common interaction (48.7% of total). On arrival at a waterhole, matriarchs were the last individual in the family group more than expected by chance (first 47/189, middle 62/189, last 80/189, $\chi^2=219.47$, $df=1$, $p<0.0001$, Fig. 1.4). Expected frequencies were calculated using three independent methods, giving similar results. First, group size was averaged in entries where matriarchs were present in the family ($n=189$, 9.95 ± 0.5 , Fig. 1.2b), and

probabilities were assigned to positions (first 0.1, middle 0.8, last 0.1) based on the average group size. Secondly, probabilities were assigned to positions based on the frequency of each group size (n=189, Fig. 1.2b), and these probabilities were averaged (first 0.15, middle 0.70, last 0.15). Matriarchs were also significantly in the last position more than expected when observed frequencies were compared to these values ($\chi^2=110.71$, df=1, $p<0.0001$). Third, group sizes were averaged based on 24/25 family group associations, and expected probabilities were calculated for each family and then averaged for an overall total (n=24, first 0.11, middle 0.78, last 0.11). One family group was never seen entering with their matriarch, so this family was excluded. The matriarch was also last more than expected when observed probabilities were calculated for each family group and then averaged ($\chi^2=23.05$, df=1, $p<0.0001$), yielding consistent results with the overall average compared with expected. In these analyses, only group entries where a matriarch was present in the group (189/387) were used.

Matriarchs were also significantly in the first position more than expected by chance, using all three calculation methods (overall average; $\chi^2=46.42$, df=1, $p<0.0001$, group size average; $\chi^2=14.43$, df=1, $p=0.0001$, family average; $\chi^2=4.80$, df=1, $p=0.028$). However, matriarchs were significantly last more than first using the first two methods (overall average and group size average; $\chi^2=8.57$, df=1, $p=0.003$) but not when only one value was used per family ($\chi^2=1.00$, df=1, $p=0.31$). This is most likely due to the small sample size in this analysis method. Matriarch position in the entering group did not affect group interactions ($\chi^2=1.74$, df=4, $p=0.78$), and did not differ based on interaction type (Agonistic: $\chi^2=2.40$, df=2, $p=0.30$, Avoidance: $\chi^2=0.21$, df=2, $p=0.90$, Non-threatening: $\chi^2=3.19$, df=2, $p=0.20$). However, matriarch position varied with family

group size; average group size was larger (11.9 ± 0.8 individuals) when matriarchs were in the middle position ($F=4.23$, $df=2$, $p=0.02$, Tukey post-hoc $\alpha < 0.05$).

The likelihood that a matriarch was with her family did not differ across the six kinship groups ($\chi^2=0.0064$, $df=5$, $p=0.89$). Interacting groups with matriarchs were significantly larger than groups without matriarchs (with= 10.51 ± 0.59 , without= 5.49 ± 0.70 , $F=22.63$, $df=1,188$, $p < 0.0001$). However, group size was not significant in determining group interaction when matriarchal and non-matriarchal groups were analyzed separately (matriarchal: $F=1.39$, $df=6,109$, $p=0.22$, non-matriarchal: $F=0.61$, $df=6,86$, $p=0.73$). To control for the interaction between group size and matriarch presence, group sizes were divided into two categories; small-average (1-10, mean= 5.2 ± 0.22) and large (>10 , mean= 17.1 ± 0.96). Ten was chosen as the separation point because this is the average group size for matriarchal groups. Small to average groups made up 73% (145/199) of total group interactions where group number was known. Interaction behaviors in the avoidance category (pass away and turn back, Table 1.3) were separated to differentiate between degrees of avoidance for approaching matriarchal and non-matriarchal groups in all subsequent analyses. For small to average group sizes, matriarch presence significantly determined group interaction type for the categories of agonistic, non-threatening, and pass away or turn back behaviors, ($\chi^2=14.14$, $df=3$, $p=0.002$ Fig. 1.5). Groups with matriarchs were more likely to avoid an attendant group by performing a pass away movement (Fig. 1.1C.i), as opposed to exhibiting the more submissive behavior of turn back (Fig. 1.1C.ii) and halting their approach to the waterhole. For interactions between large groups, matriarch presence was not a significant factor ($\chi^2=4.91$, $df=3$, $p=0.17$). However, only 13% of groups (7/54) with

more than 10 individuals did not include a matriarch, so sample sizes were highly uneven in this subset.

The difference in age between the matriarchs in the interacting groups influenced group interaction type. Agonistic behaviors occurred more when the matriarch of the approaching group was older than the matriarch of the attendant group (approaching mean age=40.76±2.54 y, attendant mean age=36.17±2.65 y, $F=5.57$, $df=3,60$, $p=0.0019$). For these analyses, only interactions in which matriarchs were present in both groups were used ($n=74$). Interestingly, if the attendant matriarch was older than the approaching matriarch, the interaction was more likely to be non-threatening (Lsmeans contrasts $F=11.41$, $df=1,60$, $p=0.0013$), rather than avoidance. Overall, the frequency of avoidance interactions was low (10/74) when only matriarchal groups were interacting. Also, kinship groups differed in mean matriarch age when they were attendant groups ($F=8.64$, $df=5,60$, $p<0.0001$, see Table 1.3). However, since kinship groups did not differ in the most frequent type of interaction (Mix, Fig 1.1D.i), it is unlikely that group identity was controlling this effect.

Influence of Relatedness and Group size

Agonistic or avoidance interactions occurred between families from different kinship groups proportionally more than between families within the same kinship group ($\chi^2=29.59$, $df=1$, $p<0.0001$, Fig. 1.6). Kinship groups were significantly different in the interaction type that was most common ($\chi^2=19.16$, $df=10$, $p=0.038$), but this relationship was driven entirely by one kinship group that only exhibited non-threatening interactions (the H-kinship group). Attendant groups gave way to approaching groups in the majority of agonistic interactions (65% of interactions). This was true across kinship groups with

the exception of the H-group, which only gave way in 30% of the observed interactions. However, inclusion or omission of this kinship group had no differential effect on subsequent analyses. No kinship group was significantly more likely to win an agonistic interaction at the shared resource ($\chi^2=1.11$, $df=5$, $p=0.95$). Group interactions were influenced by the size of the group (repeated measures ANOVA $F=2.49$, $df=6,186$, $p=0.024$); larger groups were more likely to have an agonistic interaction, while smaller groups were more likely to exhibit avoidance behaviors. However, kinship groups did not differ by average group size (mean= 8.5 ± 0.5 , $H=3.57$, $df=5$, $p=0.61$), so it is unlikely that kinship group identity was controlling this effect.

Matriarch Chemosensory Behavior

Matriarch chemosensory behavior differed based on social context. The proportion of matriarchs that performed horizontal sniff and periscope sniff behaviors was higher when other kinship groups were present at a waterhole than when only members of their own kinship group were present (18/24 versus 8/24, $\chi^2=8.39$, $df=1$, $p=0.0038$ Fig. 1.7). Horizontal and periscope sniffs are likely to detect odors from a distance rather than from the ground because the trunk is raised above a 45° angle to the ground (Table 1.2). Additionally, matriarchs performed more touch behaviors with the trunk tip to other individuals when multiple groups were present at the waterhole than when only their group was present ($t=2.05$, $df=23$, $p=0.05$). Trunk touches occurred quickly and the contacted individual could not always be identified. Hence, while most touches were likely to occur to family members because of physical proximity, the kinship membership of the individual contacted could not be analyzed reliably. There were also a significantly larger number of elephants at the waterhole when multiple

kinship groups were present ($t=6.69$, $df=23$, $p<0.0001$), but number of elephants was not a significant predictor of rate of periscope and horizontal sniffs ($R^2=0.09$), so this was not considered a covariate.

Matriarch behavior also was compared with behavior of non-matriarchal females of similar age. Rates of behaviors were averaged across social context for this analysis to control for total focal length (20.07 ± 0.44 min for matriarchs, 9.91 ± 0.50 min for non-matriarchs). However, all females over 40 y in the population behave as matriarchs, so the two groups (matriarch/non-matriarch) varied significantly in average age (matriarch mean= 39.54 ± 1.67 , non-matriarch mean= 29.89 ± 1.88 , $t=3.83$, $df=41$, $p=0.0004$). However, age was not a significant factor in determining behavior ($R^2<0.05$, $F<2.37$, $df=1,42$, $p>0.13$). Six of the 24 matriarchs exhibited flehmen behaviors during focal observations, compared to none of the 19 non-matriarchal adult females. Flehmen is considered the most complex chemosensory behavior in terms of the physical movements of the trunk as the trunk tip goes from a substrate to the roof of the palate (Schulte and Rasmussen 1999, see Table 1.2 for definition). Flehmen behaviors were evenly distributed across age among matriarchs, and evenly distributed across social context. Because non-matriarchal females never displayed flehmen during the focal observations, matriarchs showed significantly higher rates of flehmen behaviors than non-matriarchal females ($H=5.35$, $df=1$, $p=0.021$, Fig. 1.8).

Discussion

Matriarchs play a critical role in everyday interactions between groups of African elephants. The presence of a matriarch in approaching elephant groups determined their response to attendant groups at waterholes. Approaching groups with the matriarch

present were more likely than groups without the matriarch to behave agonistically toward an attendant group, and were less likely to display the more submissive behavior of turn back (Fig1.1C.ii). If the matriarch was present in the approaching group, the group displayed pass away behavior from the attendant group as opposed to stopping the approach entirely (i.e., turn back). This behavior allowed matriarchal groups to access water sooner than non-matriarchal groups. Matriarchs are leadership figures in female elephant groups, coordinating long-distance movements and group defense (Douglas-Hamilton 1972, Dublin 1983, Poole and Moss 1989, Wittemyer and Getz 2007). Matriarchs also respond more appropriately to vocalizations of unfamiliar elephants (McComb et al. 2001); however, it is not only during migration or relatively rare situations involving interactions between unfamiliar elephants that matriarchs influence group behavior. As shown in the present study, matriarchs appear to evaluate group characteristics such as relatedness and group size of familiar groups with whom they share resources on a regular basis, and respond accordingly to the presence of other groups.

Matriarchs were the last individual in the group upon entering the waterhole area more than they were in any other position. This is unusual, since leaders frequently are the first individuals during group movements of social mammals (Dumont et al. 2005, Fischhoff et al. 2007). However, a preliminary study in Tanzania indicated that adult females were both first and last upon entry, so these findings are consistent (M. Groover, unpublished data). Matriarchs were also in the first position more than expected by chance, though the most common position for a matriarch was in the rear. Matriarchs may be aware of more resource sites than younger females in the population (Dublin

1983), and coordinate group movements to these resources. However, since elephant groups were only observed entering the waterhole area in this study, it is possible that matriarchs initiate movements between resource sites, but do not maintain the lead position during the final approach. Other individuals may move ahead in anticipation of using the resource (e.g., I have witnessed younger elephants rushing forward during the final approach to a waterhole), but it would be unusual for the entire family to pass the matriarch. An alternative explanation is that the matriarch brings up the rear of the group to oversee group movement and maintain group cohesiveness. Elephants are aware of the relative position of other elephants with which they are traveling (Bates et al. 2008) and are likely to keep in contact through vocal and chemosensory communication (Poole and Moss 1989, Langbauer 2000, Soltis et al. 2005a). Captive elephants exhibit short-range alternating vocal communication, implying that conversations between elephants are occurring (Soltis et al. 2005a), which could be a method that matriarchs use to influence group behavior. From the present study, it is clear that other group members are aware of her presence in the group even if she is in the rear. In many cases, a family group reduced the distance between individuals when approaching another family at the waterhole, potentially waiting for the matriarch to signal what is the most appropriate group interaction behavior (personal observation).

Relatedness and group size also influenced interaction type; groups that were more closely related were more likely to display non-threatening behavior (Fig 1.1D) and smaller groups displayed avoidance behaviors (Fig. 1.1C) more frequently than larger groups. Kin selection theory states that resource sharing will correlate directly with degree of relatedness (Isbell and Young 2002, Spong and Creel 2004). This is especially

true in social mammals like elephants (Archie et al. 2006b), where individuals live in groups of related females and exhibit allomothering behavior (Lee 1987). Families within kinship groups were more willing to share resources and thus had fewer agonistic interactions than families less closely related. However, overall, most group interactions were non-agonistic, even between unrelated families.

Group interactions are very common in fission-fusion social systems (Goodall 1986, Cross et al. 2005, Archie et al. 2006b). Since interactions occur at shared resource sites such as waterholes, they generally involve competition between groups over a limited resource. The type of group interaction that occurs is based on the willingness of groups to share that resource, and the ability of one group to assert control over the resource. In large-bodied, long-lived species such as elephants where extreme agonistic interactions may result in serious injury or even death, dangerous interactions are likely to be avoided (Crowley 2001, Archie et al. 2006a). Thus, even interactions defined as agonistic in this study were non-violent in nature and were not generally overtly dangerous to the individuals' involved (personal observation). However, agonistic interactions do prevent the submissive group from accessing the resource, so there is an associated cost with turn back behavior (Wittemyer and Getz 2007, Wittemyer et al. 2007). Smaller groups are more likely to lose a potentially dangerous altercation, so these groups are more likely to avoid interactions despite the ecological costs (Sterck et al. 1997).

