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Age Effects on Social and Investigative Behaviors in a Closed Population of African Elephants

Christen Eileen Merte
Georgia Southern University

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AGE EFFECTS ON SOCIAL AND INVESTIGATIVE BEHAVIORS IN A CLOSED
POPULATION OF AFRICAN ELEPHANTS

by

CHRISTEN E. MERTE

(Under the Direction of Bruce A. Schulte)

ABSTRACT

In this study of African elephants (*Loxodonta africana*), I examined two competing hypotheses to explain the development of social and reproductive behaviors. The reproductive hypothesis states that behaviors change around the time when an individual begins successfully reproducing, while the social dominance hypothesis states that behaviors change throughout the life of an individual, reflective of changes in social rank. These hypotheses were explored in male and female elephants during the entry to a signal-rich waterhole and in female African elephants across seasons. Chemosensory and social behaviors were recorded in Addo Elephant National Park between May 2004 and June 2005 using focal animal sampling. During the approach to a waterhole, investigation of chemical signals differed by age and sex. The social dominance hypothesis was supported by the proportion of sniffs performed to feces, while the average rate of sniffs supported the reproductive success hypothesis. Social behaviors changed between the younger (calf - juvenile) and older (pubescent - adult) stages for females, and most behavioral measures supported the reproductive success hypothesis. Raised sniffs and aggressive behaviors supported both hypotheses, suggesting that social dominance and reproductive success may interact to affect the development of social and investigative behaviors for African elephants.

INDEX WORDS: African elephant, Chemical signal, Chemosensory, Communication, Development, *Loxodonta africana*, Seasonal effects, South Africa

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CHRISTEN E. MERTE

B.S., Michigan State University, 2002

B.A., Michigan State University, 2002

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Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

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CHRISTEN E. MERTE

Major Professor: Bruce A. Schulte

Committee: James B. Claiborne
Lorne M. Wolfe

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CHAPTER I
CHEMOSENSORY BEHAVIOR OF AFRICAN ELEPHANTS ON APPROACH TO A
WATERHOLE

Introduction

Dominance and reproductive success are important factors impacting when and how an individual develops communicative behaviors. The importance of dominance can be seen in spotted hyenas, where social rank is inherited and young hyenas display different behaviors depending on where they fall in the hierarchy (Holekamp and Smale 1998). The effects of reproductive maturity are evident in many mammals, where changes in chemosensory behaviors or odor preferences occur once the animals reach a certain age, such as puberty (Crowell-Davis and Houpt 1985, Solomon and Rumbaugh 1997). These two factors also may be interlaced such that dominance is correlated with lifetime reproductive success (Cote and Festa-Bianchet 2001, Clutton-Brock et al. 1986). Higher rank may yield greater reproductive success; or, more successful individuals may rise in rank. Because African elephants (*Loxodonta africana*) display sexual dimorphism in the timing of reproductive success and live in a ranked society that is separate for the sexes, they are good subjects for investigating the roles of social dominance as well as sex differences in the development of behavioral responses.

Social dominance or rank is an important factor affecting the behavior of many mammals. A dominance hierarchy is established and maintained by communication between individuals, and such behaviors may be displayed at a young age. For instance, wolves develop postural cues indicative of status early in life (McLeod 1996). African elephants also utilize dominance within their sexually dimorphic social systems. Males

are either solitary or loosely associated with other males, contacting females primarily for breeding (Poole 1989b, Poole and Moss 1989). In contrast, females live in family units composed of female relatives and their offspring of various ages (Moss 1988, Poole and Moss 1989, Wittemyer et al. 2005). Both sexes grow throughout their lives (Poole 1994), so age and size are strongly correlated. Intrasexual size-based dominance hierarchies exist for both sexes (Poole 1994, Archie et al. 2006a). Dominance for males is also influenced by musth, a state characterized by higher testosterone levels and aggression than in non-musth bulls (Poole and Moss 1981, Poole et al. 1984, Rasmussen et al. 2002, Ganswindt et al. 2005). In Asian elephants, males emit different musth signals based on their age. Young post-pubescent males emit a honey-like *moda* or immature musth signal, allowing them to avoid conflicts with larger bulls, whose musth odor is pungent (Rasmussen et al. 2002). These rank changes with increased size also may be influenced by the transition from pre-reproductive to reproductive status.

Reproductive maturity may occur at different times for males and females. In elephants, both sexes live with the family unit for the first ten years of their life, and thereafter the social systems begin to diverge. Upon weaning, male calves spend more time further from their mother than females (Lee 1986), beginning the gradual process of separation until dispersal. Between the ages of 12-15 years, males have separated from their family as they transition into adult society (Poole 1994). Both sexes are capable of producing viable gametes between 9 and 15 years of age (Moss 1988, Poole 1994). Yet, females in the wild begin producing calves between 10 -16 years (Poole 1994, Whitehouse and Hall-Martin 2000), while males are unable to compete successfully for mates until they reach the ages of 20 - 25 years. Males may not father offspring until

between 30-35 years of age (Moss 1988, Poole 1994), reaching peak reproductive success from the ages of 40-55 years (Hollister-Smith 2005). Thus, males and females achieve reproductive success at different points in their life. When females are birthing their first calves, they are likely reproducing with males over twice their age, suggesting that the use of “adult-like” communication has occurred at different rates in the sexes.

While many modes of communication can be used to locate and identify potential mates, chemical signals often are reliable indicators of identity, reproductive state, or overall condition and health because they are linked to physiological condition (Kappeler 1998). Chemical signals can serve various functions, including reproduction (finding mates or triggering gamete production), assessing relative dominance, individual recognition, and maintenance of geographic spacing (Solomon and Rumbaugh 1997). A pheromone is a type of chemical signal that triggers a particular response in a conspecific (Karlson and Lüscher 1959, Wilson 1968) for both intra- and inter-sexual communication (Eisenberg and Kleiman 1972). In sexually dimorphic species, pheromones may have different importance to the two sexes, and this importance may either change throughout their lifetime or at a specific time, such as when they reach reproductive maturity. In adult elephants, sex differences exist in the investigation and production of signals. As Asian male elephants mature they become more adept at detecting female pheromones and using those signals to find and guard receptive mates (Rasmussen et al. 2005). Poole and Moss (1989) suggested that African elephant females seek out males by following urine trails. In addition, females prefer larger, older males as mates, and this preference increases when the male is in musth (Moss 1983, Hollister-Smith 2005). This difference in behaviors suggests that signal investigation behaviors will change as elephants age and

become reproductively active. Because the sexes are often spatially separate as adults, individuals are likely to seek out mates by investigating areas of common use, such as waterholes.

Many large and small mammals, including elephants, visit waterholes regularly, which are sites for contact between conspecifics and other species, as well as providing a central location for signal deposition through urination and defecation (Weir and Davison 1965, Ayeni 1975, Ritter and Bednekoff 1995). Urine and feces are recognized signal sources; they are used commonly by mammals such as elephants for inter- and intra-sexual communication, including advertising reproductive status or identity (Eisenberg and Kleiman 1972, Coblentz 1976, Ziegler et al. 1993, Poole and Moss 1989, Rasmussen et al. 1997, Rasmussen and Schulte 1998, Wyatt 2003, Bagley 2004). Waterholes are ideal locations for signaling among elephants because of the high probability of other elephants coming to the site, and thus good vantage points for studying investigatory behaviors by male and female elephants of various ages.

While the specific effects of dominance and reproductive success have not been explored, previous studies on African elephants at Addo Elephant National Park in South Africa found that there were differences between the sexes, and between different ages within each sex with regards to overall chemosensory behavior (Bagley 2004, Loizi 2004). For both sexes, a higher proportion of adult than younger animals investigated general environmental stimuli with their trunks, and the proportion of animals responding to urine and feces was highest in adult males (Loizi 2004). In a study examining only male elephants, calves performed a higher rate of some investigative behaviors than older animals (Bagley 2004). This result was not produced by a higher proportion of calves

performing the behavior, but rather by three individuals with very high rates (Bagley pers. comm.). These previous studies indicate that there are differences between both the ages and sexes in investigative behaviors. To further explore the age and sex differences in chemosensory investigative behaviors, I observed elephants as they entered signal-rich waterholes. My objectives were to examine sexual dimorphism and age-class developmental patterns of chemosensory investigations involving the trunk. For the sexual dimorphism objective, I determined if males and females differed in their rates of trunk behaviors. My prediction was that at whatever age class dimorphism was established, it would remain evident through the older age classes. In addition, I predicted that females would exhibit higher rates of investigation in general to all signal sources. Adult male elephants may develop more highly refined investigation skills to conspecific signals, which would be evidenced by an increase in investigation of feces and urine.

For the developmental objective, I investigated two competing hypotheses. The social dominance hypothesis predicts that response to signals would increase with rank as determined by an increase in age throughout their lifetime. This increase across the ages would enable competition avoidance and mate choice. The alternative, termed the reproductive success hypothesis, predicts that an increase in chemosensory behaviors would occur when an elephant begins producing offspring. In contrast to the change in responses across multiple ages predicted by the social dominance hypothesis, this hypothesis predicts a step function with a single change in response rates at the time of offspring production. As female elephants achieve reproductive success earlier in life, I expected their rates of chemosensory behavior to increase at an earlier age than males.

Methods

Study Site

The study was conducted in Addo Elephant National Park (AENP), 72 km NE of Port Elizabeth in South Africa's Eastern Cape region. All observations occurred in the main elephant camp, a fenced area of 13,500 hectares that contains approximately 360 elephants. Vegetation is primarily succulent thicket with some scattered grasslands (Paley and Kerley 1998). The park was established in 1931 with eleven African elephants from which the current population is descended (Whitehouse and Hall-Martin 2000). In addition, four adult male elephants were introduced in April 2002 from a population in Kruger National Park to increase genetic diversity (K. Gough, Nelson Mandela Metropolitan University, personal comment). All individuals in this population have been identified and recorded (Whitehouse 2001), and ongoing research adds current information about births and deaths, providing reliable age data for animals born since 1996 (Whitehouse 2001, Bagley 2004, Loizi 2004).

Data collection

Data were collected from May 2004 to June 2005. Average monthly rainfall for these months was not collected during the study, but was determined after by using the South African Weather Service website (SAWeather.com). This average monthly rainfall was used to categorize the elephants to check for any confounding effects of precipitation (Table 1.1). Samples were not distributed equally across the months for two age and sex combinations (Table 1.2). For the juvenile males and adult males, there were one or two months each that had a very high representation of the total number of focal samples. The rate of sniffs was compared between the high months and the other months, and no

significant differences were found (t-test: juvenile males $t_{16} = -2.01$, $p = 0.06$, adult males $t_{17} = 0.21$ $p = 0.84$). While for juvenile males the rate of sniffs was somewhat lower (2.12 ± 1.92 sniffs/minute) during the over-represented months than the others (4.31 ± 2.70 sniffs/minute), the variation was high in both periods.

Because fecal piles are a potential signal source, the number present at the time of the focal was recorded. A fecal pile consisted of a group of feces that appeared to be the same age, based on color and consistency, and located within a one-meter radius. If this fecal count was not conducted prior to entry of the elephants, it usually was conducted as soon as possible after, subtracting any known deposits made by the incoming group. Out of 135 days on which focal observations were conducted, fecal piles were counted on 124 days (91%). For the 150 focal observations at six waterholes, there were on average 87 ± 4.5 piles present (Table 1.3).

In addition to fecal piles, elephants entering with the focal animal or those present at the site already may emit chemical signals. As each focal animal was chosen, a count of the number of elephants entering with them was conducted. A running total was kept of elephants at the waterhole, so that the number present prior to the focal animal's entrance could be obtained. On average, 7.78 ± 0.63 elephants entered (range 1- 40 elephants), while 6.85 ± 1.09 elephants were present (range 0 - 50 elephants) during a focal observation.

Observations

Elephants were observed (primarily using binoculars) from a vehicle parked at a waterhole. Seven artificial waterholes are maintained with pumps throughout the year, while various others are ephemeral depending upon recent rainfall. For this study, it was

necessary to be able to view the elephant's trunk for the duration of the entry period. An abundance of vegetation at some waterholes made it difficult to view, so only six of the available sites were used. Over 65% of all observations were performed at one waterhole known as Hapoor (Fig. 1.1). Taking into account variation in the number of fecal piles at each site, there were no differences in the rate of behaviors between Hapoor and all other sites ($F_{1,150} = 0.03$, $p = 0.87$).

Elephants were categorized by sex and age, reflecting times of major social and developmental transitions. Age categories included calves from 0 - 4 years old, juveniles from 5 - 9 years, pubescents from 10 -19 years, and adults from 20 years and older. Calves are dependent on their mother for nutrition and rarely stray far; juveniles are weaned and begin to spend more time away from their mother; pubescent animals are physiologically capable of producing gametes and for females their first offspring; and adults rise in social and reproductive status, declining slightly after 50-60 years. All elephants were distributed evenly within age categories (Table 1.4), and females in the pubescent and adult stages were equally distributed with regards to reproductive status (Table 1.5).

As a group of elephants approached the waterhole region, one focal individual was chosen based on a previously determined random order for the eight possible combinations of age and sex. If one age/sex combination was not present, the next one available in the order was used. As the focal elephant walked toward the water, all behaviors performed were noted, as well as the substrates investigated, including urine, feces, ground, air, or water. While approaching the waterhole, the elephants were always

walking and touches to or from another elephant were not noted as they occurred very rarely (pers. observ.).

Other behaviors performed included trunk positions, such as down or curled, as well as any chemosensory investigation (Table 1.6). Chemosensory behaviors included three forms of sniffing, check, place, and flehmen. Because elephants walked quickly and were observed from a distance, any downward chemosensory behavior that could not be accurately determined was scored as a sniff. As a result, it is possible that some of these sniffs were actually “check” or “place” behaviors (Table 1.6). Sniff behaviors were distinguished by vertical levels of the trunk: a downward sniff was directed at the ground, horizontal sniff from above the ground to the height of the jaw, and a periscope sniff was directed at or above head level. Because horizontal and periscope sniffs were directed at the air, the source of the sniff could not be identified. For downward sniffs, the source was distinguished as either excrement (usually elephant feces and sometimes urine or the two combined) or non-feces (including ground, vegetation, and water).

Duration of the observation was calculated beginning when the elephants crossed an obvious landmark at each waterhole after which trunk movements could be clearly viewed. Measurements of these distances using a rangefinder for the start and finish points yielded an average of 93 m (ranging from 43 to 140 m, Table 1.3). Each observation was terminated when the focal animal reached the water and began either drinking or mudding. At times there was a large group of elephants present which obscured visibility as the elephants came within 1-2 body lengths of the water, and the observation was terminated when the individual was not visible.

Analysis

All behaviors scored were analyzed as rates (behaviors per minute). At times, it was difficult to identify elephants from a distance, so some individuals were sampled more than once. When this occurred, the two samples were averaged. All rates and proportions were tested for normality using the Kolmogorov-Smirnov test, and non-parametric analogs were used if the test failed. If the data were normal, two-way analysis of variance on age class and sex was performed using Statistica software (1999 edition, copyright 1995-1999 by StatSoft, Inc.). If a significant interaction was found between the variables, then either comparisons were made between the two sexes for each age class or the simple effect of age within each sex was examined. Unless otherwise noted, descriptive statistics are presented as mean \pm 1 SEM. For determining *a posteriori* significance between ages, Tukey's HSD test was used. All statistical tests used $\alpha=0.05$.

Results

Confounding variables

I first examined whether sniff responses varied because of the number of elephants entering, time to reach the waterhole, the number of fecal piles present, date of the focal, average monthly rainfall during each focal, and number of other elephants present during the focal. The number of elephants entering with the focal animal and the rate of horizontal sniffing showed no significant relationship (Fig. 1.2). The average time taken to reach the waterhole for all age and sex classes (2 sexes and 4 age classes) was 1.49 ± 0.07 minutes, and did not differ by rainfall ($N = 148$, $r = 0.01$, $p = 0.89$). Time to reach the waterhole differed among the four age classes but not between the sexes (Table 1.7, row 1). Adults took longer to reach the water than both juveniles and calves (Tukey

HSD: adult – calf $p = 0.02$, adult – juvenile $p = 0.0006$, adult – pubescent $p = 0.10$) (Fig. 1.3). Finally, the rate of all investigative behaviors ($14.7 \pm 1.1 - 20.9 \pm 1.6$ behaviors/min) differed with rainfall level (Table 1.1; $F_{2,121} = 8.75$, $p = 0.0002$; Tukey HSD Low - Moderate $p = 0.002$, Low -High $p = 0.001$, Moderate – High $p = 0.83$).

I compared the relationship between the number of fecal piles, date, and rate of sniffing (Fig. 1.4). The average number of fecal piles decreased over time, but was not correlated to the average rate of sniffs (to all stimuli). There was no correlation between either sniffs to feces or non-feces with date. As the number of fecal piles increased, the average rate of sniffs decreased, but the correlation explained little of the variation ($N = 206$, $r = -0.40$, $p < 0.0001$).

All elephants were walking during the entire focal, and trunk movements or positions were primarily trunk down or curled (Table 1.6). On average, $99.5\% \pm 1.82\%$ of all sampled elephants performed a trunk down, while $89.4\% \pm 3.08\%$ performed a trunk curl. Trunk shake was performed by $10.1\% \pm 3.41\%$, and all remaining behaviors were performed by less than 1% of the observed elephants. Contacts were not observed between the elephants, either through the trunk touching or the whole body, such as would occur in a pushing or rubbing incident.

Trunk position can be used as a gauge of whether all elephants had the same potential for sniffing, horizontal sniffing, and periscope sniffing, based on whether the trunk was pointed toward the ground or the air. All elephants had similar proportions of their total behaviors spent with the trunk either down ($36.6 \pm 2.9\%$) or curled ($16.8 \pm 2.8\%$)(Fig. 1.5). The average rate at which elephants performed each of the two trunk positions (trunk down, trunk curl) showed no difference by age class or sex (Table 1.7,

rows 2-3). All elephants, then, had the same potential for chemosensory behaviors directed at the ground (trunk down) and the air (trunk curl).

Sexual dimorphism

I predicted that differences between the sexes would manifest at some stage and then persist. Between 85% and 100% of the elephants in each age-sex category performed horizontal sniffs (Table 1.8). Since horizontal sniffs were directed at the air, a potential factor impacting their rates was the number and identity of any elephants already present at the waterhole (Fig. 1.6). When between one and fifty elephants were present the number of elephants present did not affect the rate of sniffs ($R^2 = 0.03$, $p = 0.30$), but this pattern changed when the data were analyzed separately for low (1-15 elephants) or high (15-50 elephants) numbers.

The rate of horizontal sniffs increased as the number of elephants present increased during focal observations on females but not for males when there were between one and fourteen elephants at the waterhole. This was impacted largely by a high rate of sniffing when 14 elephants were present, and may have been influenced by the lack of data when 8-14 elephants were present. All individuals sampled when 12 - 14 elephants were present were sexually mature elephants, and comparison with rates of behavior of younger animals was not possible. When more than 15 elephants were present, there was an increasing linear relationship, but it was only significant for males. This analysis compared four adult males and three younger males with four adult females and four younger, with between 1 – 20 elephants entering at the same time. Although there were not many elephants, they were representative of a variety of ages and different situations.

Social dominance hypothesis

The first developmental hypothesis tested was that behaviors changed with social dominance, which predicts differences in the investigatory trunk behaviors between each age class for both sexes. The overall rate per minute of horizontal sniffs performed by all age-sex classes were similar with means ranging from 3.41 ± 0.66 to 5.45 ± 0.65 (Table 1.7, row 4). The chemosensory behaviors most commonly observed were various types of sniffs, indicative of olfactory investigation. Other chemosensory behaviors, namely check, place, and flehmen, were rarely seen. For the 148 different elephants observed, $95 \pm 1.2\%$ performed one or more sniff behaviors (Table 1.8).

The average proportion of behaviors an individual performed that were sniffs partially supported the social dominance hypothesis, where age but not necessarily sex differences were predicted (Table 1.7, row 5). While not significant, there was a trend towards a sex difference as well, so further investigation is required. On average, sniffs composed a higher proportion of total behaviors performed for adults ($48.5 \pm 5.2\%$) than for calves ($33.8 \pm 5.6\%$) (Tukey HSD calf – adult $p = 0.03$). Overall, the average rate of sniffs to fecal piles was low (0.31 ± 0.06 sniffs per minute). Calves performed a lower rate of sniffs to feces than adults (Fig. 1.7; Table 1.7, row 6; Tukey HSD: calf – juvenile $p = 0.96$, calf – pubescent $p = 0.37$, calf – adult $p = 0.04$). Within the sexes, adult males performed a higher rate of sniffs than younger animals, yet no pattern was present for females (Table 1.7, row 6a-6b; Planned comparison among males: adult – calf, juvenile, and pubescent $F_{1,57} = 7.15$, $p = 0.01$). Both the proportion of elephants sniffing and the rate of actual sniffs support the social dominance hypothesis with changes between the

intermediate stage age classes indistinguishable from the previous age class but overall change from low in calves to high in adults.

The proportion of elephants that sniffed feces was low throughout all age classes, especially among calves and juveniles (6% - 13%). The number of individuals of all ages sniffing feces was too low to perform statistical analysis (4.6 ± 1.4 individuals, ranging from 1-13 individuals per age class), but some general trends were observed. For only those animals performing the behavior, among females the proportion of elephants increased between the juvenile (13%) and pubescent (33%) ages. For males, there were two increases in the proportion of elephants sniffing feces, between juvenile (11%) and pubescent (33%) age groups and then a large jump between pubescent and adult (72%) age groups. This pattern of differences between each age class supports the social dominance hypothesis.

Reproductive success hypothesis

Male and female elephants begin successfully producing calves at different ages, so this hypothesis predicts a change in behaviors at different points for each sex. The average rate at which elephants sniffed all substrates showed differences by both sex and age (Table 1.7, row 7). Males performed sniffs at a higher average rate (3.87 ± 0.32 sniffs per minute) than females (2.72 ± 0.32), and the increase in rates appeared to occur at a different point in development (Fig. 1.8). For females, calves sniffed less than all older elephants (Table 1.7, row 7a), while the rate of sniffs changed later for males, between the juvenile and pubescent stages (Table 1.7, row 7b). This supports the prediction of a single change of behaviors occurring at different ages for the males and females. Among only those elephants performing a sniff behavior (Fig. 1.9), there was

no significant interaction between age and sex, but males exhibited significantly higher rates than females (Table 1.7, row 8). The observed pattern of behaviors suggests that rates may be lowest for calves, but does not show a significant difference. Female calves exhibited lower rates of behavior than older females (Table 1.7, row 8a), but there was no difference between the age classes for males (Table 1.7, row 8b).

The reproductive success hypothesis also was supported by the proportion of elephants performing check and place trunk movements (see Table 1.6), which were performed by $4\% \pm 1.8\%$ of the elephants overall. Only one calf and no juveniles were recorded performing this behavior, so only sexually mature elephants could be compared. For adult and pubescent aged elephants, $7\% \pm 2.8\%$ of the animals performed a check or place; this percentage was largely driven by the pubescent (22%) and adult (17%) males. Only one pubescent female performed a place. Among those animals performing checks or places, four individuals (male and female) performed the behavior to feces; the proportion of total checks performed to feces was on average $6\% \pm 0.7\%$ (range 4.3% - 8.0%).

