

Male and female developmental differences in chemosensory investigations by African elephants (*Loxodonta africana*) approaching waterholes

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Abstract Although communication is vital for members of a social species, the sexes may differ in the type and degree of information sought. In many polygynous societies, males search for reproductively active females and compete intrasexually for access to females with older males often being most successful. In social mammals, females may mature sooner than males and thus at an earlier age behave more like adults. This maturation may include the assessment of potential mates directly or via indicative signals. In this study, we observed the behavior of African elephants (*Loxodonta africana*) during their approach to waterholes. Waterholes provide an opportunity for elephants to investigate conspecific chemical signals from feces and urine, and each other. We examined the presence of sexual dimorphism in behaviors of the trunk that are indicative of olfactory investigation. We predicted that upon approach to a waterhole, adult males would show greater interest than females in conspecific chemical signals. Females were predicted and observed to exhibit adult-like rates of investigatory behavior at a younger age than males because females mature sooner. Adult males took the longest to

reach the waterhole in the last 100 m of approach; they also demonstrated greater investigatory rates to conspecific feces. Each sex showed adult-type investigative behaviors with the trunk before the age of reproduction. Rather than showing a common chronological developmental pattern across sex, the exhibition of investigatory, chemosensory behaviors reflected sex-specific changes in reproductive development, perhaps reflective of the relative strength of intra- and intersexual selection on communication patterns.

Keywords African elephant · Chemosensory behavior · Behavioral development · Investigation

Introduction

Communication plays a crucial role in the social dynamics of group-living species. Factors such as social dominance and sex influence the behaviors of senders and receivers (Holekamp and Smale 1998). Males and females have different objectives in evaluating any given signal, based on social status and the dynamics of the male and female segments of the group (Moss and Poole 1983; Lonsdorf 2005). Social dominance affects the degree of reproductive success in many mammals (Cote and Festa-Bianchet 2001; Clutton-Brock et al. 1986), and dominance hierarchies are established and maintained by communication between individuals. Animals often display such communicative behaviors at a young age; for instance, in wolves, postural cues indicating status develop early (McLeod 1996). Mathisen et al. (2003) suggested that males and females of sexually dimorphic species express different developmental and behavioral patterns, including the timing of reproduction and associated behaviors. For example, as young males, horses exhibit higher rates of flehmen than

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females of the same age (Crowell-Davis and Houpt 1985). Behavioral development may coincide with reproductive success, as illustrated by some primates. 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).

Developing male and female African elephants (*Loxodonta africana*) live with their maternal family. Despite this similar social structure, sexual differences in behavior are evident even before physical separation. For example, after weaning, male calves begin the gradual process of separation until dispersal by spending more time further from their mother than do females (Lee 1986). Lee and Moss (1999) suggest that male calves may be more exploratory than female calves based on their greater likelihood to be more than 5 m from their mother. Young females also show less interest in urine and feces than similar-aged males (Meyer 2006).

For elephants, intrasexual size-based dominance hierarchies exist in the social structure of both sexes, with size correlated to age (Poole 1994; Archie et al. 2006; Archie et al. 2007). Hierarchies also exist between female groups (Wittemyer and Getz 2007; Esposito 2008). Hence, both sexes may benefit by detecting signs of same-sex conspecifics as they move across their habitat.

Male and females also benefit by locating reproductively active conspecifics. Between the ages of 12 and 15 years, males have separated from their family as they transition into adult society (Buss 1961; Laws and Parker 1968; Croze 1974). Although both sexes are capable of producing viable gametes between ages nine and 15 (Poole 1994), females in the wild begin producing calves between 10 and 16 years of age (Whitehouse and Hall-Martin 2000; Moss 2001), while males are unable to compete successfully for mates until they at least reach age 20–25 (Poole 1994). Typically, male peak reproductive productivity occurs from 35 to 50 years of age (Hollister-Smith et al. 2007). Thus, males and females achieve reproductive success at different points in their life. For their early pregnancies, females have likely mated with males over twice their age, suggesting that the use of adult-like communication has developed at different rates in the sexes. Alternatively, young, post-puberty males also may perform adult-like communication but be unsuccessful in procuring mates.