Dominance is clearly an important factor in group interactions (Sterck et al. 1997, Archie et al. 2006a, Wittemyer et al. 2007). For example, more dominant groups spend more time near waterhole resources in the dry season (Wittemyer et al. 2007). However,

there was no evidence in the current study of a reliable dominance hierarchy in this population of elephants. Differences in matriarch age between family groups were significant in predicting whether an interaction would be agonistic, avoidance or non-threatening, but this was not consistent across contexts. Matriarch age is a significant factor in dominance interactions between groups in elephant populations (Wittemyer and Getz. 2007). Thus, I predicted that families with older matriarchs would be involved in more agonistic interactions as the approaching group, and as the attendant group receive more avoidance interactions than younger matriarchal groups. This was partly true. When the approaching matriarch was older, the interaction was more likely to be agonistic, but if the attendant matriarch was older then the group behavior was more likely to be non-threatening. This is likely due to the waterhole having higher resource value for approaching versus attendant groups, so attendant matriarchs are willing to share it with younger approaching matriarchs. Frequency of threatening interactions was low in this subset, and there was also an interaction between location relative to the waterhole (attendant or approaching) and matriarch age. Because of these confounding factors, dominance hierarchies between family groups could not be reliably identified, if they exist.

Matriarchs showed heightened rates of investigatory behaviors in more complex social contexts. More matriarchs performed horizontal sniff and periscope sniffs when there was a different kinship group in addition to their own present at a waterhole. Periscope sniff and horizontal sniff behaviors investigate signals from outside the immediate vicinity of the individual. This increased interest in olfactory signals may help a matriarch respond more quickly to a potential threat from another kinship group, or

allow her family to make way for an approaching group to avoid a confrontation. Additionally, matriarchs performed more touch behaviors when multiple kinship groups were present. Females reinforce social bonds by touching in captive African elephant groups (Meyer et al. 2008), so increased touching may reinforce bonds within kinship groups in the presence of non-kin.

Matriarchs also performed higher rates of flehmen behaviors in comparison to adult, non-matriarchal females. Complexity of chemosensory behavioral repertoire has been shown to increase with age in African elephants (Merte 2006), and flehmen is considered the physically most complex chemosensory behavior (Schulte and Rassmussen 1999). Matriarchs were the only focal individuals to perform these behaviors during observation, which would be expected because they are the oldest females in their family groups. However, younger matriarchs (20-40y) performed the highest rate of flehmen behaviors (Fig 1.8), so the age relationship was not supported within the matriarch subgroup. My results support the idea that matriarchs are more aware of their environment than other adult females, regardless of absolute age of the matriarch. This furthers their role as leaders in the family group.

Communication plays an important role in interactions between individuals and groups (Bain 1986, Langbauer 2000). Several communication modalities are used by African elephants to gather information about their surroundings and respond appropriately. For example, elephants use odor and garment color to distinguish between human African ethnic groups, which are differentially threatening to elephant populations (Bates et al. 2007). By focusing on differences in communication behaviors of group leaders and non-leaders, we can gain insight into how leaders influence the defensive

behavior (McComb et al. 2001) or movement behavior (Dumont et al. 2005, Fischhoff et al. 2007) in groups of social mammals. Additionally, studying communication behaviors demonstrates how leaders communicate within groups about factors that influence group interactions, such as group size and relatedness. Leader individuals are aware of the location of other elephants that they are traveling with and other elephants in the vicinity (Bates et al. 2008), whether or not the leader is physically in front of the group. Without the presence of the leader, elephant groups lack this central point of communication and respond in a more ecologically costly manner to social interactions (McComb et al. 2001). In fission-fusion social systems exhibited by large-brained mammals, group interactions are common and responses are highly variable (Douglas-Hamilton 1972, Moss and Poole 1983, Goodall 1986, Christal and Whitehead 2001, Archie et al. 2006b). Key individuals, notably leaders, may play an important role in mediating these interactions.

The present study demonstrates the importance of matriarch communication to interactions that occur daily between groups of familiar individuals in the long-lived, socially complex African elephant. Matriarchs varied their rate of exploratory behaviors based on social context, and they performed more investigatory behaviors than other adult females. This indicates that matriarchs serve as focal points in communication between groups, which was supported by the observed matriarchal effects on group interactions. The presence of a matriarch in the approaching group resulted in the group behaving more agonistically and less submissively, characteristics that also were influenced by inter-group relatedness and group size. Previous research on group interactions in social mammals have focused on relatedness and dominance effects on

interactions (Spong and Creel 2004, Archie et al. 2006a, Wittemyer et al. 2007); the present study illustrates the importance of leaders such as matriarchs in interactions. Matriarchs play a crucial role in the movements and interactions that occur between elephant groups, and may be communicating relevant information to other group members. More research is needed to determine the specific mechanisms of matriarchal influence on group behavior.

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CHAPTER II

THE EFFECT OF GROUP CHARACTERISTICS ON FITNESS AND CHEMOSENSORY BEHAVIOR OF FEMALE AFRICAN ELEPHANTS

(*LOXODONTA AFRICANA*)

Abstract

Female African elephants (*Loxodonta africana*) live in a social hierarchy composed of families, groups of frequently-associating families (kinship groups) and kinship groups that share the same range (clans). Families are led by the matriarch and consist of related females. Kinship groups are made up of related families and are led by the grand matriarch. I analyzed two competing hypotheses for how matriarch age influences group fitness. First, older matriarchs lead groups with greater sociality; and second, older matriarchs provide their groups greater access to limited resources. A null hypothesis was that behavioral differences between elephant kinship groups have no fitness payoff but indicate the presence of behavioral signatures. Two clans consisting of six kinship groups and 25 families were studied in Addo Elephant National Park, South Africa from January to July, 2007, using continuous focal observations and instantaneous scan sampling on family groups. Additionally, five years of demographic data were compiled as a measure of kinship group fitness. Calf-to-female ratio increased with the age of the grand matriarch ($R^2=0.82$), but this was not influenced by sociality and only weakly by waterhole use. Behavioral differences between kinship groups most likely represent behavioral signatures. Large-scale socio-ecological factors like home range quality and energy budgets may be more influential to increased fitness of older matriarchal groups, rather than daily sociality or resource access.

Introduction

Resource distribution and competition over resources are considered the first-order determinants of inter- and intra-group dominance structure in group-living mammals (Sterck et al. 1997). Social organization is generally structured by these and other ecological factors including predation risk (Wrangham 1980). In situations where resources are widely dispersed and not easily defensible, group dominance structure will be flexible and agonistic interactions rare (Isbell and Young 2002). Though this relationship was initially proposed for illustrating the effects of resource distribution on primate groups, it has since been applied to other mammals exhibiting similar social structures (e.g. cetaceans, Christal and Whitehead 2001; elephants, Wittemyer et al. 2007; bats, Popa-Lisseanu et al. 2008). The social structure in these mammals is such that group membership is flexible, and groups exhibit frequent splitting and merging often based along lines of relatedness (Archie et al. 2006b). Dynamic group structures of this nature are referred to as fission-fusion for that reason.

Flexibility in group membership of fission-fusion systems allows for optimization of group characteristics such as group size, daily movements and seasonal range based on resource availability and predation risk, which are also non-static properties of the ecosystem. However, the ability to optimize group characteristics based on socio-ecological factors may be variable between groups and will have associated fitness consequences. Group characteristics such as group number, territory quality, home range size, and characteristics of group leaders have been shown to influence direct or indirect fitness in a number of fission-fusion species (McComb et al. 2001, Wittemyer et al. 2007, Popa-Lisseanu et al. 2008). The characteristics of leaders, especially age and size, dictate

dominance rank in socially complex species (Robbins et al. 2005, Wittemyer and Getz 2007). Leaders can influence many aspects of sociality including group movement, territory defense and recognition of other groups (McComb et al. 2001, Dumont et al. 2005). Leaders also may control optimization of group size in fission-fusion systems. The ability to optimize group size may covary with dominance and be influenced by the age of the leader.

Female elephant social structure has been demarcated into six tiers: mother-calf units (tier 1), families (tier 2), kinship groups (tier 3), clans (tier 4), subpopulations (tier 5), and populations (tier 6) (Wittemyer et al. 2005). The family consists of one or more adult females and their offspring in which the oldest, largest member is the matriarch (Douglas-Hamilton 1972). Matriarchs are the leaders of the family group. Kinship groups are made up of families that consistently fuse together into larger aggregations at frequent intervals (Douglas-Hamilton 1972, Dublin 1983, Moss and Poole 1983, McComb et al. 2003), and I termed the oldest female in the kinship group the grand matriarch. Clans are kinship groups that share the same home range (Moss and Poole 1983). Since families within kinship groups and clans associate with each other more frequently, individuals within kinship groups and clans are expected to be more behaviorally similar to each other than to other individuals in the population; therefore, in the present study fitness was quantified at the kinship level.

In African elephants, matriarch age has been correlated with direct fitness (number of offspring) measurements of individuals in elephant groups (McComb et al. 2001), but the proximate causes of this relationship have not been fully examined. One hypothesis is that older matriarchs are better able to optimize fission-fusion properties of

elephant social structure, and this conveys a fitness benefit to members of their family or kinship groups (McComb et al. 2001). For example, groups with older matriarchs may better optimize group size based on ecological factors such as resource availability or predation risk. Thus, families with older matriarchs would exhibit fission and fusion more regularly than families with younger matriarchs. This is termed the social association hypothesis.

Resource access is also an important factor in inter-group competition and consequently fitness. This presents an alternative hypothesis for how groups of older matriarchs secure higher fitness for group members, called resource access. Dominant groups of African elephants have small home ranges centered on permanent water sites compared to subordinate groups during the dry season (Wittemyer et al. 2007). If dominant groups are able to monopolize limited resources by making use of them more or staying in the immediate vicinity for longer, this could incur a fitness advantage for more dominant groups, that is, groups with older matriarchs (Wittemyer and Getz 2007).

Finally, a null hypothesis is that differences between groups of elephants are arbitrary and incur no obvious fitness benefits to the respective groups. Differences in behaviors of this nature are considered behavioral signatures (Miller 2005). These behavioral signatures of groups could be considered a form of culture, which has been shown in other mammals such as primates (Nakamura and Nishida 2006, Miller 2005) and cetaceans (e.g. Rendell and Whitehead 2004). Differences in types of communication behaviors, methods of using tools, and other seemingly arbitrary behaviors exist between groups in these instances. For example, groups of female sperm whales (*Physeter macrocephalus*) living together exhibit distinct vocalization repertoires when compared

with other groups (Rendell and Whitehead 2004). Since the social structure for sperm whales is similar to that of elephants (Connor et al. 1998), group differences in communication behavior may be found in elephants as well, but these differences may not be related to matriarchal characteristics or fitness.

Female African elephants commonly communicate via auditory vocalizations and chemosensory signals (Langbauer 2000, Bagley et al. 2006, Goodwin et al. 2005, 2006). Auditory communication is often long-distance (McComb et al. 2003, O'Connell-Rodwell et al. 2006), though there is evidence of captive elephant individuals performing alternating vocal communication behaviors, implying short-range communication (Soltis et al. 2005). Chemosensory communication, which involves the transmission and reception of chemical signals such as pheromones, occurs over relatively short distances but longer time spans (Karlson and Lüsher 1959, Eisenberg and Kleiman 1972). These signals may be deposited in the form of excretions or secretions at information centers such as waterholes, and they may be present for minutes to days before the arrival of the focal elephant (Napora 2007). Chemical signals convey information about individuals previously using the resource relating to age, sex, sexual state and possibly individual identity (Rasmussen and Schulte 1998).

The number of chemosensory behaviors performed is related to the number of signal sources that are available (Merte 2006), which is in turn related to the number of individuals that visit the area on a regular basis. Family groups in a large clan share the majority of their home range with a greater number of individuals, so the increased level of available clan-specific information may lead to an increase in investigatory behaviors for a larger versus a small clan. Also, differences in chemosensory behaviors may be a

source of signature behaviors for elephants, since differences in acoustic communication behaviors make up the behavioral signature for socially similar sperm whales. I examined differences in chemical communication behaviors between individuals in different clans and kinship groups for possible behavioral signatures.

I hypothesized that groups with older matriarchs would have ecological advantages that lead to fitness benefits. I predicted that groups led by older matriarchs would have a higher calf-to-adult-female ratio (higher fitness) than groups with younger matriarchs. I examined two hypotheses explaining the proximate causes of this relationship, termed social association and resource access. If increased sociality drives this fitness benefit, I predicted that groups with older matriarchs would associate with members outside their family more than groups with younger matriarchs. Thus, older matriarchal family groups would exhibit less cohesion and consistency in association, and group fluidity (i.e., rates of fission and fusion) would correlate positively with matriarch age. If resource access drives fitness, I predicted that the amount of time spent near a limited resource such as a waterhole would correlate positively with matriarch age, and fission-fusion properties would be constant across groups. Alternatively, differences between groups may have no obvious fitness benefit, and may instead serve as signature group behaviors, similar to those demonstrated in other species. The null hypothesis was that behavioral differences would exist between kinship groups but these would have no fitness benefit, and I predicted that these would not correlate with matriarch age.

