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Sexually Dimorphic Developmental Patterns of Chemosensory Behaviors in African Elephants (Loxodonta Africana)

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SEXUALLY DIMORPHIC DEVELOPMENTAL PATTERNS OF CHEMOSENSORY BEHAVIORS IN AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*)

by

DHAVAL K. VYAS

(Under the Direction of Bruce A. Schulte)

ABSTRACT

Like many polygynous mammals, African elephants exhibit social dimorphism in which females reside in matriarchal groups while males often travel alone or in bachelor groups. Males search for receptive mates who may advertise their condition through chemical and other signals. The difference in adult lifestyles suggests that the developmental pattern of communication for the two sexes should diverge when the social environment and reproductive opportunities of males and females begin to differ. In this study, I examined the differences between the sexes and across four age classes (calves, juveniles, subadults and adults) in the performance of chemosensory behaviors. African elephants were studied at a waterhole in 2004-5 at Ndarakwai Ranch, Tanzania. I identified 277 elephants and 26 distinct female-offspring groups. Sex differences in the chemosensory repertoire and rate of behaviors were evident for subadults but not for the younger age classes. Males showed a higher rate of chemosensory behaviors than females and adults performed chemosensory behaviors more often than calves. Chemosensory responses to a standard stimulus increased in each subsequent age classes for males, but showed no age class differences for females. The observed responses supported the hypothesis that chemical communication patterns would diverge during early puberty, indicating that the development of chemosensory behaviors occurs differently in the sexes in preparation for their disparate adult lifestyles.

INDEX WORDS: Chemosensory, Development, *Loxodonta africana*, Sexual Dimorphism, Tanzania

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DEDICATION

This thesis is dedicated to my friends in Tanzania: Bila ninya, sinakitu.

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INTRODUCTION

Development can be studied by documenting the changes in the life history of a species. Life history refers to the ages that are associated with behavioral or physiological changes during development (e.g. weaning and puberty) (Geary 1999). The physiological, morphological and behavioral development that occurs during the pre-adult stages of infancy, juvenility, and adolescence is a product of genes and the environment. Genotype variations have explained the migratory patterns of adult blackcap warblers (*Sylvia atricapilla*) (Berthold & Pulido 1994) and the food preferences of newborn garter snakes (*Thamnophis elegans*) (Arnold 1981). Environmental variables also affect the development of individuals. In mice (*Mus musculus*), embryonic hormone exposure affects the level of aggression in adults (vom Saal et al. 1983). Imprinting experiments on the beak color of the zebra finch (*Taeniopygia guttata*) have demonstrated the relationship between nestling experience and adult sexual behavior (Vos 1995). Cross-fostering experiments with cockatoos have shown that a gene-environment interaction influences the development of behavior (Rowley & Chapman 1986). For many species, the life histories for males and females differ, leading to sexually dimorphic patterns of development.

Mathisen et al. (2003) suggested that males and females of sexually dimorphic species express different developmental and behavioral patterns. Sexual dimorphism is common in polygamous societies where the dimorphism (e.g. size or color) is associated with differential reproductive success. In polygynous species, a male's likelihood of winning competitions and therefore access to females is dependent on his body size or secondary sex characteristics such as horns, antlers or tusks (Alexander et al. 1979;

Székely et al. 2000). The delayed maturation of male satin bowerbirds (*Ptilonorhynchus violaceus*) has been linked to the acquisition of experience in young males. Collis and Borgia (1992) found that young male satin bowerbirds spend time observing older males and practicing bower building and display behaviors. An extended juvenile period for males faced with intense male-male competition may allow them to prepare for the challenges of successful reproduction. The suspension of maturation for one sex and not the other may reflect the different reproductive demands for males and females.

Achieving reproductive status is a significant stage in the development of individuals. Multiple modes of communication are used to convey reproductive status: touch (Dewsbury 1988), visual cues (Petrie et al. 1991), sound (Bower & Kitchen 1987) and olfactory signals (Gosling & Roberts 2001). Of the different modes of communication, olfaction is ubiquitous among mammals (Gosling & Roberts 2001). Chemical signals come in diverse forms and convey several messages. Reproductive success is dependent on the ability to hold and defend resources, genetic relatedness and sexual status; information which can be derived from chemical signals. Secretions from scent glands demarcate territories (Sillero-Zubiri & Macdonald 1998), body odor conveys kinship (Porter et al. 1986) and urinary compounds signal sexual receptivity (Rasmussen et al. 1997). Males and females have evolved behaviors, termed chemosensory behaviors, that allow them to assess these chemical signals.

Chemosensory behaviors are important factors in the reproduction of mammals. Many species of mammals perform a well-known and conspicuous chemosensory behavior called flehmen. Flehmen is a non-habituated chemosensory behavior used to assess the physiological state in conspecifics (Hart 1983). Excretions and secretions are sampled and chemical signals from the excretions are transferred from the tongue to the vomeronasal organ (VNO) - a sensory apparatus on both sides of the nasal septum that processes the sexually stimulating odors of urine (Estes 1972). In a variety of ungulate species, males will curl the upper lip to cover the nasal openings and inhale, sucking the chemicals from the urine or feces of females into incisive ducts on the roof of the mouth (Estes 1972; Stahlbaum & Houpt 1989; Thompson 1995). The performance of flehmen varies based on the age and sex of the performer. In a study on sable antelope (*Hippotragus niger*), flehmen rates increased with age in both sexes, but males exhibited flehmen earlier and had greater increases in flehmen rate than females (Thompson 1995). Similarly, semi-wild cattle (*Bos indicus*) displayed a bimodal development of flehmen and the rate of flehmen increased from juveniles to adults with greater rates by males than females (Reinhardt 1983). The trends in the development of flehmen among semi-wild cattle may coincide with the production of testosterone which influences sexual motivation and has a similar biphasic developmental pattern (Reinhardt 1983).

The development of chemical communication can be studied by observing the changes across age classes in the performance of chemosensory behaviors (Alberts & May 1992; Palagi et al. 2002; Waters & Burghardt 2005). Males and females of species that have differential reproductive demands (e.g. parental investment) in adulthood are likely to display developmental sex differences. The sexually dimorphic, polygynous and social characteristics of the African elephant (*Loxodonta africana*) make it an appropriate model for studies on the presence of sex differences during development (Buss 1961; Douglas-Hamilton 1972).

The social system of the African elephant is matrilineal with females staying in the natal group and with males dispersing as teenagers (Douglas-Hamilton 1972; Poole 1989b; Poole 1994). Male and female African elephants have different developmental patterns. By 9-10 years of age, males are larger than the same aged females and a ca. 17 year old male is the same size as a 40 year old female (Moss 1996). Adult males are nearly twice the size of adult females and they show marked differences in body morphology (e.g. tusk size, body width, and head shape). The behavioral differences between males and females begin to emerge during infancy. Male calves spend more time suckling and are more likely to stray from their mothers while interacting with non-familial elephants than female calves (Lee 1986; Lee and Moss 1986; Lee & Moss; 1999). Female calves spend more time with the natal group and have a greater amount of familial interactions. Lee and Moss (1999) showed that these behavioral sex differences resulted from a combination of maternal investment, environmental conditions, and the behaviors of the calves. They also suggested that differential maternal investment and calf behaviors reflect the differences in the growth rate and behaviors of older elephants.