While many modes of communication can be used to locate and identify competitors or potential mates, chemical signals are often reliable indicators of identity, reproductive state, or overall condition and health because they are linked to physiological condition (Kappeler 1998). As male Asian elephants (*Elephas maximus*) mature, they become more adept at detecting the female estrous pheromone and using female chemical signals to find and guard receptive

mates (Rasmussen et al. 2005). Female Asian elephants display different behaviors toward other females based on the reproductive status of the investigated female (Slade-Cain et al. 2008).

African elephants also use chemical signals to assess the reproductive condition of conspecifics (Bagley et al. 2006; Loizi et al. 2009). Female elephants prefer to mate with males in the rut-like state of musth, and such males dribble odiferous urine regularly, thus leaving urine trails (Poole and Moss 1981; Moss 1983; Hollister-Smith et al. 2007). Poole and Moss (1989) suggest that African elephant females investigate such urine trails to assess potential mates. Male African elephants can differentiate between the urine of females in the luteal and follicular stages of estrus (Bagley et al. 2006), and between musth and non-musth urine (Hollister-Smith et al. 2008). Waterholes provide locations for congregating and signaling among elephants, and thus provide vantage points for studying investigatory behaviors by males and females.

Our objective was to examine developmental differences in male and female behaviors related to chemosensory investigation. We focused on investigatory behaviors during entrance to a waterhole area where signs of conspecifics (e.g., feces and urine) and interactions with conspecifics would be likely. The rate of movement from a standard point to the waterhole should reveal the inclination for investigating the surroundings with the trade-off of taking longer to reach the waterhole. Adult males were predicted to take more time to reach the water due to higher rates of investigative behavior than females and younger animals. Previous research by Loizi et al. (2009) showed that male African elephants are more likely to respond to conspecific feces and urine than females. While no difference in the rate of investigation was found, the study did not observe elephants specifically upon entering a waterhole area but either after elephants had drunk or at locales other than waterholes. We predicted that adult males compared to females would exhibit higher rates of investigation to feces upon entering a waterhole area. We focus on feces because they are visible for days after deposition. Our observations indicate that elephants usually defecate when they urinate but they may not urinate when they defecate. Hence, some feces may be mixed with urine. If chemical signals in feces or urine reveal attributes such as age, status, and reproductive condition, then males would benefit by detecting these signals upon arrival. Both sexes should benefit by detecting predators and resources, so the investigation of the general surroundings, excluding elephant excretions, was predicted to be similar in males and females, but greater in older than in younger elephants. Finally, females were predicted to show adult patterns of investigatory behavior to elephant and non-elephant sources

earlier in life than males because females mature sooner, facing a different suite of social, ecological, and energetic problems than similarly aged males (Lee and Moss 1999).

Materials and methods

Study site

The study was conducted in Addo Elephant National Park (AENP), 60 km north of Port Elizabeth in South Africa's Eastern Cape region from May 2004 to June 2005. All observations occurred in the main elephant camp, a fenced area of 103 km² that contains approximately 360 elephants. All individuals in this population have been identified, and older individuals were aged based on photographic records (Whitehouse 2001) and accepted aging practices for elephants (Moss 1996). Ongoing research adds current information about births and deaths, providing reliable age data for animals born since 1996 (Bagley 2004; Loizi 2004; Gough and Kerley 2006; Merte 2006; Meyer 2006). Because of the consistent presence of observers in AENP, elephant births and deaths are often known to the day, but at least the week or month.