Materials and Methods

Study Site and Population

This study was conducted in Addo Elephant National Park (AENP) from January to July of 2007. AENP is 72 km northeast of Port Elizabeth, South Africa. A population of approximately 375 African elephants (*Loxodonta africana*) in six matrilineal groups lives in a fenced reserve of roughly 103 square km (Whitehouse and Schoeman 2003). A smaller population of some 70 elephants in the Nyathi area was not observed in this study. The vegetation is largely dense thorny thicket with a wide range of shrubs, herbs, grasses, and other plants (Paley and Kerley 1998). Throughout the park there are roads that provide access to the waterholes and other prime viewing locations for tourists and researchers.

The AENP population was established in 1931, following a near-extinction of the regional population from hunting. Eleven elephants were placed on a reserve in an effort to preserve the elephant population at the southern end of its range (Whitehouse and Hall-Martin 2000). The park was later fenced in 1954, and the current population is derived almost entirely from the original eleven individuals. From in-depth studies and an analysis of data since the park's creation in 1931, reliable matrilineal groups have been determined and these matrilineal groups are less closely related than would be expected from such an extreme bottleneck event (Whitehouse et al. 2001). Since the work by Whitehouse (2001), the identification of elephants and composition of the population in AENP have been monitored by the combined efforts of researchers at Nelson Mandela Metropolitan University (especially doctoral candidate K. Gough), Georgia Southern University and AENP personnel. The six matrilineal groups form the six kinship groups, which comprise two clans. Kinship groups served as the basis for categorizing group membership (Table 1.1).

Twenty-five family associations are known within these kinship groups (Loizi 2004, Bagley 2004, Gough & Kerley 2006, Merte 2006, Meyer 2006), which were confirmed during the current study.

Behavioral Methods

Observations focused on family units at the waterholes. At AENP elephants are habituated to vehicles in close proximity, so all observations were made from a vehicle located near elephants partaking in natural activities. Using behavior sampling with continuous recording (Martin and Bateson 1993), family group interactions were observed starting from when the group was approximately 30m from the waterhole and continuing for 10 min or until the group interaction ended. Group type, group number, group identification (ID) and arrival order (age/sex/ID of first and last elephant) were recorded for every family group. A group was defined as any assemblage of two or more elephants in which every individual was within 3 body lengths of its nearest neighbor. Groups with more adult males than females were not included. Group ID was determined by identifying the matriarch and at least two of the adult or pubescent females in the group. The ID of the oldest female in the group served as the group ID if the matriarch was not present. Additionally, 41 hours of scan sampling with instantaneous recording was completed on 24 of 25 family groups at waterholes. Scans occurred on 5-minute intervals, and the location of the group relative to the waterhole, state behavior of the group, and number of individuals in the group were recorded at this time (Martin and Bateson 1993). Locations were either within 30 m of the waterhole (WH), or 30-500 m from the waterhole in any direction. Scan observations ended when the group moved farther than 500 m from the waterhole.

The calf-to-female ratio was calculated by dividing the number of surviving calves (<5 y) by the number of post-puberty females (>15 y) in the kinship group. This compared all calves in a kinship group born in a 5-year period to all potentially reproductively active females in the kinship group during that time. No calves have been born to females younger than 10 y in this population. Reproductively active females younger than 15 y were not included because they were not sexually mature for the entirety of the study period. The H-kinship group was excluded from this analysis because it contained only a single family group. The coefficient of variation was calculated by dividing the standard deviation of group size upon entry to the waterhole area by the mean group size for each family. These were then averaged within kinship groups to obtain an overall coefficient of variation for the kinship group.

Ten-minute focal observations also were recorded for one individual of each sex and age class from every kinship group, totaling 15.5 hours of focal observations with continuous recording (Martin and Bateson 1993). Because age and sex has been shown to influence behavior (Merte 2006, Vyas, 2006, Meyer 2006), focal observations were grouped within sex into two age categories: pre-adult (0-19 y, mean=8.02±0.71) and adult (>19 y mean=36.64±1.43). Behaviors did not vary by sex in the pre-adult category ($t=1.26$, $df=38$, $p=0.21$), so males and females were combined. Within categories, age was considered a covariate, but was found not to be significant ($F<0.12$, $df=1$, $p>0.72$). Adult included all 25 matriarchs in the population, totaling 44 females. Observations on 23 females and 22 males in the pre-adult category were performed. These data were used to compare behavior of all age classes of individuals within kinship groups and clans. All

behavioral measures were made based on the definitions given in Tables 1.2, 1.3 and 2.1, and in Appendices A.1 and A.2.

Data Analysis

Data were analyzed using the JMP4 statistical program (SAS Institute, Cary, NC). Chemosensory, contact and waterhole use behavioral data were analyzed for differences between families within clans and families within kinship groups. The H-kinship group was excluded from analyses of families within kinship groups since it is made up of a single family group, so an average for family could not be obtained. Contact behaviors (Table 1.2) included all trunk touches to another elephant, but were not significantly related to any group characteristics (B.1). All descriptive statistics are reported as mean \pm SE. Analyses compared distributions using contingency tables and χ -square tests, and variation using ANOVA analysis or Kruskal-Wallis ranks analysis on non-normal data. Regression and correlation analyses were performed on kinship and family characteristics.

Results

Matriarch Age and Fitness

The age of grand matriarchs in kinship groups was a significant predictor of the kinship group calf-to-post-puberty (>15 y) female ratio ($R^2=0.82$, $F=13.87$, $df=1,3$, $p=0.034$; Fig 2.1). As predicted, this ratio increased with the age of the grand matriarch. Kinship group size did not predict the calf-to-post-puberty female ratio ($R^2=0.49$, $F=3.91$, $df=1,4$, $p=0.12$). The H-kinship group fell below the line in the regression of calf-to-female ratio and matriarch age (Fig 2.1). This kinship group was significantly less agonistic than other kinship groups in group interactions, giving it a distinct signature of

interaction behaviors. It was also unique in only containing a single family group (Table 1.1), and it was the smallest kinship group.

Social Association Hypothesis

Family group social associations (measured as the coefficient of variation in group size) did not vary between kinship groups ($H=1.42$, $df=4$, $p=0.84$). Standard deviations ranged from 23-88% of average group size for family groups and 31-55% when these were compiled at the kinship group level. There was no relationship between coefficient of variation and matriarch age ($R^2=0.03$, $F=0.59$, $df=1,22$ $p=0.45$; Fig 2.2). In addition, elephant clans did not differ in the coefficient of variation for their family groups ($t=0.63$, $df=1$, $p=0.53$).

Resource Access Hypothesis

Family group matriarch age weakly predicted the total time spent within 500 m of the waterhole ($R^2=0.16$, $F=4.10$, $df=1,22$, $p=0.055$; Fig. 2.3); time spent near the waterhole increased with matriarch age. Kinship groups differed in the proportion of scans spent in the immediate vicinity of the waterhole ($F=3.5$, $df=4,18$, $p=0.028$; Fig 2.4). Families in the A-group spent significantly less time within 30 m the waterhole than families in the B-group and the R-group (Tukey post-hoc, $\alpha=0.05$). However, this was not correlated to kinship matriarch age ($R^2=0.05$, Table 1.1). Family groups did not differ in proportion of common state behaviors (Stand, Drink, Mud, Walk, Table 2.1) while at the waterhole (B.1). No differences were found between elephant clans in either the time spent in the immediate vicinity of the waterhole or the proportion of state behaviors performed at the waterhole (B.1).

Signature Behaviors

Adult females in the larger Clan 1 performed more total chemosensory behaviors than adult females in the smaller Clan 2 ($t=2.68$, $df=42$, $p=0.01$; Fig 2.5). However, clans also differed in the total time observed because of the larger size of Clan 1 (C1:311.1 min, C2:126.1 min), which may be a confounding factor. Yet, pre-adults did not differ in these same behavioral measures by clan membership ($t=0.67$, $df=43$, $p=0.51$). Adult females in kinship groups significantly differed in the average rate of the trunk-touch behavior termed check (see Table 1.2 for definition; $H=12.64$, $df=5$, $p=0.027$; Fig 2.6). The females in the A-group (Table 1.1) performed a higher rate of check behaviors than females in the R-group (Tukey post-hoc, $\alpha=0.05$). The rate of total chemosensory behaviors did not vary between kinship groups within the age category of pre-adults (B.1).

The H-kinship group only exhibited non-threatening group interactions (Table 1.3) and at a significantly higher frequency than other kinship groups ($\chi^2=14.34$, $df=5$, $p=0.013$; Fig 2.7). Kinship groups were not different in the frequency of friendly interactions when the H-group was removed from analysis (post-hoc $\chi^2=4.45$, $df=4$, $p=0.35$). The H-group was also less likely to give way in an agonistic interaction as an attendant group. On average, attendant families from kinship groups gave way in 65% of agonistic interactions, whereas the H-group only gave way in 30% of the observed interactions. Thus, the H-group displayed a distinct “interaction” behavioral signature.

Discussion

Grand matriarch age significantly predicted the direct fitness of kinship groups (measured as the calf-to-post-puberty [>15 y] female ratio). I examined two hypotheses

about the proximate cause of this relationship. The first hypothesis states that older matriarchal groups optimize fission-fusion properties of elephant social structure in response to ecological factors, and would consequently show less cohesion than younger matriarchal groups. My second hypothesis was that older matriarchal groups use limited resources such as waterholes more than younger matriarchal groups, and this conveys a fitness benefit. The null hypothesis was that arbitrary differences between groups that convey no fitness benefit (behavioral signatures) would be apparent. Matriarch age was not related to the measure of cohesiveness for family groups, but was weakly related to waterhole use behaviors of family groups. Additionally, distinct behaviors were illustrated at the kinship group and clan level that had no relationship to fitness, which supports the presence of behavioral signatures in this population. Thus, the social association hypothesis was not supported, whereas some support was provided for the resource access and behavioral signature hypotheses.

Matriarch age was not correlated with sociality and cohesiveness measures, as predicted by the social association hypothesis. Direct fitness measures were correlated with matriarch age in the Amboseli National Park population in Kenya (McComb et al. 2001), which was attributed to increased sociality of older matriarchs. McComb et al. (2001) also illustrated that groups with older matriarchs conserve energy by exhibiting defensive responses only when defensive behaviors are beneficial (in interactions between unfamiliar groups). They hypothesized that groups with older matriarchs also have more opportunities for cooperation because of increased sociality. Cooperation provides fitness benefits such as protection from predation (Sterck et al. 1997). In the present study, families with older matriarchs did not associate more frequently with

elephants from other family groups than did families of younger matriarchs. Thus, the potential for cooperation from increased sociality was not related to age of the matriarch.

Water is a limited resource for elephant populations, and other studies have found that dominant family groups have smaller home ranges and spend more time nearer to permanent water than subordinate groups (Wittemyer et al. 2007). Food is also an important resource for elephants, but the elephant diet is broad and not restricted to rare or endemic plants (Landman et al. 2008); therefore, food availability was not considered in this study. Dominance of family groups is correlated with age of the matriarch (Wittemyer and Getz 2007), so the resource access hypothesis predicts that time spent near a waterhole will increase with increasing matriarch age. While some waterholes are maintained at AENP, overall water availability is variable within the park because of abiotic factors (Landman et al. 2008), and could be considered limiting. In the present study, measures of total time spent within 500 m of a waterhole indicate some support for this hypothesis, but only weakly. Because of the low R^2 value, it is likely that other factors besides matriarch age may be more strongly influencing time spent in the vicinity of a waterhole, though the marginal significance may be due to lack of power in detecting weak relationships with somewhat small sample sizes ($n=25$).

Proportion of time spent within 30 m of the waterhole was not related to matriarch age, group fitness, or any other group characteristics, which does not support the resource use hypothesis. Families in the A-group (grand matriarch age 51y) spent less of the scan within 30 m of the waterhole than the B (grand matriarch age 56y) and R (grand matriarch age 43y) kinship group families, but this difference was seemingly arbitrary and not related to fitness. No differences were found between kinship groups in the

proportion of time spent using the resource (drinking or mudding) as opposed to being in the vicinity of the resource but not using it (standing or walking). Seasonality may influence waterhole use behaviors; in the Samburu population of elephants of Kenya, differences in access to water between elephant groups was evident only during the dry season (Wittemyer et al. 2007). Therefore, differential use may only become apparent when resources are highly limited. The present study spanned one of the two annual peaks in rainfall (austral autumn), so dry-season impacts could not be quantified (Landman et al. 2008). The relationship between matriarch age and range size or quality may be more relevant to the fitness of individuals in a group than the time spent in close proximity to water. However, home range and movement patterns of kinship groups were not quantified in this study.