Periscope sniffs were performed by between 0 - 56% of the sampled elephants, depending on age class (Table 1.8). Because the trunk is raised above the head for periscope sniffs, elephants might access a different source of signals than when performing horizontal sniffs. Unlike the pattern for horizontal sniffs, there was no significant relationship between the rate of periscope sniffs and the number of elephants present for females (1-15 elephants present: $R^2 = 0.06$, $p = 0.37$; 16-50 elephants present: $R^2 = 0.27$, $p = 0.19$) or males (1-15 elephants present: $R^2 = 0.01$, $p = 0.74$; 16-50 elephants present $R^2 = 0.24$, $p = 0.26$). However, age and sex interacted to affect the rate

of periscope sniffs (Table 1.7, row 9). For females, juveniles performed the highest rate of periscope sniffs, whereas males did not differ by age class (Table 1.7, rows 9a – 9b) (Fig. 1.10). Juvenile females performed this behavior at approximately four times the rate of calf females and six times the rate of pubescent or adult females. While not supporting either original hypothesis, the juvenile stage is just prior to reproductive maturity, which is closer to the ideas of the reproductive success hypothesis than the social dominance. After combining horizontal and periscope sniffs into a ‘raised sniff’ category, age and sex effects were not apparent (Table 1.7, row 10).

Discussion

Distinct differences between ages and sexes were evident in the behaviors of elephants as they approached the waterhole. Of the possible repertoire of elephant behavior seen previously (see Bagley 2004, Loizi 2004, Schulte 2006 for ethograms), only a small group of movements were observed during the waterhole approach sequence. Most commonly noted were initial investigative behaviors such as sniffs, while more in-depth investigations such as check or place were exhibited infrequently. One variable that changed during the study was the number of fecal piles at a site. This number decreased with time. As the study progressed, rainfall occurred more frequently and to a greater degree, which would wash away feces and thus result in lower counts of fecal piles during observations. The lack of a decrease in sniffs over time could be because fresh fecal piles were still present, which are more likely to have signals of interest compared to older fecal piles.

Sex and age differences in behavior were supported. First, for both sexes adult elephants tended to take longer to reach the water than younger animals. This could

indicate that compared to younger individuals, older elephants are more carefully investigating their surroundings. Second, sexual dimorphism was evident in the rate of horizontal sniffing with respect to the number of elephants already present. Family sizes in AENP tend to be small (Whitehouse 2001), and group sizes between 1-15 elephants likely consist of only one or two families, possibly accompanied by some males. Females increased their horizontal sniffing when small groups were present, indicating interest in signals from up to one additional family and decreased interest or ability to investigate when larger groups were present. Males showed an increase in chemosensory behaviors when more than 15 elephants were present, but not with less than 15. With many elephants present, the signals may be more confusing (and potentially interesting), requiring more effort by the males to assess potential mates or competitors.

If social dominance is the primary variable impacting behavior, then the rate of chemosensory behaviors, including investigation of feces, would be greatest in the oldest, largest individuals. This hypothesis predicts a change in behavior between each age class with males showing both an earlier increase and overall higher responses than females. Loizi (2004) found that the proportion of elephants responding to feces increased to adulthood in males, and was higher overall for males than for females. The highest proportion of elephants performing sniffs to feces in my study was among the reproductively active males. This implies that potential chemical signals in feces, such as those indicating reproductive status, are more interesting and potentially relevant for adult males than for females and younger males.

The reproductive success hypothesis predicts that males and females should show an increase in the rate of behaviors when they begin producing offspring. Females begin

to reproduce between the ages of 10-16 (Poole 1994, Whitehouse and Hall-Martin 2000), considered part of the pubescent stage in the current study. Typically, males do not successfully reproduce until the adult stage (Poole 1994, Hollister-Smith 2005). Average rate of sniffs to all substrates increased from the calf to the juvenile stage for females, and for males the increase was from juvenile to pubescent. The increase in behavior was evident one developmental stage earlier than predicted for both sexes, which could indicate that the elephants are learning the behavior prior to needing to use it. Check and place behaviors were performed primarily by sexually mature males and females, supporting the reproductive success hypothesis. These behaviors may be associated directly with reproductive capability, but other studies with this same population of elephants have observed check, place and flehmen behaviors by calf and juvenile elephants (Bagley 2004, Loizi 2004); location and activity may explain this trend more than reproductive maturity or the factors may interact.

Finally, some behaviors did not clearly support either hypothesis. Calf and juvenile males may exhibit higher rates of sniffs than the females because they must learn which signals are important before dispersal, whereas females will have their families to learn from throughout their lifetime (Poole 1994). Asian elephants use signals to advertise their developmental status, and to avoid conflict between younger and older animals (Rasmussen et al. 2002). Younger male African elephants also may need to evaluate signals in order to avoid competition from older bulls. No differences were apparent in the rate of horizontal sniffs after accounting for the number of elephants present. Males and females of different ages also could be investigating different signals, as evidenced by the lack of differences in horizontal sniffs. Finally, there was no

difference in the proportion of elephants performing a sniff behavior, which indicates that all elephants were interested in sniffing something, but again makes no distinction about the signal source. The rate of periscope sniffs performed demonstrated differential effects for the ages and sexes. Only females showed a differential rate by age class as juveniles displayed the highest rate of periscope sniffs. Juveniles are the transitional stage between non-reproductive and reproductive females, and may have elevated interest in evaluating airborne cues (Poole 1994, Whitehouse and Hall-Martin 2000), such as the identity of nearby elephants. Males do not become reproductively active until much later (Poole 1994, Hollister-Smith 2005), when cues other than general airborne signals may be more relevant. When horizontal sniffs were combined with periscope sniffs age differences were not detectable, which merits further exploration.

Male and female elephants have different incentives and costs associated with learning which signals are relevant and important. Male elephants spend their formative years with their families (Lee 1986), exposed to breeding females and males. After leaving the family upon reaching pubescence (Poole 1994), they must rely mainly on their own skills to interpret the signals. Female elephants live with their families throughout their lives, and may still learn from their relatives after reaching pubescence (Moss and Poole 1983). However, females begin reproducing before males (Poole 1994, Hollister-Smith 2005), which may require them to assess reproductively relevant signals more quickly than males. Yet, once males have left the natal group, they will not have ready access to older, related individuals who may aid their learning. For males, mistakes about intrasexual signals related to competition for mates may be more costly than improperly assessing intersexual signals. Hence, the identity of the sender is an

important component, but one that is often difficult to determine, to understand the details of development in elephant chemosensory communication.

The initial 1-2 minutes on approach to a waterhole is not the only time that elephants will investigate signals; throughout their stay at the waterhole they are sniffing and investigating the situation. This study served to illustrate the initial responses, not the total array performed over an entire visit. One previous study showed differences in chemosensory behaviors primarily between males and females with some differences between age classes within each sex (Loizi 2004). A second study only on male elephants showed calves performing more flehmen behaviors than adults (Bagley 2004). By examining only the period of initial exposure, when any developmental differences may be magnified, a finer degree of clarification was achieved to examine the two developmental hypotheses of social dominance and reproductive success.

In many mammals there are behavioral differences between different ages and sexes (Thompson 1995, Solomon and Rumbaugh 1997, Holekamp and Smale 1998, Lonsdorf 2005). For elephants, behaviors begin to diverge between the sexes at a young age. Horses also show sexual divergence at an early age, as young males exhibit higher rates of flehmen than females of the same age (Crowell-Davis and Houpt 1985). In cattle, males increase the rate of flehmens upon reaching sexual maturity (Reinhardt 1983). Primates can be used to illustrate a developmental pattern similar to that predicted by the reproductive success hypothesis. In chimpanzees, the amount of time spent in tool use behaviors increases from almost non-existent to adult levels over a single transitional period; this transition occurs earlier in life for females than for males (Lonsdorf 2005).

The development of behavior in my study supports also demonstrates a transitional period at different times for the sexes.

Based on the results of this study, both social dominance and reproductive success are important in the development of chemosensory behaviors in African elephants. Examining investigative behaviors to chemical signals, deposited abundantly at gathering places for conspecifics such as a waterhole, provides insight into the development of communication in this social species. The development of behaviors may be modified by many factors including sex, age, reproductive maturity and social rank. Further research is needed to better refine the hypotheses outlined herein, and more completely explain the interaction between dominance and reproductive success with regards to how communication develops to its adult manifestation.

Table 1.1: Average monthly rainfall used for analysis of data collected between May 2004 and June 2005. Rainfall data and monthly rainfall categories were obtained from South African Weather Service (<http://www.weathersa.co.za>) 2004-05 monthly rainfall maps.

Rainfall	Months	Average monthly rainfall (mm)
Low	May, June, July, November	0 – 25
Moderate	September and October 2004, January and April 2005	25 – 50
High	December, February, March	50 – 200

Table 1.2: Number of focal observations on African elephants completed per age class per month (May 2004 – June 2005) in AENP. ‘Total samples’ indicates total number of observations obtained per age/sex class or month, while ‘total individuals’ is the total number of focal individuals sampled. Disproportionate sample distributions occurred in August 2004 for juvenile males and January 2005 for adult males.

	2004							Total Samples	Total Individuals
	May	Jun	Jul	Aug	Sep	Oct	Nov		
Calf Female	2	2	1	1	1	1	1	1	
Juvenile Female	4	3	2	1	0	1	2	1	
Pubescent Female	2	1	2	1	1	0	2	2	
Adult Female	2	3	2	0	0	2	3	2	
Calf Male	1	2	1	2	2	2	1	1	
Juvenile Male	0	0	0	7	1	2	0	1	
Pubescent Male	0	3	0	4	4	3	0	0	
Adult Male	3	1	1	1	2	1	0	1	
2004 Samples	14	15	9	17	11	12	9	9	
	2005						Total Samples	Total Individuals	
	Jan	Feb	Mar	Apr	May	Jun			
Calf Female	2	3	1	1	0	0	17	16	
Juvenile Female	1	1	0	0	1	0	17	16	
Pubescent Female	4	2	1	1	0	0	19	18	
Adult Female	3	2	0	0	1	0	20	17	
Calf Male	4	2	1	1	0	0	20	18	
Juvenile Male	2	1	1	0	0	3	18	18	
Pubescent Male	2	1	1	0	0	0	18	18	
Adult Male	8	2	1	0	0	0	21	18	
2005 Samples	26	14	6	3	2	3	150	139	

Table 1.3: Differences between waterholes for observations performed at AENP, May 2004 – June 2005. Mean distance (\pm SE) elephants traveled from start of observation until reaching waterhole, number of samples completed and average number of fecal piles at six waterholes. Distances were determined by measuring the point of focal starting and the point at which most elephants started drinking and calculating the distance between the two. Distances at Hapoor were an average of the distance from five points from which elephants typically entered, while at the other locations only one path of entry was used.

Waterhole	Samples completed	Estimated distance traveled (m)	Average number of fecal piles
Camp Dam	3	Not quantified	33 \pm 4.0
Carol's Rest	15	83	14 \pm 0.4
Domkrag	7	140	16 \pm 0.8
Gwarriedam	9	43	24 \pm 2.3
Hapoor	112	116 \pm 16	111 \pm 3.9
Woodlands	4	81	23 \pm 1.7
Grand Total	150	93 \pm 17	87 \pm 4.5

Table 1.4: Average age of elephants sampled in AENP, May 2004 – June 2005. Most elephants were known, and age used was age in 2004. Nine pubescent males between the ages of 10-15 could not be positively identified, and were each given an average age of 12.5 years.

Sex	Age class	Number of individuals	Average (\pm SE) age in years
Female	Calf	16	1.94 \pm 0.30
	Juvenile	15	6.73 \pm 0.34
	Pubescent	17	15.11 \pm 0.65
	Adult	17	33.35 \pm 1.97
Male	Calf	17	2.48 \pm 0.27
	Juvenile	16	6.81 \pm 0.34
	Pubescent	18	14.97 \pm 0.63
	Adult	17	30.65 \pm 2.55

* Paired t-tests for each age class revealed no difference in average age between the sexes.

Table 1.5: Number of female elephants sampled in five reproductive stages* during focal observations upon entering waterholes at AENP, May 2004 – June 2005.

	Unknown	Lactating	Estrus	Pregnant	Non-cycling	Total
Adult	6	9	0	3	1	19
Pubescent	11	8	0	2	0	21

* Lactating includes females with calves 2 years old or younger. Pregnant was determined based on calf births subsequent to sampling. Non-cycling indicates no calf produced in the last 10 years. Lactating and pregnant are not mutually exclusive; if both applied then female was categorized as pregnant.

Table 1.6: African elephant trunk movements and chemosensory behaviors performed during approach to a waterhole. Behaviors include trunk movements, positions, and chemosensory behaviors (some behaviors drawn from Loizi 2004, Bagley 2004).

Trunk movements and positions	
Pinch	Two fingers of the trunk are closed together
Trunk curl	Trunk held with openings pointing either to the side or up away from the ground
Trunk down	Trunk held with openings pointing towards the ground
Trunk shake	Distal end of trunk rapidly curled or twisted then released
Trunk swing	Trunk moves side to side with clear directional movement
Trunk wriggle	Trunk twists and then untwists once, with moderate speed
Chemosensory behaviors	
Check*	Touch substrate/substance with tip of trunk (either finger)
Flehmen*	Tip of trunk touches substrate then placed in the openings in the roof of the mouth
Genital check	Trunk tip touching genitals of another elephant
Horizontal sniff	Sniff occurring from any position ranging from just above ground level to holding the trunk out level with the mouth
Other	Any other trunk behavior not listed elsewhere
Periscope sniff	Sniff occurring from above the level of the mouth
Place*	End of trunk is placed flat on a substrate/substance
Sniff*	Trunk hovers over substrate/substance without contact

* Definitions based on Schulte and Rasmussen 1999

Table 1.7: Statistics for behavioral data collected on African elephants at AENP, May 2004 – June 2005. Tests performed were two-way analysis of variance for age, sex, and their interaction, or one-way analysis of variance for age. Kruskal – Wallis (K–W) non-parametric tests were used when the data did not meet the assumptions of normality and equal variance.

Parameter	N	Interaction		Age		Sex	
		F (3 d.f.)	p	F or H (3 d.f.)	p	F (1 d.f.)	p
1. Time to water	130	2.63	0.05	5.46	0.001	1.00	0.32
2. Rate of trunk down	143	2.34	0.08	1.31	0.27	1.12	0.29
3. Rate of trunk curl	143	0.54	0.65	0.03	0.99	0.10	0.75
4. Rate of horizontal sniffs	134	0.33	0.88	0.65	0.58	0.62	0.43
5. Proportion per individual of behaviors that were sniffs	126	0.51	0.68	3.85	0.01	3.03	0.08
6. Sniffs to feces	128	1.48	0.22	2.74	0.05	2.34	0.13
6a. Within females	71			1.33	0.27		
6b. Within males	57			2.43	0.07		
7. Rate of sniffs to all substrates	137	0.47	0.7	4.92	0.03	3.61	0.01
7a. Within females	73			6.24	0.01		
7b. Within males	67			7.03	0.03		
8. Sniff - among elephants performing a sniff behavior	124	0.52	0.67	2.34	0.08	5.27	0.02
8a. Within females	58			4.95	0.03		
8b. Within males	66			2.91	0.09		
9. Rate of periscope sniffs	128	4.54	0.005	5.45	0.001	8.82	0.004
9a. Within females (K-W)	69			10.16	0.02		
9b. Within males (K-W)	67			5.71	0.13		
10. Rate of raised sniffs	134	0.43	0.72	1.52	0.21	1.68	0.2

Table 1.8: Percentage of sampled African elephants performing chemosensory behaviors upon entering waterholes at AENP, May 2004 – June 2005. See Table 1.2 for total N per age/sex class. Average (\pm SE) for females, males, and all elephants included. Flehmen and rub behaviors were not seen during any focal observation.

	Sniff	Horizontal sniff	Periscope sniff	Check	Place
Calf Female	81.3	100.0	31.3	0	0
Juvenile Female	75.0	100.0	56.3	0	0
Pubescent Female	95.0	85.0	15.0	5.0	5.0
Adult Female	88.2	94.1	17.6	5.9	0
Calf Male	83.3	94.4	22.2	5.6	0
Juvenile Male	83.3	94.4	16.7	0	0
Pubescent Male	100.0	100.0	0.0	22.2	0
Adult Male	94.1	94.1	11.8	17.6	0
Average for Females	84.9 \pm 4.3	94.8 \pm 3.5	30.0 \pm 9.4	2.7 \pm 1.6	1.3 \pm 1.3
Average for Males	90.2 \pm 4.1	95.8 \pm 1.4	12.7 \pm 4.7	11.4 \pm 5.2	0
Average overall	87.5 \pm 3.0	95.4 \pm 1.7	21.0 \pm 5.9	7.0 \pm 3.0	0.6 \pm 0.6

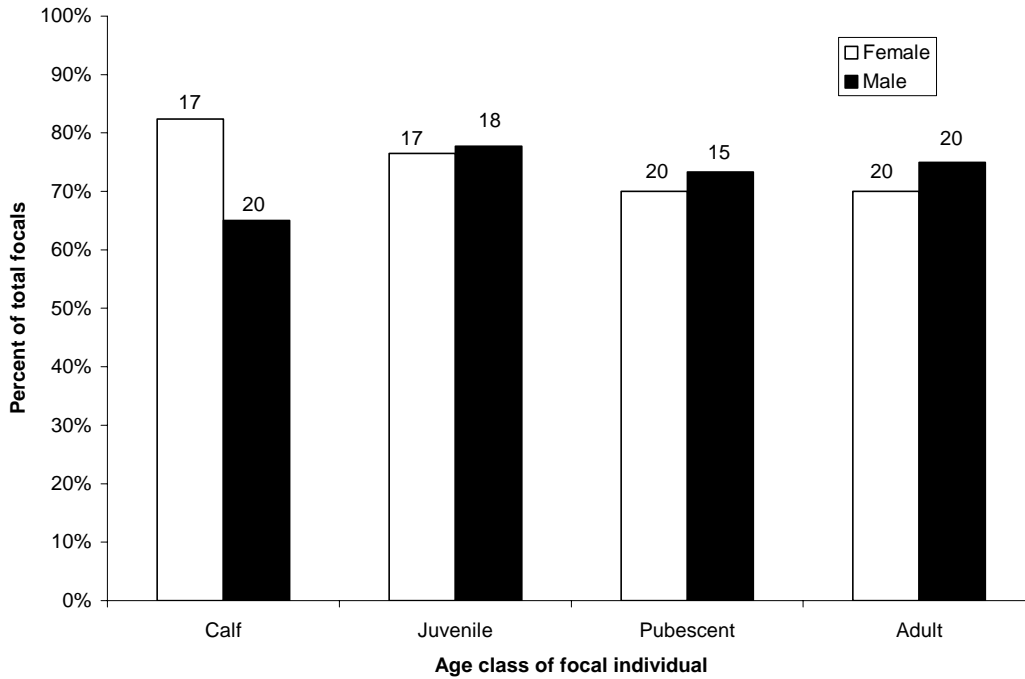


Figure 1.1: Proportion of focal observations completed at Hapoor water hole in AENP, categorized by age and sex, May 2004 - June 2005. Calf ages 0-4 years, Juvenile 5-9 years, Pubescent 10-19 years, Adult 20+ years. The total number of focal observations completed at all waterholes is shown above each bar.

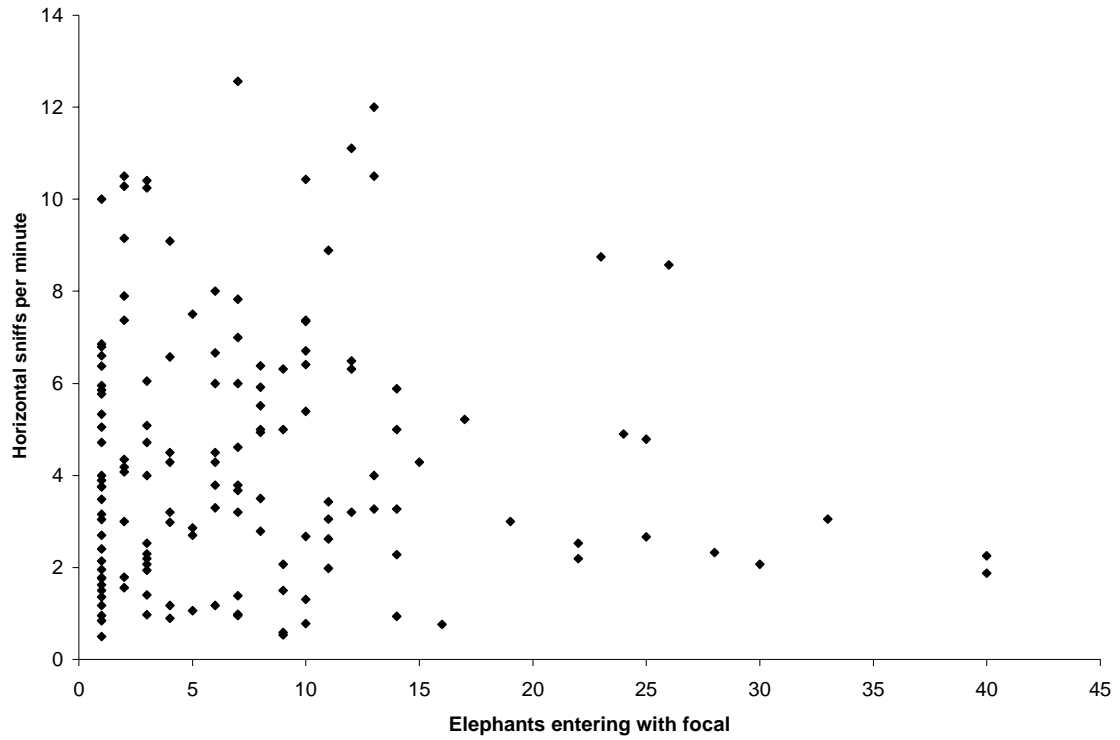


Figure 1.2: Average rate of horizontal sniffs performed by focal individuals versus the number of elephants entering at the same time, May 2004 - June 2005. N = 142 focal samples. No significant correlation was seen between the two variables ($r = -0.03$, $p = 0.72$).