Data collection

Elephants were observed (primarily by CEM with some assistance from BAS) from a vehicle parked at six natural or artificial waterholes. Elephants were categorized by sex and age, reflecting times of major social and developmental transitions (Moss 1996). We sampled between 16 and 19 male and female elephants within four age categories: calves from 0 to 4 years old ($N=34$; $\bar{x} \pm SD=2.2 \pm 1.2$ years), juveniles from 5 to 9 years ($N=34$; 6.8 ± 1.3 years), pubescents from 10 to 19 years ($N=36$; 15.5 ± 2.7 years), and adults from 20 years and older ($N=34$; 32.0 ± 9.3 years). The ages of the sexes per age class did not significantly differ for animals in our observations.

We based our age classifications on Moss (1996). 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 females generally produce their first or sometimes second offspring. We combined 1A (10–14.9 years) and 1B (15–19.9 years) described by Moss (1996) into our pubescent category, which Evans and Harris (2008) term adolescence, to be consistent with a previous study (Loizi et al. 2009). Five of our pubescent females were 15 years of age with six older and seven younger. Adults rise in social and reproductive status with increasing age. Males reach the height of adult

females by age 20, although they may not experience musth until their mid-twenties or later (Poole 1989, 1994; Hollister-Smith et al. 2007). The observed adult females ranged in age from 23 to 49 with three under age 25 ($N=17$; $\bar{x} \pm SD=33.4 \pm 8.1$ years), while the observed adult males ranged in age from 20 to 51 with six under age 25 ($N=17$; $\bar{x} \pm SD=30.6 \pm 10.5$ years).

As a group of elephants approached the waterhole region, one focal individual was selected 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 observed. As the focal elephant walked toward the water, all trunk behaviors performed were noted as well as the substrates investigated, including urine, feces, ground, air, or water. We did not have data on investigations of feces or urine deposited by known individuals. While approaching the waterhole, the elephants were always walking, and since touches to or from another elephant occurred very rarely, they were not considered in the analyses. Only one male in our data set was in musth, and his responses fell within the range of those from other males; therefore, his values were included in the analyses.

We noted the position of the trunk (down or curled), and chemosensory behaviors that we typically recorded are check, place, and flehmen. These involve touching the trunk to the substrate and in the case of flehmen, bringing the trunk tip to the orifices of the vomeronasal organ duct in the dorsal palate (Schulte 2006). In waterhole approaches, these contact trunk behaviors were relatively rare, so our analyses focused on the sniff behaviors. The three types of 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 with the trunk at a maximal position approximately parallel to the ground, and a periscope sniff was directed at or above head level with the trunk above an angle parallel to the ground. Horizontal and periscope sniffs (together termed raised sniffs) were directed at the air, so 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). We refer to downward sniffs as “sniffs” henceforth in keeping with previously published work (Schulte and Rasmussen 1999; Bagley et al. 2006; Meyer et al. 2008; Slade-Cain et al. 2008; Loizi et al. 2009), and we refer to horizontal and periscope sniffs as raised sniffs.

At each of the six waterholes used in this study, the duration of an observation was calculated beginning when the elephants crossed an obvious landmark 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 depending on the waterhole). Each observation was terminated when the focal animal reached the water and began either drinking or wallowing in the mud. At times, a large group of elephants was present, thus obscuring visibility as they came within one to two body lengths of the water. In such cases, the observation was terminated when the individual was not clearly distinguishable.

Fecal piles were counted on 124 out of 135 days of observations (92%). On 11 days, elephants arrived before fecal piles could be counted and with elephants present, counting feces was difficult and inaccurate. 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 1-m radius from the center of the pile.

Analysis

We focused our analyses on downward and raised sniff behaviors because they were observed frequently. The frequency of each behavior observed per individual was divided by the observation time to yield an individual rate for each behavior. At times, it was difficult to identify an elephant from a distance, but as it approached, identification was clarified. Hence, some individuals were sampled more than once. When this occurred (15 times), the two samples were averaged. We tested the data for normality using the Kolmogorov–Smirnov test. We used two-way analysis of variance on age class and sex using Statistica software (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, we present descriptive statistics as mean \pm 1 standard deviation. For determining a posteriori significance between ages, we performed Tukey's honestly significant difference (HSD) test. All statistical tests used $\alpha=0.05$.