Differences in apparently arbitrary behaviors between groups, termed behavioral signatures have been identified in other species (Rendell and Whitehead 2004, Nakamura and Nishida 2006, Miller 2005). Behavioral signatures have been equated to a form of culture. Culture is the non-hereditary transmission of an acquired behavior set that is more similar among individuals within a group than between groups (Nakamura and Nishida 2006). In animal societies, culture can be determined by observing differences between groups in particular behaviors, as well as observing transmission within a group of a novel behavior (Whiten et al. 2005). Adult females from two of the six kinship groups (A and R) differed in the rate of trunk-touch chemosensory behaviors and frequency of group interaction behaviors they performed, but this was not related to any group characteristics beyond group identity. Interestingly, the same groups that differed from each other in waterhole use behavior (A from B and R) were also the groups that

differed in the rate of check behavior. In studies of other mammals, differences exist between spatially separated populations of individuals, but the elephant kinship groups studied herein are members of the same population and their home ranges overlap in AENP, so differences were expected to be small. Additionally, elephants in the AENP population are related within the past century, though they are genetically more diverse than would be expected given this recent bottleneck event (Whitehouse and Hall-Martin 2000). This recent divergence could also contribute to the small scale of behavioral signatures.

The H-kinship group also exhibited a distinct “interaction” behavioral set when compared to the other 5 kinship groups in the population. All interactions initiated by the H-group were non-threatening, even though only 16% of these interactions occurred between subsets of the H-kinship group. This group also was less likely to move away from a resource as another group approached. This presents a unique behavioral signature such that this kinship group was never agonistic and rarely submissive towards other groups, but instead had more non-threatening interactions than any other group.

One explanation contrary to a behavioral signature is that this is the dominant kinship group in the population, since dominant groups or individuals receive more submissive behaviors from subordinates than vice versa (Anestis 2005, Archie et al. 2006a, Wittemyer and Getz 2007). However, dominant individuals also behave aggressively towards subordinates to maintain the linear dominance structure (Robbins 2005), which is incongruous with the inter-group behavior of the H-group. Additionally, the H-group had the second lowest calf-to-post-puberty female ratio in the population (Fig 2.1), which suggests that there is not a fitness advantage related to their social

position. Unique interaction behaviors and lower fitness may be influenced by the other unique characteristics of this group. For example, the H-group is the smallest kinship group in AENP, comprised of a single family (Table 1.1). The matriarch in the H-group was present in 66% of group entries, which is the largest ratio of all kinship groups (range: 50-61% for rest). For 50% of the entries when the H-group matriarch was not present in the approaching group, she was at the waterhole area but farther than 30 m away; in each case, she approached the waterhole with the remainder of the H-kinship group shortly after the initial group (personal observation).

Female elephants in this group also responded to an abnormal development more than two other kinship groups. They fully investigated the path park rangers had taken to remove a drowned elephant calf of the B-group from a waterhole, even though this had occurred hours before the family's arrival at the location. In contrast, families from the B- and M/P-kinship groups paid only minimal attention to the dead calf and none at all to the chain of events leading up to its removal. Group interaction and contextual investigatory behavior make up the unique behavior set that defines the H-kinship group.

Support is provided in this study of arbitrary differences in behavior (behavioral signatures) existing between kinship groups in terms of waterhole use, interaction and investigatory behaviors. Development and transmission of culture could be a viable explanation of behavioral differences between elephant groups.

The two elephant clans differed in their rate of total chemosensory behavior; members of the larger clan performed a higher rate. Chemosensory behaviors are used to investigate shared resource sites such as waterholes for information on the sex, sexual state and identity of other individuals who have used the area within a timeframe of a few

days (Langbauer 2000, Napora 2007). Family groups in the larger clan share the majority of their home range with a greater number of individuals, so the increased level of available clan-specific information may explain their higher rate of chemosensory behaviors.

Groups in fission-fusion systems often contain a dominant individual regarded as the leader (Lazaro-Perea 2001, Robbins et al. 2005, Archie et al. 2006a). The characteristics of leaders, especially age and size, dictate dominance rank in socially complex species (Robbins et al. 2005, Wittemyer and Getz 2007). Leaders influence group movement, group defense and interactions with other groups (McComb et al. 2001, Dumont et al. 2005, Fischhoff et al. 2007). Optimization of group characteristics such as group size, daily movements and seasonal range based on resource availability and predation risk may be an important facet of leadership. The ability to optimize group characteristics based on socio-ecological factors will have associated fitness benefits, but leaders may only gain this ecological skill with age.

Since evidence only weakly supported the resource access hypothesis and the social knowledge hypothesis was not supported, the proximate cause of the positive relationship between higher group fitness (i.e., a higher calf-to-post-puberty female ratio) and grand matriarch age cannot be clearly identified at this time. Arbitrary differences in behavior between individuals in kinship groups were illustrated, which indicates that behavioral signatures may be present in elephants. The higher calf-to-post-puberty female ratio was not related to daily resource use or the fission-fusion properties of elephant social structure. However, matriarch presence influences group interactions such that matriarchal groups perform group interaction behaviors which lead to earlier access to the

resource and thus may have a lower energetic cost (Chapter 1), and groups with older matriarchs also conserve energy by responding more appropriately to auditory signals (McComb et al. 2001). Energy conservation may pave the way for higher fecundity in groups with older matriarchs. Additionally, range size and quality may vary between kinship groups based on matriarch age but not small-scale usage behavior, which could conserve additional energy and lead to higher fitness. Thus, larger-scale factors need to be examined to discern proximate causes of increased fitness for kinship groups with older grand matriarchs.

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Table 1.1: Female group relatedness and organization of living elephants in AENP South Africa during 2007 (note: Lumka and Lizzy were no longer alive in 2008).

Clan	1				2	
Kinship Group	A	B	H	M/P	L	R
Oldest Matriarch in Kinship Group (year born): the Grand Matriarch	Andiswa (1956)	Tania (1951)	Hettie (1950)	African Slurpie (1949)	Lumka (1953)	Rebecca (1964)
Number of individuals	73	67	24	86	45	47
Number of Families in Kinship Group	8	4	1	6	3	3
Family descriptions: Matriarch (year born), number of members	Andiswa (1956) 12	Tania (1951) 26	Hettie (1950) 24	African Slurpie (1949) 13	Lumka (1953) 15	Rebecca (1964) 14
	Aloe-vera (1961) 17	Catherina (1970) 16		Mary (1963) 14	Lizzy (1956) 13	Ruth (1971) 19
	Little Agatha (1963) 5	Bluebell (1976) 12		Megan (1965) 10	Little Left Tusk (1968) 17	Rita (1973) 14
	Amanda (1969) 12	Bridie (1980) 13		Mandisa (1972) 16		
	Allissa (1972) 9			Tipperary (1973) 20		
	Apple (1974) 11			Phyllis (1981) 13		
	Amber (1977) 5					
	Annake (1985) 3					

Table 1.2: Ethogram event behaviors performed by wild African female elephants during behavior and focal sampling with continuous recording at AENP South Africa in 2007 (Loizi 2004; Bagley 2006).

Event behavior categories and defined event behaviors		Definition	
<i>Trunk to Ground Substrate, Air or Conspecific</i>	Check*	Touch ground with tip of either finger	
	Flehmen*	Tip of trunk touches substrate or conspecific then placed in the VNO ducts in the roof of the mouth	
	Horizontal sniff	Trunk raised parallel to ground, sniffing air	
	Periscope sniff	Trunk raised above head, sniffing air	
	Pinch	Tips of trunk touch each other	
	Place*	Entire nasal opening is placed on ground or conspecific and held momentarily	
	Sniff*	Nasal openings hover over ground or conspecific without contact	
	<i>Trunk Tip to other Female/Male</i>	Anus	Area under the tail and above perineum
		Body	Torso or areas not listed
		Genital	Penis or vulva region between rear legs of elephant
Head		Forehead and superior most point of head	
Mouth		Area around and/or inside maxilla and mandible (e.g. lips, jaw, etc.)	
	Temporal gland	Point of TG secretion on side of head in front of ear	
	Trunk	Portion of trunk starting from mouth area, down to tip	

*Chemosensory definitions derived from Schulte & Rasmussen (1999)

Table 1.3: Ethogram used to record group interactions between family groups of African elephants at AENP South Africa in 2007.

Category of interaction	Interaction	Label	Description
Agonistic ¹	Displace ⁴	DIS	Approaching group causes attendant group to move, but does not take vacated spot
	Pass Towards	PT	Approaching group changes trajectory towards attendant group but attendant group does not move and approaching group continues by attendant group
	Supplant ⁴	SUP	Approaching group causes attendant group to move, and takes the vacated spot
Avoidance ²	Pass Away	PA	Approaching group gets within 2 body lengths of attendant group, and changes trajectory away from attendant group
	Turn Back	TB	Approaching group comes within 2 body lengths of attendant group, then halts approach and turns back from attendant group
Non-threatening ³	Mix	MIX	Approaching and attendant groups become indistinguishable
	Pass By ⁵	PB	Approaching group gets within 2 body lengths of attendant group, but does not change trajectory and continues by attendant group

¹Agonistic: Approaching group moves toward the attendant group without mixing

²Avoidance: Approaching group moves away from the attendant group

³Non-threatening: Approaching group combines with attendant group or moves tangentially to attendant group with no motion toward or away

⁴Based on aggressive interaction definition from Leong et al. (2005)

⁵Based on Ortolani et al. (2005)

Table 2.1: Ethogram used to record state behaviors performed by wild African elephants during scan sampling with instantaneous recording at AENP South Africa in 2007.

State behavior categories and defined state behaviors	Definition	
Stand	Remains in the same location for at least two seconds with none of the following trunk behaviors observed	
Walk	Leaves location while all four legs are moving in a steady pace with none of the following trunk behaviors observed	
<i>Trunk Behavior</i>	Drink	Takes water into the trunk and immediately placing water into the mouth
	Eat	Takes nutrients into the mouth via the trunk
<i>Care</i>	Dust	Uses the foot or trunk to place dirt particles on the body
	Lay	One side of the torso in contact with the ground
	Mud	Uses the trunk to throw mud particles on the body or moving body rapidly in a mud hole
Other	Other behaviors observed, but not listed in ethogram	
Not Visible	Elephant has moved out of sight	

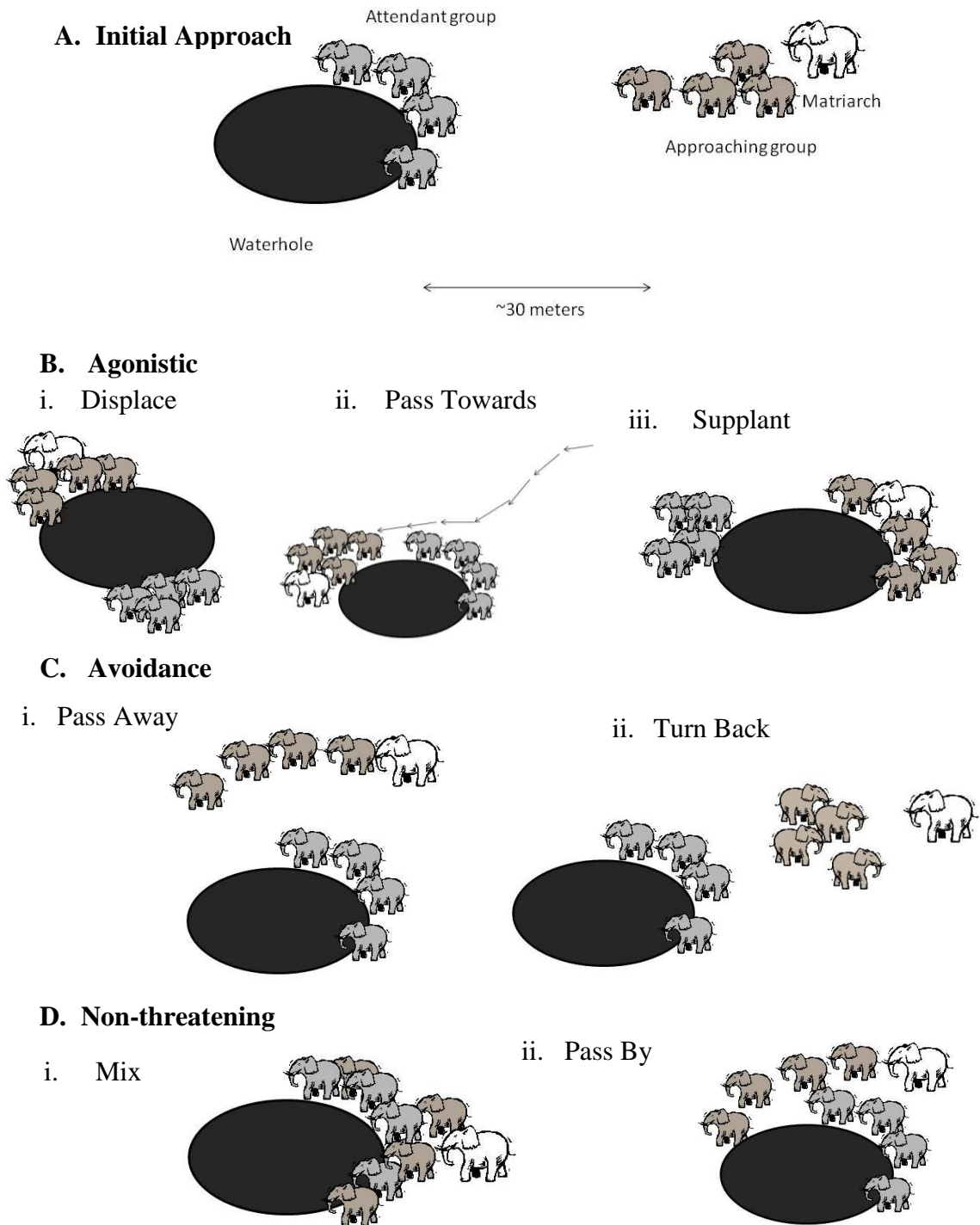


Figure 1.1. Diagrams of observed group interactions at AENP in 2007. For definitions, see Table 1.3. A. Initial approach corresponds to all interactions. B.i-iii agonistic, C.i-ii avoidance, D.i-ii. non-threatening.