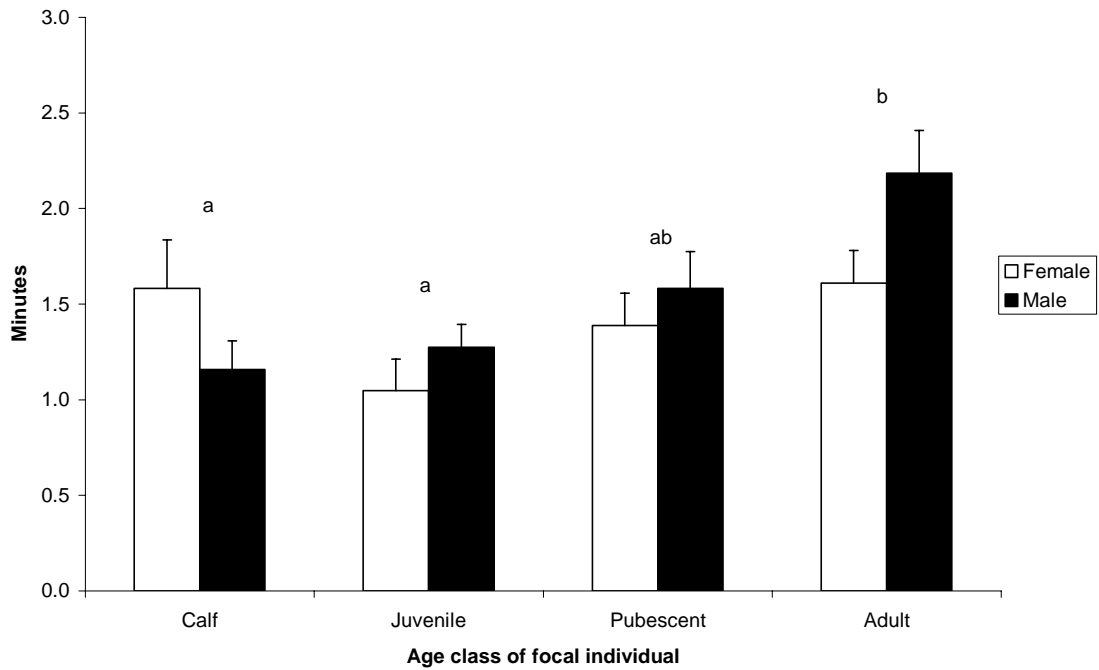


Figure 1.3: Mean (+ SE) time African elephants in AENP took to reach the waterhole, categorized by age and sex. Adults took longer to reach the water than juveniles and calves (Table 1.7, row 1). Different letters indicate significant differences by age class with both sexes combined.

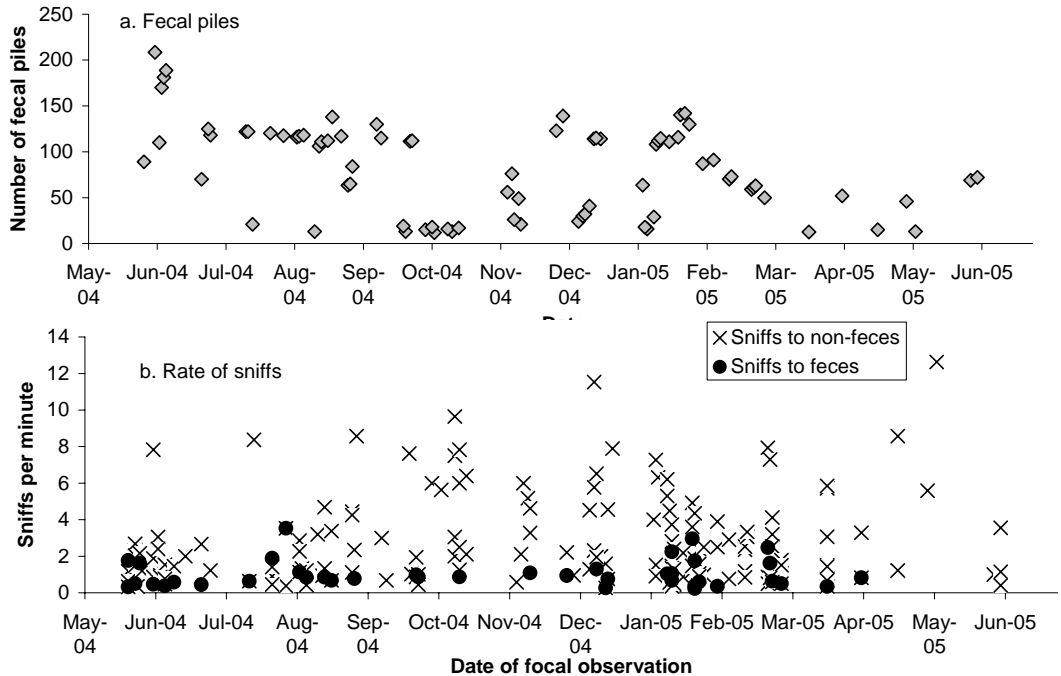


Figure 1.4: Average number of fecal piles and average rate of sniffs in AENP, May 2004 - June 2005. Non-feces signals included the ground or vegetation. The average number of (a) fecal piles decreased through time ($r = -0.42$, $p < 0.0001$), but there was no decrease in (b) the average rate of sniffs (to feces or non-feces) over the same period (feces: $r = 0.01$, $p = 0.93$; non-feces: $r = 0.13$, $p = 0.10$).

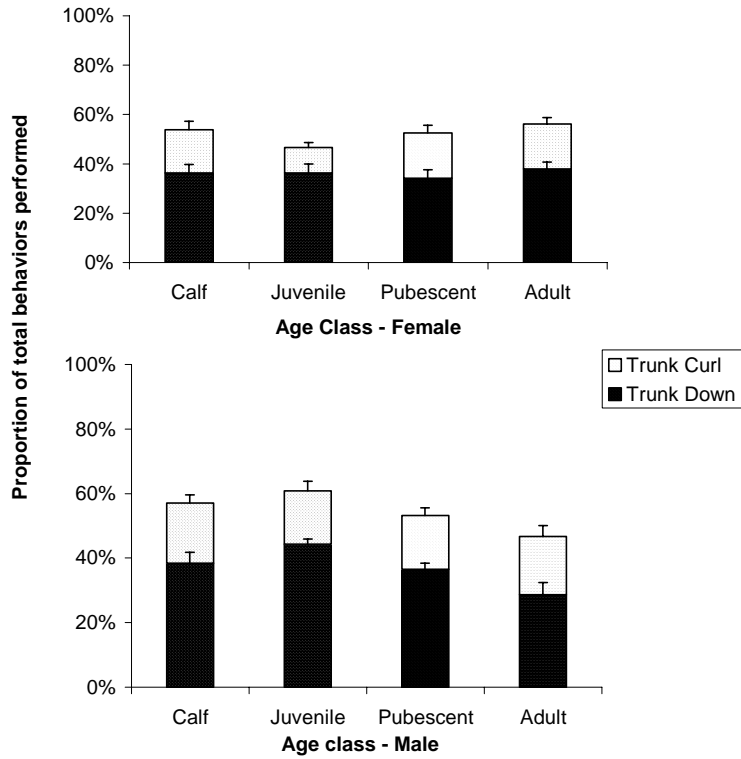


Figure 1.5: Trunk positions performed as a percentage of all behaviors (chemosensory) and positions (trunk) performed by individual elephants in AENP, May 2004 - June 2005. Females and males are presented separately, and non-parametric tests of ages within each sex showed no difference in the proportions of behaviors for trunk curl or trunk down (see Table 1.6) (Females $X^2 = 0.42$, $p = 0.93$; Males $X^2 = 6.56$, $p = 0.08$).

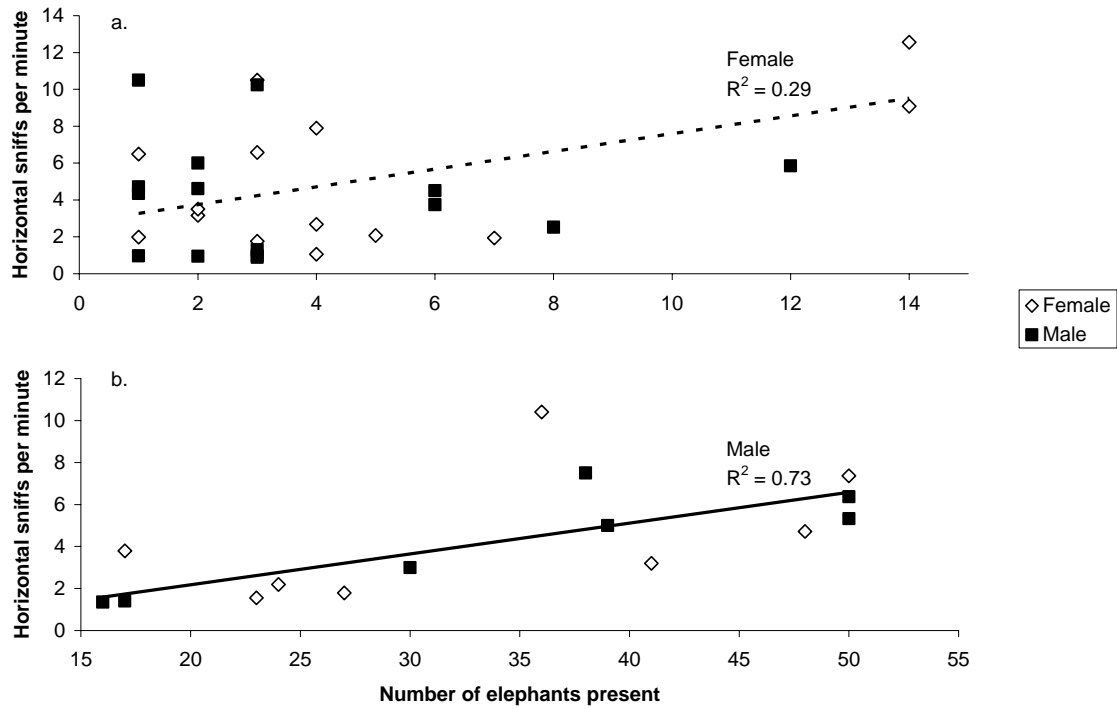


Figure 1.6: Average rate of horizontal sniffs performed by elephants in AENP when: (a) 1- 14 elephants were present and (b) 15-55 elephants were present. One focal of a male elephant with 100 elephants present was excluded because of no comparable focal observations with female elephants. The number of elephants present refers to the number of elephants at the waterhole when the focal animal entered. Each data point indicates one focal with 22 males and 22 females total. The rate of sniffing increased for females ($p = 0.04$), when 1-14 elephants were present, but not for males ($R^2 < 0.0001$, $p = 0.99$). Males showed an increase in sniffing when 15-50 elephants were present ($p = 0.01$), but females did not ($R^2 = 0.27$, $p = 0.19$)

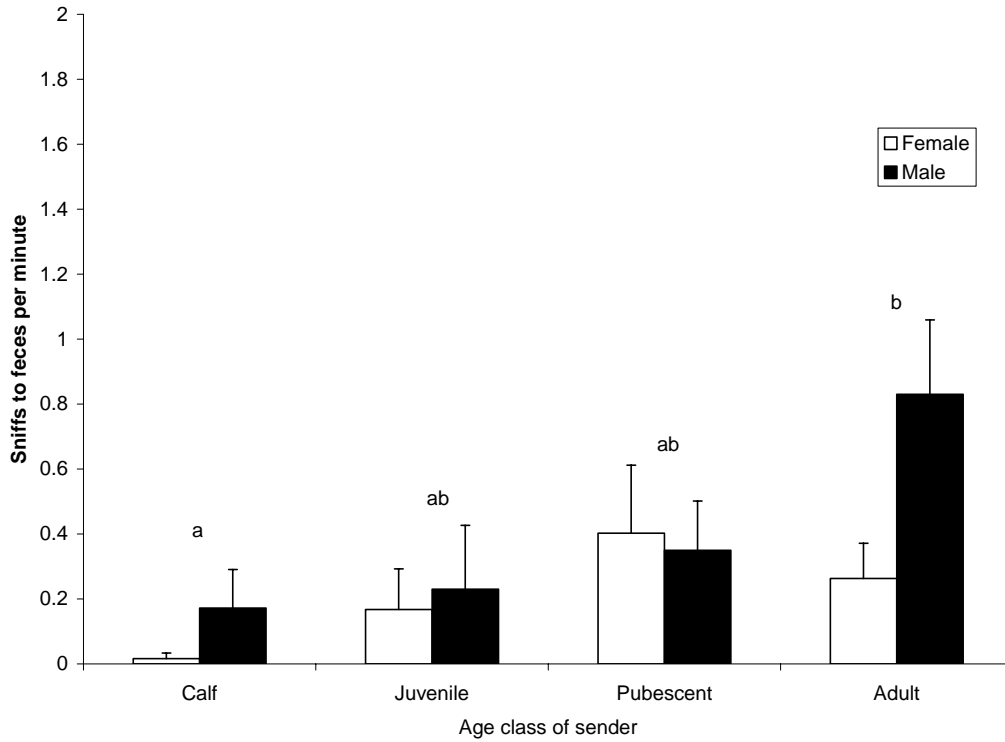


Figure 1.7: Average rate of sniffs performed to feces by elephants in AENP, May 2004 - June 2005. The average rate of sniffs was lower for calves than for adults (Table 1.7, row 6). Different letters indicate significant differences between age groups for males and females combined.

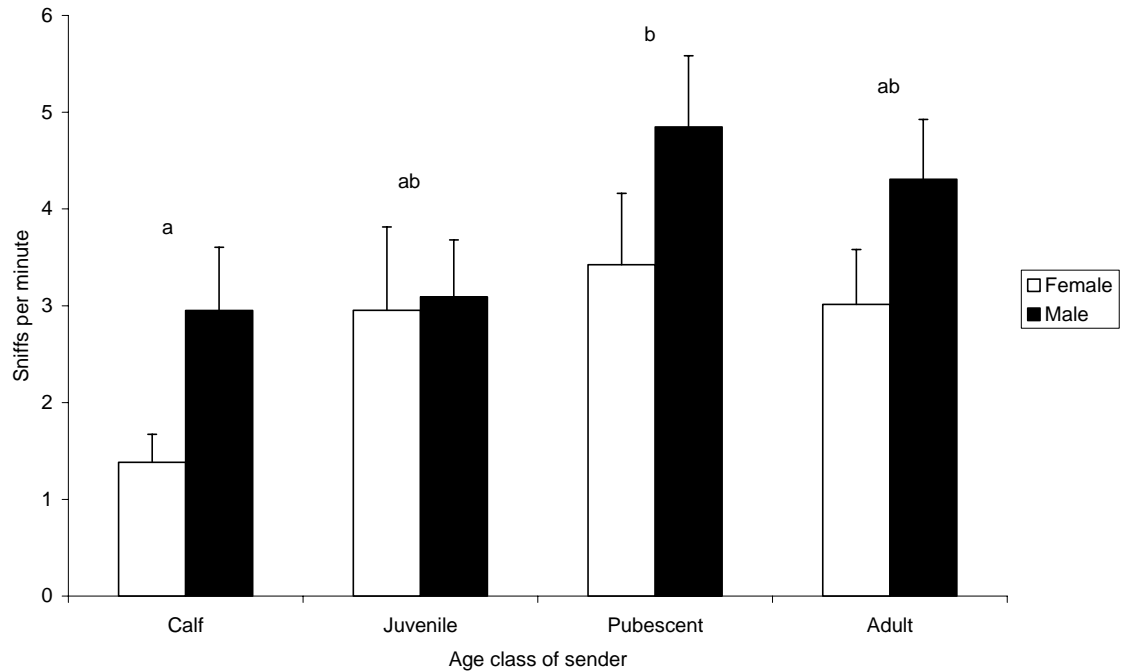


Figure 1.8: Average rate of sniffs (#/min) to all substrates for male and female elephants from four age classes upon entering waterholes at AENP, May 2004 – June 2005. Males performed sniffs at a higher rate than females, and pubescent animals had a higher rate of sniffs than calves (Table 1.7, row 7; Tukey HSD: calf – juvenile $p = 0.53$, calf – pubescent $p = 0.01$, calf – adult $p = 0.07$). Different letters indicate significant differences between age groups for both sexes combined.

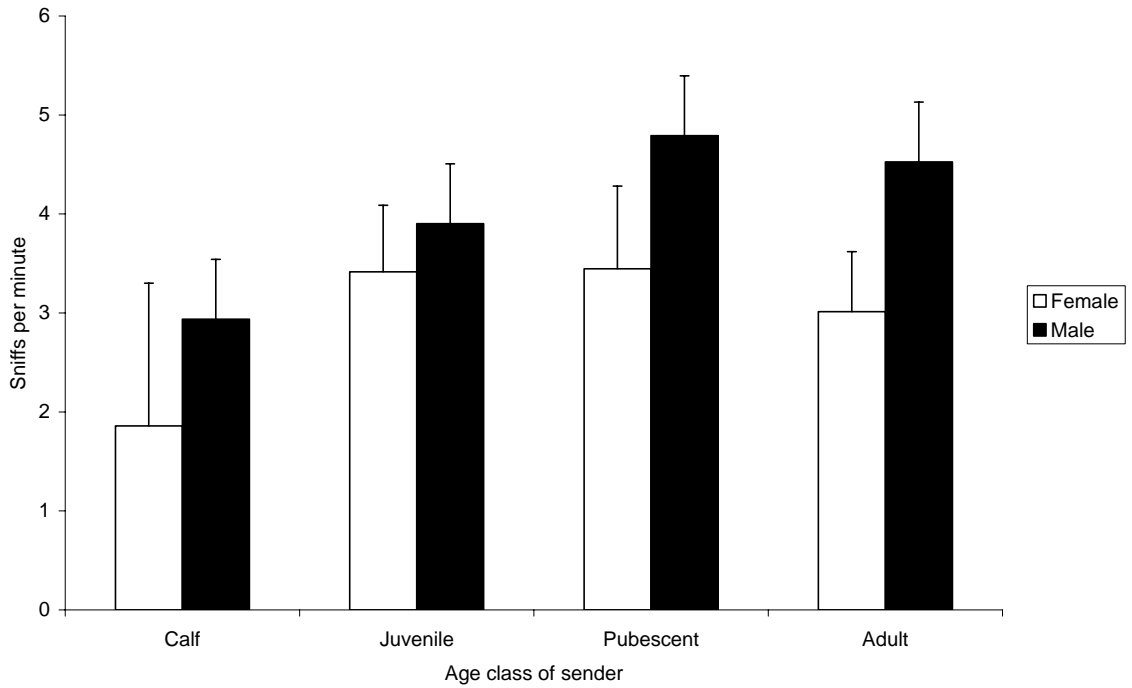


Figure 1.9: Average rate of sniffs (see Table 1.6) among elephants performing a sniff behavior in AENP, May 2004 – June 2005. Males performed more sniffs on average than females, and within the sexes there were differences by age for females but not for males (Table 1.7, row 8).

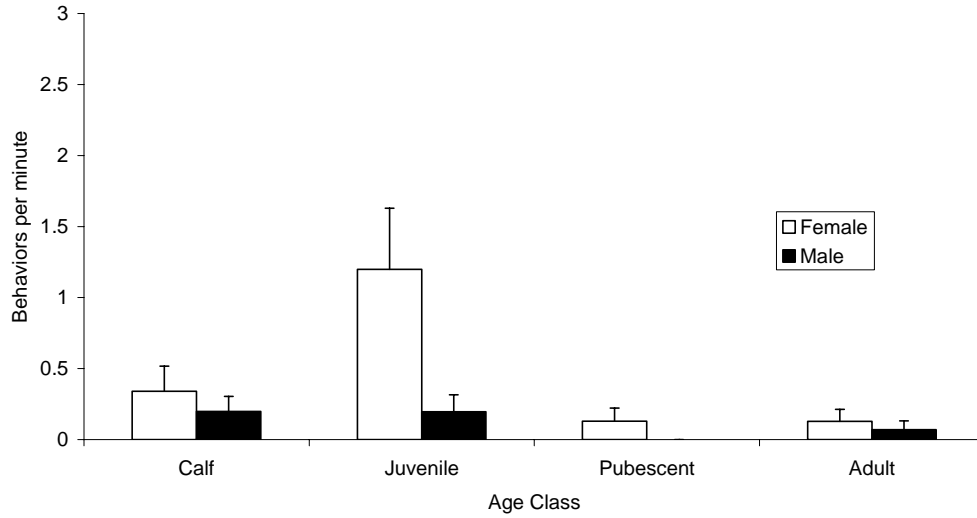


Figure 1.10: Average rate of periscope sniffs performed by male and female elephants in four age classes in AENP, May 2004 - June 2005. A significant interaction occurred between age and sex and within each sex; females differed significantly by age, while males did not (Table 1.7, row 9).

CHAPTER II

DEVELOPMENT OF BEHAVIOR IN FEMALE AFRICAN ELEPHANTS

Introduction

Behaviors develop and change as animals mature. In long-lived species where an entire generation cannot be studied, similarities and differences between young animals and adults can provide an understanding of when different behaviors are performed and how they relate to adult roles. In addition, pinpointing when a behavior changes from a juvenile form to an adult manifestation can be useful in determining the meaning of the behavior. While some behaviors are practiced early in preparation for adult life, others may be more important at the juvenile stage and not as relevant later (Stamps 2003). The rate of change also is interesting, whether the behaviors change at key life stages or whether there is a more gradual change. Observing behaviors from the same individuals over time can provide insight into whether season or time of year has any impact on behaviors.

Communication occurs when a signal is transmitted from a sender to a receiver (Kappeler 1998). Based on models, selection often will favor signals that are both honest and accurate (Bradbury and Vehrencamp 2000). Communication can take a variety of forms, including auditory, tactile, visual, or chemical signals (Langbauer 2000). Many animals use chemical signals to exchange information between and within the sexes. Chemical signals are useful because they persist over time in the absence of the sender (Eisenberg and Kleiman 1972, Alberts 1992). Because they are often composed of metabolic byproducts, chemical signals are also reliable indicators of body condition or reproductive status (Kappeler 1998), often making them more honest signals (Poole

1989a). Intersexual chemical signals have been demonstrated in a wide variety of mammal species, primarily used in finding mates and for demarcating territories (Eisenberg & Kleiman 1972, Ziegler et al. 1993, Converse et al. 1995, Thompson 1995, Solomon and Rumbaugh 1997, Kappeler 1998, Swaisgood et al. 2000). Social dominance or rank affects signal investigation, particularly when the signals are used to establish dominance, to reduce aggression or fighting, or to facilitate reproductive interactions (Solomon and Rumbaugh 1997). Within the reproductive context, communication may be used in mate competition or to advertise reproductive status (Eisenberg and Kleiman 1972, Poole and Moss 1989, Ziegler et al. 1993, Schulte and Rasmussen 1999). In addition, behaviors involved in investigating reproductive signals may not change until an animal is capable of producing offspring. These two factors of rank and reproduction also could interact to impact how communication and social behaviors develop.

Elephants can be used as a model to explore the development of communication and social behavior. Over a long lifespan and within a highly organized social structure, communication facilitates social interactions both between and within the sexes. Adult female elephants face a different set of social challenges from adult males. Males disperse at puberty from the natal group, whereas for females, integration into a linear hierarchy within the natal group is the key feature of adult society (Moss 1983; Poole and Moss 1989, Archie et al. 2006a). Play prepares young animals for adulthood, and an emphasis on different modes of communication may diverge at an early age. Females concentrate their early interactions with family members (Lee 1986, Lee and Moss 1999), which prepares them for integration within the family unit. Interactions such as trunk

touches and contacts may be elevated in younger animals in preparation for this later integration. In addition, juvenile females display a variety of caretaking behaviors toward younger siblings (Dublin 1983, Lee 1987). Caretaking behaviors may include either affiliative contacts or trunk touch investigations. In addition to a variety of more play-oriented behaviors, caretaking may provide the basis for skills that will be required by adult elephants as is known for other social mammals such as rats (Spinka et al. 2001). Thus, the age of reproductive maturity may be a critical period in the acquisition of adult behaviors for African elephants.