The physiological aspect of sexual maturation for males and females occurs at the same age. Gamete production starts in the early teens (Laws 1969), but young males are not able to compete with older males for females until their late teens or early twenties (Poole and Moss 1989). By their mid-twenties, males start to express musth, a state of heightened sexual activity and increased testosterone (Poole and Moss 1981; Hall-Martin 1987; Poole 1989a). Females actively seek out and prefer to mate with males in musth (Poole 1989b). Older males in musth mate more often than younger males in musth (Poole 1989b) and musth males sire more offspring than non-musth males (Hollister-

Smith 2005). Males communicate their musth status by emitting an odorous temporal gland secretion (TGS), leaving trails of strong smelling urine (Poole & Moss 1981; Hall-Martin 1987), and producing low frequency calls (Poole & Moss 1989). Adult male Asian elephants (*Elephas maximus*) in musth release a sex pheromone called frontalin that elicits mating responses only from females in follicular stage of estrus (Rasmussen & Greenwood 2003). Rasmussen and Greenwood (2003) found age class discrepancies among males exposed to frontalin with subadult males displaying avoidance behaviors and adult males showing indifference.

As adults, male and female African elephants remain spatially isolated and mainly associate for reproduction. Elephant estrous cycles have a ca. 10-week luteal and a ca. 5-week follicular phase culminating with ovulation (Hess et al. 1983; Plotka et al. 1988; Kapustin et al. 1996). Females are fertile for a 2-10 day period in a ca. 15-week estrous cycle and because of the lengthy 22 month gestation and extended nursing period, females often cycle only once every four to five years (Plotka et al. 1988; Moss 1983). The relatively short receptivity period, long interbirth interval, and spatial isolation of the sexes (Poole & Moss 1989) make it critical for sexually active individuals to find and identify each other. If the male cannot reach a female before ovulation, reproductive success for both sexes will be delayed. Females and males may facilitate this process by exhibiting conspicuous signs of their reproductive status. Specific behaviors (Short 1966; Moss 1983), vocalizations (Poole 1989a; Leong et al. 2003), and chemical signals in excretions and secretions (Rasmussen et al. 1982; Fieß et al. 1999; Ganswidt et al. 2005) are emitted by elephants to convey their sexual condition.

Vocalizations may signal the presence of reproductively active males and females (Langbauer et al. 1991; Poole 1999), but they do not appear to give information on a female's proximity to ovulation (Leong et al. 2003). Elephant secretions and excretions carry chemical signals that communicate information about the identity (Rasmussen 1995) and precise sexual status of an individual (Rasmussen et al. 1982; Poole 1989a, b; Slade et al. 2003). Both species of elephant show differential responses to urine from various stages of the estrous cycle. Male and female elephants perform behaviors indicating that they can discern between urine from the luteal versus follicular estrous phase (Rasmussen et al. 1982; Slade et al. 2003; Bagley et al. 2006). A suite of chemosensory behaviors, including flehmen, are used to assess the information contained in various elephant chemical messages (Schulte & Rasmussen 1999b).

The change in the performance of chemosensory behaviors across age classes and between sexes of elephants has received limited attention. Evidence from the social development of male and female calves, the pronounced sexual dimorphism and differential opportunities for reproduction in African elephants makes it probable that the development of chemosensory behaviors differs between males and females.

This study examined the developmental patterns of chemosensory behaviors by male and female African elephants (*Loxodonta africana*). I hypothesized that the changes in the social environment across age classes and the differential opportunities for reproduction between males and females would lead to sex differences in the development of chemosensory behaviors. The study was conducted in two parts. For Part I, the first objective was to determine the pattern of change in chemosensory behaviors across age classes within each sex. Young elephants may use chemosensory behaviors to gain information about their environment, but the role that these behaviors play for older elephants in finding and identifying receptive mates was expected to affect the rate of chemosensory responses. For both sexes, the rate of chemosensory responses was predicted to be lowest for calves and greater for each subsequent age class. The second objective was to detect at what stage of development males and females begin to show sex differences in the rate of chemosensory behaviors. Since subadult females are reproductively active before subadult males and the latter have approximately ten years before they are ready to mate, sex differences were expected to be found first in the subadult stage and to be present in the adult age class. Communication requires a sender and a receiver. Hence, behaviors by receivers may differ with the identity of the sender. Part II focused on identifying sexually dimorphic patterns of chemosensory responses to the feces and urine of an elephant whose identity was known in order to further examine the predictions of Part I.

Developmental trends in communication can be found in the repertoires of many species. Studies on bird songs have shown that properties of vocal communication among birds follow developmental patterns, many of which are limited to one sex (Nelson & Marler 1994; Kipper 2004). For both parts of the study, I examined whether the chemical communication of African elephants followed sexually dimorphic developmental patterns. Three hypotheses about the change in the chemosensory repertoire were tested. First, the null hypothesis predicted that there was no change across age classes in the size and composition of the repertoire. The second and third hypotheses predicted that the repertoire size and composition would increase or decrease, respectively, across age classes. I also hypothesized that males and females would display different chemosensory repertoires. Differential development of the sexes as calves and juveniles with the divergent lifestyles of adults indicates that chemosensory repertoire may be sexually dimorphic.

PART I. SEXUALLY DIMORPHIC DEVELOPMENTAL PATTERNS OF CHEMOSENSORY RESPONSES TO NATURALLY EXISTING STIMULI

METHODS

Study Site and Population

This study was conducted from September 2004-June 2005 on free-ranging African elephants at Ndarakwai Ranch, Tanzania. Ndarakwai Ranch is a privately owned area of ca. 4300 ha located in northern Tanzania in the Kilimanjaro District (S03º00.663’ E037º00.113’) (Fig. 1). During the colonial era, the area was owned by German and British cattle ranchers. After Tanzania’s independence in the 1960’s, the land was acquired by Tanzania Breweries Ltd. for agriculture and cattle grazing (pers. comm. Peter Jones). Peter and Margot Jones purchased the land in October 1995 from Tanzania Breweries Ltd. and have managed Ndarakwai Ranch as a semi-protected area without fences and with ranger patrols. Ndarakwai Ranch is in the greater West Kilimanjaro Area (WKA), which is in proximity to three national parks: Arusha to the south (ca. 30km), Kilimanjaro to the east (ca. 20km), and Amboseli to the north in Kenya (ca. 40km; Fig. 1).

Ndarakwai Ranch’s western and southwestern borders are demarcated by the Ngare Nairobi (North) River. The river is dry during most of the year and the main water sources on the property include smaller streams and a permanent man-made waterhole. The ca. 4,300 m^2 waterhole (Appendix A) is fed with water diverted from the Ngare Nairobi (North) River and attracts a variety of wildlife. Adjacent to the waterhole is a six meter high platform that serves as a viewing station for observing wildlife.

Mixed acacia woodland dominates the western section of the ranch and the remaining area is mainly grassland. The major species of *Acacia* include *A. abyssinica A. depranolobium, A. mellifora* and *A. tortilis*. Scattered patches of *Commiphera africana* are found with the acacia and other species of vegetation (Appendix B). The exact density and composition of the fauna prior to the purchase by Peter and Margot Jones are not known. Observers have identified mammal species from several orders including Primates, Carnivora, Ungulata, Proboscidae, Perissodactyla, and Artiodactyla. A recent bird survey conducted by the resident field guide counted over 200 species of birds. In a concurrent one-year study at the waterhole, I counted 27 species mammals and 117 species of birds (Appendix C).