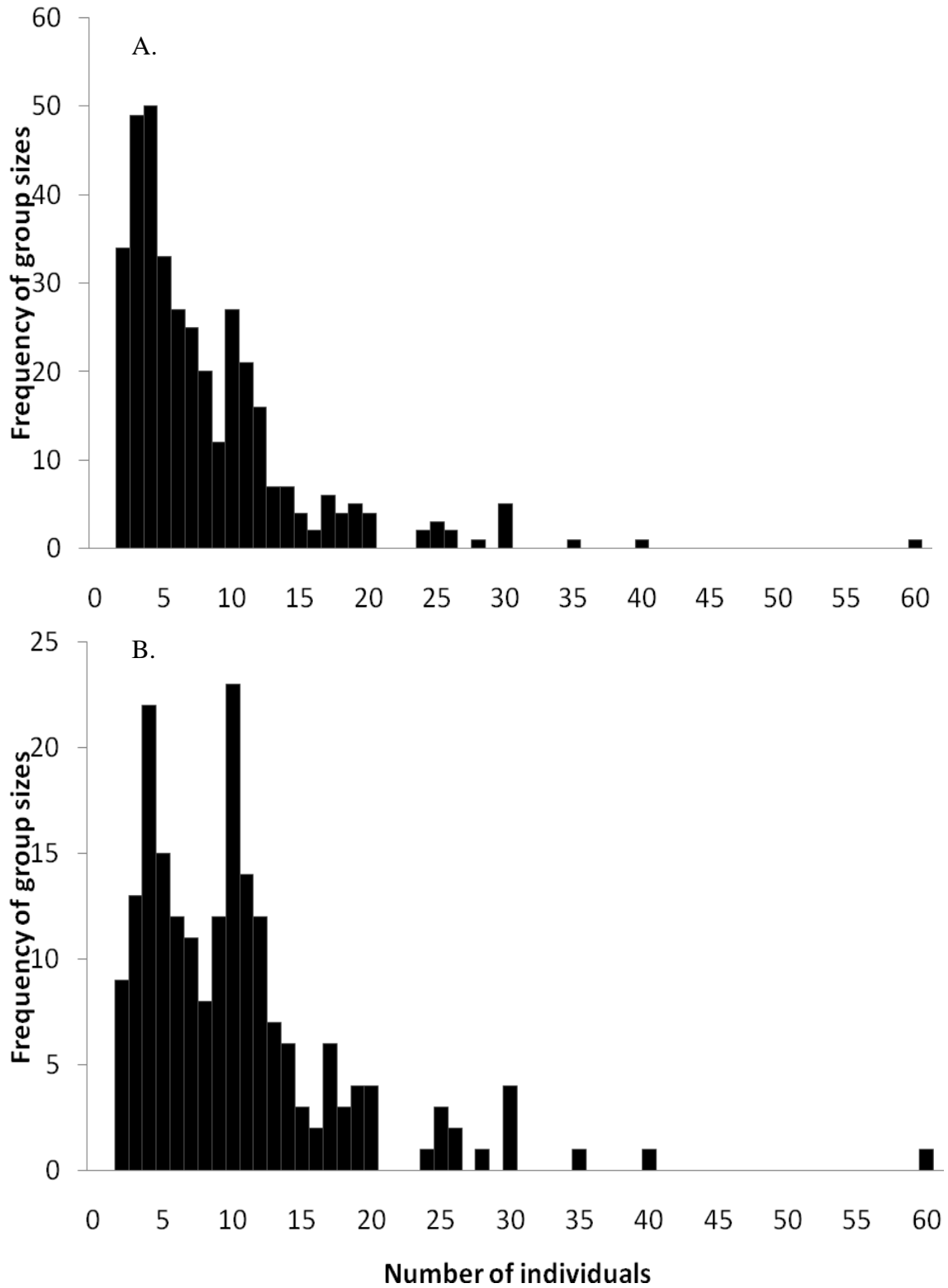


Figure 1.2. Frequency of A. all (n=371, mean=8.5, SE=0.5) and B. matriarchal (n=189, mean=9.95 SE=0.5) group sizes of African elephants families on approach to a waterhole at ANEP South Africa in 2007.

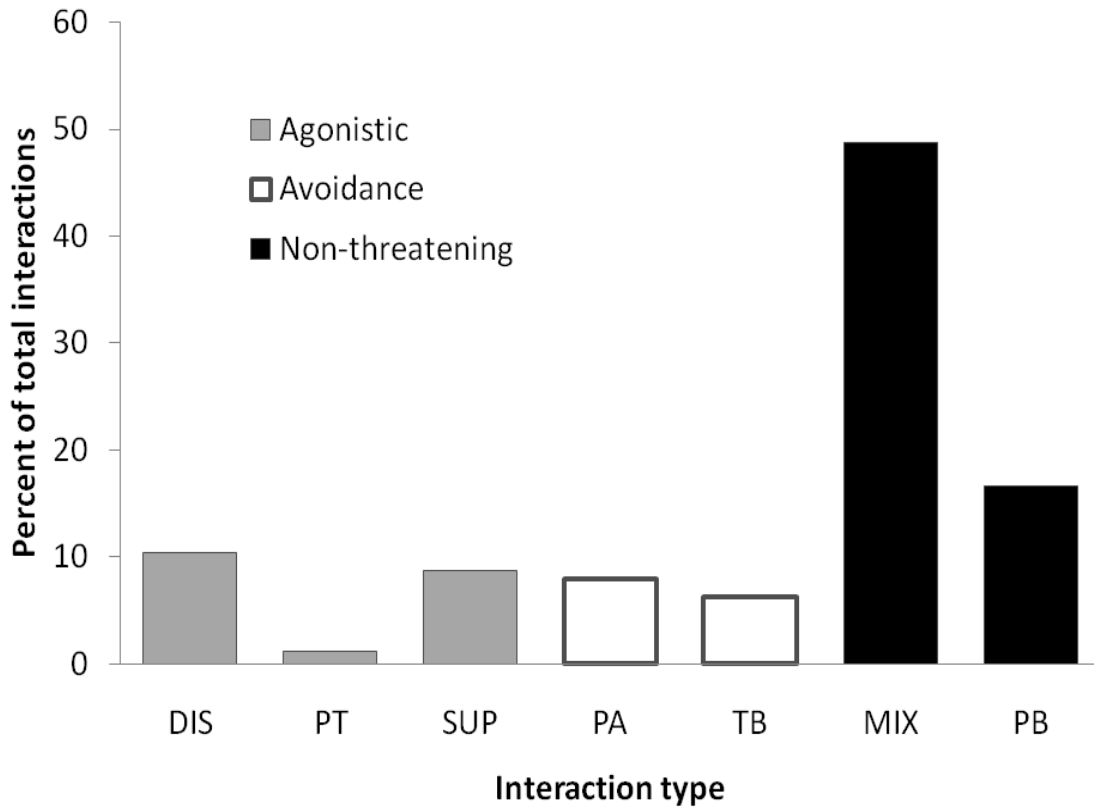


Figure 1.3. Percent (n=240) of observed group interactions between African elephant families at ANEP South Africa in 2007. Most group interactions were non-threatening, with mix being the most common (48% of total).

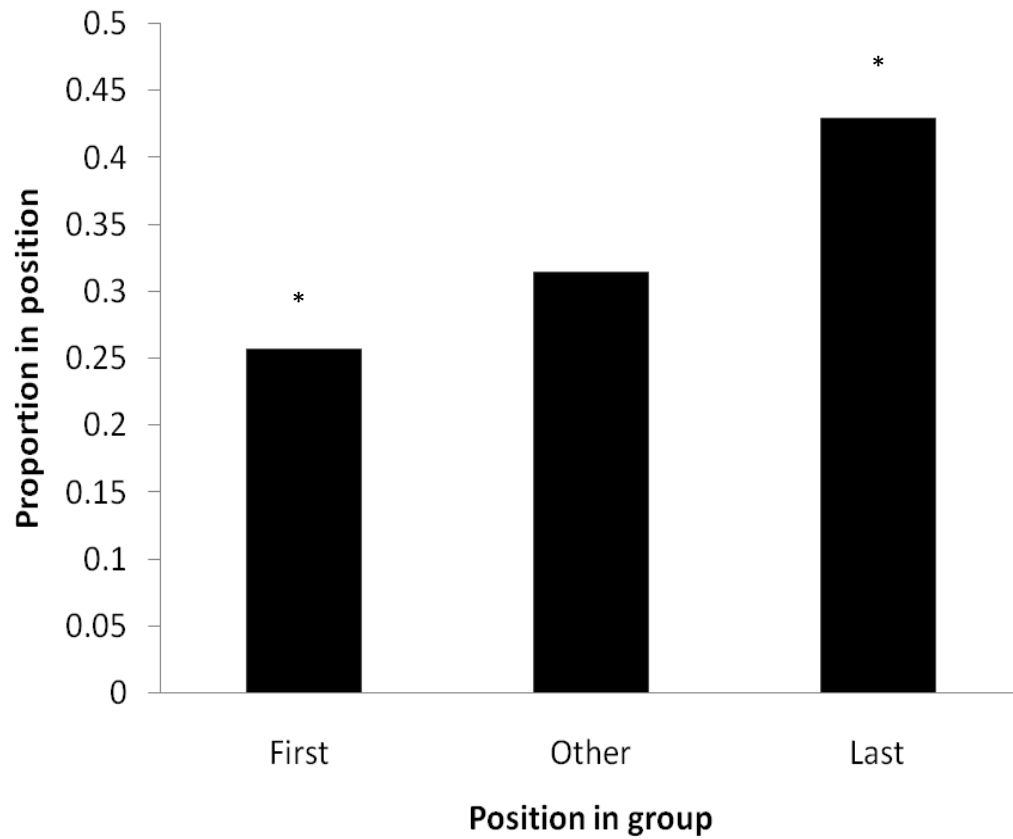


Figure 1.4. Proportion of positions (n=189) of African elephant matriarchs in the family group upon entering a waterhole at ANEP South Africa in 2007. Matriarchs were last in 43% of observed entries.

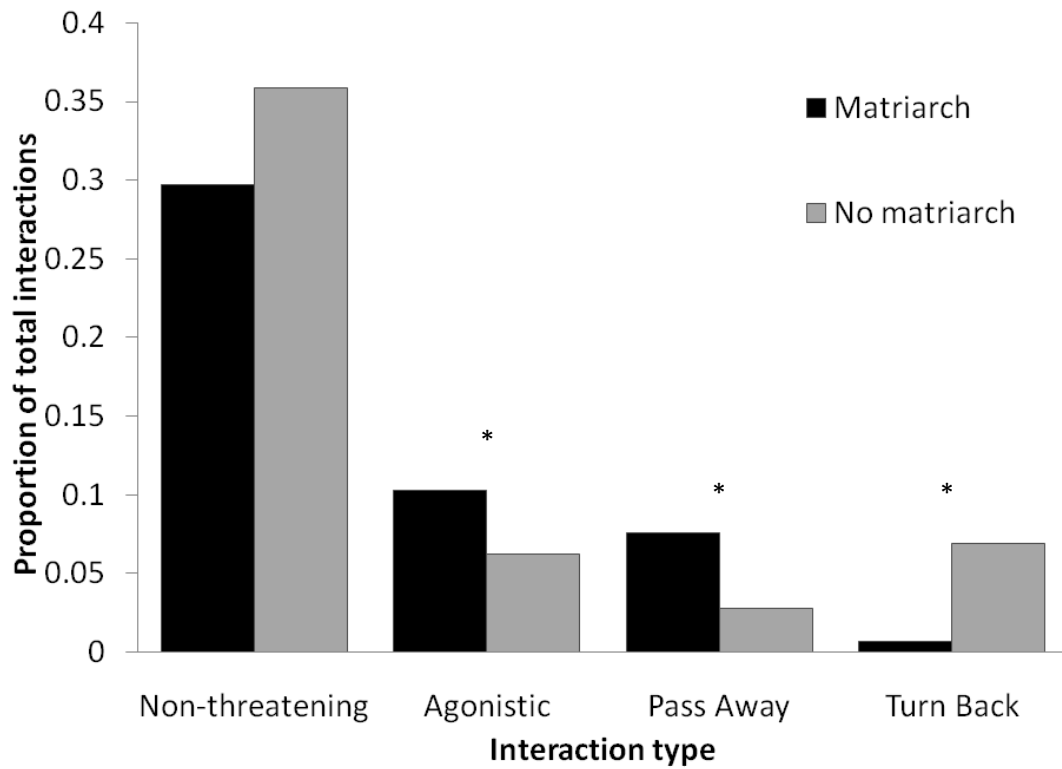


Figure 1.5. Proportion of total group interactions (n=145) between families of African elephants at ANEP South Africa in 2007 with and without a matriarch present in the approaching group. Matriarch groups passed away (Fig1.2f), whereas non-matriarchal groups turned back (Figure1.2.e) when approaching another family.