The development of adult behaviors also may reflect the rank in female elephant society. Rank is correlated positively with age (Archie et al. 2006a), and female elephants benefit reproductively from the leadership of an older matriarch (McComb et al. 2001). In captive elephants, subordinate females receive more aggressive contacts and vocalize less than dominant females, but these differences are only apparent during the ovulatory and not the anovulatory phase of estrus (Leong et al. 2005). Female elephants advertise their reproductive status through signals in their feces and urine (Slade et al. 2003, Bagley 2004), which, unlike vocal signals used for short-range communication (Leong et al. 2003, Leong et al. 2005), do not require any additional effort on the part of the female. If the relevance of signals must be learned, this information may be transferred from their mothers or other members of their social group at a particular developmental stage such as at reproductive maturity, or be acquired gradually as females rise in rank throughout their lifetime. Imposed upon this large temporal scale of development, the timing of behavioral ontogeny may be influenced seasonally by changes in biotic or abiotic factors.

Signals both between and within the sexes are affected by seasonal changes in group composition and environmental conditions. For African savanna elephants, sets of related females and their offspring form a family group (Archie et al. 2006b). The family group rarely divides into smaller units, regardless of alterations in environmental conditions (Western and Lindsay 1984, Wittemyer et al. 2005). However, during some seasons, family groups may associate closely with more distantly related elephants, forming bond groups or more expansive social groupings (Western and Lindsay 1984, Poole 1994, Wittemyer et al. 2005, Archie et al. 2006b). Seasonal association differences also may be reflected in the use of different forms of communication. For example, when elephants are widely dispersed in the dry seasons, there may be more use of persistent signals such as chemical messages deposited in urine or feces. During rainy seasons, when elephants aggregate in large groups, other cues such as volatile chemicals emitted from the temporal glands or tactile cues gained from directly touching another elephant may be more important. Seasonal effects may be impacted by either biotic or environmental variation. Biotic variation would be evident if there were particular months when calves were born, or when there were more reproductively active adults. In other populations, seasons determine the amount of water and food available (Western and Lindsay 1984, Leggett et al. 2003, Dublin 1996). Higher temperature and humidity increase the evaporation rate of signals (Alberts 1992), and extensive rainfall may eliminate previously deposited signals. Therefore, greater rates of chemosensory behaviors would be predicted as rainfall increases to a point, after which signals would be eliminated more quickly than they can be investigated. Understanding the maturation of

chemosensory behaviors in African elephants requires field studies that consider the long-term developmental patterns and potential seasonal perturbations.

Previous studies on elephants in Addo Elephant National Park, the site of this current work, have been conducted on chemosensory and other communicative behaviors. One study provided an overview comparison of the behavior of males and females (Loizi 2004), while a second looked exclusively at males (Bagley 2004). The current study continued this exploration of developmental patterns by examining female elephants.

I compared two hypotheses to determine what factors influence the development of social behaviors and communication in female African elephants. The reproductive success hypothesis predicts a definitive change in behavior patterns at the age of first reproduction. Juvenile females should exhibit increased contact and trunk touching behavior to younger siblings as they prepare for having their own calves. Chemosensory behaviors also should show a clear transition at the age of first mating. The alternative hypothesis is that behaviors would change with social rank or dominance. Younger elephants are still exploring their social world, and may interact indiscriminately with all ages and both sexes. Older females are more interested in maintaining social bonds and finding mates; they may be more discriminatory in who they interact with and whether those interactions are friendly or aggressive. The social dominance hypothesis predicts that contact, trunk touches and chemosensory behaviors will change over multiple age classes from immature to mature patterns. Because developmental patterns may be influenced by seasonal influences or only detectable under particular conditions, I considered seasonal effects as part of my investigation of these hypotheses.

Methods

Site description

This study was conducted in Addo Elephant National Park (AENP) between May 2004 and May 2005. AENP is located approximately 72 kilometers northeast of Port Elizabeth in the Eastern Cape region of South Africa. Vegetation in this region is primarily succulent thicket, as described in Paley and Kerley (1998).

Approximately 400 elephants live in this park, divided into two separate fenced sections. Studies ongoing since 1996 have identified all elephants and their family relationships (Whitehouse 2001, Bagley 2004, Loizi 2004). All research was conducted in the main elephant camp, an area of 103 km² (Whitehouse and Harley 2002). During 2004, there were 179 females in six matrilineal lines and 175 males, ranging in date of birth from 1949 to 2004 (Fig. 2.1). Three demographic shifts have occurred in the past three years, two introductions and one removal of male elephants. Two sets of four male elephants were introduced from Kruger National Park in 2002, one to each section of the park (pers. comm. K. Gough, and H. Loizi 2004). In addition, in July 2005, after completion of the current study, 15 bulls were transferred from the park to private game reserves in the Eastern Cape region.

Observation location

The site for each day's work was chosen based on the habits of the elephants in the preceding week. If the elephants had been seen consistently at one particular waterhole, then the day's work would consist of waiting at that site for the elephants to come drink. If the elephants' movements had been more sporadic, moving around to a variety of different locations, an alternate strategy was employed. One option was to

drive along Zuurkop ridge, which offers a high vantage from which the location and possible movements of the elephants were determined (See Appendix B). A second option was to drive in a circuitous route through the park, stopping for a time at each waterhole and trying to observe whether there were any elephants in the vicinity.

Observations were conducted at 17 locations. Elephants are dependent on water, and visit some source of water daily (Weir and Davison 1965, Ayeni 1975). As such, waterholes provide a centralized location where there is a high potential for interaction between elephants and their environment. This potential is higher at a waterhole than in the bush, where elephants are primarily concerned with feeding. In addition, waterholes provide an open area where the entire trunk is visible; in foraging areas, vegetation often obscures visibility. For these reasons, focal studies were conducted at or near the various waterholes in the park. Some waterholes were supplied with pumped water year round, while others filled only after rainfall. Of the 17 sites, the largest waterhole with between 3 and 4 available pools at any given time was Hapoor, where 46% of all the focal observations were conducted. Gwarriedam was the next most frequented site where I conducted 21% of the focal observations. The remaining 33% of observations were performed at 15 sites with no site accounting for more than 10% of the total (Table 2.1).

Focal animal selection

The study encompassed both a longitudinal and a cross-sectional component, using continuous focal animal sampling for 20 minutes (Altmann 1974). For the longitudinal component, approximately 30 female elephants from each of four different age classes and six matrilineal lines were chosen as potential subjects (Appendix A). Age classes were chosen based on life stage transitions of elephants; calves (0 – 4 years)

were still dependent on their mother, juveniles (5 – 9 years) were beginning to be weaned, pubescent (10 – 19 years) females have begun to reproduce, and adults (20+ years) have multiple offspring and increase in rank with age. Age of an individual in 2004 was used throughout the analyses. The group of 120 potential subjects was distributed evenly across age classes and matriline. Care was taken to avoid inclusion of both females and their current dependent offspring whenever possible.

Each month I attempted to obtain focal observations on each elephant in the longitudinal data set (N=120). Over a 379 day period, 262 days for a total of 1484 hours, or approximately 5.7 ± 0.17 hours per day, were spent in the field watching elephants, searching for elephants, or awaiting their arrival at a waterhole. It was never possible to observe all the females in a single month. Hence, as the months progressed, this process became more selective. I concentrated on females with previous focal observations, opting for more repetitions on fewer females rather than more individuals with fewer repetitive observations, in order to increase sample size for longitudinal analyses.

When there were no longitudinal focal animals present, observations were obtained on whichever females were present. These data were used in a cross-sectional analysis of all behaviors across the 12-month period. Overall, 148 females were sampled one or more times, or approximately 83% of the available female elephants. Between 73% and 90% of each age group was sampled (Table 2.2). In total, 786 focal observations were conducted, 715 on individuals who were repeated three or more times. On average, three observations were completed each day, and at least one focal observation was completed on 76% of the days in the field (199 days).

Observations

At a site, as elephants were entering, the number of animals and identities were established, both of families and individuals. If an individual was a potential longitudinal candidate, that animal was used for a focal study. If more than one longitudinal individual was present, then one that was easiest to observe for twenty minutes was selected. Criteria for selection included speed of entry, visibility, and location with regards to bushes or animals that may have obscured viewing. If multiple families were present, the family to start with was chosen based on which animals appeared easiest to follow for a full twenty minutes. A second criterion for selection was age class, which was selected randomly without replacement whenever possible.

Once the focal animal was selected, she was observed for a period of twenty minutes or until out of view, using continuous focal recording (Altmann 1974). Four categories of behaviors were created, namely, state behaviors, and three categories of events: trunk tip touches, body contacts and chemosensory behaviors (Appendix C). States were defined as major body behaviors that lasted for more than five seconds (Table 2.3), and the duration of each state was recorded. Trunk tip touches could occur to self or another elephant. The identity of the animal touched or touching the focal animal and the body region were noted (Table 2.4). Body contacts made or received by the focal animal and the identities of the elephants were recorded (Table 2.5). Trunk on back, tail touch, and lean were combined into one category of affiliative behaviors for analysis, and examined based on age of the focal and identity and sex of their interactive partner. I also noted all chemosensory behaviors by the focal elephant including the substrate or individual investigated (Table 1.6). Horizontal and periscope sniffs were distinguished

from the other sniffs as occurring when the trunk was directed at the air above the ground. These were combined into one category (raised sniffs) for analysis.

Following a focal observation, a new animal was chosen if elephants were available. Whenever possible, the immediate relative (mother or daughter) or elephant nearby the previous focal animal was not selected. The above process was repeated until all available animals were out of view. The number of other elephants present was counted whenever a focal was completed, and ranged from one to two hundred elephants. The number of new calves was determined by field observations of how many calves were born in a given month. The average number of musth bulls likely to be present in the park each month was calculated based on minimum and maximum numbers. Minimum was the number of bulls actually seen in musth in a month, while maximum was the number of bulls who were not seen that month, but judged likely to be in musth based on observations from previous or subsequent months (Table 2.6). Estimations of these numbers were facilitated by other researchers and tour guides operating in the park.

Analysis

Analyses were carried out using Statistica software (StatSoft 1999). All behaviors were tested for normality using the Kolmogorov – Smirnov test, for equal variance using Levene’s test, and, if applicable, a test for parallelism of covariates. If assumptions of parametric analysis were not met, comparable non-parametric techniques were used. All tests were two-tailed with $\alpha = 0.05$. All age classes used refer to the age class an animal belonged to in May 2004.

Seasonal effects were examined in four different ways. I examined whether the number of elephants present, number of calves born per month, and number of potential

musth bulls in the park each month influenced the behaviors recorded in this study. More elephants present during a focal observation could mean more immediate signals available, while elevated numbers of new calves or musth bulls could result in more potentially interesting signals in the park in general. I also examined the abiotic effect of rainfall, and whether this was correlated with the other biotic variables.

Three biotic factors (number of elephants present, number of new calves, and number of musth bulls) were used to separate the focal observations into either three or five groups, depending on sample sizes. For each individual, all focal observations falling into a given group were averaged. Each individual was represented in only one group such that there was an even number of individuals within each group for each age category. Total contact, chemosensory, and trunk touch behaviors were examined using linear regressions or correlations to examine the causative effect or general relationship of these biotic factors on elephant responses.

The effect of average monthly rainfall was tested by placing each date of a focal observation into a corresponding rainfall category (Table 1.1). Average monthly rainfall categories were based on data from the South African weather service website (SAWeather.com), and temperature or humidity data were not available. Rainfall data were not collected at the time of the study and this information was the most reliable available for analysis. For each individual, all focal observations falling into a given block were averaged to achieve one score per individual for each block of rainfall. For some analyses, those individuals with a score in each block were analyzed using a repeated-measures ANOVA. In other cases, individuals with scores in multiple blocks

were combined and one score per individual was randomly selected without replacement to achieve an even distribution across ages and rainfall blocks.

Behaviors performed during a focal observation were categorized as states, trunk touches, contacts, and chemosensory behaviors (Tables 2.3-2.5, Table 1.6). For each behavior, only those individuals that performed the behavior were included in the analyses (range 26 – 147 elephants). Unless noted otherwise, zeros were excluded from all analyses. Proportion of time spent in each of five main states (Table 2.3) was calculated for each focal, then an average for each individual was used. In addition, all states which had definite start and end times (eliminating the first and last state of a focal bout, as well as those bracketing periods when the elephant was not visible) were used to calculate the average bout length of a state for each individual. These times were used for comparison among age classes.

For each category, rate of behavior (behaviors per hour) was calculated for each individual for each date they were observed. Trunk touch and contact behaviors were separated into sender and receiver categories. Averages for each individual per time period were calculated. Individuals were selected randomly so that values were evenly distributed across both ages and whichever categorization (rainfall, new calves, or bulls in musth) was appropriate (Appendix D). All behaviors were compared with two-way analysis of variance (ANOVA) or analysis of covariance (ANCOVA). If significant differences were found, Tukey HSD tests were used to test for differences within main effects. In addition, all behaviors were analyzed based on the interacting partner (mother and offspring, relative, or non-relative), using two-way ANOVA. Where there were interactions between main effects (e.g. between rain and age class), data were analyzed

for one effect within the other (e.g. age class at different levels of rainfall). Finally, trunk touch behaviors were examined by location of touch (Table 2.4). These behaviors were divided by the absolute number seen performed to each location; out of 495 behaviors performed to or received by a focal female, most (166) were performed to the body. The three next highest were combined into one category: mouth (104), legs (96), and nipples (67). The other ten locations on the elephant were combined with a total of 62 touches.

Two analyses were used for chemosensory behaviors. Data from those individuals that were represented in each period were analyzed using a repeated measures ANOVA and Tukey HSD. To achieve a cross-sectional sample with larger N, all other individuals were selected randomly for even distribution across age classes and rainfall levels so that no individuals were repeated (as shown for contacts in Appendix D). The data from individuals were compared using ANCOVA with rainfall as the covariate.

Results

The ensuing sections examine each of the major response categories (states, chemosensory behaviors, trunk touch behaviors and contact behaviors) for variation resulting from seasonal effects and for developmental patterns in light of predictions of the reproductive success and social dominance hypotheses. Seasonal effects include three biotic factors of interest (number of elephants present during observation, and number of calves or musth bulls in park during the month of the observation) and the abiotic factor of average rainfall level. Average monthly rainfall was not correlated to either the number of bulls in musth in the park each month or the number of new calves born each month, but was positively correlated with the number of elephants present

during the focal observation (Pearson correlation: musth bulls $r = 0.30$, $p = 0.32$; calves $r = 0.24$, $p = 0.42$; elephants present $r = 0.31$, $p = 0.02$).

States

All elephants allocated their time equally to various states, which did not support the predictions of either the social dominance or reproductive success hypotheses. There was a significant relationship between the percent of time an elephant spent standing and the number of elephants present, but it explained less than 5% of the variation (Table 2.7, row 1a). Elephants of all ages spent a similar proportion of their focal walking, standing, or mudding (Table 2.8, rows 1a-1c; Fig. 2.2). Calves spent a lower proportion of their focal drinking ($17.4 \pm 1.9\%$) than either juveniles ($28.3 \pm 2.8\%$) or adults ($28.2 \pm 2.5\%$) and the difference with pubescents ($26.7 \pm 2.8\%$) approached significance (Table 2.8, row 1d; Tukey HSD calf – juvenile $p = 0.015$, calf – pubescent $p = 0.07$, calf – adult $p = 0.02$). When time spent suckling was included with the time spent drinking by calves, then all ages spent similar proportions of time suckling or drinking (Table 2.8, row 1e). The average amount of time an elephant spent in a single bout of walking (2.8 ± 0.10 minutes) and standing (1.7 ± 0.11 minutes) did not differ between the age classes; drinking approached significance and mudding differed (calves spent slightly longer than others in both activities) (Table 2.8, row 2). Despite these differences in bout length, since mudding accounted for no more than ten percent of a focal observation, all elephants had approximately equal opportunities to perform all other behaviors.

Chemosensory behaviors

Chemosensory behaviors were impacted by two seasonal variables, and individual behaviors supported the reproductive success hypothesis. The average number of new

calves or musth bulls present in the park did not affect the rate of chemosensory behaviors (Table 2.7 rows 2a, 3a). The number of elephants present during a focal observation showed a weak but significant positive, linear relationship with the average rate of performing any chemosensory event (Table 2.7, row 1b) and with monthly rainfall, both for all observations and for a select group (chosen to minimize repeated individuals and days) (Fig. 2.3). Rainfall affected the overall rate of chemosensory events observed (Fig. 2.4). More chemosensory events were performed when moderate (25-100mm) levels of rain fell per month than when rainfall was low (0-10mm) or high (100-200mm) (Table 2.9, row 1; Tukey HSD: low - moderate $p = 0.0004$, low - high $p = 0.004$, moderate - high $p = 0.75$). In addition, the overall rate of chemosensory events supported the reproductive success hypothesis; across rainfall levels the calf - juvenile ages performed fewer behaviors than pubescent - adult females (planned comparison $F_{1,48} = 7.49$, $p = 0.009$).

The rate of raised (horizontal and periscope) sniffs performed also supported the reproductive success hypothesis. When a repeated measures analysis was performed on thirty individuals who were sampled during each of three rain categories (Table 1.1), the rate of raised sniff differed by rain category and between age classes (Table 2.9, row 2). Pubescent females performed more raised sniffs (50.9 ± 5.4 sniffs/min) than juveniles (32.4 ± 5.7 sniffs/min; Tukey HSD juvenile - calf $p = 0.31$, juvenile - pubescent $p = 0.02$, juvenile - adult $p = 0.15$, calf - adult $p = 0.99$; Fig. 2.5). This supports the prediction of a single transitional period in the development of a behavior. To increase the sample size, all individual focal elephants were included in a linear regression with age for each of three levels of monthly rainfall (Fig. 2.6). When rainfall was high (51 - 200 mm), the

rate of raised sniffs increased with age, but no pattern was evident with low (0 – 25 mm) or moderate (26 - 50 mm) rainfall. Pooling the samples across rainfall, when only young (0-10 years old) or mature (11 – 50 years old) elephants were analyzed, there were no linear trends (young $R^2 = 0.0004$, $p = 0.87$; mature $R^2 = 0.03$, $p = 0.19$). For elephants between the ages of 6-12 years old, sniffs increased with age, but this only explained a small percentage of the variance ($R^2 = 0.05$, $p = 0.05$). These data indicate that behaviors increase during a transitional period between the juvenile and pubescent stages.

Adult chemosensory behaviors generally would be directed at potential signal sources, so the detection of a developmental transition period may be facilitated by isolating different sources of potential signals, specifically other elephants, their excretions, or the general environment. Young (calf and juvenile) elephants performed targeted (sniff and horizontal sniff) sniffs at a higher rate that approached significance (Table 2.9, row 5) than older (pubescent and adult). The animal being sniffed (the focal animal's mother or offspring, any other relative, or a non-related elephant) did not affect this combined rate of sniffs and horizontal sniffs (Fig. 2.7). Sniffs to other elephants were then combined with sniffs to urine or feces as elephant stimuli. Sniffs were performed at a higher rate to elephant (25.8 ± 2.9 sniffs/hour) than to environmental (20.7 ± 2.5 sniffs/hour) stimuli (Fig. 2.8; Table 2.9 row 8). Checks also were performed by juvenile, pubescent, and adult animals, but the sample sizes were too low to detect any significant difference between ages or stimulus types ($N = 11$, Kruskal-Wallis (2 d.f.), $H = 2.30$, $p = 0.31$). These findings reveal that when elephants were performing sniffs they more often were investigating potential signal sources known to be from elephants than

environmental stimuli, which would be predicted by both the reproductive success and social dominance hypotheses.

Trunk touch behaviors

Trunk touch behaviors could be performed or received by elephants, and examining both sender and receiver of the action supported both the uses of the trunk as a communication avenue as well as indicating that the behaviors are influenced both by reproductive success and social dominance. For the reproductive success hypothesis, trunk touch behavior was predicted to change at pubescence. The social dominance hypothesis predicted that trunk touches would vary across all age classes along with changes in dominance status. The biotic seasonal variables did not impact the rate of trunk touches performed or received by elephants (Table 2.7, rows 1c - 1d, 2b – 2c). As rainfall decreased, the average rate of trunk touches each female performed to herself decreased (Table 2.7, row 4a). Rainfall was not correlated with the rate of trunk touches performed either to or from another elephant (Table 2.7 row 4b). A two-way ANOVA on age class and rainfall showed differences between the ages and between levels of rainfall (Fig. 2.9; Table 2.9, row 3). When rainfall was low, juvenile females performed more self-touches (37 ± 4.9) than all other ages (19 ± 2.4 to 20 ± 3.5). At high levels of rain, calf females performed more touches to other elephants (17 ± 1.8) than adults (10 ± 1.2) (Table 2.8, row 3).

A behavioral transition at pubescence was supported with two measures of trunk touch behaviors. Young (calf and juvenile) elephants are still learning their place in the family, and were predicted to display more trunk touch behaviors both to themselves and to other elephants, while juvenile females were predicted to have elevated rates of

touches to relatives (such as younger siblings) in preparation for their own reproduction. When the focal animal was the sender, there were differences in the rate of trunk touches within mother-offspring pairs, but not when the elephant being touched was any other relative or a non-relative (Fig. 2.10; Table 2.10, row 1). Calves and juveniles appeared to perform a higher rate of touches to their mother than mature females performed to their offspring. When the focal animal received trunk touches, there were no differences between ages within interactive pairs (Table 2.10, row 1). This indicates that the behavioral differences are most evident when the elephant is performing the investigation, not in the rates of receiving attention from others.

Finally, differences in the rate of trunk touches to specific locations reflected a transitional period on reaching reproductive success. Trunk touches were conducted to a variety of specific locations on the elephant, as well as to the body in general (see Table 2.4). The rate of trunk touches to the body did not differ by age (Fig. 2.11a; Table 2.10, row 2). When the location was the mouth, legs or nipples, mother-offspring pairs showed differences, but no differences were evident within relative or non-relative pairs (Fig. 2.11b; Table 2.10, row 3). Mothers received touches to these locations from their offspring, but offspring did not receive touches to these regions from their mothers. Finally, touches elsewhere on the body (anal region, ears, feet, genitals, head, pinnae, tail, trunk, tusk, and temporal glands) differed by age for interactions between non-relatives (Fig. 2.11c; Table 2.10, row 4). The difference in touches to these specific locations in mature females supports the reproductive success hypothesis, with differences between immature (calf-juvenile) and mature (pubescent-adult) females.

The proportion of trunk touches an elephant performed to their own mouth supported the social dominance hypothesis. With rainfall as a covariate, different proportions of trunk touches were performed by elephants to their own mouth (Table 2.8, row 4; Fig. 2.12). After adjusting for the effects of rainfall, calves performed a higher proportion of trunk touches to their mouth ($82 \pm 0.04\%$) than adults ($63 \pm 0.06\%$) (Tukey HSD: calf – adult $p = 0.03$). The lack of difference between intermediate stages suggests a change at multiple ages for this behavior, as predicted by the social dominance hypothesis.