Reports of elephants at Ndarakwai and the surrounding area before 1995 are mainly anecdotal and few. A census by Poole and Reuling (1997) in Kilimanjaro National Park reported an elephant population of 220 ± 88 individuals of which many were known to migrate out and west of the park. The westward track of these migrations included villages adjacent to Ndarakwai Ranch. Several brief unpublished reports by the School for International Training (SIT) from 1997-2000 provide additional information on the presence of elephants and other fauna at Ndarakwai Ranch and the surrounding WKA. Two concise SIT reports in 2000 and my photo-ID study from June-August 2001 estimated a population of ca. 70-80 elephants at Ndarakwai. Kikoti (2002*)* surveyed five villages neighboring Ndarakwai Ranch from November 2000-February 2001 and recorded means (± standard errors) ranging from 8.50 ± 2.36 to 27.00 ± 4.24 elephants per village. Seventy percent of Kikoti's 90 elephant photographs were recognized by Amboseli Elephant Research Project (AERP) personnel, leading Kikoti to suggest that elephants travel through the area encompassing Ndarakwai as they move between Amboseli and WKA (Kikoti 2002). The high likelihood of Ndarakwai being a migratory junction and the lack of continuous monitoring made it difficult to gauge accurately the demographics of the elephant population.

I confirmed an annual presence of elephants on Ndarakwai Ranch. Two hundred and thirty elephants in 26 individual groups were identified during the study period (Appendix H). This total does not include solitary adult males of which 44 were identified. Elephants were seen during each month, but the sightings showed seasonal variation (Fig. 2). Data collection started on September 23, 2004 and continued through June 30 2005 except for two periods from January 30-February 23 and from June 18-23 when no data collection occurred.

Identification of Elephants

Elephants were identified using methods described by Ian Douglas-Hamilton (1972) and Moss (1996). Ear morphology (e.g. vein patterns, holes, or tears), missing or broken tusks and bent or bald tails distinguish one individual from another. From August 2004-September 2004, index cards were created including sketches and notes of individual elephants and served as identification files. Starting from September 2004 to the end of the study, identification files of elephants were created from photographs using an Olympus C-765 UltraZoom digital camera. The images were transferred to a laptop computer and assigned number and letter codes designating the date and month photographed. Each elephant was given a name and number-letter code to facilitate identification.

The majority of the photographs were taken from the six meter high tree house adjacent to the waterhole. Adults were the easiest to photograph and had the most obvious distinguishing traits (e.g. missing tusks and scars). The small size and lack of distinctive features of young juveniles and calves made their individual identification difficult. In addition to relying on photographs, recognition of the older females provided a reliable means of identifying the younger elephants. Whenever possible, a photograph of the entire herd was taken to show the total number of elephants and their relative sizes. Subsequent photographs of the individuals were categorized together under the name of an identified adult female in the herd. After identifying one or two older females in a herd, it was possible to identify reliably the younger elephants since they were unlikely to be found in multiple family units without their familial females (Moss & Poole 1983; Wittemyer et al. 2005; Archie et al. 2006a).

There were no known ages for any of the elephants at Ndarakwai Ranch. Using a system developed by Moss (1996), morphological features (e.g. shoulder height and tusk length approximations, Appendix D) were used to estimate ages. Based on the estimations, elephants were placed into four age classes: calves (0-4 yrs), juveniles (5-9 yrs), subadults (10-19 yrs), and adults (>19yrs). This differentiation was used by Bagley (2004), Loizi (2004) and Merte (2006) with elephants of known ages in Addo Elephant National Park in South Africa and it allowed larger sample sizes while incorporating the major developmental stages (calves: nursing; juveniles: weaned but largely with family unit; subadults: capable of gamete production, reproduction (females) or decreased association with family unit (males); adults: capable of reproduction) of elephant behavior.

Behavioral Observations

Behavioral observations were recorded from the six meter high platform adjacent to the ca. 4,300 m^2 waterhole from morning to afternoon hours. The platform served as a hide, allowing for safe observations of elephants without the risk of disturbing their behavior. Data collection was limited to the waterhole for three reasons: 1) it allowed for clear observations of subtle trunk behaviors, 2) it permitted the non-intrusive observation of large numbers of elephants and 3) it had a large concentration of elephant feces and urine that emit chemical signals. A pair of Swift Ultralite binoculars with a magnification of 8X42 was used to observe elephants. The age class and sex of focal elephants were selected one day prior to the time of observation. Selection of the age class and sex of the focal elephants was random until the sample size became skewed with an abundance of focal elephants from one sex or age class. In order to maintain equal observation time across age classes and between sexes, haphazard selection (Lehner 1996) replaced random selection of the age class and sex of the focal. If one age class/sex was being sampled more than others, it was not included in the pool of possible candidates for focal individuals.

Several possible focal animals were chosen in the case that the desired individual of the pre-selected age class and sex was not encountered. Individual focal elephants were selected based on their visibility and order of appearance. Once the elephant was selected, continuous focal sampling (Altmann 1974) was used to record behaviors based on an ethogram for 20 minutes (Table 1). Data collection was terminated before the 20 minute period if the focal elephant or the trunk was out of sight for three continuous minutes and another focal elephant was selected. The number of elephants observed and the mean focal duration (min) were relatively equal across age classes and between sexes (2-way ANOVA age class: $F_{3,162} = 0.10$, $P = 0.96$; sex: $F_{1,162} = 0.17$, $P = 0.68$; interaction: $F_{3,162} = 0.27$, $P = 0.84$; Fig. 3). The mean age of calves and juveniles was estimated to within one year by taking the average of a minimum and a maximum possible age. Among juveniles, the distribution of samples from each age range was skewed towards older ages for females and younger ranges for males (Table 2). Subadult males and females were categorized as 10-14 or 15-19 years old. Adult males had three possible ranges and adult females had two possible ranges: males were 20-24, 25-39, or 40-60 years old and females were 20-34 or 35-50 years old. All age ranges were based on morphological features including tusk lengths and shoulder height approximations (Moss 1996).

The behaviors recorded for each focal were categorized as either states or events and as non-investigatory or investigatory. States were behaviors that had measurable durations and events were instantaneous occurrences of behavior (Martin & Bateson 1993). Non-investigatory behaviors included state behaviors (e.g. walking) and body contacts with conspecifics. Investigatory responses were event behaviors that involved the trunk tip to examine conspecifics or to explore stimuli. The investigatory responses were categorized into two groups depending on whether the stimulus was environmental (e.g. substrate) or of elephant origin (e.g. conspecifics, feces or urine). On many occasions the distance between focal elephants and the observer made it difficult to distinguish between sniffs, checks and places (see definitions, Table 1). These three chemosensory responses and flehmen were combined and termed SCPF (Schulte & Rasmussen 1999b; Schulte et al. 2005). SCPF and raised sniffs accounted for 90%

(SCPF = 305/570, Raised sniff = 208/570) of all chemosensory responses to any type of stimulus (e.g. environmental or of elephant origin). The two responses were analyzed separately for differences in the performance of chemosensory behaviors across age classes and between sexes. An attempt was made to record the age class and sex of all sender and recipients of body and trunk tip contacts.