Results

The rate of movement from a standard point to the waterhole should reveal the inclination for investigating the surroundings, which may be inversely related to the motivation to drink. For all age and sex classes (two sexes and four age classes), the average time taken to reach the waterhole from approximately 100 m away when observations began was 1.48 ± 0.81 min. Time to reach the waterhole was influenced by the age and sex of the elephant as determined by the significant interaction term (interaction, $F_{3,130}=2.63$, $p=0.05$; age, $F_{3,130}=5.46$, $p=0.001$; sex,

$F_{1,130}=1.00$, $p=0.32$). Adults took longer (females, 1.61 ± 0.71 min; males, 2.18 ± 0.94 min) to reach the water than both juveniles and calves (range, 1.05 ± 0.64 to 1.58 ± 1.01 min; Tukey HSD: adult–calf, $p=0.02$; adult–juvenile, $p=0.0006$; adult–pubescent, $p=0.10$; Fig. 1). The difference in time of travel by age was driven by a significant difference between the ages for the males (range, 1.16 ± 0.64 to 2.18 ± 0.94 min; $R^2=0.22$, $p<0.0001$), but not for the females (range, 1.05 ± 0.64 to 1.61 ± 0.71 min; $R^2=0.04$, $p=0.08$).

Potential signal sources included fecal piles and the other elephants in the area. For the 153 focal observations (138 different elephants with 15 repeats) at six waterholes, there were on average 87 ± 53 fecal piles present. The rate of sniffs to fecal piles by all age and sex classes was 0.31 ± 0.60 sniffs per minute. Calves performed a lower rate of sniffs to feces than did adults (Fig. 2; interaction, $F_{3,128}=1.48$, $p=0.22$; age, $F_{3,128}=2.74$, $p=0.05$; sex, $F_{1,128}=2.34$, $p=0.13$). Within the adult age class, males performed a higher rate of sniffs (0.83 ± 0.94 sniffs/min) to feces than females (0.28 ± 0.45 sniffs/min; $F_{1,31}=4.47$, $p=0.04$).

The other potential signal sources were from elephants entering with the focal animal or from those already present at the site. On average, 7.78 ± 7.67 elephants entered (range, one to 40 elephants), while 6.85 ± 13.2 elephants were present (range, zero to 50 elephants) during a focal observation. There was no correlation between the number of raised sniffs displayed and the number of elephants entering with the focal individual ($n=142$, $r=0.019$, $p=0.82$). The number of elephants present also did not affect the rate of raised sniffs for the focal animal ($n=142$, $r=0.077$, $p=0.36$).

For the 138 elephants observed, all performed one or more types of sniff behaviors, indicative of olfactory investigation. Examining all raised sniffs (horizontal and

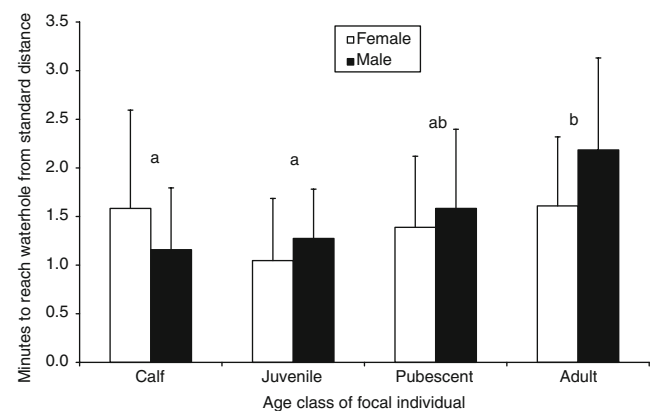


Fig. 1 Mean (+SD) time African elephants in Addo Elephant National Park took to reach the waterhole, categorized by age and sex. Different letters indicate significant differences by age class with both sexes combined