Contact behaviors

Results for the rate of performing various contact behaviors were mixed as to which, if either, of the two hypotheses were supported. Contact behaviors were influenced by partner and analyzed separately by whether the focal animal was the sender or receiver of the action. Little variation was explained by any of the seasonal variables. More contact behaviors were performed when a greater number of bulls in the park were in musth, but a linear fit explained very little variation (Table 2.7, row 3b). Contact behaviors did not vary by the number of elephants present during a focal observation (Table 2.7, row 1e). Rainfall did not impact contact behaviors (Table 2.9, row 4).

When the focal animal initiated the contact (focal animal as sender), significant differences were evident in the average rate of body rubs (see Table 2.5). Comparing the rate of body rubs between females and their immediate relative (mother or offspring), there was a significant difference between age classes (Table 2.8, row 5a; Fig. 2.13a). Calves and juveniles were not significantly different from one another, but both performed a higher rate of body rubs than pubescent females (Tukey HSD: calf – juvenile

$p = 0.71$, calf – pubescent $p = 0.0006$, juvenile – pubescent $p = 0.01$). Calves also performed a higher rate of body rubs than adult females (Tukey HSD: calf – adult $p = 0.0008$). A change in behaviors occurred between the juvenile and pubescent stages, as predicted by the reproductive success hypothesis. Age class of the sender and sex of the receiver interacted when the receiver was any other relative (Fig. 2.13b; $F_{3,95} = 2.71$, $p = 0.05$). When the receiver was male the rate of body rubs differed by age, but not when the receiver was female (Table 2.8, rows 5b-5c).

Differences in the rate of affiliative behaviors (trunk on back, tail touch, and lean) supported the reproductive success hypothesis. Affiliative behaviors changed between the age classes (when the focal animal was the sender) for interactions between mother-offspring pairs (Table 2.8, row 6a) but not between their other relatives (Table 2.9, row 9; Fig. 2.14). Juvenile females performed a lower rate of affiliative behaviors to their mother than pubescent females did to their offspring (both sexes combined) (Fig. 2.14a; Tukey HSD juvenile – calf $p = 0.97$; juvenile – pubescent $p = 0.04$; juvenile – adult $p = 0.21$). With contacts to other relatives, all ages contacted males at a higher rate than females (Table 2.9, row 9; Fig. 2.14b).

The average rate of aggressive (trunk wrap, push, back into, head butt, and push) contact behaviors (see Table 2.5) changed by age of the focal female and sex of the partner (Fig. 2.15), partially supporting each hypothesis. When the female contacted an unknown elephant, behaviors changed between the juvenile and pubescent stages but not in the rate of contacts to calf-juvenile (male and female) or pubescent-adult (females only) partners (Table 2.9, row 6; Fig. 2.15a). Juvenile females performed a higher rate of contacts (10.5 ± 0.6 contacts/hour) than pubescent (5.5 ± 0.7 contacts/hour) or adult

females (6.2 ± 1.4 contacts/hour)(Tukey HSD juvenile-calf $p = 0.25$, juvenile-pubescent $p = 0.001$, juvenile-adult $p = 0.005$). However, only adult females performed aggressive behaviors to pubescent or adult males; if age is correlated to rank (Archie et al. 2006a), this supports the social dominance hypothesis.

When the focal animal was the receiver of body rub behaviors, the evidence supported the social dominance hypothesis. Calves received fewer rubs from their mother than mature animals received from their offspring, and juveniles were intermediate (Fig. 2.16a; Table 2.8, row 5d; Tukey HSD calf – juvenile $p = 0.64$, calf – pubescent $p = 0.002$, calf – adult $p = 0.04$). When the sender was any other relative, age and sex differences were evident (Table 2.9, row 10). Males performed more body rubs to all ages of females than females performed (Fig. 2.16b).

Differences in the rate of affiliative behaviors received provided evidence for developmental changes, but not the predicted patterns (Fig. 2.17). Calves received higher rates of contact from their mother than juveniles, and this rate also was higher than the rate of behaviors performed to adults by their offspring (both sexes) (Table 2.8, row 6b; Fig. 2.17a). When the sender was any other relative (including mature, independent offspring), there were no differences in the rate of behaviors by either age class of the receiver or sex of the sender (Table 2.9, row 11; Fig. 2.17b).

Aggressive behaviors did not differ by age of the receiver, but a difference by sending partner supported the reproductive success hypothesis (Table 2.9, row 7; Fig. 2.15b). Calf and juvenile (CJ) elephants (male or female) performed aggressive contacts at a higher rate to all ages (5.7 ± 0.9 contacts/hour) than either pubescent-adult (PA)

females (4.5 ± 0.5 contacts/hour) or males (4.2 ± 0.7 contacts/hour)(Tukey HSD CJ (both sexes) - PA (female) $p = 0.04$, CJ (both sexes) - PA (male) $p = 0.05$).

Discussion

Variation in social behaviors was largely independent of seasonal factors. The proportion of time elephants spent in the four main states (i.e. walk, stand, drink or nurse, and mud) was comparable across the ages and all elephants had similar opportunities to conduct all event behaviors. Calves spent a lower proportion of the focal drinking, but this difference was due to increased time spent suckling. Elephants displayed variability in social behaviors across ages and by interactive partner (Table 2.11). Separating these factors is often difficult and complicated by external factors such as other elephants and their reproductive status (males in musth or females with new calves). Reproductive status of the focal female likely had some effect on the behaviors (See Appendix F), but samples were not high enough to explore this possibility in depth. Other elephant populations display clear differences in group size and association with season (Wittemyer et al. 2005). These differences in group size were predicted to be correlated with behavioral differences. In the Addo population, although group size and chemosensory behaviors differed by season, social behaviors remained consistent over the year of this study. Therefore, differences by age class in social behaviors can be more readily attributed to developmental than seasonal factors. Finally, for the chemosensory behaviors, when elephants performed investigations, there was a high probability that they were investigating elephant signals because sniffs occurred at a higher rate to elephant (feces, urine or other elephants) than to environmental stimuli.

Four behavioral measures showed some support for the social dominance hypothesis, which predicts differences in behaviors from calves through to adults (Table 2.11). Raised sniffs were performed at higher rates as age increased, which may have reflected transitions during multiple age classes, although this was complicated by rainfall effects. For the rate of trunk touches performed by elephants to their own mouth, calves were higher than adults, but no difference was evident in the intermediate stages. Previous work showed that most interactions between a calf and its mother were body rubs or greeting behaviors, while with other relatives there were more trunk touches (Lee 1987). In the current study, differences in the rate of body rubs received by focal animals also supported the hypothesis that behaviors decrease from calf to adult. Social bonds are formed early with overt behaviors and then maintained with less obvious signals later in life. Aggressive behaviors may be involved in dominance interactions or competition for resources (Archie et al. 2006a), which would be evidenced in increased aggression with dominance. Contrary to this, aggression decreased with age. Older, higher ranking females may use more avoidance or subtle aggressive behaviors that were not recorded, so this hypothesis cannot be eliminated based on the observed decrease in aggression with age. Finally, only adult females were recorded performing aggression to pubescent or adult males, which may be related to their heightened social dominance.

Evidence for the reproductive success hypothesis was found in each of the three categories of behaviors examined (Table 2.11). Reproductive success occurs at pubescence for female elephants, and the reproductive success hypothesis predicts that calves are not different behaviorally from juveniles, but both differ from pubescent and adult animals. Chemosensory behaviors provided evidence in the rate of raised sniffs,

especially when examining the rate of behavioral change during the hypothetical transition period. Investigative behaviors performed to other elephants also differed between the immature and mature ages.

The rate of trunk touches to other elephants also supported the reproductive success hypothesis (Table 2.11). Calf elephants are more interested in exploring their environment than older animals, as shown in previous studies at AENP with higher rates of some behaviors in calves than adults, for both males and females (Bagley 2004, Loizi 2004). Calves and juveniles performed different rates of touching, both in general and to specific locations, than older animals, but this was influenced by the identity of the elephant with which they interacted. As social bonds are crucial for elephants (Lee 1986, Lee and Moss 1999), calves are possibly using trunk touch behaviors to establish or reinforce those bonds.

Contact behaviors also supported the reproductive success hypothesis (Table 2.11). Affiliative contacts are used to cement social relationships, such as when juvenile females carry out acts of allomothering or comfort (Dublin 1983, Lee 1987). Affiliative behaviors were performed less frequently from juveniles to their mother than from pubescent females to their offspring, indicating that these behaviors increase in importance once a female has offspring to care for or that juveniles are spending more time with siblings and not their mother. However, all ages performed more affiliative behaviors to male relatives (non-offspring) than to female. Previous studies have found that male calves spend more time away from their mother than females (Lee and Moss 1999), so the increased rates of behavior could be a result of increased opportunity for relatives other than the mother to contact male calves. Aggressive contacts were

performed at a higher rate by calf and juvenile animals, with a drop at pubescence, as predicted by the reproductive success hypothesis. These aggressive contacts may have been more play-oriented, as the young animals are developing a sense of place in the social order. Thus, while the transition in behaviors occurred at pubescence, different behaviors performed by older females provide evidence for the importance of dominance as well.

Some behavioral measures provided support for neither hypothesis (Table 2.11). State behaviors did not differ by age. Sniff behaviors in general did not differ by age, but they did differ in the substance investigated. The lack of an age difference in these findings could be related to the fact that the precise signal was not known. Young animals may exhibit moderate rates of behavior to a wide variety of interesting signals, while adults exhibit high rates to a select group of signals, but this study lacked the power to distinguish between specific signal types, such as existing fecal piles that may have been deposited by musth or non-musth males. When elephants were the recipients of affiliative behaviors, the rate dropped from calf to juvenile, which was one age class earlier than predicted by the reproductive hypothesis. Such a change could indicate an early preparation for later independence.

Similar to other social animals, elephants develop a variety of skills early in life. Interest in elephant stimuli, and in friendly contacts with relatives, help a young animal develop the social bonds that are crucial to effective functioning in adult society. In other species, behaviors are important only during some life stages, perhaps at very young ages and then not until adulthood (Stamps 2003). This pattern of variability by ages is upheld, even after accounting for a variety of seasonal factors. Seasonality, while important in

patterns of movement and aggregation, did not appear to be an overriding factor impacting development of social behaviors, but did influence rates of chemosensory behaviors. Instead, attaining reproductive success and social rank may have interacted to influence many behaviors and their development.

Behavioral development in other species also follows the patterns predicted by the social dominance and reproductive success hypotheses. In spotted hyenas, behaviors change at five points corresponding to changes in social structure and maturity (Holekamp and Smale 1998). For chimpanzees some behaviors are modified during a single developmental period while others develop over the entire lifetime (Lonsdorf 2005). In elephants, sexual dimorphism becomes apparent at a young age. Both social rank and reproductive capabilities interact to produce different patterns of development for males and females. Further research on the chemical signals various ages and sexes respond to will help in better understanding of adult behaviors and the developmental pathway to reach that adult stage. Using a longitudinal approach, external variables have been shown to impact the rate of behaviors, which will become important in designing future research, while a cross-sectional analysis allowed for larger sample sizes. Differences between the ages and sexes are magnified during the initial approach to a signal-rich area (see Chapter 1), and may be evident even before the elephants are visible to researchers. Further exploration of this and other questions will help to further refine the interactions of social dominance and reproductive maturity on development in African elephants and other social mammals.

Table 2.1: Percent of total focal samples conducted on female African elephants at various locations in AENP, May 2004 – May 2005. Additional locations detailed in Appendix E.

Location	Percentage of total	Number of focal observations completed
Gwarriedam	20.6	162
Hapoor	46.4	365
Marion Baree	9.15	72
Woodlands	5.8	46
All other locations	18.05	142

Table 2.2: Focal samples completed on female elephants in four age classes in AENP, May 2004 – May 2005. Calves were between 0 – 4 years old, juveniles from 5 – 9 years, pubescent from 10 – 19 years, and adults from 20 years and older. Ages refer to an individual’s age in 2004, and the number of observations conducted per individual is included in Appendix A.

Age class	Average age (± SE)	Number of focal observations completed	Individuals sampled		Percent of available females sampled
			1-2 times	3+ times	
Calf	1.7 ± 0.21	177	13	23	87.8
Juvenile	6.7 ± 0.21	183	12	25	90.2
Pubescent	14.4 ± 0.46	180	10	22	72.7
Adult	31.4 ± 1.5	246	12	31	81.1
Total		786	47	101	82.7

Table 2.3: State behaviors recorded for elephants at AENP. Start and stop times were recorded for each behavior. Some behaviors taken from Lee 1987, Schulte 2006.

Behavior	Definition
Defecate	Release of feces
Dig	Using trunk, foot, or tusk to dig into ground, resulting in substrate being shifted
Drink	Uptake of water into trunk and transferred inside mouth
Dust	Using trunk to throw dirt over body
Eat	Consuming food, whether gathering with trunk, lifting to mouth or chewing
Mud	Either wallowing in mud or waterhole, or using trunk to spray mud over body
Not visible	Elephant has moved out of sight
Other	Other state behavior not explicitly defined
Play	Use of the trunk to manipulate objects or environment, or vigorous but not aggressive head-to-head sparring and trunk wrestling, mounting, chasing, and rolling on another
Stand	Elephant stays stationary in one location for more than two seconds
Suckle	Contact with the nipple with less than 30s of time off the nipple
Urinate	Release of urine
Walk	Locomotion where all four legs are moving at a steady pace
Wrestle	Face to face contact, trunks intertwined, pushing and shoving

Table 2.4: Trunk touch behaviors performed to or from a focal elephant at AENP. Trunk tip was used to explore different areas of either themselves or another animal. Some definitions were drawn from Loizi 2004, Schulte 2006.

Location	Definition
Anal	Area under the tail and above perineum
Body	Any part of the elephant not specifically noted elsewhere
Ears	External entrance to ear canal
Feet	Area from ankle down
Genitals	Contact to penis or vulva
Head	Forehead, top of head
Legs	From hip or shoulder to ankle
Mouth	Area around and/or inside maxilla and mandible (e.g. lips, jaw, etc.)
Nipples	Nipple region of mammary gland
Pinnae	External portion of the ear
Tail	From the base of the tail to the tip of the hairs
Temporal gland	Gland opening behind eyes
Trunk	From the mouth area to trunk tip
Tusk	Contact to the visible tusk

Table 2.5: Contact behaviors recorded between elephants at AENP. Some definitions drawn from Bagley 2004, Loizi 2004, and Schulte 2006.

Behavior	Definition
Back into	Elephant reduces distance between itself and another elephant by moving backwards and touching the other elephant with hindquarters
Body rub	Elephant walks past another elephant and side of torso rubs against the conspecific
Climb on	Placing the body on top of another elephant which is either standing or lying down, from any position except directly from the rear
Head butt	Use of the forehead or base of the trunk to contact another, either head-to-head or head-to-body
Incidental	Contact with another elephant that is not intentional
Kick	Elephant lifts leg and uses foot to touch or push another elephant
Lean	Elephant places body weight against another elephant
Other	Any contact between two elephants not explicitly listed elsewhere
Push	Elephant uses the body to displace another elephant
Tail touch	Tail is outstretched and touches another elephant
Trunk on back	Entire trunk rests on back area for at least 2 seconds
Trunk on head	Entire trunk rests on superior region of head for at least 2 seconds
Trunk slap	Use of the trunk to sharply contact the body or head of another elephant
Trunk wrap	Trunks are intertwined, often combined with pulling or pushing

Table 2.6: Average (\pm SE) numbers of musth bulls likely to be present during each month in AENP and average (\pm SE) rate of chemosensory behaviors during those months, May 2004 – May 2005.

Average (\pm SE) likely musth bulls¹	Months	Average (\pm SE) rate of chemosensory behaviors²
1 \pm 0	August 04 – September 04	57.66 \pm 3.02
1.6 \pm 0.4	June 04, July 04, October 04, January 05	51.92 \pm 2.53
2.5 \pm 0.3	May 04, November 04, December 04	49.33 \pm 2.45
3.5 \pm 0.4	February 05, May 05	84.55 \pm 4.94
4.75 \pm 1.1	March 05, April 05	88.57 \pm 4.19

¹ Each number of musth bulls is an average of the minimum (number of musth bulls actually sighted) and maximum (number of bulls not sighted but who were in musth in previous or successive months) likely musth bulls per month.

² The average rate of chemosensory behaviors is the average of all focal observations during a level. Individual elephants may be repeated.

Table 2.7: Correlation between seasonal variables and behaviors performed by female elephants in AENP, May 2004 – May 2005.

Variable	Behavior (average performed per hour across all ages)	Correlation or regression coefficient	p
1. Average number of elephants present during a focal			
1a.	Percent of observed time spent standing	$R^2 = 0.04$	<0.001
1b.	Chemosensory behaviors	$R^2 = 0.09$	0.03
1c.	Trunk touches to self	$R^2 = 0.01$	0.22
1d.	Trunk touches to or from other elephants	$r = 0.09$ (Spearman)	0.30
1e.	Contact behaviors	$R^2 = 0.002$	0.63
2. Total number of new calves born each month			
2a.	Chemosensory behaviors	$R^2 = 0.002$	0.75
2b.	Trunk touches to self	$r = -0.02$	0.83
2c.	Trunk touches to or from other elephants	$r = 0.13$	0.13
3. Average number of musth bulls in park at time of data collection			
3a.	Chemosensory behaviors	$R^2 = 0.006$	0.56
3b.	Contact behaviors	$R^2 = 0.04$	0.02
4. Average monthly rainfall			
4a.	Average rate of trunk touch to self behaviors	$R^2 = 0.13$	0.003
4b.	Average rate of trunk touches to other elephants	$r = 0.05$	0.55
5. Low monthly rainfall	Raised sniffs	$R^2 = 0.03$	0.27
6. Moderate monthly rainfall	Raised sniffs	$R^2 = 0.02$	0.52
7. High monthly rainfall	Raised sniffs	$R^2 = 0.10$	0.03

Table 2.8: Statistics for one-way ANOVA on state and behavioral data collected from elephants in AENP, May 2004 – May 2005. Four age categories were used; degrees of freedom are noted (d.f.).

	N	Focal animal sender or receiver	F (3 d.f.)	p
1. States (proportion of visible time)	147			
1a. Walking		Sender	2.53	0.06
1b. Standing		Sender	0.32	0.81
1c. Mudding		Sender	1.95	0.12
1d. Drinking		Sender	4.13	0.007
1e. Drinking and suckling		Sender	0.83	0.48
2. States (average bout length)	148			
2a. Walking		Sender	0.53	0.66
2b. Standing		Sender	0.65	0.59
2c. Mudding		Sender	4.16	0.008
2d. Drinking		Sender	2.48	0.06
3. Trunk touches				
3a. Proportion of trunk touches performed to mouth	105	Sender	2.82	0.04
4. Average rate of trunk touches performed to self				
4a. Low rainfall	38	Sender	5.8	0.003
4b. Moderate rainfall	38	Sender	0.008	0.99
4c. High rainfall	38	Sender	3.5	0.02
5. Average rate of body rub				
5a. Mother – offspring pairs	88	Sender	10.82	< 0.0001
5b. Male relatives (not offspring)	19	Sender	4.42	0.02
5c. Female relatives (not offspring)	75	Sender	1.75	0.16
5d. Mother – offspring pairs	70	Receiver	4.99	0.003
6. Average rate of affiliative behaviors				
6a. Mother – offspring pairs	91	Sender	3.30	0.02
6b. Mother – offspring pairs	80	Receiver	5.01	0.003

Table 2.9: Statistics for two-way ANOVA of data collected from elephants in AENP, May 2004 - May 2005. Degrees of freedom (d.f.) are indicated.

Average rate of:	N	Interaction		Age		Rainfall		
		F (6 d.f.)	p	F (3 d.f.)	p	F (2 d.f.)	p	
1. Chemosensory behaviors	52	0.33	0.92	2.87	0.05	8.56	0.0004	
2. Raised sniffs	30	0.51	0.8	3.33	0.03	4.73	0.01	
3. Trunk touches to self	38	3.54	0.004	2.17	0.11	16.8	< 0.0001	
4. Contact behaviors	80	1.01	0.42	3.03	0.03	0.92	0.4	
Average rate of:	Focal animal sender or receiver	N	Interaction		Age		Partner ¹	
			F	p	F	p	F	p
5. Targeted sniffs	Sender	52	1.77 (2 d.f.)	0.18	3.26 (1 d.f.)	0.07	1.93 (2 d.f.)	0.16
6. Aggressive behavior	Sender	71	1.49 (3 d.f.)	0.22	3.52 (3 d.f.)	0.02	0.002 (1 d.f.)	0.97
7. Aggressive behavior	Receiver	93	0.60 (6 d.f.)	0.73	0.32 (3 d.f.)	0.81	3.32 (2 d.f.)	0.04
Average rate of:	N	Interaction		Age		Stimulus ²		
		F	p	F	p	F	p	
8. Sniffs	144	0.06 (3 d.f.)	0.98	0.58 (3 d.f.)	0.63	43.0 (1 d.f.)	< 0.0001	
Average rate of:	Focal animal sender or receiver	N	Interaction		Age		Sex	
			F	p	F	p	F	p
9. Affiliative behavior	Sender	98	0.23 (3 d.f.)	0.87	0.58 (3 d.f.)	0.63	6.62 (1 d.f.)	0.01
10. Body rubs (to other relatives)	Receiver	87	1.89	0.14	2.65	0.05	4.03	0.05
11. Affiliative behavior	Receiver	84	0.17	0.91	2.28	0.08	0.04	0.85

¹ 'Partner' refers to the identity of interacting partner: mother or offspring, other relatives, or non-relatives. When the focal animal was the sender for aggressive behaviors (row 6), non-relatives were excluded.

² 'Stimulus' could be either elephant (urine, feces, other elephant) or environmental (ground, vegetation, water).

Table 2.10: Results from Kruskal - Wallis tests for trunk touch behavioral data obtained on elephants in AENP, May 2004 – May 2005. Data were tested for four age categories and three categories of partner: mother-offspring, relative, and non-relative; degrees of freedom (d.f.) are noted.

	N	Focal animal sender or receiver	H (3 d.f.)	p
1. Total trunk touches between:				
Mother – offspring	31	Sender	9.9	0.02
Relatives	59	Sender	3.6	0.30
Non - relatives	17	Sender	1.8	0.62
Mother – offspring	39	Receiver	1.6	0.66
Relatives	38	Receiver	4.6	0.20
Non - relatives	28	Receiver	2.4	0.49
2. Trunk touches to body between:				
Mother – offspring	39	Receiver	5.83	0.12
Relatives	38	Receiver	1.86	0.60
Non - relatives	28	Receiver	5.12	0.16
3. Trunk touches to mouth, legs, or nipples between:				
Mother – offspring	39	Receiver	9.99	0.02
Relatives	38	Receiver	3.34	0.34
Non - relatives	28	Receiver	4.07	0.25
4. Trunk touches to other locations between:				
Mother – offspring	39	Receiver	5.70	0.13
Relatives	38	Receiver	0.52	0.91
Non - relatives	28	Receiver	7.61	0.05

Table 2.11: Summary of seasonal variables impacting data and support for or against the proposed hypotheses. Seasonal variable are only listed when they significantly affected the behaviors. Hypotheses are explained on pp. 53-54.