Opportunities for the trunk tip to perform chemosensory behaviors were reasoned to be reduced if elephants were performing certain state behaviors and if this occurred disproportionately across age and sex classes, then the results on the chemosensory responses could be misconstrued. Drinking, mudding and wallowing (see Table 1 for definitions) were termed water activities because their utilization of water would occupy the trunk such that its ability to explore stimuli would be reduced.

As the approaching elephant(s) became visible, the number, approximate ages, and group type of the individuals were recorded. Group type was defined as bull, cow/calf, mixed or solitary based on definitions from Moss (1996). A cow/calf group was composed of adult females and their offspring and if at least one adult male was in the group, it was considered a mixed group. Bull groups were made up of all males. Other variables included air temperature, which was recorded from a thermometer at the viewing platform, and number of conspecifics present. Air temperature (°C) and number of elephants at the waterhole were examined to see whether these variables affected chemosensory behaviors.

Data Analysis

All event behaviors were analyzed as mean rates (frequency/hour) and the durations of state behaviors were assessed as mean bout durations (minutes). A bout was any singular occurrence of a behavior with a known start and stop time (e.g. a three minute stand was one bout of standing). The first and last state behaviors, as well as truncated behaviors under the not visible category, of a focal observation were not included in calculating the mean bout duration because their full durations were unknown. Chemosensory repertoire was assessed by analyzing the differences in the mean number (size) and mean relative proportion (richness) of the chemosensory behaviors. Four of the 170 focal elephants were observed more than once, but no more than three times, and their responses were averaged.

Data that did not meet the normality (tested with Goodness of Fit tests) and homogeneity of variance (tested with Levene's tests) assumptions for parametric tests were analyzed with non-parametric tests. Spearman rank correlations were used to examine relationships between two variables. Analysis of variance (ANOVA) was used to determine the effect of age class and sex on the dependent variables. Arcsine transformations were made for proportions that failed the assumptions of parametric tests. Tukey-Kramer HSD and Mann-Whitney *U* tests (see Dunn 1964) were used *a posteriori* for all pair-wise comparisons. For the post hoc Mann-Whitney *U* and X^2 tests, the *P*-values were adjusted using the Hochberg method (Sokal & Rohlf 1995), a sequential Bonferroni adjustment that protected against Type I errors. An outlier was defined as any focal individual that was at the waterhole under abnormal circumstances (e.g. injured or high level of human activity). All statistical tests were two-tailed and the significance level was $\alpha = 0.05$, except for Mann-Whitney *a posteriori* tests. Unless stated otherwise, all descriptive statistics are presented as mean ± standard error. JMP IN 4.0.4 (SAS Institute 2000) for Windows operating systems was used for all statistical analyses.

RESULTS

Some measures of elephant behavior varied with air temperature and the number of elephants present at the waterhole. Temperature was negatively related to the duration of drinking bouts (Spearman rank correlation: $r_s = -0.20$, $N = 169$, $P = 0.01$), but had a positive relationship with the rate of chemosensory behaviors ($r_s = 0.27$, $N = 169$, $P < 0.001$). The number of elephants at the waterhole had a positive correlation with the duration of wallowing bouts ($r_s = 0.20$, $N = 170$, $P = 0.001$) and a negative relationship with the duration of mudding bouts ($r_s = -0.19$, $N = 170$, $P = 0.01$). The rate of chemosensory behaviors decreased as the number of elephants at the waterhole increased ($r_s = -0.23$, $N = 170$, $P = 0.002$). In all cases, the correlations coefficients were low, so temperature and the number of elephants at the waterhole were not considered to have a strong impact on the main analyses.

Bout durations of water activities did not correlate strongly with the chemosensory rates of males or females (Males: $r_s = -0.20$, $N = 83$, $P = 0.06$; Females: $r_s = 0.09$, $N = 84$, $P = 0.40$). For males, there was a slight negative correlation that was close to being significant. The time spent mudding and wallowing followed opposite trends across age classes. From calves to adults, the duration of mudding bouts increased, but the duration of wallowing bouts decreased (Fig. 4). Females had significantly longer bouts of drinking than did males and adult females had the longest duration of drinking bouts (Tables 3, I and 4, I). The sexes did not differ in the time spent walking, but the duration of walking bouts was significantly longer for calf females than for adult females (Tables 3, III & 4, III).

Males and females responded differently to environmental stimuli and to stimuli of elephant origin. Three times as many elephants performed chemosensory behaviors to environmental stimuli (e.g. substrate) (N = 94/170 elephants) than to stimuli of elephant origin (e.g. conspecifics, feces or urine) (N = 30/170 elephants) (X^2 = 53.93, df = 1, P = <0.001). The proportion of males or females that performed chemosensory behaviors to either type of stimulus did not differ across age classes. A similar proportion of subadult and adult males performed chemosensory behaviors to stimuli of elephant origin (Subadult: N = 6/20; Adult: N = 9/26) (X^2 = 0.11, df = 1, P = 0.74). A significantly greater proportion of subadult and adult males performed chemosensory behaviors than did subadult and adult females to stimuli of elephant origin (Subadults: Males = 6/20 elephants, Females = 0/20 elephants; Adults: Males = 9/26 elephants, Females = 2/20 elephants) (Fig. 5). Comparisons between mean chemosensory responses to environmental stimuli and to stimuli of elephant origin could not be made because of the low number of individuals that exhibited chemosensory responses to the latter category. No significant differences were found when analyzing responses from only focal elephants that performed chemosensory behaviors. Unless stated otherwise, the following results are for chemosensory behaviors from all focal individuals with no distinction between environmental stimuli and stimuli of elephant origin.

Rates of Chemosensory Behaviors

The proportion of males that exhibited chemosensory responses (N = 58/86 elephants) was greater than the proportion of females (N = 44/84 elephants) (X^2 = 4.03, df = 1, P = 0.04) and males came close to having a higher mean rate of chemosensory behaviors than females (mean rate ± SE Males = 22.9 ± 4.93 Freq/hr, N = 86; Females =

11.8 ± 2.03 Freq/hr, $N = 84$) (Table 5, II). Neither males nor females showed differences across age classes in the mean rate of chemosensory behaviors (Table 5, III; Fig. 6). The maximum mean rate of chemosensory responses for females occurred in the juvenile stage (14.9 ± 4.09 Freq/hr, $N = 21$), whereas for males, the peak occurred in the adult stage (34.0 ± 12.69 Freq/hr, $N = 26$). The mean rate of chemosensory responses between adult males and adult females was not significantly different (Adult males = 34.0 ± 12.69 Freq/hr, $N = 26$; Adult females = 14.2 ± 4.84 Freq/hr, $N = 20$) (t-test test: $t_{44} = -1.31$, $P = 0.19$). There was considerable overlap between the range of chemosensory rates of adult males (3.64-324.74 Freq/hr) and females (8.33-80.08 Freq/hr). The high level of variation among adult males was caused by two males whose chemosensory rates were elevated (Focal #39: 104.52 Freq/hour; Focal #85: 324.74 Freq/hr). Removal of these two individuals caused a reduction in the difference between adult males and females (mean rate ± SE Adult males = 18.97 ± 4.19 Freq/hr, $N = 24$) ($t_{42} = -0.75$, $P = 0.45$).