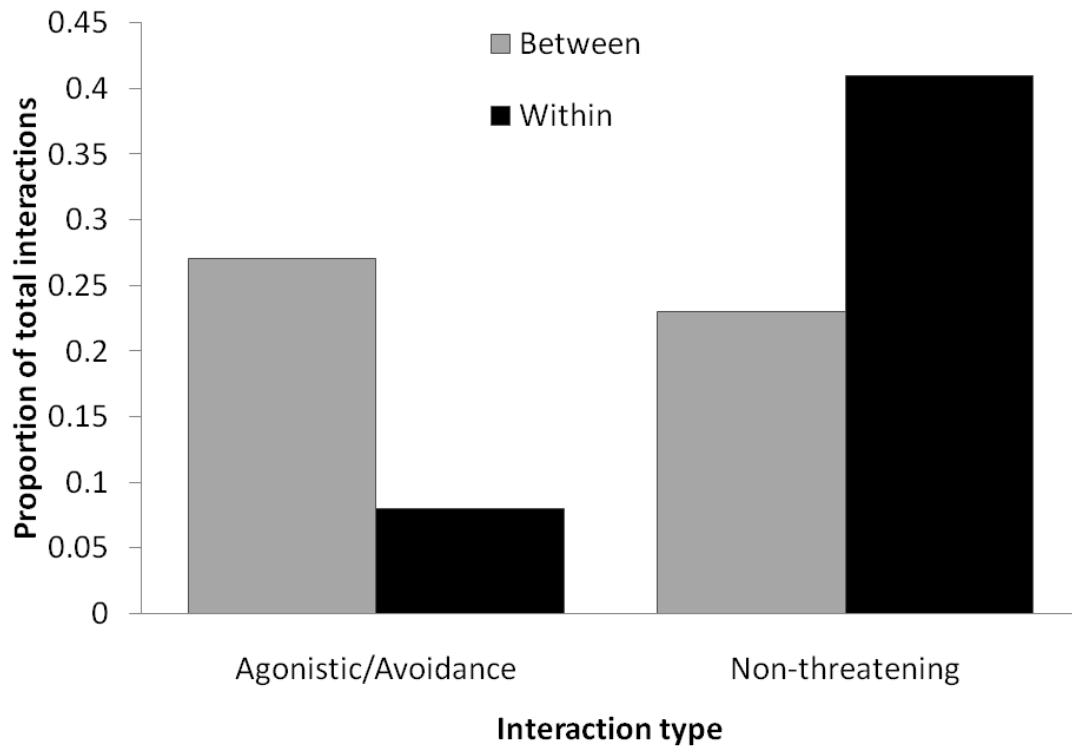


Figure 1.6. Proportion of group interactions (n=95 between, n=94 within) involving families from different (between) and the same (within) kinship groups of African elephants at ANEP South Africa in 2007. Agonistic/avoidance interactions occurred more between families from different kinship groups than families from the same kinship group.

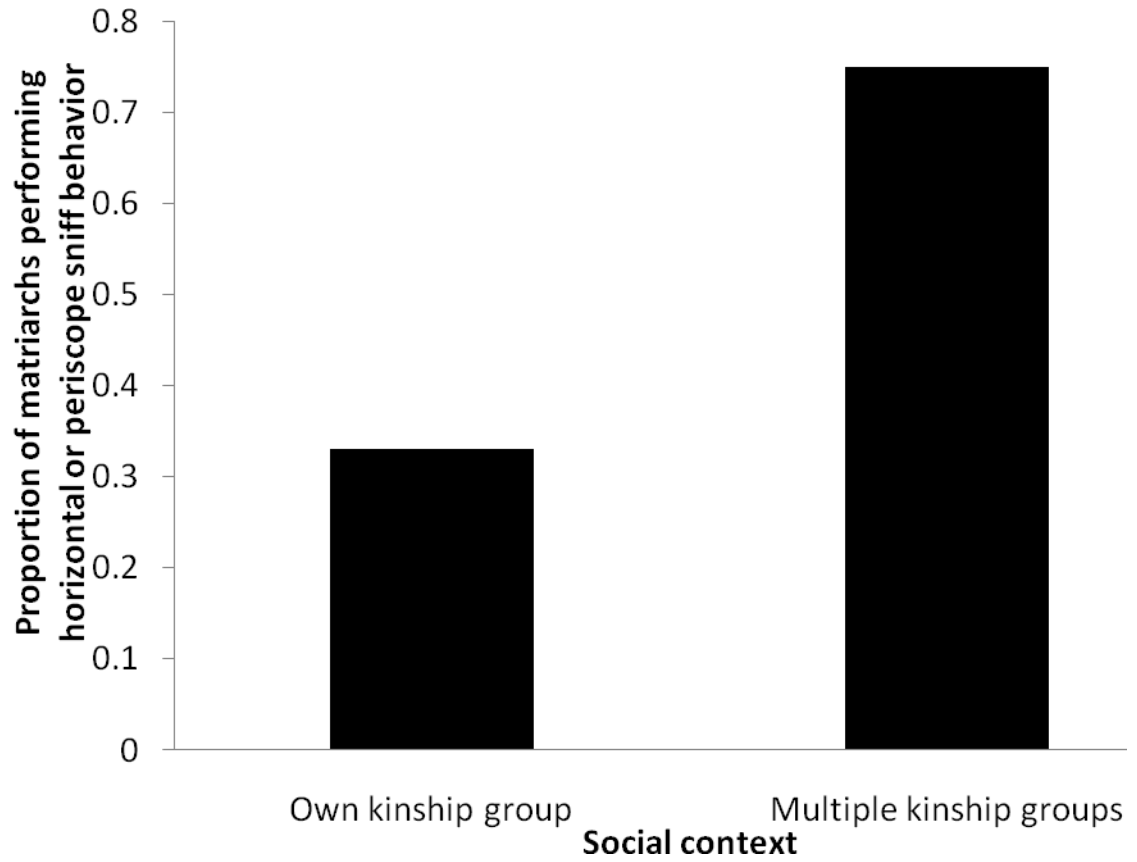


Figure 1.7. Proportion of African elephant matriarchs (n=24) performing long-distance chemosensory behaviors (horizontal or periscope sniff) in different social contexts at ANEP South Africa in 2007. More matriarchs performed these behaviors when multiple kinship groups were present at the waterhole.

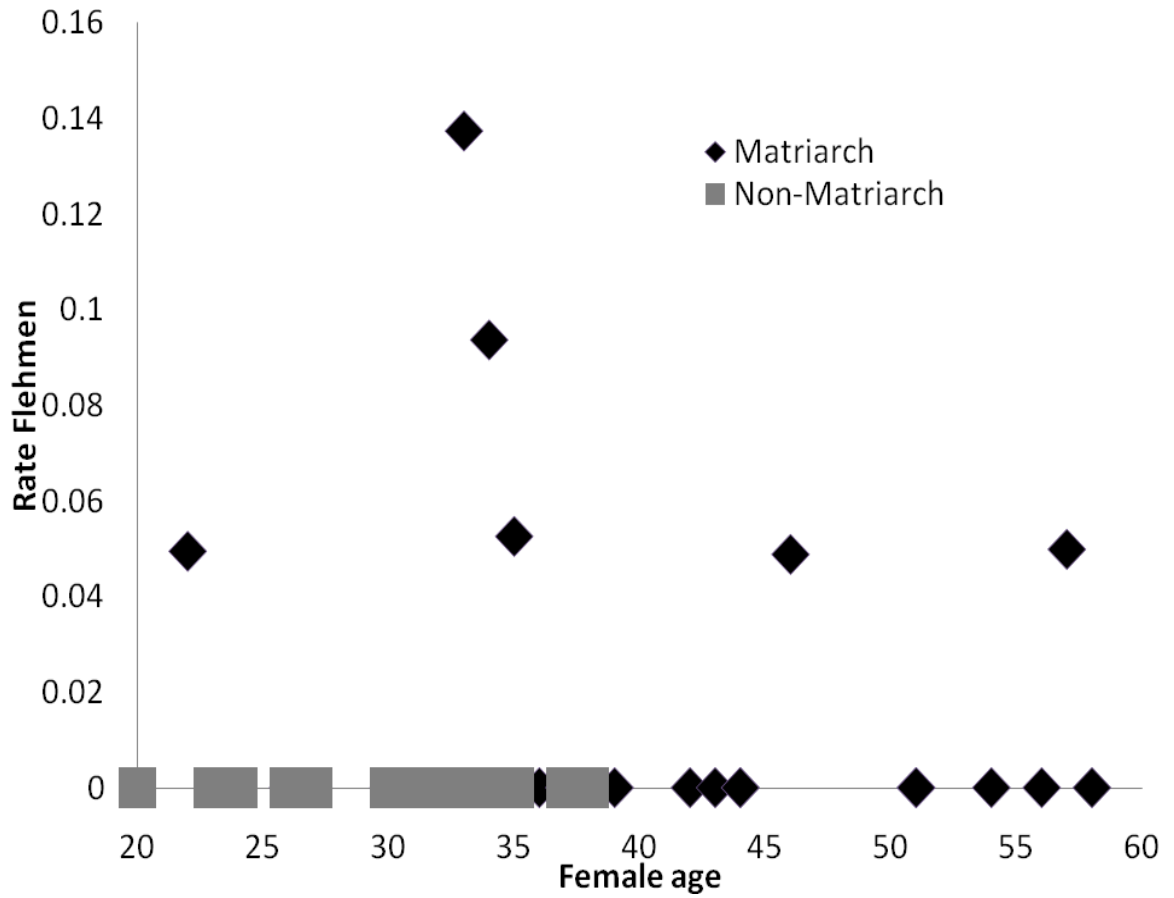


Figure 1.8. Rate of flehmen behaviors from matriarchal and non-matriarchal female African elephants at ANEP South Africa in 2007. No non-matriarchal females performed flehmen behaviors over the 10-min focal observations.

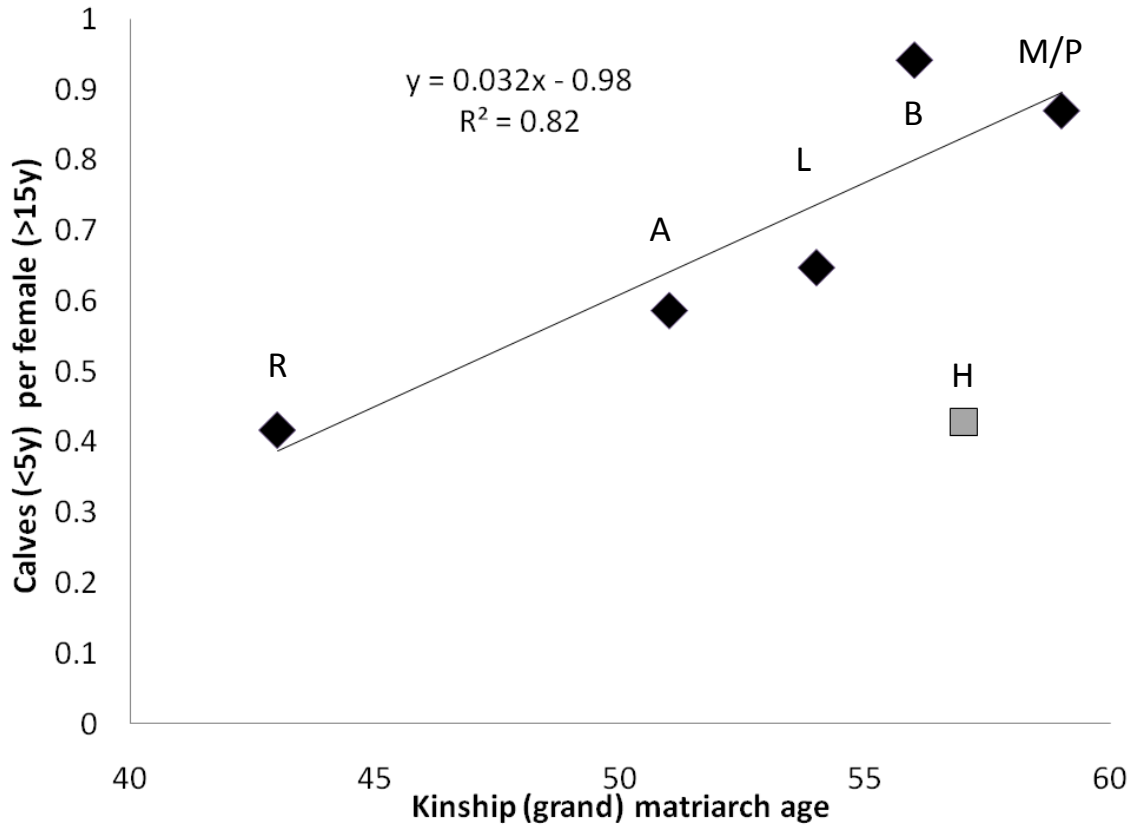


Figure 2.1. Calf-to-post-puberty female ratio (number of calves to post-puberty [>15 y] females) compiled over five years by grand matriarch age for kinship groups (indicated by letters) at AENP South Africa in 2007. Grand matriarch age significantly predicted the calf-to-female ratio ($F=13.87$, $df=1,3$, $p=0.034$). The H-group was composed of only a single family, so it was excluded from analysis.