Category	Behavior	Seasonal variables ¹	Social Dominance	Reproductive Success	Figure
States		Elephants present	No	No	2.2
Chemosensory Behaviors		Rain	No	Yes	2.4
	Raised sniffs	Elephants present	Yes	Yes	2.5 – 2.6
	Sniff or horizontal sniff performed to elephants	Rain	No	Yes	2.7
	Sniff to different stimuli		No	No	2.8
Trunk touch²					
	Trunk touches to self	Rain	No	No	2.9
	Trunk touches sent		No	Yes	2.10
	Trunk touches received		No	Yes	2.11
	Trunk touches performed to mouth		Yes	No	2.12
Contact behaviors²		Musth bulls in park			
	Body rub Focal animal sender		No	Yes	2.13
	Affiliative Focal animal sender		No	Yes	2.14
	Aggressive Focal animal sender		Yes	Yes	2.15
	Aggressive Focal animal receiver		No	Yes	2.15
	Body rub Focal animal receiver		Yes	No	2.16
	Affiliative Focal animal receiver		No	No	2.17

¹ Seasonal variables include number of elephants present, number of musth bulls or new calves in the park, and rainfall. Further explanations can be found in the Analysis section, pp. 59-61.

² Trunk touch and contact behaviors were also influenced by the elephant that was interacted with; see Results section pp. 66 – 70.

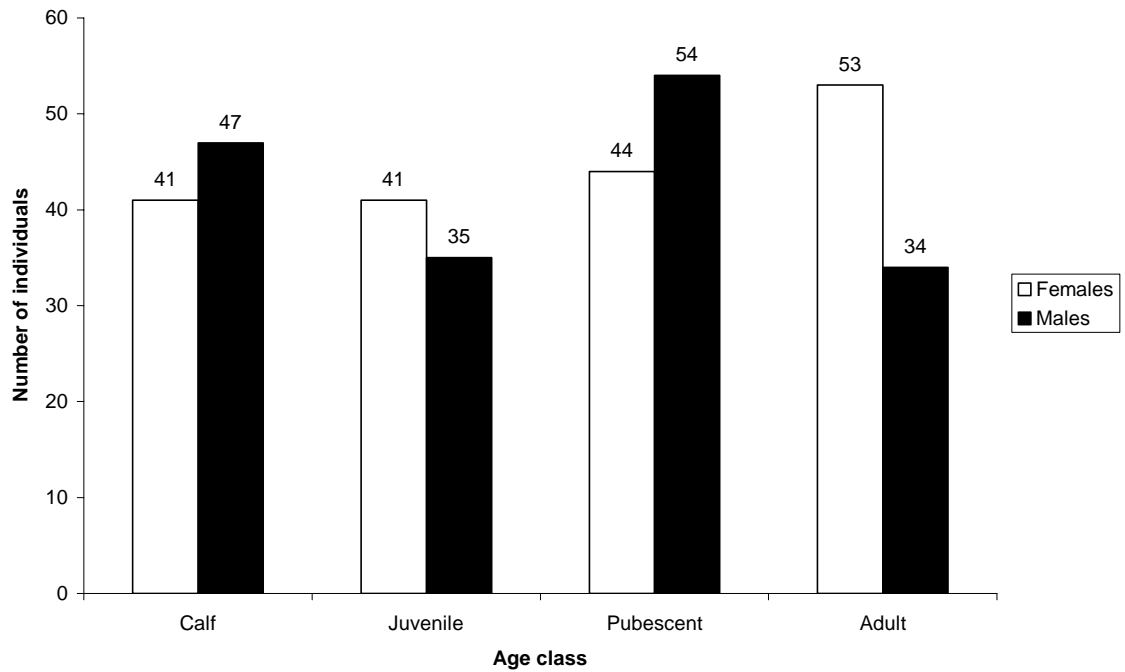


Figure 2.1: Age class distribution in December 2004 of male and female African elephants in AENP. Number of individuals is indicated above each bar. Calves were between 0 – 4 years old, juveniles from 5 – 9 years, pubescent from 10 – 19 years, and adults 20 + years.

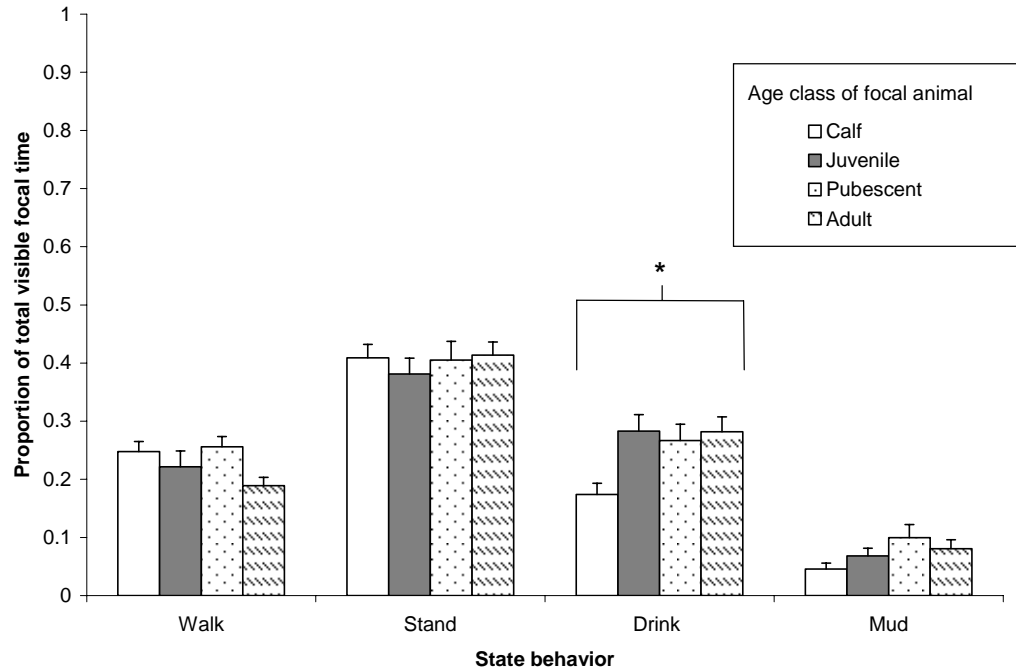


Figure 2.2: Average proportion of visible focal length spent in four states by female elephants in AENP, May 2004 - May 2005. All ages spent the same proportion of time walking, standing, and mudding (Table 2.8, row 1). * Drink (without suckling included) accounted for a lower proportion of the focal length for calves than for juvenile or adult age classes (Tukey HSD calf – juvenile $p = 0.015$, calf – pubescent $p = 0.07$, calf – adult $p = 0.02$).

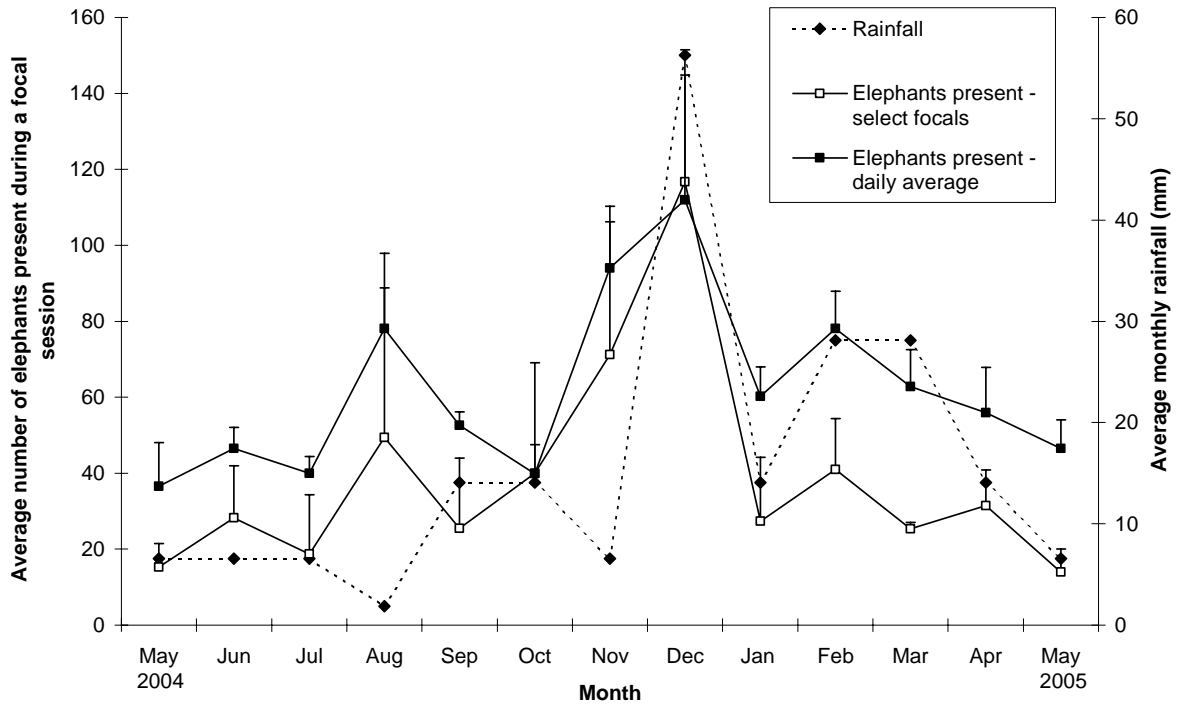


Figure 2.3: Average (+ SE) number of elephants present each month versus average monthly rainfall, May 2004 - May 2005 in AENP. For select focal observations, between 2 and 7 elephants were included each month, N = 50 total individuals. The number of elephants present during a focal observation increased with increased rainfall, $r = 0.31$, $p=0.02$. There was also a significant positive correlation between the average number of elephants present each day a focal was conducted (N = 199) and average monthly rainfall, $r = 0.20$, $p = 0.004$.

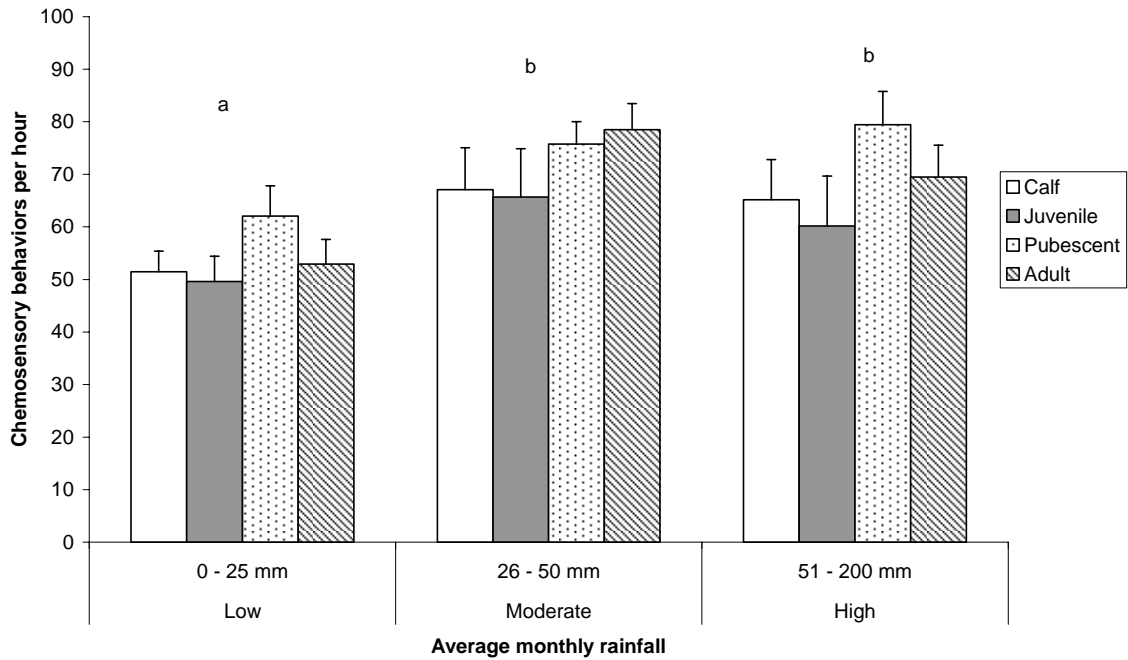


Figure 2.4: Average rate (+ SE) of all chemosensory behaviors performed by four age classes of elephants in AENP, across 3 levels of average monthly rainfall (see Table 1.1). N=11, 9, 14, 18 for calf, juvenile, pubescent, and adult age classes, respectively. Chemosensory behaviors differed by both age and rainfall (Table 2.9, row 1). Differing letters refer to significant differences in rates of chemosensory behavior by rainfall levels across age classes.

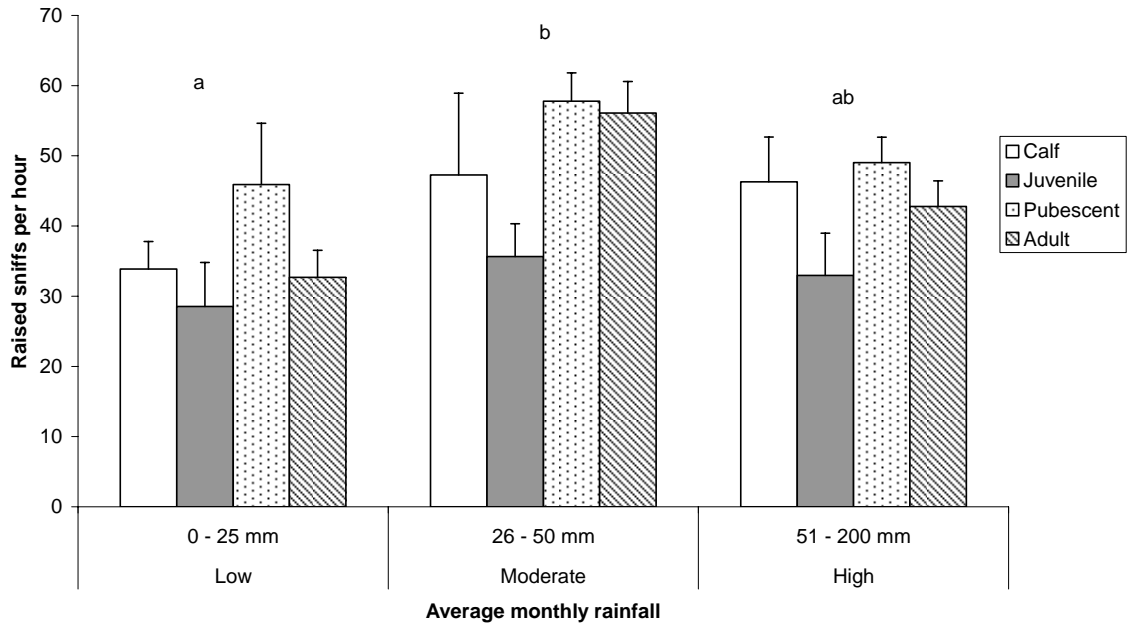


Figure 2.5: Average rate of raised (horizontal and periscope) sniffs performed by 30 individuals in AENP during three rainfall blocks, May 2004 - May 2005. N = 7, 4, 6, 13 for calf, juvenile, pubescent, and adult age classes, respectively. Differing letters refer to significant differences in rate of raised sniffs by rainfall levels for all ages combined (Tukey HSD low – moderate $p = 0.004$, low – high $p = 0.28$, moderate – high $p = 0.18$). For all rainfall levels, pubescent females performed more sniffs than juvenile females (Table 2.9, row 2).

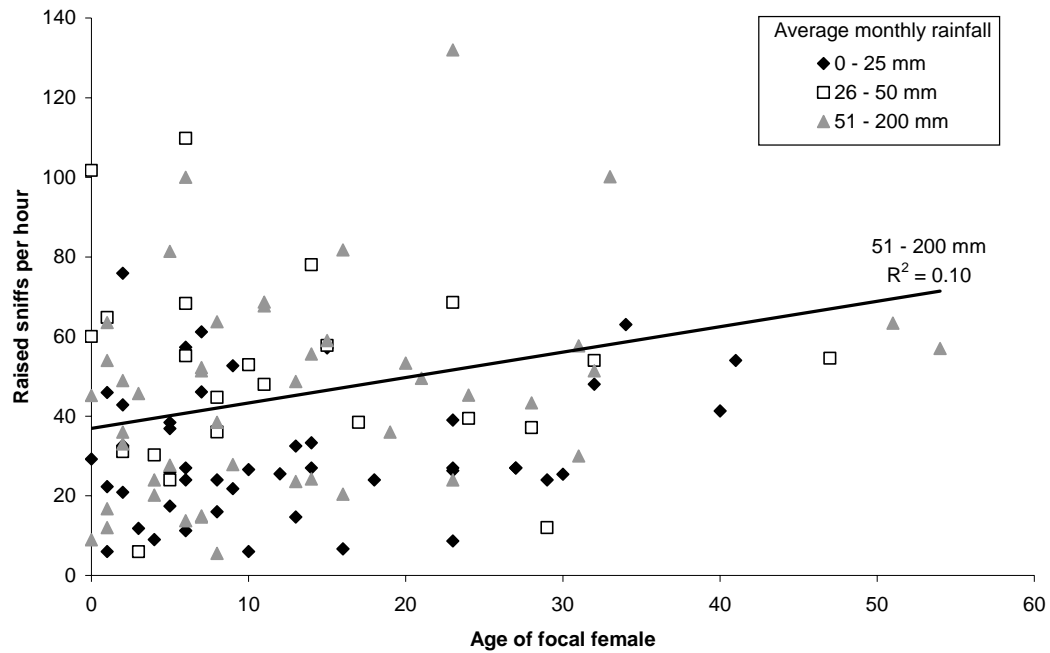


Figure 2.6: Average rate of raised (horizontal and periscope) sniffs performed by female elephants in AENP, May 2004 – May 2005. Samples were categorized by three levels of average monthly rainfall, with N = 44 for Low (0-25 mm) rain, N = 21 for Moderate (26-50 mm) rain, and N = 44 for High (51-200 mm) rain (Table 2.7, rows 5 – 7).

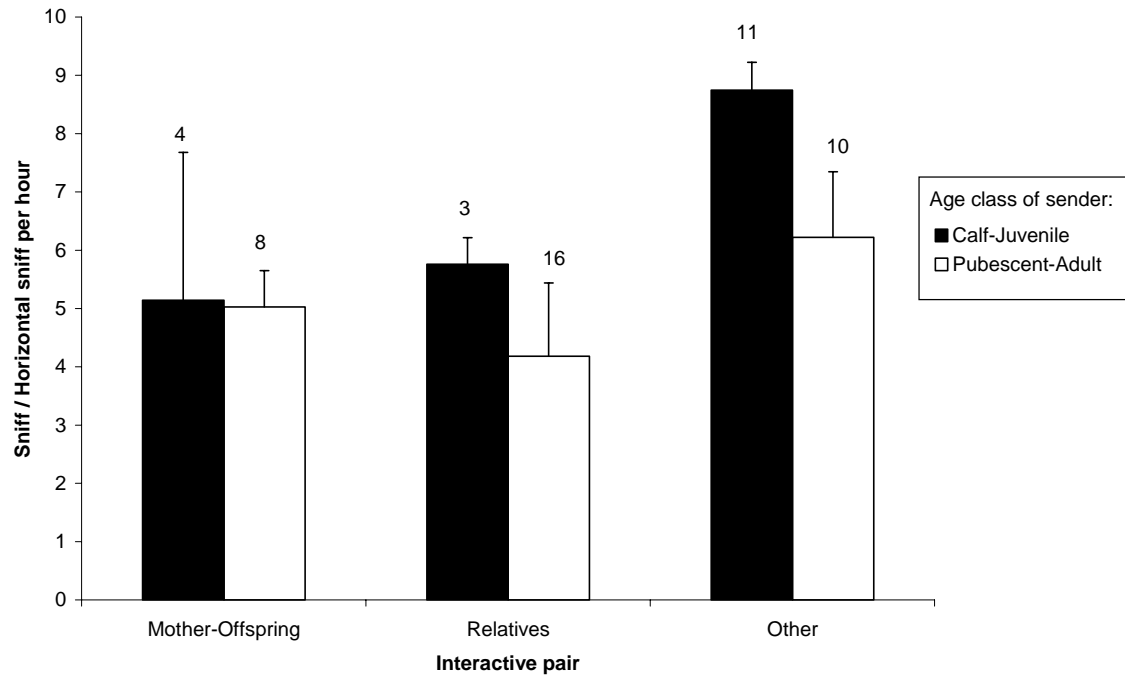


Figure 2.7: Average rate (+ SE) of sniff and horizontal sniff performed to another elephant, categorized by age class of sender and identity of receiver. Number of individuals is indicated above each bar. There were no significant differences between age classes (Table 2.9, row 5).

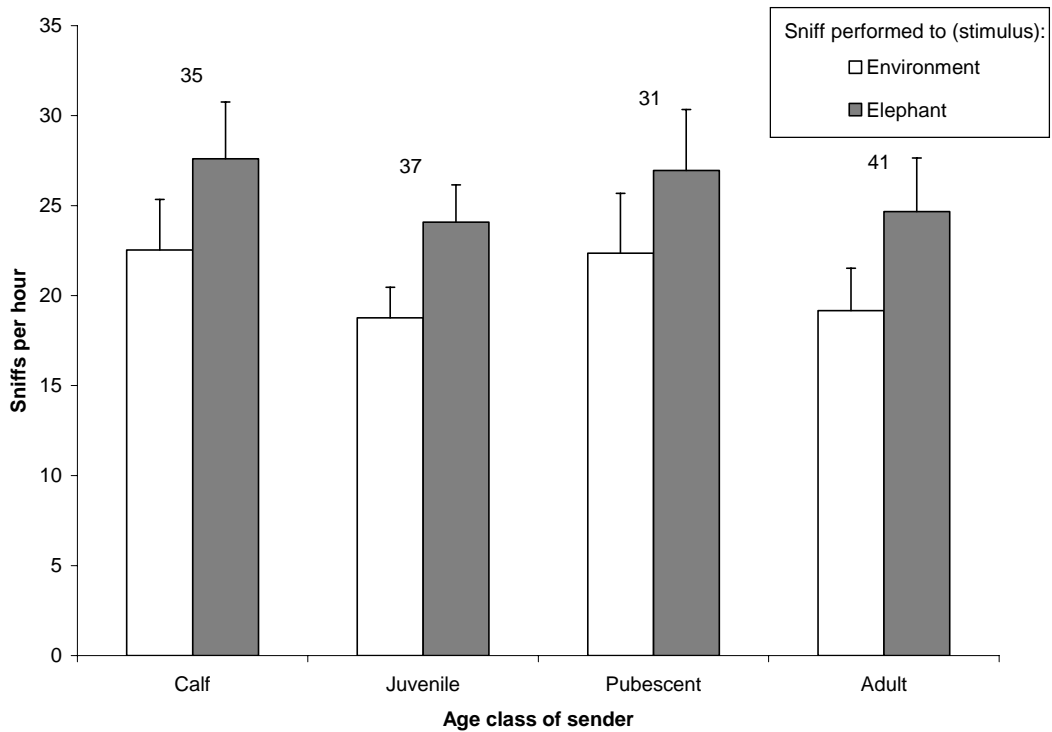


Figure 2.8: Average rate of sniffs (+ SE) to environmental (ground, vegetation, water) and elephant (urine, feces, or other elephants) stimuli for four age classes of female elephants in AENP, May 2004 - May 2005. Number of individuals sampled is indicated above each bar. A higher rate of sniffs was performed to elephant than to environmental stimuli (Table 2.9, row 8).