Sex differences were found in the rate of sniff, check, place and flehmen combined (SCPF); the four most commonly performed chemosensory behaviors. Of all male and female focal elephants, a significantly greater proportion of males than females performed SCPF (Males: $N = 33/86$ elephants; Females: $N = 17/84$ elephants) (Table 5, IV). The prediction that subadult males and females would be the first to display significant sex differences was supported: significant sex differences emerged in the subadult stage and sex differences also were close to being significant among adults (Table 5, V & VI). The proportion of elephants that exhibited any combination of SCPF did not differ across age classes within each sex. Males performed SCPF significantly more often than did females (Fig. 7; Table 5, VII Sex), although the difference was mainly from the higher occurrence of SCPF in subadult and adult males. Calves and juveniles of both sexes showed similar rates of SCPF and differences between the sexes in SCPF rate did not emerge until the subadult stage when males had a significantly higher rate than females (Subadults: males = 11.8 ± 5.01 Freq/hr, $N = 20$; Females = 0.6 ± 0.65 Freq/hr, $N = 20$) (Table 5, VIII). As with the rate of all chemosensory responses, the SCPF rate was not significantly different between adult males and females (Adult males = 27.2 ± 12.49 Freq/hr, $N = 26$; Adult females = 8.09 ± 3.88 Freq/hr, $N = 20$) ($t_{44} = -1.30$, $P = 0.20$). There were no significant differences among or between the sexes in the number of elephants that displayed raised sniffs or in the rate of raised sniffs. Unlike SCPF, the rate of raised sniffs was not different between the sexes at any developmental stage.

Chemosensory Repertoire

For males and females, the juvenile and subadult stages marked the appearance of behaviors that were absent in the previous developmental stage(s). Trunk wriggling and rubbing were first observed in juveniles and pinching did not occur before the subadult stage. Although flehmen responses were observed only in focal subadult ($N = 5/20$ elephants) and adult males ($N = 8/26$ elephants), calf males and adult females that were not focal animals were seen performing flehmen. Out of the 15 flehmens from focal males to stimuli of elephant origin, nine were to female elephants (Adult females $N = 5$, Subadult females $N = 4$) and six were to elephant excretions of unknown individuals (urine $N = 3$; feces $N = 3$). All flehmens to conspecifics occurred after the males had contacted the genital area of the females, so it is possible that urine was the stimulus eliciting the behavior. The range of different chemosensory behaviors performed was larger for males than for females (Males = 0-9 behaviors; Females = 0-3 behaviors) and males had a significantly larger repertoire size (Fig. 8). Within each sex, the size of the chemosensory repertoire of elephants that performed chemosensory behaviors did not differ across age classes. There was no evidence that the age class of an elephant affected the number of different chemosensory behaviors performed. Although males had a larger repertoire size than that of females, statistically significant sex differences were not found in any age class.

Sniffs were the most common chemosensory response with no significant difference in the mean proportion of sniffs that made up the chemosensory repertoires of males and females (age class: $F_{3,94} = 1.19$, $P = 0.32$; sex: $F_{1,94} = 0.28$, $P = 0.60$; interaction: $F_{3,94} = 0.78$, $P = 0.51$). Check, place and flehmen made up small proportions of the total repertoire for males and females. The composition of the repertoire between males and females differed in the proportion of sniff, check, place, and flehmen responses (SCPF) and raised sniffs. These two types of responses accounted for relatively equal proportions of all chemosensory behaviors for males (mean proportion ± SE SCPF = 0.43 ± 0.06, $N = 58$; Raised sniffs = 0.45 ± 0.06, $N = 58$) (t-test: $t_{114} = 0.31$, $P = 0.76$), but the repertoire of females was made up of significantly more raised sniffs than SCPF (mean proportion ± SE SCPF = 0.29 ± 0.06, $N = 44$; Raised sniffs = 0.61 ± 0.07, $N = 44$) ($t_{86} = 3.43$, $P = 0.001$). Sexually dimorphic developmental trends too were found. For males, SCPF made up a non-significantly greater proportion of the chemosensory repertoire for adults than for calves or juveniles and raised sniffs accounted for a significantly greater proportion of the chemosensory repertoire for juveniles than for adults (Tables 6 & 7, II). Unlike males, the chemosensory repertoire for females showed a lesser composition of

SCPF for each proceeding age class from calves to subadults. The proportion of SCPF was similar between calves (0.32 ± 0.15, $N = 10$) and juveniles (0.25 ± 0.10, $N = 15$), and was lowest in subadult females (0.09 ± 0.09, $N = 9$). The proportions of SCPF were greatest among the adult age class for both sexes (Table 6). Overall, males had a greater proportion of SCPF than did females (Table 6). The initial occurrence of this sex difference during the subadult stage supports the idea that the differential social environments and reproductive opportunities affect the performance of chemosensory behaviors. Aside from SCPF and raised sniffs, the remaining category of behaviors was termed Accessory trunk behaviors (Table 1), but these behaviors occurred too infrequently and were performed by too few individuals for statistical analyses.

Trunk Touches

Chemical information can be exchanged via contacts from the trunk tip to particular body regions. Trunk touches to and from other elephants were too infrequently observed for conducting statistical tests on these data. In the limited amount of data, there were indications that age class and sex affected the body area and type of conspecifics investigated with the trunk. Among males, the most commonly touched area by calves was the mouth, whereas subadults and adults directed the majority of their trunk touches to the genitals (Table 8). Calf males and females touched the most number of body regions and showed a relatively even spread of the proportion of body areas touched: no one area composed more than half of all the areas touched. For subadult females and subadult and adult males, more than half of the trunk touches were to the mouth and genitals, respectively. Calves touched other calves more than any other age class (Table 9). After the calf stage, the majority of trunk touches from males were to older or same aged elephants and the greatest proportion of trunk touches from females was to calves. No focal adult females were observed to trunk touch other elephants and only one adult female was observed trunk touching a focal elephant of any age and sex.

PART II: SEXUALLY DIMORPHIC DEVELOPMENTAL PATTERNS OF CHEMOSENSORY RESPONSES TO STANDARD STIMULI

In Part I, the nature of the chemical signals that elicited the chemosensory responses was highly variable (i.e. the identity of the sender was unknown). Differences in the chemosensory responses from the focal elephants could be attributed to the variability of the signal, rather than developmental or sexually dimorphic patterns. In an attempt to reduce the uncertainty of the chemical signals eliciting chemosensory responses, bioassays were conducted using excretions from a habituated 6-7 year old juvenile female African elephant (*Loxodonta africana*) as the main stimuli. The exact chemical properties of the excretions from this individual were unknown; however, it was reasoned that reproductive signals were absent from these samples since most female elephants do not begin to experience estrus until after 10 years of age. The samples from this elephant were considered to be standard throughout the study.

Adult male and female chemosensory response levels were used as baselines for determining at what stage of development younger elephants begin to resemble adults. For males, it was predicted that adults would have the highest rate of chemosensory responses and that subadults, although unable to compete for females, should show a level of interest in chemical signals that is similar to that of adults. In Asian elephants, older and more dominant adult males often ignore the subordinate subadults who signal their subordinance by emitting chemical signals (Rasmussen et al. 2005). If performing chemosensory behaviors does not incur costs to subadults, their level of interest in conspecifics and reproductive signals should be similar to that of adults. Juvenile and subadult females were expected to show higher levels of interest than calf and adult females. The young age of the juvenile female that provided the stimuli may be of more interest to similar aged female elephants than younger or older individuals. The chemosensory repertoire composition and size were predicted to change across age classes. Differences between males and females in their chemosensory responses were expected to occur first in the subadult class, the developmental stage when the sexes begin to differ in their social environments and opportunities for reproduction.