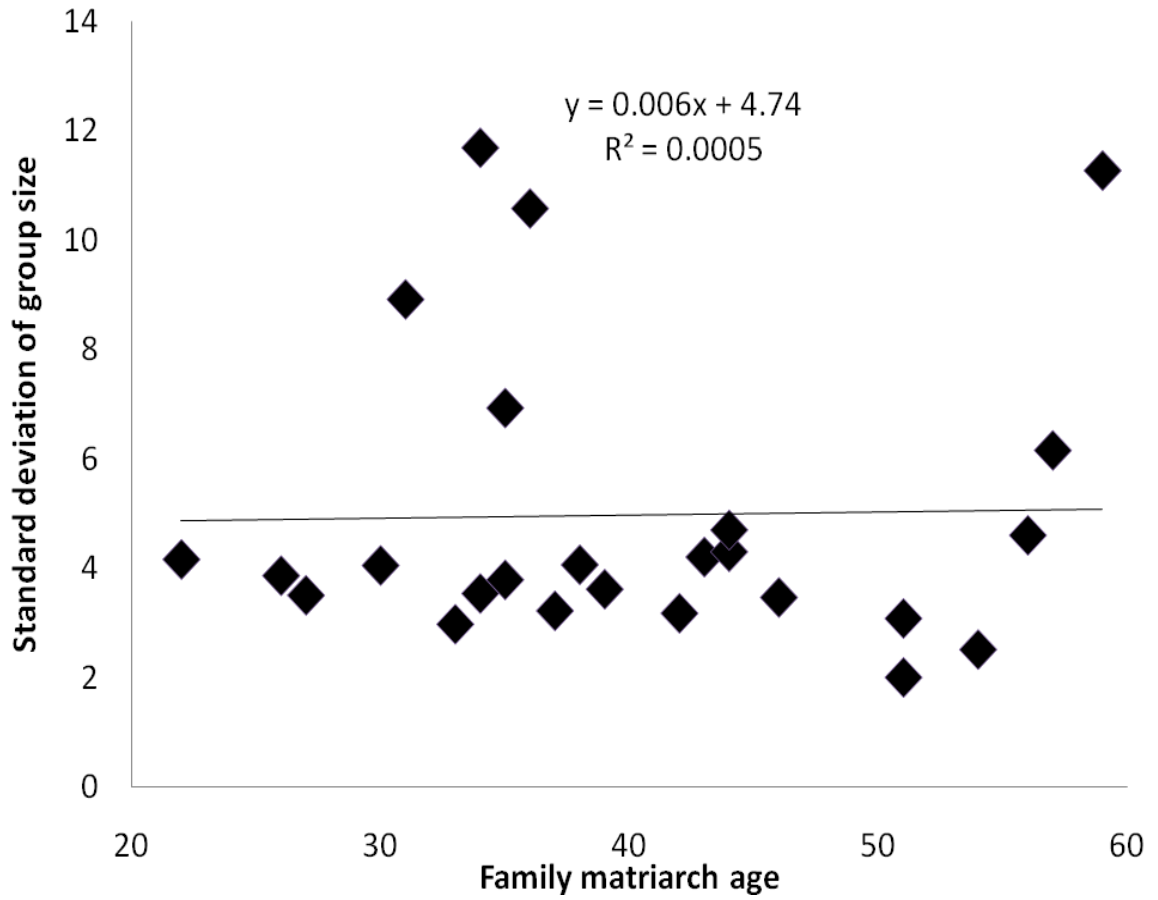


Figure 2.2. Coefficient of variation for family groups by family matriarch age during behavioral sampling of group entries at AENP South Africa in 2007. Matriarch age did not predict the coefficient of variation for family groups ($R^2=0.031$, $F=0.59$, $df=1,22$, $p=0.45$).

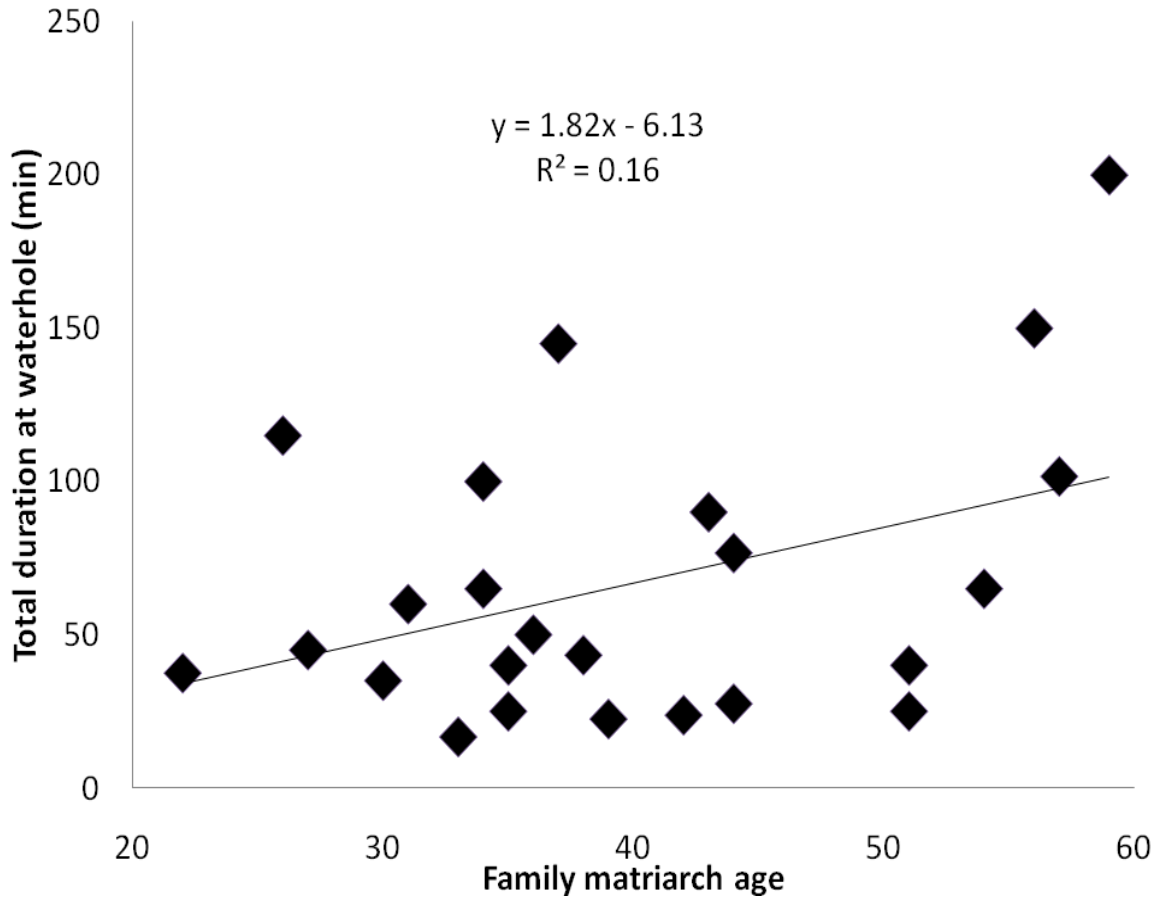


Figure 2.3. Total time (min) spent within 500 m of the waterhole by family matriarch age during scan sampling of family groups at AENP South Africa in 2007. Matriarch age weakly predicted the time spent near the waterhole ($R^2=0.16$, $F=4.10$, $df=1,22$, $p=0.055$).

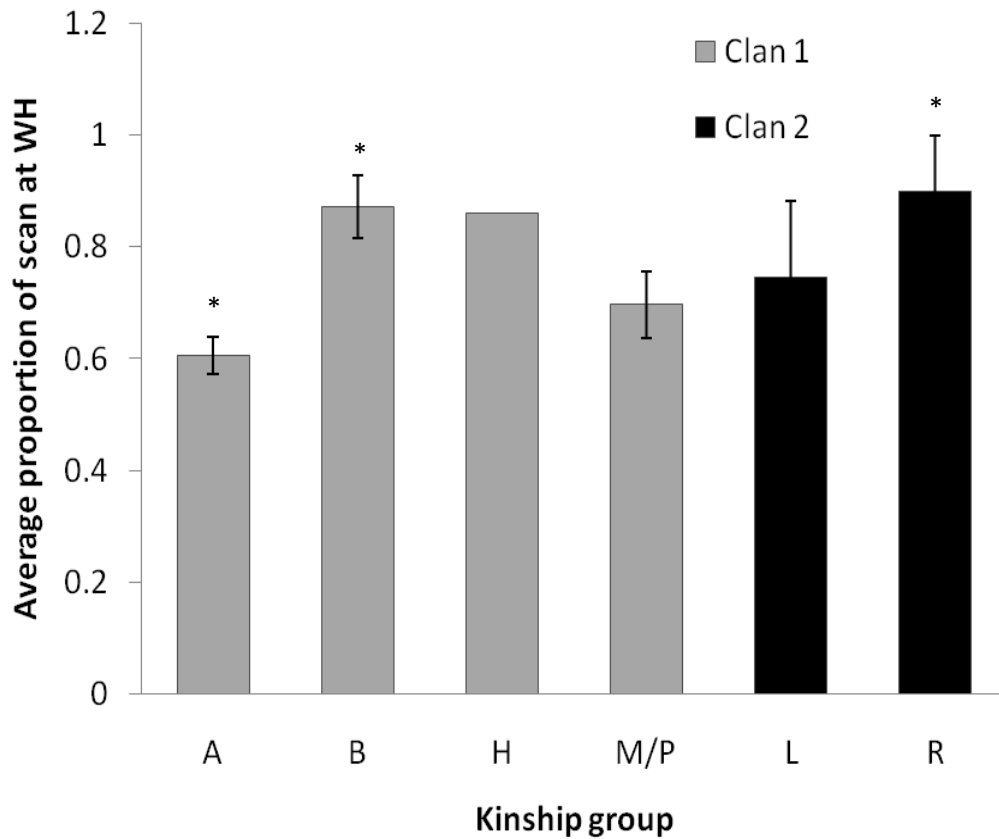


Figure 2.4. Average proportion of time spent in the immediate vicinity of the waterhole during scan sampling of family groups at AENP South Africa in 2007. Groups were significantly different in the proportion of scans observed at the waterhole ($F=3.5$, $df=4,18$, $p=0.028$) with the A group exhibiting a difference between the B and R groups (Tukey post hoc, $\alpha=0.05$).