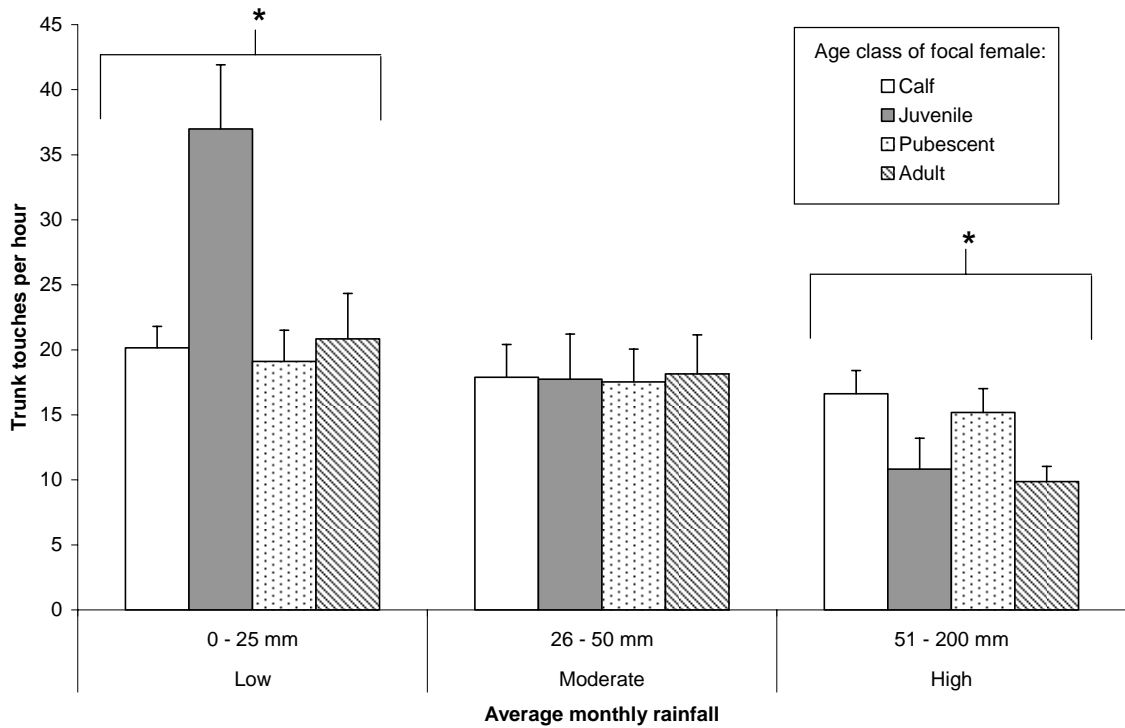


Figure 2.9: Average rate of trunk touches (+ SE) performed to any part of themselves by elephants in AENP for four age classes and three rainfall levels (see Table 1.1). N = 8, 6, 7, and 9 for calf, juvenile, pubescent, and adult respectively. Age class and rainfall interacted significantly (Table 2.9, row 3). *Age differences were seen in Low and High rainfall categories (Table 2.8, row 4).

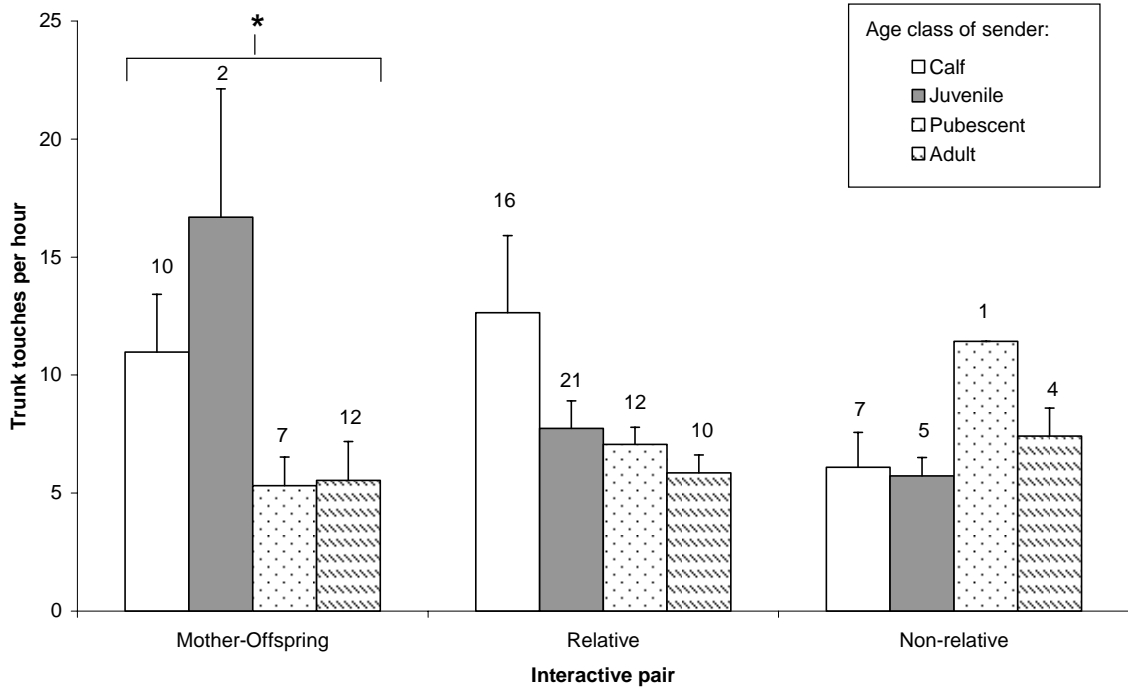


Figure 2.10: Average rate of trunk touches from a focal animal to their mother (calf-juvenile) or offspring (pubescent – adult), to another relative, or to a non-relative by elephants in AENP. Significant differences in the average rate of trunk touches by age were evident in the mother-offspring pair (*), but not within relatives, or within non-relatives (Table 2.10, row 1).

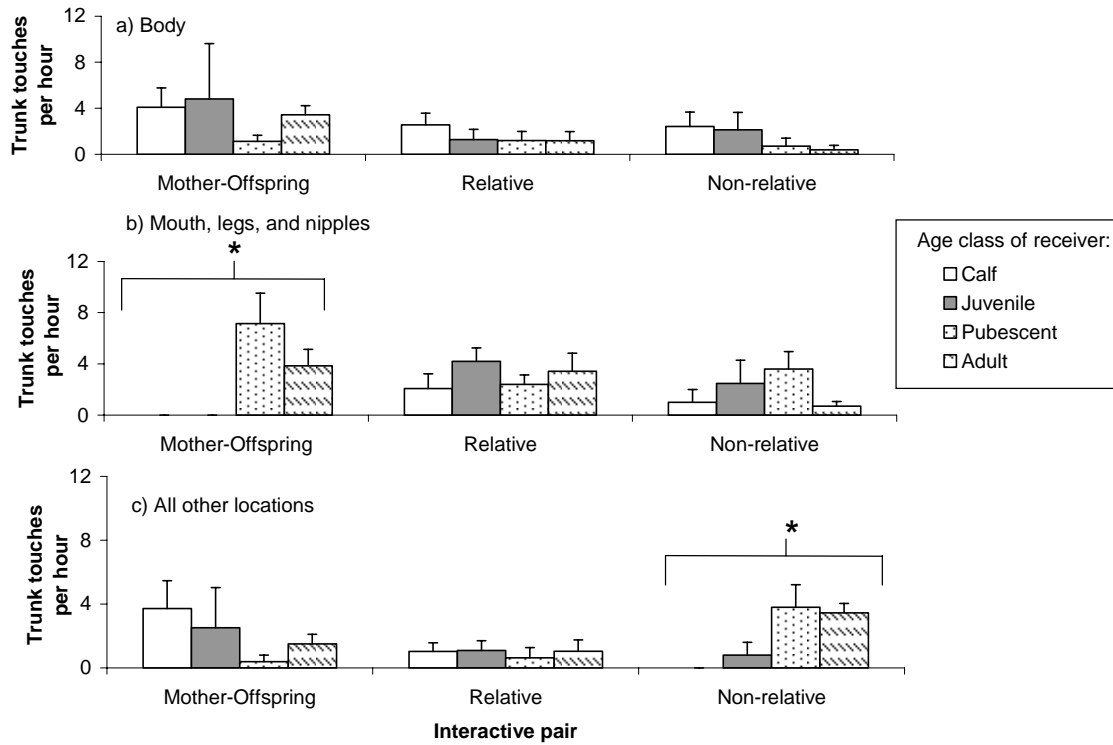


Figure 2.11: Average rate (+ SE) of trunk touches performed to a) the body, b) the mouth, legs, and nipples and c) other parts of the body by elephants in AENP. The other parts touched included anal region, ears, feet, genitals, head, pinnae, tail, trunk, tusk, and temporal glands (see Table 2.4).

* Differences between age classes were apparent in the rate of trunk touches performed between mother-offspring pairs to the mouth, legs, and nipples, and between non-related females to other specific locations (Table 2.10, rows 2 - 4).

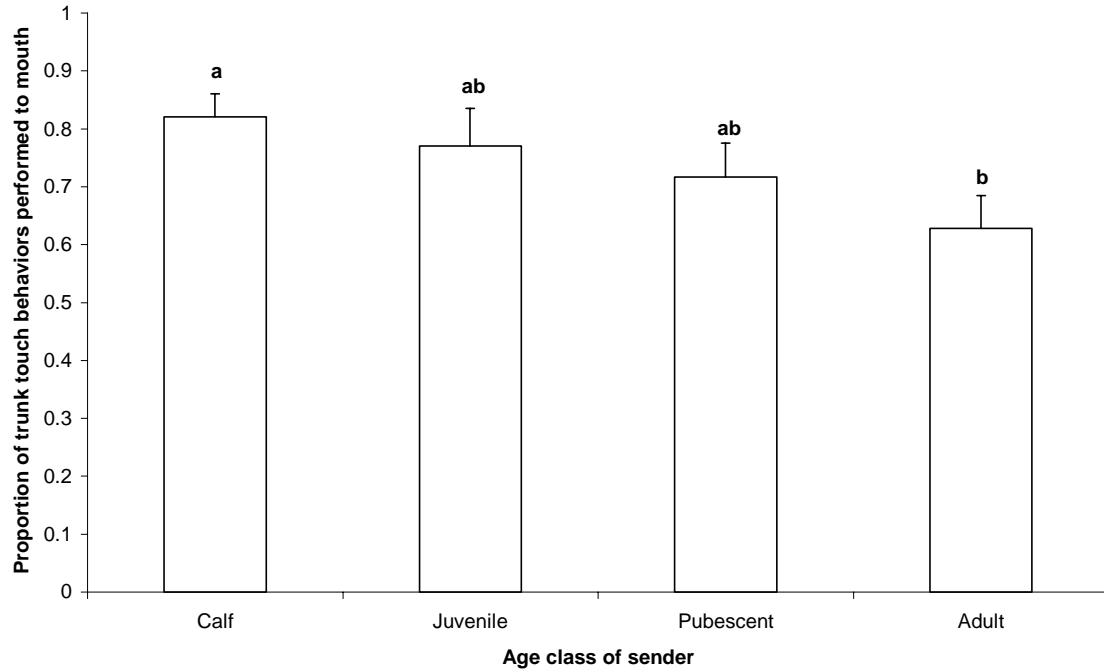


Figure 2.12: The average proportion (+ SE) of all trunk touches to own mouth performed by elephants in AENP, May 2004 – May 2005. N = 35 for calf and adult age classes, N=20 for juvenile and pubescent age classes. Average monthly rainfall was included as a covariate. Differing letters refer to significant differences by age class (Table 2.8, row 4).

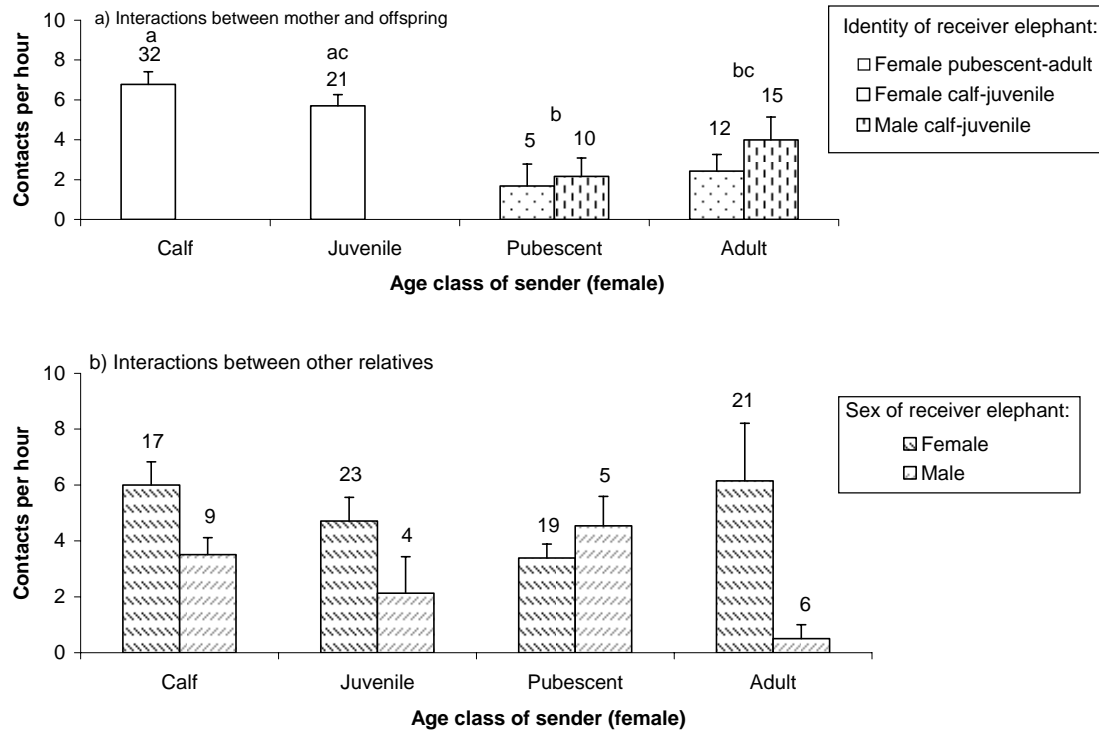


Figure 2.13: Average rate (+ SE) of body rubs performed by focal elephants in AENP, May 2004 - May 2005. Average number of musth bulls (see Table 2.6) was included as a covariate. Age class refers to the sender of the behavior, and the number of individuals in each age class is indicated above every bar. When the receiver was (a) the mother (calf and juvenile age classes) or the offspring (pubescent and adult age classes), different letters indicate significantly different age classes (Table 2.8, row 5a). When the receiver was (b) any other relative, age differences in the rate of body rubs were evident when the receiver was male but not female (Table 2.8, rows 5b-5c).

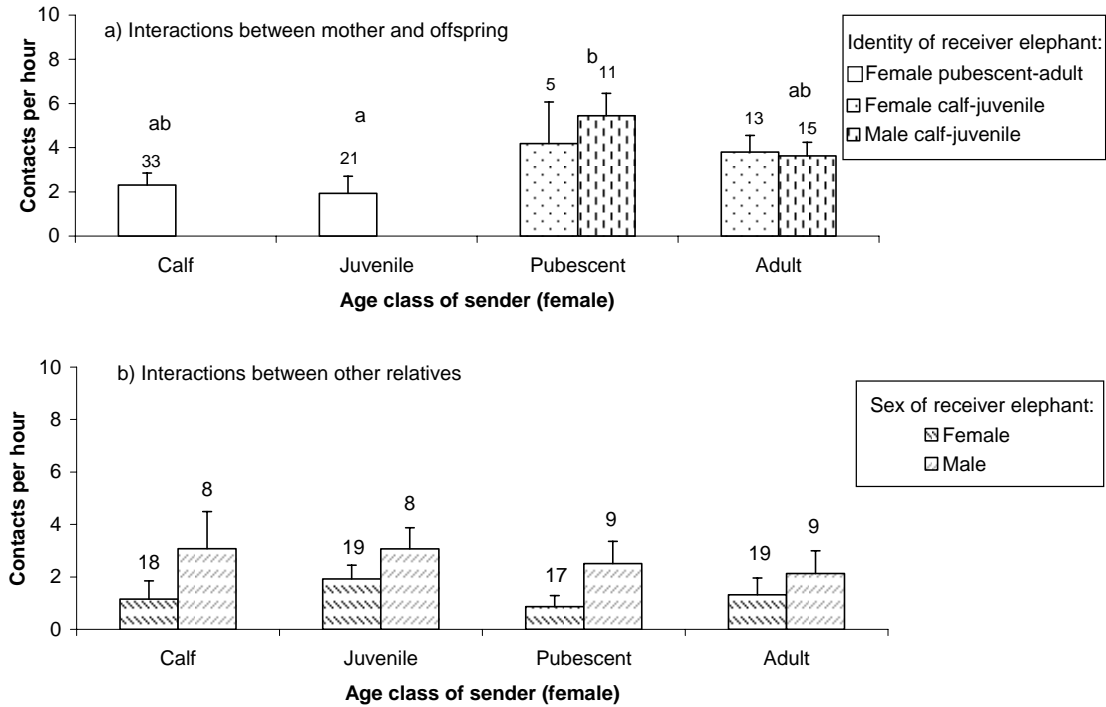


Figure 2.14: Average rate (+ SE) of affiliative contacts (trunk on back, tail touch, and lean) performed by focal elephants in AENP, May 2004 - May 2005. Average number of musth bulls (see Table 2.6) was used as a covariate. Age class refers to sender of contact and the number of individuals sampled is included above each bar. Differing letters indicate differences between the age classes when the interaction was between mother-offspring (Table 2.8, row 6a). Male relatives (non – offspring) received more contacts than females (Table 2.9, row 9).

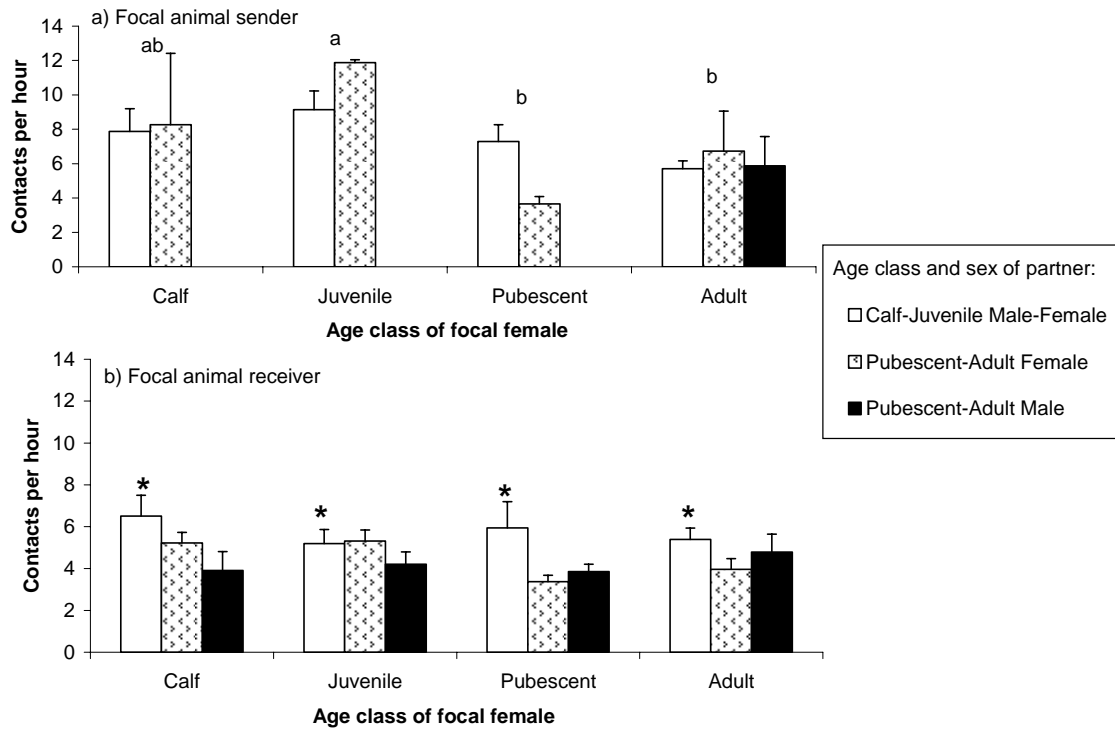


Figure 2.15: Average rate of aggressive contacts between focal animal and a non-identified partner in AENP, May 2004 – May 2005. Aggressive contacts were trunk wrap, push, back into, head butt, and kick (see Table 2.5). When the focal female elephant a) contacted a non-identified elephant, there was a difference by age of sender, indicated by differing letters above the bars (Table 2.9, row 6). When the focal female elephant was b) contacted by a non-identified elephant, behaviors were affected by sending partner but not age (Table 2.9, row 7). The calf - juvenile class was different (*) than both pubescent - adult males and females.

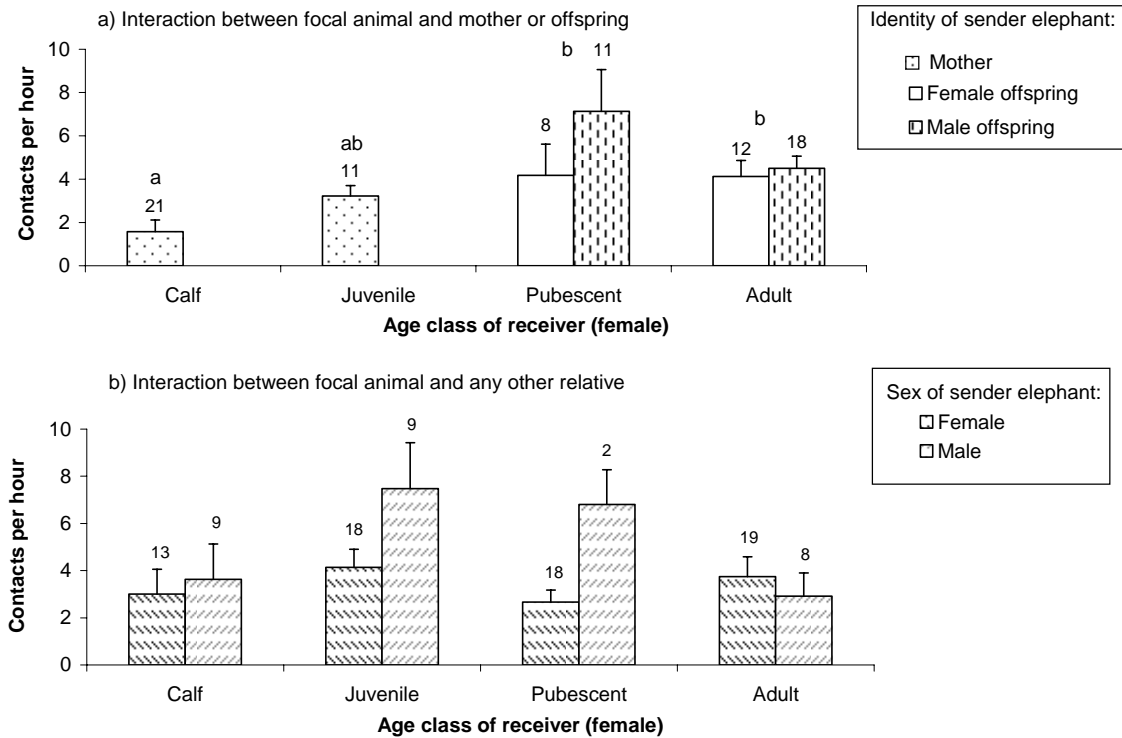


Figure 2.16: Average rate (+ SE) of body rubs received by female elephants in AENP, May 2004 - May 2005. Number of individuals is indicated above each bar. When the focal animal received body rubs from a) their mother or offspring, differing letters indicate differences between the age classes (Table 2.8, row 5d). There were also differences by age and sex of the sender in the rate of body rubs received from b) any other relatives (Table 2.9, row 10).