METHODS

Study Site

Bioassays were conducted at Ndarakwai Ranch from September 2004-June 2005. All aspects of the field site were the same as those of Part I and samples were placed around the same 4,300 m^2 waterhole used in Part I (Appendix A). Observations and chemosensory responses were recorded from the ca. six meter high platform.

Bioassay Samples

Samples for bioassays included the feces and urine from a habituated juvenile female elephant (Enkarsis) and a vanilla extract solution. Access to freezers was unavailable and since chemical degradation can be confounding, only one to two day old samples of the excretions were used. Enkarsis's caretakers provided her feces and urine in plastic bags and sealed containers, respectively. After collecting the excretions, the samples were stored in a dark and temperate room before use. The room was not temperature controlled, but since all bioassay samples were stored over one ($N = 88$) or two ($N = 21$) nights, it was assumed that each type of sample was exposed to the same duration of nighttime temperatures prior to the day of the bioassay. The exact weights of fecal matter could not be obtained, but effort was made to standardize the mass of matter by using four similar sized boluses. Three different samples, namely a fecal slurry, urine and a vanilla extract solution, were used for each bioassay.

The fecal slurry was created ten minutes before placing the fecal samples at the waterhole using the feces collected from Enkarsis a day prior to the bioassay. Four boluses, of relatively equal dimensions, were placed in a 10-liter plastic jug and diluted with five liters of water from the stream feeding the waterhole. The mixture was churned with a wooden stick for approximately 15 rotations until a discernable amount of liquid was produced. One liter of this slurry was used for the bioassays. Water was not available on 13 of the 129 placements of feces; instead, the boluses were used as the samples.

Urine was provided by the caretakers of Enkarsis in plastic containers. Attempts were made to collect similar amounts of urine. When water was available in a nearby stream, a urine-water solution was made of five-hundred milliliters of urine and five-hundred milliliters of stream water. If the stream was dry, five-hundred milliliters of undiluted urine were used. Most urine samples had settled overnight and had to be stirred before combining with the water.

Vanillin is a compound that is found in Asian elephant excretions and is known to elicit a low-level response from Asian and African elephants (Schulte & Rasmussen 1999a; Slade et al. 2003; Loizi 2004; Bagley 2004). Imitation vanilla extract, which contains vanillin (Belay & Poole 1993), was used successfully as a control in bioassays by Loizi (2004) and Bagley (2004). For those studies, a control was necessary because the researchers were comparing chemosensory responses to different samples. For this study, there was no intention of comparing the responses between the different types of samples. A vanilla extract and water solution was used to measure the responses to a novel stimulus. The solution was made by combining five milliliters of Tone's® synthetic vanilla extract with one liter of stream water.

Bioassay Protocol

For use in another concurrent study, the area surrounding the waterhole was divided into four sections (NE, NW, SE and SW) and four zones. The sections were based on the four cardinal points of a compass and the zones were determined by the distance (meters) from the edge of the waterhole to a designated area. This division facilitated the identification of the areas where elephants were most likely to come into contact with the placed samples. Bioassay samples were placed at six sites around the waterhole: one in NE, one in NW, and two each in SE and SW (Appendix A). Different sites were used to maximize the probability that an elephant would encounter a sample. The sites were chosen after observing how often elephants used particular sections and zones. At each site, there were three locations for the placement of urine, slurry, and control (e.g. 1sl=site 1-slurry, 2ur=site 2-urine, 3co=site 3-control); each location was separated by about one meter. The shortest distance between any two sites was six meters. No two samples were placed at the same site.

The site and location of the samples were determined one day before the bioassay and randomized to prevent the repetitive use of one site by any one stimulus. Samples were placed 30 minutes after arriving at the waterhole and replenished three to four hours afterwards; observations lasted six to eight hours. Earlier samples were replenished with the same volume as that of the sample of feces or urine that was initially placed. The substrate of each area was rubbed beforehand with the shoes of the observer to control for the presence of human scent. After placement of the sample, the sites were marked with branches arranged in the shape of an “X” to assist visual identification from the platform. These markers were placed ca. one meter from the sample and attempts were made to render these markers indistinguishable from the surrounding substrate (e.g. only fallen branches from trees at the waterhole were used). At the end of the day, each location was rinsed with water from the waterhole and the “X” markers were removed.

Data collection began as an elephant approached to within one body length of any of the samples; this was scored as a “proximity”. A “near” was recorded when an elephant came to within one trunk length of the sample and the trunk was in a down position. This distance was reasoned to be the minimum space needed between the trunk tip and the sample for chemosensory behaviors to occur. Distances were relative to the size of the elephant so a calf body length would be shorter than an adult body length. The bioassay was terminated once the animal created a distance greater than one body length from the sample or was out of sight for three minutes. An attempt was made to record the duration of each bioassay, but logging the length of bioassays was made difficult when a procession of elephants approached and rapidly passed a sample. Cursory onsets and offsets of proximities to the stimulus were designated as durations of less than two seconds. In the event of an approach as a group, the most visible individual was selected and sampled. If numerous elephants approached all three samples, the list of pre-selected focal elephants was consulted to choose which age class and sex to observe. Behaviors according to an ethogram (Table 1) were recorded using continuous focal sampling (Altmann 1974) along with details about the focal elephant (e.g. sex, minimum and maximum age estimations). Additional variables included temperature, number of conspecifics, location of the sample and qualitative notes on the weather conditions (e.g. cloud cover).

Focal elephants of a specific age class and sex were chosen one day prior to the bioassay. The age classes and mean ages were calculated in the same manner as the one used in Part I. The unpredictable nature of elephant abundance at Ndarakwai Ranch made it difficult to find and observe consistently the desired focal individuals. On most occasions, focal elephants were selected haphazardly (Lehner 1994). The sample sizes did not differ significantly across age classes within each sex (Males: $X^2 = 3.44$, df = 3 $P = 0.33$; Females: $X^2 = 3.30$, df = 3, $P = 0.09$). There were no differences in the number of males versus females that were observed. The distribution of the estimated ages of the focal elephants was based on the same methodology as that in Part I (Table 10).

Data Analysis

All behaviors were recorded as events. Rates were calculated as the frequency of the behavior per proximity. Unlike in Part I, the rate of chemosensory responses was not divided into separate categories because SCPF made up over 80% of all chemosensory behaviors. A separate analysis of SCPF rate from that of the rate of all chemosensory responses showed no differences between the two. Proportions included only those focal elephants that performed chemosensory behaviors. JMP IN 4.0.4 (SAS Institute 2000) for Windows operating systems was used for all statistical analyses. All statistical procedures were similar to those described in Part I. Unless stated otherwise, all descriptive statistics are presented as mean ± standard error.

RESULTS

Bioassay samples were placed around the waterhole on 129 of the 172 days spent in the field from September 2004- Jun 2005. Focal elephants were observed coming into proximity of the samples on 35 of the 129 days that samples were placed. The 94 other days either lacked elephants at the waterhole or the samples were not approached to within one body length.