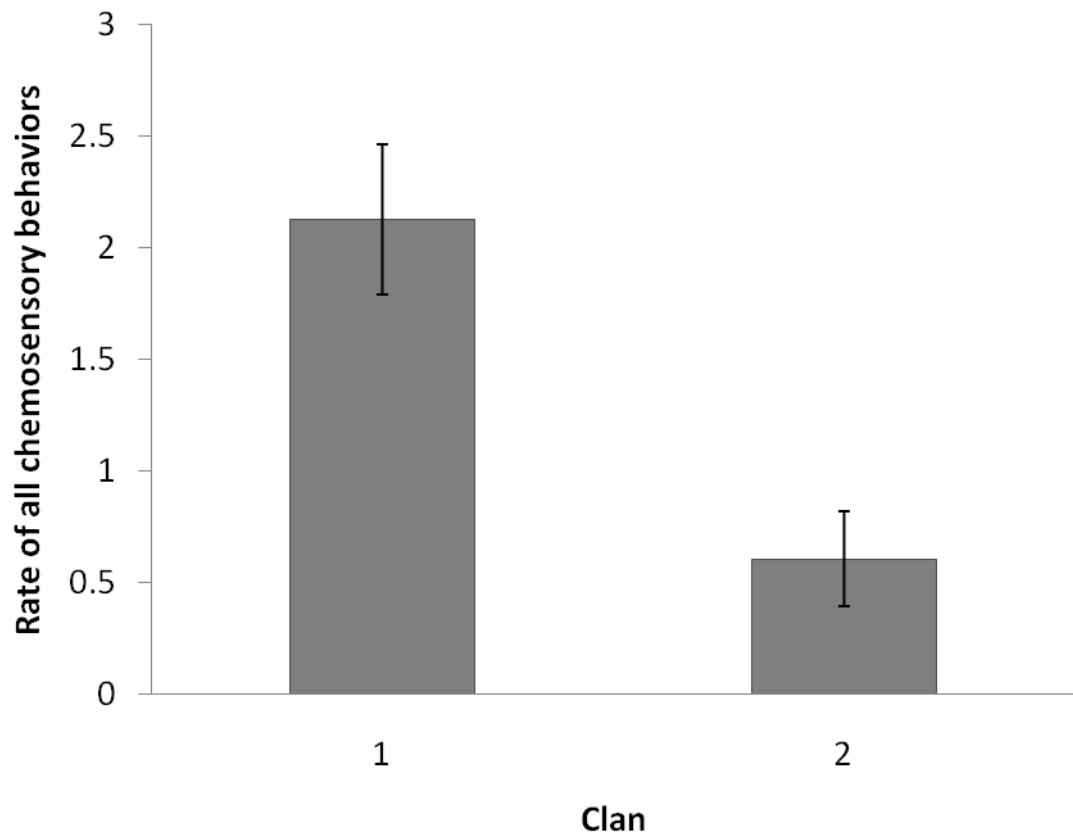


Figure 2.5. Rate of total chemosensory behaviors for adult females at AENP South Africa in 2007. Females in Clan 1 performed a higher rate of chemosensory behaviors than females in Clan 2 ($t=2.68$, $df=42$, $p=0.01$).

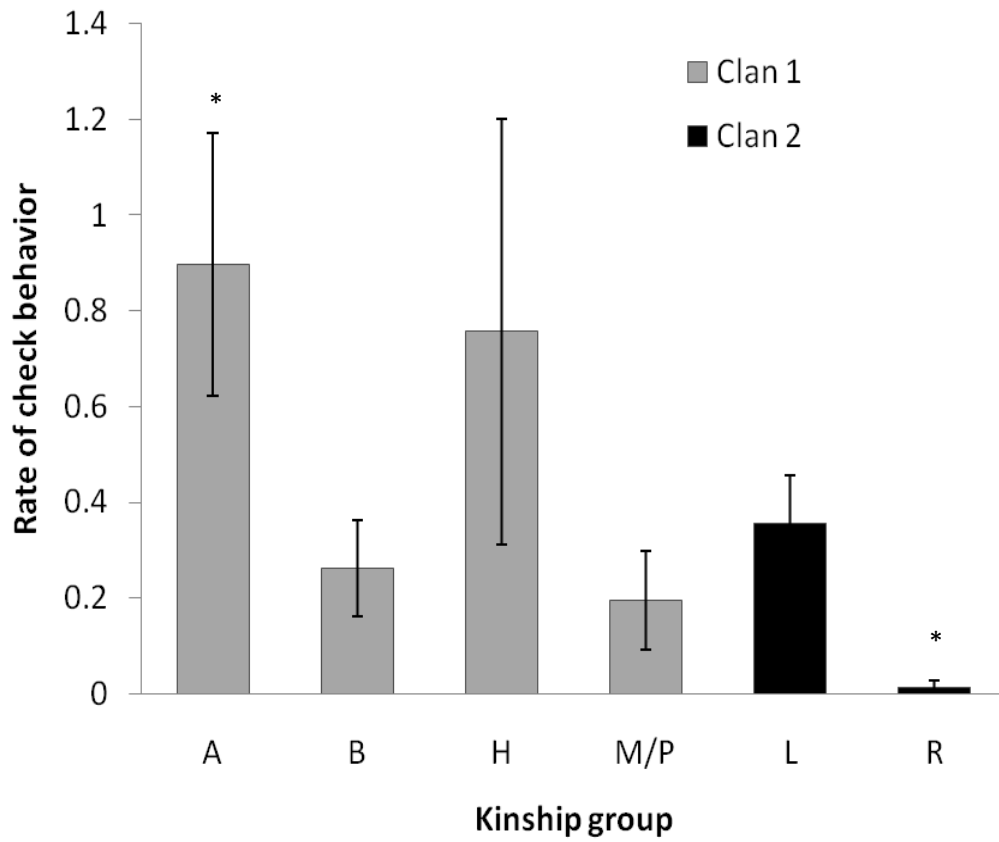


Figure 2.6. Rate of check behaviors for adult females (>20y) in kinship groups at AENP South Africa in 2007. The A-group performed significantly more check behaviors than the R-group ($H=12.64$, $df=5$, $p=0.027$, Tukey post-hoc, $\alpha=0.05$).

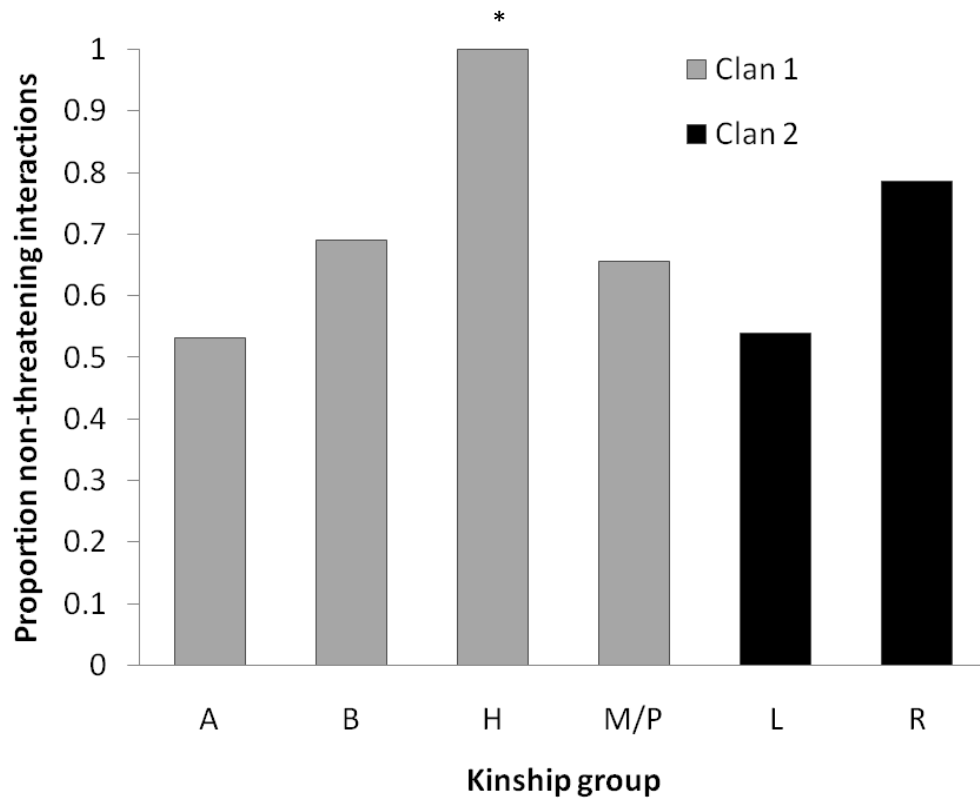


Figure 2.7. Proportion of non-threatening approaching group interactions for families in kinship groups at waterholes at AENP South Africa in 2007. The groups differed significantly in the proportion of non-threatening interactions ($\chi^2 = 14.34$, $df=5$, $p=0.013$). (See Table 1.1 for definition of non-threatening).

APPENDIX A. COMPLETE ETHOGRAM

Table A.1: Ethogram to record state behaviors performed by wild African male and female elephants during focal continuous observations.

State Behaviors	Definition
Chasing	One elephant is pursuing another
Defecate	Release feces
Dig	Using trunk, foot, or tusk to dig into ground, resulting in substrate being shifted
Stand	Remains in the same location for at least two seconds with none of the following trunk behaviors observed
Suckle	Nipple contacts separated by less than 30 s of time off nipple (Lee 1986)
Urinate	Release urine
Walk	Leaves location while all four legs are moving in a steady pace with none of the following trunk behaviors observed
Trunk Behavior	
Drink	Taking water into the trunk and immediately placing water into the mouth
Eat	Taking nutrients into the mouth via the trunk
Object Play	Using the trunk to manipulate an inanimate object or splashing the tip of the trunk into water
Rest trunk	Placing approximately ¼ of the lower trunk on the ground and allowing it to remain there for at least two seconds
Sparring	Entwine trunks/tusks and push against another
Care	
Dust	Using the foot or trunk to place dirt particles on the body
Lay	One side of the torso in contact with the ground
Mud	Using the trunk to throw mud particles on the body or moving body rapidly in a mud hole
Other	Other behaviors observed, but not listed in ethogram
Not Visible	Elephant has moved out of sight

(Compiled by H. Loizi and K. Bagley; additions from Schulte & Rasmussen 1999, Slade et al. 2003, Ortolani et al. 2005 where noted)

Table A.2: Ethogram used to record event behaviors performed by wild African male and female elephants during focal continuous observations.

Event behavior categories and defined event behaviors	Definition
<i>Trunk to Ground Substrate or Conspecific</i>	
Check*	Touch ground with tip of either finger
Flehmen*	Tip of trunk touches substrate or conspecific then placed in the VNO ducts in the roof of the mouth
Flick Trunk	Flick trunk tip out from body
Horizontal sniff	Trunk raised parallel to ground, sniffing air
Periscope sniff	Trunk raised above head, sniffing air
Pinch	Tips of trunk touch each other
Place*	Entire nasal opening is placed on ground or conspecific and held momentarily
Rub	Trunk in place position and moved in a circular motion
Sniff*	Nasal openings hover over ground or conspecific without contact
Trunk shake	Shake trunk
<i>Trunk Tip to other Female/Male</i>	
Anus	Anal region underneath tail of elephant
Genital	Penis or vulva region between rear legs of elephant
Body	Torso or areas not listed
Head	Forehead and superior most point of head
Mouth	Area around and/or inside maxilla and mandible (e.g. lips, jaw, etc.)
Temporal gland	Point of TG secretion on side of head in front of ear
Trunk	Portion of trunk starting from mouth area, down to tip
Feet	Area below ankle
Tail	From the base of the tail to the tip of the hairs
Ears	External entrance to ear canal, including hairs projecting from opening (Slade et al.)
Legs	From hip or shoulder to ankle
Tusk	Contact to the visible tusk
<i>Body Contact to Females/Males</i>	
Back into	Intentionally walks backward into the body of another individual
Body rub	Using the torso to brush against another individual's torso
Present	Turn backside toward another

Lean	Focal animal placing body weight on the body of another individual
Trunk on Head	Placing the entire length of the trunk on the head and holding position for at least two seconds
Trunk over Back Resting	Placing trunk on the back and rests it there for at least 2 sec. while stationary (1-2 steps allowed)
Trunk over Back Driving	Placing trunk on the back and pushes forward (both moving for more than 2 steps (Ortolani et al. 2005))
Head butt	Quickly using the head to make contact with the body of another individual. (Slade et al. 2003)
Push	Using the body to displace another elephant from their location
Kick	Using legs to strike at another
Mount	Standing on hind legs, forelegs resting on body of a standing elephant
Rolling	One elephant is on the ground, while other is on top
Leg Grab	Trunk wrapped around another individual's leg, exerting force (Ortolani et al. 2005)
Trunk Wrap	Trunks are intertwined
Tail slapping	Lift tail erect then slap it between own legs into genital area (Slade et al. 2003)
Tail grab	Trunk wrapped around tail, pulling
Tail touch	Using the tail outstretched to touch another elephant
Incidental	Any contact that is not intentional

*Chemosensory definitions derived from Schulte & Rasmussen (1999)

APPENDIX B. NON-SIGNIFICANT BEHAVIORAL SIGNATURE ANALYSES

Table B.1: Statistical table for non-significant state and event behaviors recorded during scan sampling with instantaneous recording and focal sampling with continuous recording at AENP South Africa in 2007.

Comparison	Behavior	Analysis	Statistic	df	p-value
Family waterhole state behaviors within kinship groups	Drink	ANOVA	F=0.88	5,18	0.51
	Mud	ANOVA	F=0.92	5,18	0.49
	Stand	ANOVA	F=0.45	5,18	0.80
	Walk	ANOVA	F=0.63	5,18	0.68
Family waterhole state behaviors within clans	Drink	t-test	t=1.54	22	0.14
	Mud	t-test	t=0.36	22	0.72
	Stand	t-test	t=0.27	22	0.79
	Walk	t-test	t=1.46	22	0.16
Chemosensory event behaviors of pre-adults within kinship groups	Sniff	ANOVA	F=1.02	5,39	0.42
	Check	ANOVA	F=1.24	5,39	0.31
	Total chemo	ANOVA	F=0.84	5,39	0.53
Trunk-to event behaviors of adult females within kinship groups	Body	ANOVA	F=0.61	5,38	0.69
	Genital	ANOVA	F=1.04	5,38	0.41
	Head	ANOVA	F=1.04	5,38	0.41
	Mouth	ANOVA	F=0.33	5,38	0.88

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