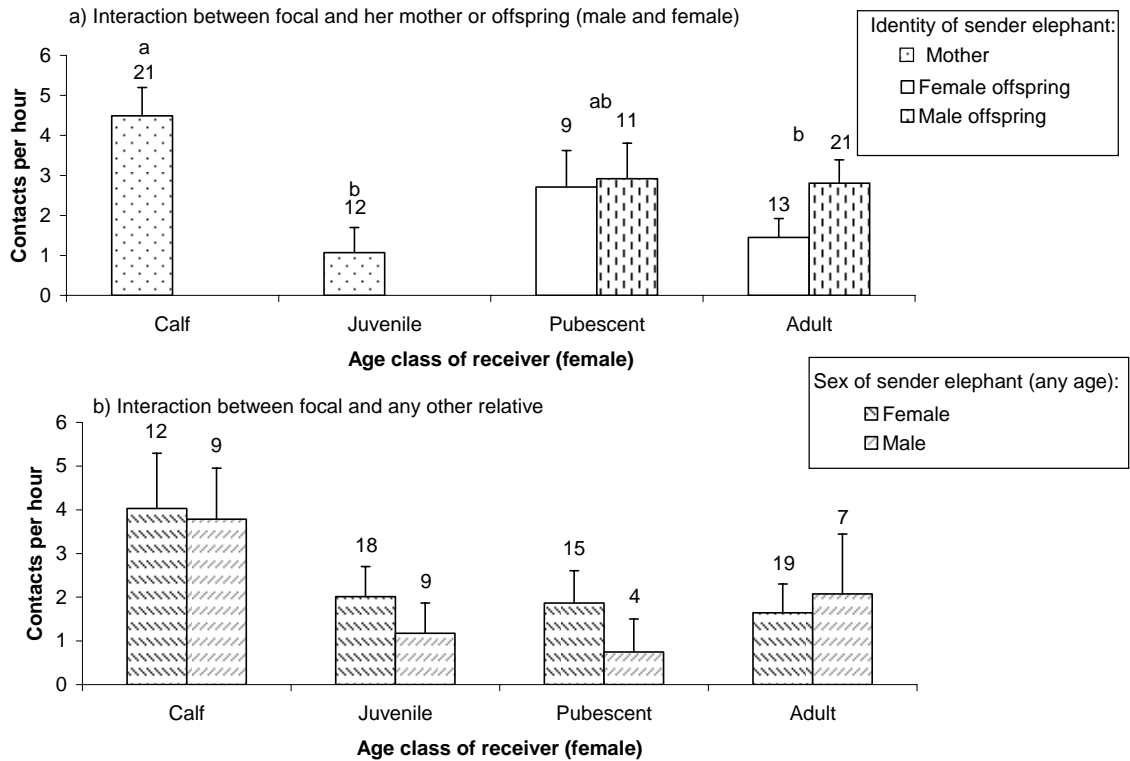


Figure 2.17: Average rate (+ SE) of affiliative contacts (trunk on back, tail touch, and lean) received by female elephants in AENP, May 2004 - May 2005. Average number of musth bulls (see Table 2.6) was used as a covariate. When the sender was a) either the mother or dependent offspring, different letters indicate differences in the rate of affiliative contacts between the ages (Table 2.8, row 6b). When the sender was b) any other relative (including pubescent and adult immediate offspring), there were no differences in the rate of contacts by sex of the sender or age class of the receiver (Table 2.9, row 11).

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APPENDIX A

CANDIDATES FOR LONGITUDINAL STUDY

Table includes how many focal observations (focals) were completed on each individual and date of birth (DOB) of the individual.

Calf females (0 – 4 years old)					
Focal Animal ID	DOB	Focals Completed	Focal Animal ID	DOB	Focals Completed
AKI	2005	1	RAH	2002	2
PIN	2005	2	SAR	2002	7
APR	2004	11	SHE	2002	9
FER	2004	6	STE	2002	2
HAI	2004	11	SUS	2002	2
LUN	2004	7	ZEL	2002	1
MOT	2004	3	CRY	2001	5
AJA	2003	7	FLO	2001	2
ERB	2003	2	MOS	2001	6
LEX	2003	6	CGE	2000	9
LYD	2003	4	OLG	2000	2
MOE	2003	3	ONY	2000	4
OCH	2003	1	ORI	2000	8
OLY	2003	1	ZOE	2000	9
ORC	2003	2			
SAL	2003	1			
ACO	2002	2			
ANA	2002	12			
CAS	2002	4			
HES	2002	9			
LAV	2002	3			
NAO	2002	6			
PAN	2002	6			
			Total	37	178

Appendix A. (cont.)

Juvenile females (5 – 9 years old)					
Focal Animal ID	DOB	Focals Completed	Focal Animal ID	DOB	Focals Completed
AGN	1999	5	PEP	1997	3
AZU	1999	2	POL	1997	5
FLE	1999	5	ANI	1996	1
GAY	1999	1	BIR	1996	9
GLA	1999	1	BUN	1996	1
HEA	1999	8	HAZ	1996	4
LOL	1999	6	MIA	1996	9
ZIL	1999	8	MIN	1996	2
ALG	1998	2	PEA	1996	1
ASH	1998	6	PEG	1996	12
AZA	1998	5	ROX	1996	3
DUE	1998	1	AIL	1995	10
FEL	1998	9	AME	1995	7
MAL	1998	2	ARI	1995	1
MKA	1998	5			
RAF	1998	7			
REN	1998	8			
RUB	1998	1			
ARU	1997	8			
BEZ	1997	9			
LIE	1997	6			
LOR	1997	3			
MAX	1997	7			
			Total	37	183

Appendix A. (cont.)

Pubescent females (10 – 19 years old)					
Focal Animal ID	DOB	Focals Completed	Focal Animal ID	DOB	Focals Completed
BUL	1994	7	BIV	1988	2
MAB	1994	5	BRY	1988	5
RHE	1994	1	LIS	1988	8
AUD	1993	6	ANT	1987	2
MIL	1993	1	MEL	1987	8
ROB	1993	8	BHU	1986	6
LAN	1992	1	PHO	1986	9
MYR	1992	11	REI	1986	10
AMO	1991	7	ANN	1985	10
BIA	1991	2	LUC	1985	5
LOU	1991	2			
MAD	1991	2			
ADE	1990	1			
BWI	1990	10			
LYN	1990	4			
PRU	1990	1			
ROW	1990	9			
AST	1989	4			
MIR	1989	5			
POP	1989	11			
PRI	1989	7			
RON	1989	1			
ARA	1988	10			
			Total	33	181

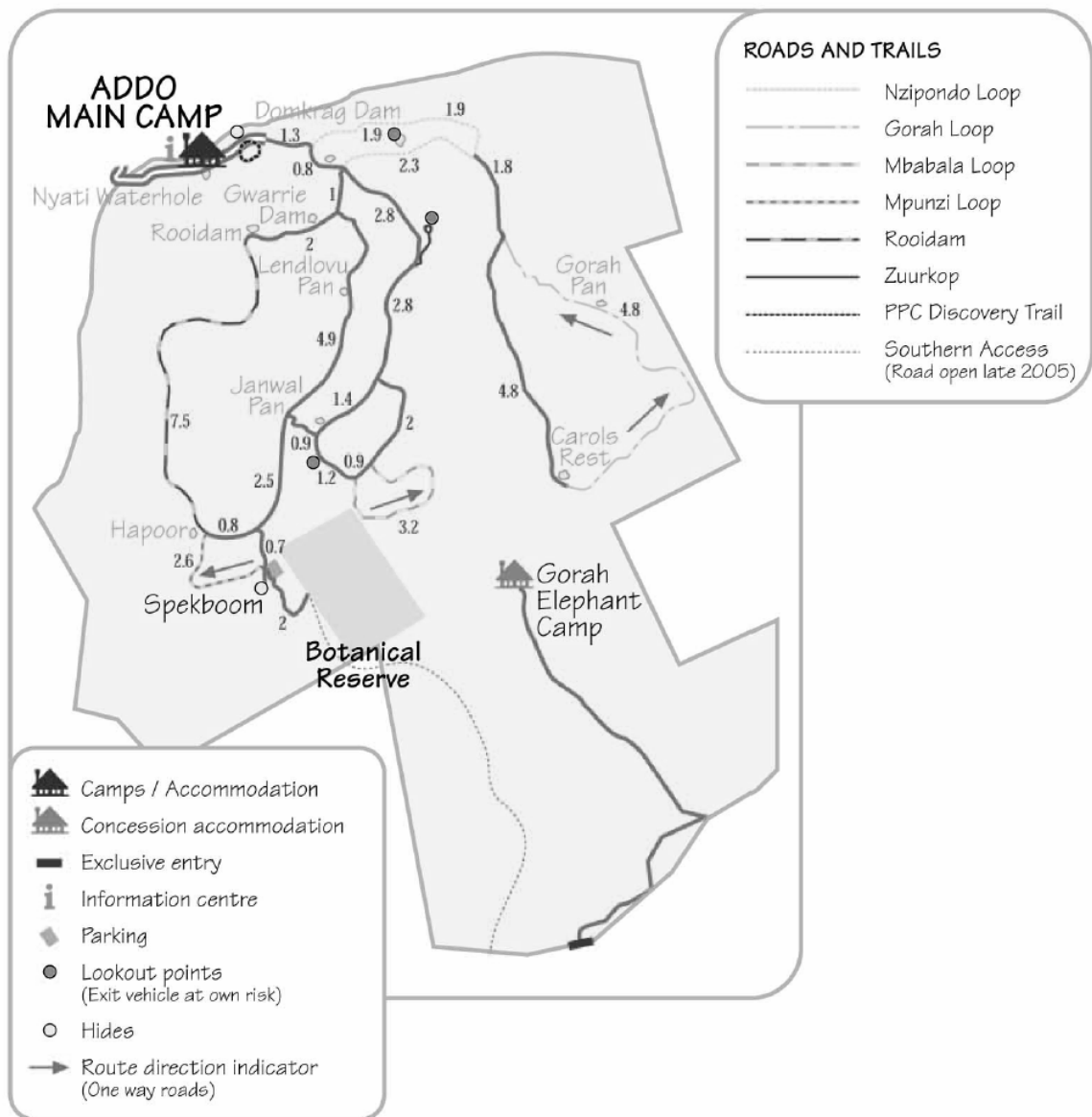
Appendix A. (cont.)

Adult females (20 + years old)					
Focal Animal ID	DOB	Focals Completed	Focal Animal ID	DOB	Focals Completed
PUM	1984	8	AVI	1973	9
BUB	1983	3	PTI	1973	10
MUS	1983	9	RIT	1973	5
AKH	1981	2	BAR	1972	4
ARR	1981	9	HEI	1972	2
HAN	1981	7	LAU	1972	1
LEO	1981	4	MAN	1972	12
LOT	1981	4	RUT	1971	11
MOL	1981	10	BCA	1970	8
MON	1981	2	LIT	1968	7
ROS	1981	3	MEG	1965	9
BRI	1980	3	REB	1964	4
POR	1980	1	MAR	1963	9
ANG	1979	8	AND	1956	1
RHI	1979	8	LIZ	1956	7
AMB	1977	1	LUM	1953	5
RHO	1977	5	BTA	1951	10
BLU	1976	2	HET	1950	10
HIL	1976	8	PAF	1949	10
LUL	1975	1			
ROZ	1975	2			
APP	1974	9			
BCH	1974	2			
			Total	42	245

APPENDIX B

MAP OF ADDO ELEPHANT NATIONAL PARK

Map shows main elephant camp, as reproduced from Addo Elephant National Park Official Guide (2005). Map credits to Gillian Morgenrood, South African National Parks.



APPENDIX D

SELECTION OF DATA FOR CROSS-SECTIONAL COMPONENT

This table shows the average rate of affiliative contact behaviors for individual calves when various numbers of bulls were in musth in the park. Scores of zero were given when an animal performed any non-affiliative contact behavior. Bold print indicates those scores to be used in the cross-sectional analysis. Selection was made to ensure even distribution within an age group and across the five musth categories, and zeros were not included.

Focal Animal ID	DOB	Average bulls in musth in the park				
		1	1.6	2.5	3.5	4.75
AKI	2005					7.83
PIN	2005					10.00
FER	2004	4.81				
HAI	2004	2.92	0.00			
LUN	2004	0.00		3.00	3.00	
AJA	2003	8.31	0.00			
LEX	2003			5.45		
LYD	2003				3.00	
OLY	2003		7.20			
ANA	2002		8.89			
CAS	2002				0.00	
HES	2002	9.84				
LAV	2002			5.45		
PAN	2002		5.45	0.00		
RAH	2002				0.00	
SUS	2002		0.00			
ZEL	2002			2.90		
CRY	2001				1.88	
CGE	2000	3.00		9.11	3.00	3.19
OLG	2000				9.00	
ZOE	2000	0.00				

APPENDIX E

FOCAL OBSERVATION LOCATIONS

Number and percentage of focal observations (focals) conducted at various sites, as well as whether there was water to drink (waterhole) or not (other).

Location	Waterhole or Other	Focals Completed	Percentage of total
Buffelskop	Other	1	0.13%
Camp	Waterhole	27	3.43%
Carols Rest	Waterhole	17	2.16%
Domkrag	Waterhole	21	2.67%
Grasvlakte	Other	1	0.13%
Gwarriedam	Waterhole	162	20.58%
Hapoor	Waterhole	365	46.38%
Kilani	Waterhole	22	2.80%
Korhan flats	Waterhole	6	0.76%
Marion Barea	Waterhole	72	9.15%
Marion Barea Hill	Other	1	0.13%
Near Domkrag	Other	1	0.13%
Near Hapoor	Other	1	0.13%
Roodam	Waterhole	7	0.89%
Spekboom	Waterhole	20	2.54%
Wayne's Valley	Waterhole	17	2.16%
Woodlands	Waterhole	46	5.84%
Total		787	100%

APPENDIX F

FEMALE ELEPHANT REPRODUCTIVE STATUS

This section details supplementary information regarding differences between adult and pubescent elephants depending on their reproductive status, May 2004 – May 2005. All methods are the same as in earlier chapters; in brief, 20 minute focal observations were conducted mainly at waterholes on a sample of females in AENP.

All females who were 10 years or older were placed into one of five reproductive status categories (Table F.1). An average rate of behavior within each stage was calculated for each individual. If an individual had focal observations conducted in multiple stages, I used the responses from a single stage by selecting one that provided the most even distribution across ages and stages. I used all females with a focal in the ‘estrus’ stage for the analysis. Females with focal observations in ‘pregnant’, ‘lactating’, and ‘new calf’ were selected so that there were even numbers of individuals represented in each category. All behaviors were then analyzed using a one-way ANOVA.

Female elephants in various stages of the reproductive cycle were predicted to vary in the rates of signals and contacts both sent and received. Females in estrus would be predicted to have elevated levels of chemosensory behaviors, as they are actively trying to mate. Females with new calves may receive more interest from other elephants, while pregnant females may actively avoid aggressive encounters. In AENP, among females performing the behaviors, estrous females exhibited higher average rates of chemosensory behaviors than both pregnant females and those who were suckling a calf 6 months or younger (Fig. F.1) (Tukey HSD estrus – pregnant $p = 0.009$, estrus – new calf $p = 0.02$, pregnant – new calf $p = 0.69$).

Reproductive status also had an impact on the rate of trunk touches sent or received, but not on the rate of contact behaviors. Females with calves 6 months or younger performed or received trunk touches at a higher rate than pregnant, lactating, and unknown females (Fig. F.2). There were no differences in the average rate of contact behaviors performed between the reproductive stages ($F_{4,69} = 0.65$, $p = 0.63$).

Therefore, my predictions were partially supported. Females who were ready to mate performed more chemosensory behaviors. This could indicate the use of chemical signals to either find mates or avoid other estrous females who would be potential competitors. Trunk touches were elevated to females with new calves, indicating that not only new elephants but also their mothers were potentially more interesting subjects to investigate. The lack of differences in contact behaviors seen may be due to the lack of distinction between interactive partners as well as between types of behaviors.

Table F.1: Number of female elephants sampled for 5 reproductive status categories in AENP, May 2004 - May 2005.

Reproductive status	Description	Maximum number of individual elephants sampled
Estrus	Elephant was seen in estrus on the day behavioral data were collected	3
Lactating	New calf was born 7-24 months prior to the day of data collection	18
New calf	New calf born 0-6 months prior to the day of data collection	13
Pregnant	New calf born 0-22 months after the day of data collection	16
Unknown	No new calves or estrous behavior observed	30

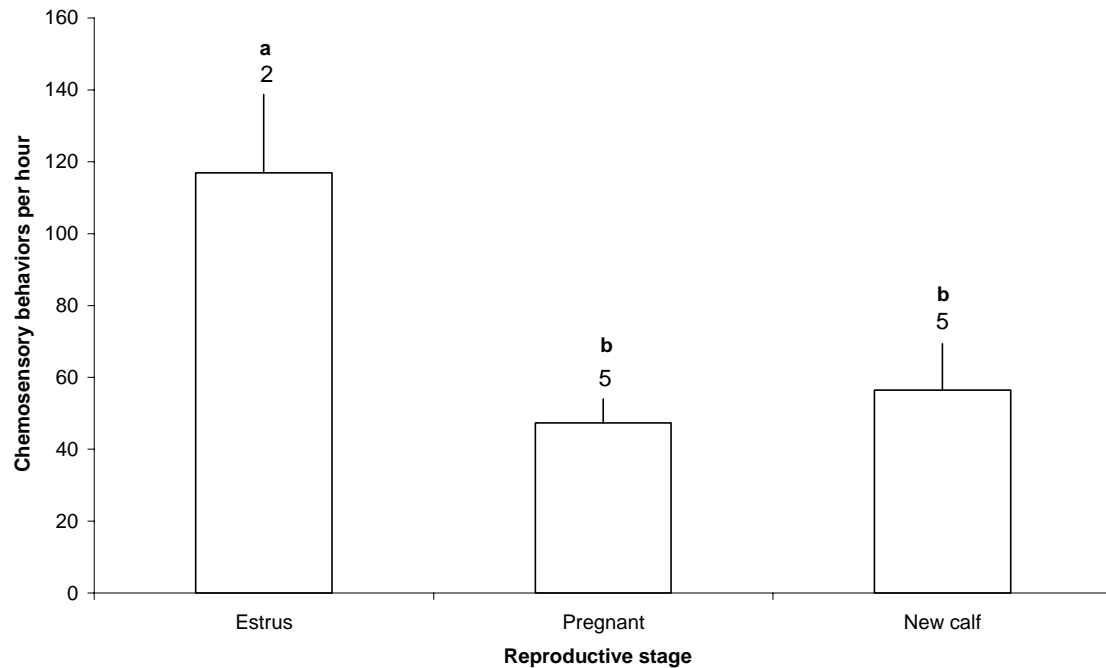


Figure F.1: Average rate (+ SE) of chemosensory behaviors performed by female elephants in AENP, May 2004 – May 2005. Only females performing the behaviors included, and females were categorized into one of three reproductive stages (see Table F.1). Sample size is indicated above each bar, and females in estrus performed behaviors at a higher rate than both pregnant females and those with new calves ($F_{2,8} = 4.86$, $p = 0.04$).

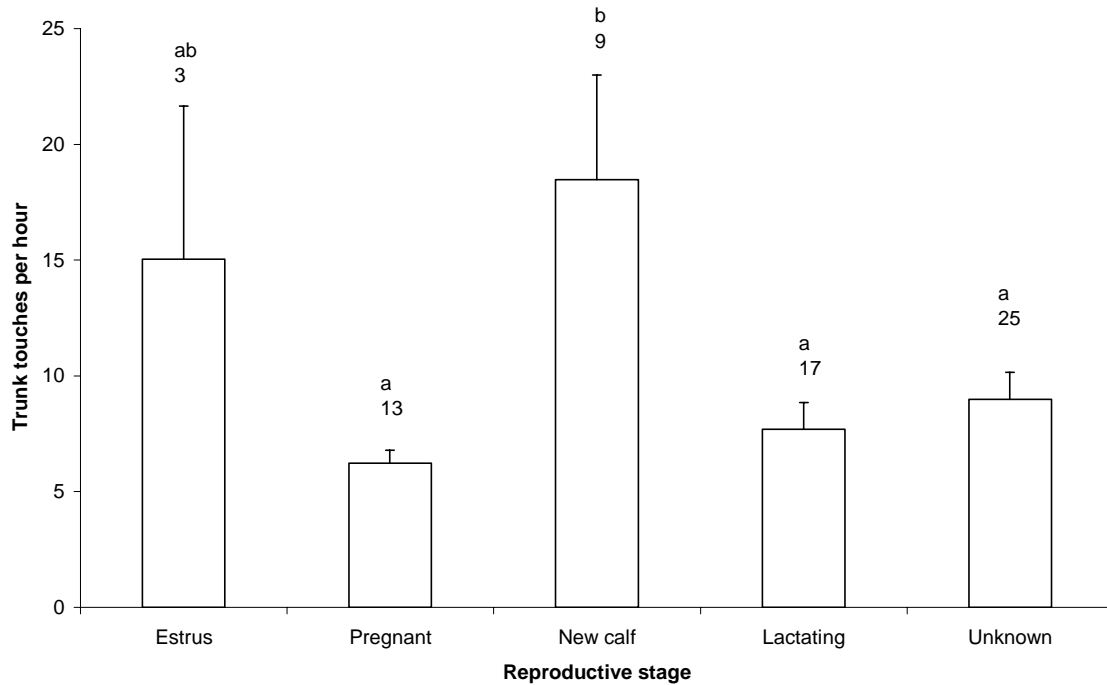


Figure F.2: The average rate (+ SE) of female elephant trunk touch interactions in AENP, May 2004 – May 2005. Only those females performing the behavior were included; females were in various reproductive stages (see Table F.1). ‘New calf’ females performed or received trunk touches at a higher rate ($F_{4,61} = 5.33$, $p = 0.001$) than pregnant ($p = 0.003$), lactating ($p = 0.01$), and unknown ($p = 0.04$), but not estrous ($p = 0.97$) females.