The rate of chemosensory behaviors was dependent on the type of excretion and there section of the waterhole. Feces, urine and vanilla extract were placed the same total number of times (N = 129), but the number of times that each was in a particular section differed (Table 11). Urine elicited a higher rate of chemosensory responses than did feces and the samples in the SW section of the waterhole yielded higher rates of chemosensory responses than did the other three sections (Table 12). The differences between the four sections were inconsequential and chemosensory responses to placed stimuli from the four sections were lumped. Elephants came into proximity to vanilla samples twice, but never came near these samples, so no chemosensory responses occurred to the vanilla solution. Chance events (e.g. elephants headed in direction around location of vanilla extract sample) rather than avoidance are likely reasons for the low score of proximity to vanilla extract. There were no differences in the rate or number of different chemosensory responses to one-day old urine versus two-day old urine (number of different chemosensory responses: $t_{65} = 1.60$, $P = 0.11$; rate of chemosensory responses: $t_{107} = -0.43$, $P = 0.67$) . The relationship between the air temperature (°C) and the number of elephants at the waterhole with the chemosensory responses approached significance (temperature & number of different chemosensory responses: $r_s = -0.20$, $N =$

73, $P = 0.09$, temperature & rate of chemosensory responses: $r_s = -0.15$, $N = 139$, $P = 0.19$; number of elephants & number of different chemosensory responses: $r_s = -0.16$, $N = 76$, $P = 0.16$, number of elephants & rate of chemosensory responses: $r_s = -0.14$, $N = 142$, $P = 0.08$).

For each age class and sex, more than half of the elephants that were in proximity to the samples came near the samples (Fig. 9). A significantly greater proportion of adult males came near the samples than did calf and juvenile males (Table 13, Ic & Ie). Chemosensory responses to the samples could not be performed if the individual was greater than one trunk-length away from the sample. Of the elephants that came within one trunk length of the placed sample, a significantly greater proportion of adult males performed chemosensory behaviors than calf males and adult females (Fig. 10).

The rate of chemosensory responses followed different patterns for males and females. As expected, the rate of chemosensory behaviors among males was greater for each subsequent age class from calves to adults (Fig. 11). Adult males had the highest rate of chemosensory behaviors, but it was significantly different only from that of calves (Adult males = 4.1 ± 0.76 Freq/proximity, $N = 26$; Calf males = 1.3 ± 0.64 Freq/proximity, $N = 17$) (Table 15, I). No other age class closely resembled adults, but the rate of chemosensory behavior between subadults (2.6 ± 0.77 Freq/proximity, $N = 15$) and adults was most similar. The rate of chemosensory responses among females showed little variation (range = 2.2-2.6 Freq/proximity) and no differences were found across age classes. Sex differences were not found at any developmental stage, but adult males came close to having a higher rate of chemosensory behaviors than adult females.

For elephants that performed chemosensory behaviors, the size of the chemosensory repertoire did not change across age classes as expected. For both sexes, the mean number of different chemosensory behaviors per age class was approximately two (Fig. 12). Although few calves were seen to perform chemosensory behaviors, the repertoire size for calves (Males = 2.7 ± 0.48 behaviors, $N = 4$; Females = 2.5 ± 0.50 behaviors, $N = 4$) was slightly larger than that of adults (Males = 2.5 ± 0.30 behaviors, $N = 21$; Females = 2.0 ± 0.23 behaviors, $N = 11$), while the repertoire size of subadults (Males = 2.4 ± 0.34 behaviors, $N = 10$; Females = 2.0 ± 0.22 behaviors, $N = 7$) most closely resembled that of adults. Males performed slightly more different chemosensory behaviors than females (Males = 2.5 ± 0.20, $N = 45$; Females = 2.0 ± 0.14, $N = 31$), but significant sex differences were not found in any of the developmental stages (Table 15, VII - XII).

The composition of the chemosensory repertoire was skewed toward one behavior in each age class with sniffing making up at least half of the chemosensory repertoire of for males and females. The proportion of the repertoire made up by sniffs was not different across age classes or between sexes (2-way ANOVA age class: $F_{3,75} = 2.31$, $P = 0.08$; sex: $F_{1,75} = 0.50$, $P = 0.48$; interaction: $F_{3,75} = 0.08$, $P = 0.97$). Juveniles and adults had a similar relative proportion of sniffs, while the proportion of sniffs was similar between calves and subadults (Table 16). Small sample sizes prevented statistical analyses of behaviors other than sniffs. Flehmens to the placed samples were observed only in subadult ($N = 4/15$ elephants) and adult ($N = 3/26$ elephants) males. Of the four main chemosensory behaviors (sniff, check, place and flehmen), places and flehmens were the least common. Checks occurred in small proportions, but showed similar patterns as did sniffs. The other chemosensory behaviors, termed Accessory trunk behaviors (Table 1), were performed by few individuals per age class and composed small proportions of the chemosensory repertoire (Table 17). Interestingly, every focal elephant that did accessory trunk behaviors also performed SCPF, but every elephant that did SCPF did not exhibit accessory trunk behaviors. Although a few behaviors were found in only one sex (e.g. flehmen in males and dig in females), the chemosensory repertoires were similar among and between males and females.

DISCUSSION

Sex differences in the performance of the main chemosensory responses were evident in the subadult age class but not younger age classes, confirming the prediction these behaviors are sexually dimorphic at the developmental stage when the sexes experience differential reproductive opportunities and social environments. The prediction that chemosensory behaviors would be performed more often in older age classes was not supported. Neither males nor females showed higher rates of chemosensory behaviors in each of the subsequent age class from calves to adults. Chemosensory repertoire size was sexually dimorphic and the proportion of some chemosensory behaviors differed between subadult males and females; further supporting the prediction that the timing of sex differences happens at the subadult stage in development. The sex and age class differences in the proportion of elephants responding to a standard stimulus provide stronger evidence of a sexually dimorphic developmental pattern of chemosensory behaviors.

An obvious indicator of interest in an object is whether it is investigated. Sexually dimorphic levels of interest in stimuli were evidenced by the proportion of subadult and adult males that responded to stimuli of elephant origin. Investigation of feces, urine or conspecifics may provide information about the sexual status of individuals. Since males do most of the mate searching, it would be beneficial to investigate as many pertinent chemical signals as possible. Subadult and adult females may spend energy and time at the waterhole performing behaviors that offer more benefits than does investigating stimuli. The longer duration of drinking bouts for adult females suggests that acquiring resources (e.g. water) has a higher priority than chemosensory investigations. Although bout durations of water activities did not correlate with the rate of chemosensory responses, more time spent drinking could reduce the likelihood of coming across chemical signals. An analysis on activity budgets would provide information on how waterhole use affects chemosensory behaviors.

The lack of an ability to perform chemosensory behaviors by subadult females is not a possible explanation for the sex differences since subadult females performed these behaviors during the bioassays in Part II. Results from this study confirm prior research showing that males and females in each age class are able to perform chemosensory behaviors (Loizi 2004; Bagley 2004; Merte 2006). The lack of sex differences in chemosensory behavior before the subadult age class may be explained by the similar social environments and reproductive inactivity shared by calves and juveniles of both sexes. The subadult stage of development marks the onset of emigration from the natal herd for males and mating opportunities for females. These divergent lifestyles, which are retained through adulthood, reflect the sexually dimorphic interest displayed by subadults and adults towards stimuli of elephant origin. The proportion of subadult and adult males that performed chemosensory behaviors was similar because males in both stages of development have the physiological ability to mate, so signals of sexual status would arouse interest from each group of males.