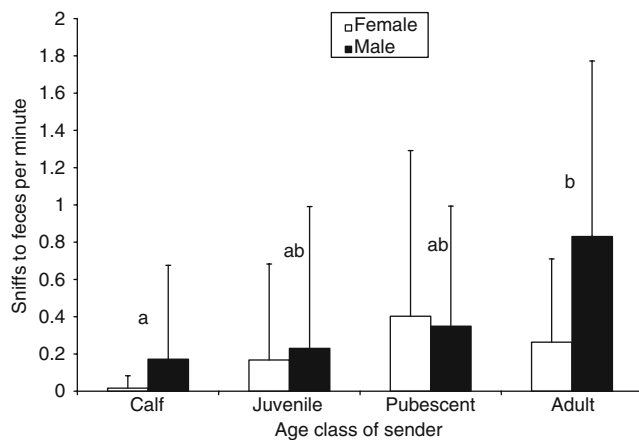


Fig. 2 Average rate of sniffs (number/min) performed to feces by elephants in Addo Elephant National Park, May 2004 to June 2005. Different letters indicate significant differences between age groups for males and females combined

periscope), a significant age effect was apparent (interaction, $F_{3,136}=0.69$, $p=0.56$; age, $F_{3,136}=2.70$, $p=0.05$; sex, $F_{1,136}=1.20$, $p=0.27$). When the sexes were combined, juveniles sniffed more (5.77 ± 3.55 sniff/min) than pubescent elephants (3.95 ± 2.73 ; Tukey HSD juvenile–calf, $p=0.40$; juvenile–pubescent, $p=0.053$; juvenile–adult $p=0.99$). Considering only periscope sniffs, there was a significant interaction between age and sex (interaction, $F_{3,128}=4.54$, $p=0.0046$). Within females, juveniles had a higher rate (1.2 ± 1.72 sniffs/min) than all other age classes (0.20 ± 0.50 sniffs/min; $F_{3,70}=5.29$, $p=0.0024$; Tukey HSD juvenile–calf, $p=0.044$; juvenile–pubescent, $p=0.0043$; juvenile–adult, $p=0.0054$). Juvenile males showed no similar difference by age in periscope sniff rates ($F_{3,74}=1.42$, $p=0.24$). The overall rate per minute of just horizontal sniffs performed by all age-sex classes did not differ significantly, with means ranging from 3.41 ± 2.71 to 5.45 ± 2.61 (interaction, $F_{3,134}=0.33$, $p=0.80$; age, $F_{3,134}=0.65$, $p=0.58$; sex, $F_{1,134}=0.62$, $p=0.43$).

The rate at which elephants sniffed all substrates differed by both sex and age (interaction, $F_{3,137}=0.47$, $p=0.70$; age, $F_{3,137}=0.70$, $p=0.03$; sex, $F_{1,137}=3.61$, $p=0.01$). Males performed sniffs at a higher average rate (3.87 ± 2.80 sniffs/min) than females (2.72 ± 2.64 sniffs/min), and pubescent animals had a higher rate of sniffs than calves (Tukey HSD: calf–juvenile, $p=0.53$; calf–pubescent, $p=0.01$; calf–adult, $p=0.07$). In addition, the increase in rate of sniffs from juvenile to adult levels occurred at different stages for the two sexes. Males increased from the juvenile to pubescent stage ($F_{3,67}=7.03$, $p=0.03$), while females increased between the calf and juvenile stages ($F_{3,73}=6.24$, $p=0.01$; Fig. 3). Examining only the rate of sniffs performed to non-excrement (substrates other than urine and/or feces), the rate of sniffs differed by sex but not age (interaction, $F_{3,131}=0.74$, $p=0.53$; age, $F_{3,131}=2.18$, $p=0.09$; sex, $F_{1,131}=4.21$,

$p=0.04$). Males performed sniffs at a higher average rate (3.45 ± 2.52 sniffs/min) than females (2.58 ± 2.47 sniffs/min).

We examined how the substrate, specifically feces, affected the likelihood of investigatory behavior by age and sex. For female elephants that sniffed some substrate, 6.25% calf (1/16), 12.5% juvenile (2/16), 33% pubescent (6/18), and 29% adult (5/17) females sniffed feces. For males that sniffed some substrate, 11% calf (2/18), 11% juvenile (2/18), and 33% pubescent (6/18) males sniffed feces, but 72% (13/18) of adult males sniffed feces. Overall, of those elephants that performed a sniff, the percentage of elephants that sniffed feces increased with age class (C, 9%; J, 12%; P, 33%; A, 51%). Elephants from the two younger age classes (C+J, 10%) were less likely to sniff feces than elephants from the two older age classes (P+A, 42%) (Yates corrected $\phi_1^2 = 9.56$, $p=0.002$). Pubescent females (33%), pubescent males (29%), and adult females (33%) had similar likelihoods of sniffing feces relative to all substrates, so we combined these groups to compare to adult males. While adult males were the most likely to sniff feces, the proportion of adult males that sniffed feces (72%) did not differ in a statistically significant manner from the combined proportion of adult females and pubescent elephants (32%) that sniffed feces (Yates corrected $\phi_1^2 = 2.42$, $p=0.12$).

Discussion

African elephants exhibited developmental and sexual differences for investigatory behaviors as they approached waterholes. Adult males spent more time traveling the final 100 m to the waterhole than other elephants, and showed the highest rates of chemosensory investigation to elephant feces during this time. While we had predicted similar rates of general

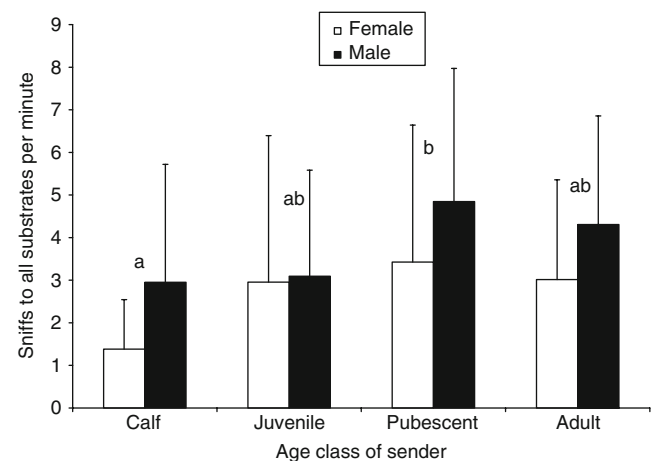


Fig. 3 Average rate of sniffs (number/min) to all substrates for male and female elephants from four age classes upon entering waterholes at Addo Elephant National Park, May 2004 to June 2005. Different letters indicate significant differences between age groups for both sexes combined

investigation for males and females, or even higher for females if detecting predators was an important part of investigation, males actually exhibited higher rates. Water for drinking is likely the primary motivation for visiting a waterhole, but socializing and acquiring signals are additional benefits. The time investigating signal sources upon approach briefly lengthens the time until drinking, and this trade-off can be revealing about the potential benefits of investigation to elephants of different age and sex.

Male and female elephants have diverse incentives and costs associated with learning about relevant signals (Lee and Moss 1999), which translate into differences in the rate of investigation. 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 either on their own skills to interpret signals or take cues from other males (Evans 2006, Evans and Harris 2008). 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. 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 et al. 2007), which may require them to assess reproductively relevant signals sooner in life than males. Because of the potentially high costs of intrasexual competition for males (Poole 1989), the consequences are likely to be more severe for mistakes about intrasexual compared to intersexual signals for elephants and other polygynous mammals.

Investigative behaviors in elephants are performed in part for reproductive functions, so we predicted that both males and females should show an increase in the rate of such behaviors once they begin reproducing. Females begin to reproduce between the ages of 10 and 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 well into the adult stage (e.g., >25 years old, Poole 1994; >26 years, Hollister-Smith et al. 2007). Thus, the rates of investigation that we observed were shown to increase at the developmental stage just before reproductive maturity for both male and female elephants as if priming elephants for the impending changes in their social and sexual environment.

Juvenile elephants, notably females, showed the highest rate of periscope sniffs. When the trunk is in this position, elephants arguably are detecting odors from a further distance than sniffs or horizontal sniffs, which are often directed at individuals or objects. For the juvenile elephants, and apparently especially females, the periscope

position of the trunk may be necessary to sample the less immediate odor field, which may become of greater interest as these juvenile female elephants approach maturity. The initial approach to a waterhole revealed differences in the developmental timing of investigatory trunk behaviors displayed by each sex. Our findings indicate that as individuals approach maturity, a wider range of signals becomes important. While we did not determine what information was obtained, our results suggest that elephants are investigating signs of conspecifics that may be potential mates or competitors.

Typically, mammals display greater interest in odors of the opposite sex (Brown 1979, Heymann 1998, Ferkin 1999), indicating the importance of chemical communication in reproduction. Polygynous males search and compete for receptive females, while females may maximize reproductive success by selecting the best males (Clutton-Brock 1989). Sexual selection theory states that intrasexual competition also will play a role in reproductive success (Clutton-Brock 2007). Hence, these polygynous males would also exhibit interest in odors from other males, who are potential competitors. In the present study, we could not identify the depositor of the feces, but because males would be interested in feces (and urine) from both sexes, we predicted greater investigation by males, especially adults. This prediction was supported by higher rates of sniffs to feces by adult males, and pubescent and adult elephants were more likely to investigate feces than were calves and juveniles. Although not statistically significant, adult males appeared more likely than adult females and pubescent elephants to sniff feces on approach to the waterhole.

We would expect that the interest in feces by males in a heightened reproductive condition, such as musth in elephants, would be greater than that exhibited by other males. Similarly, females approaching ovulation also would be expected to show greater interest in male excretions and secretions, compared to non-reproductively active females. We were surprised at the low rate of response to fecal piles by pubescent and adult females, but perhaps females rely more on olfactory signals in air currents. The odor of a musth male is detectable to a human nose from some distance (personal observations), so females may detect musth males using elevated sniffs. Furthermore, the elephants at AENP are quite familiar with each other and with their surroundings. Hence, mature females may display greater investigatory behavior in places where they have a higher chance of interacting with unfamiliar elephants or where other factors such as predators and human impacts are more variable. In addition, females may rely on the matriarch (Esposito 2008) or other forms of communication to obtain information. Currently, we are examining these hypotheses to evaluate further the role of chemical signals in mating choices by African elephants.

Elephants, like many mammals, live in a society structured by both reproductive success and social dominance, and there are complex interactions between both age and sex for a range of olfactory communication behaviors. By exploring the initial response to a signal-rich environment, this study demonstrates differences between males and females and shows that some behaviors increase from juvenile to adult levels prior to reproductive maturity. Adult males have greater costs associated with misinterpretation of signals, which translates to more interest in signals, as evidenced by their longer travel time to reach the water, higher probability of examining fecal piles (also supported by Loizi et al. 2009), and higher rate of investigation to those feces.

In a range of social mammals, studies have investigated not only the differences between the sexes but also the developmental patterns and underlying evolution (e.g., Lande 1980, Hedrick and Temeles 1989, Mathisen et al. 2003). Similar to the elephants in the current study, young female meerkats (*Suricata suricatta*) show more adult-like responses than similarly aged males, but in the case of meerkats, the response is to alarm calls (Hollén and Manser 2006). In mammals, the development of large body size, fighting abilities, and high social status is important in male mating success (Clutton-Brock et al. 1982). The investigative ability to locate and identify receptive mates is an important addition to this list (Johansson and Jones 2007). Our work on elephants ties into this body of work by underlining some of the fundamental patterns in mammalian development, as well as to provide an avenue for continued research in other taxa. As in other social mammals, adult male and female elephants face separate challenges that impact their social development (Geary 1999, Lonsdorf 2005). Further exploration of the interactions between age and sex in elephants and other group-living species will help to clarify the influence of intra- and intersexual selection on communication patterns of social species.

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