Age class and sex affected how many elephants responded to stimuli of elephant origin, but not to environmental stimuli. The broad range of information emitted from environmental stimuli may have attracted similar levels of interest from all age classes. Much of the environmental stimuli included substrate material (e.g. grass and dirt) that could have signaled location of food or presence of predators. Once the signal source was specified to feces and urine, sources known to emit information about conspecifics (e.g. sexual status), interest in subadult and adult males was higher than that of similar aged females. In Part I, little was known about the sources of the stimuli that elicited chemosensory responses, so signal variation could have affected the proportion of elephants that performed chemosensory behaviors. The results from Part II showed that when presented with a standard stimulus, sex differences were found in the proportion of adults elephants that performed chemosensory responses. There were no differences in the proportion of elephants that came near bioassay samples, so each age class and sex had similar opportunities to investigate the samples. As adults, males are reproductively active and able to compete for mates, so they should seek information about the reproductive states of nearby females. Even though the information found in the excretions from Enkarsis would likely have signaled a lack of sexual receptivity, a male in search for mates would benefit from inspecting all pertinent stimuli.

A hierarchy of chemosensory behaviors may exist among elephants. Evidence for this hypothesis was found from Part II where accessory trunk behaviors were found in conjunction with sniffs, checks, places and flehmens (SCPF), but not without the latter behaviors. Accessory trunk behaviors are thought to increase sample detection, bind odorants and communicate interest (Rasmussen et al. 2003; Schulte et al. 2005). The lower occurrence of these behaviors suggests an auxiliary role to the SCPF responses. When specifying the analyses to SCPF, the premier suite of chemosensory behaviors used by elephants when investigating stimuli (Loizi 2004; Bagley 2004; Schulte et al. 2005; Merte 2006), differences by sex were found among subadults. Studies on large ungulates have found that chemosensory behaviors, particularly flehmen, follow sexually dimorphic developmental patterns with males developing higher rates of flehmen earlier than females (Reinhardt 1983; Stahlbaum & Houpt 1989; Thompson 1995). Female and other age classes of elephants were seen to perform flehmen, but the frequency and prevalence of this behavior was predominant among subadult and adult males.

The sex differences in SCPF responses support the hypothesis that the different social environments and reproductive opportunities experienced by subadult males and females produce sexually dimorphic patterns of chemosensory responses. The social environments of males and females begin to differ in the juvenile stage where males spend greater amounts of time away from their families and females remain close to the natal group members (Lee 1986; Lee & Moss 1999). As subadults, both sexes undergo physiological transitions into puberty and begin producing gametes. Two important sex differences develop during this stage that may affect the performance of chemosensory behaviors: males disperse from the natal group and females begin reproducing.

If a male disperses at the onset of the subadult stage (ca.10 years), he has approximately 10 years before he is sexually mature and ready to compete for mates. Females have a shorter period of maturation and can conceive as early as 10 years of age. Delayed maturation for males of species that experience intense male-male competition is beneficial as it allows time for refining physical, cognitive and behavioral skills that are related to reproductive demands (Geary 1999). In young birds, the ontogeny of several aspects of courtship behaviors has been associated with experience and practice (Shettleworth 1984). Dispersal and an extended period of immaturity for male elephants provide them time to gain the skills, which cannot be accessed in the natal herd, necessary for male-male competition (see Main and Coblentz 1990).

Sexual dimorphism of a behavior or set of behaviors can be assessed by examining how much of the male and female behavioral repertoire is consisted of the behavior(s). The proportion of the repertoire made of sniff, check, place and flehmen (SCPF) and raised sniffs was found to be different among subadult males and females. Since SCPF is associated with investigating sexually stimulating chemical signals, this suite of behaviors may not provide subadult females at the waterhole with relevant information (e.g. location of food or presence of predators). Instead, subadult females used raised sniffs to investigate the environment at the waterhole. Subadult males could be preparing for adulthood by developing their skills at deciphering chemical messages by continuing to use SCPF. It is possible that the stimuli present at the waterhole were salient enough to elicit SCPF from subabdult males, but not from subadult females. Variability of the stimuli is a likely explanation since the standard stimulus produced a repertoire composition of similar proportions among all groups of elephants. Sexually dimorphic sensory apparatuses too can affect the performance of chemosensory behaviors (Segovia & Guillamón 1993). Anatomical studies on elephants have not revealed whether the VNO system is sexually dimorphic (Rasmussen & Hultgren 1990). Previous studies on flehmen recognized testosterone as the underlying factor that influenced sexual motivation, thus producing sexually dimorphic developmental patterns in flehmen responses (Reinhardt 1983). A greater concentration of testosterone in post-pubertal male than female elephants may be a proximate explanation for the sex differences in SCPF responses.

Interestingly, sex differences in SCPF responses were absent after the subadult age class. Although the rate of SCPF responses between sexes of adults approached significance, SCPF made up similar proportions of the repertoire of both sexes. It is likely that both sexes deploy the same suite of chemosensory behaviors at equal proportions, but differ in how often these behaviors are performed. This hypothesis needs further testing in order to explain the chemosensory responses among subadults versus subadults.

If males and females live divergent lifestyles as adults, adult-like behaviors may be found at different stages of development. For females, adult levels of chemosensory responses were found among juveniles and may occur early during development because parturition and parental care are possible during the subadult stage. The similarity between juvenile females and adult females in the rate of chemosensory responses reflects an early maturation of these behaviors. The ability to process chemical signals as juveniles would benefit females later in life as they would have learned which signals are salient. Delayed maturation for males would reduce the requirement of an early development of chemosensory behaviors. Similarities between subadult and adult males in the proportion of elephants that performed chemosensory responses to feces and urine and in their chemosensory repertoires show that although subadult males usually mate as adults, their interests are similar to those of adults in stimuli that contain information about reproductive status. For both sexes, adult-like levels of behaviors were reflected in an earlier stage of development (see Loizi 2004, Figs. 7&8).

Elephants usually begin to mate after the juvenile stage and since chemosensory behaviors facilitate mate searching and discrimination between sexual states, it was predicted that both sexes would show a greater rate of chemosensory behaviors in each following age class with maximum rates occurring among adults. The rate of chemosensory responses for males in Part II supported this prediction, and the rate of chemosensory responses from Parts I and II showed a sexually dimorphic developmental pattern. Direct comparisons of the rate of chemosensory responses between Parts I and II could not be made because the rates were calculated per hour and per proximity, respectively. As predicted for males, adults had the highest rate of responses, but the variation in response rate prevented a significant sex difference among adults in Parts I and II.

Experience may contribute to how often an adult male needs to investigate a stimulus before his inquiry is satisfied. Male elephants are known to disperse from the natal herd as young as 8 years of age or as old as 20 years of age (Poole 1994; Lee & Moss 1999). If sex differences in performing chemosensory behaviors were dependent on divergent social environments, then the variation in the age of dispersal would affect sexual dimorphism. The aptitude for chemosensory behaviors in a male who disperses later in life may not be as developed as that of a male who dispersed earlier. Sixty-five percent of the adult males in this study were estimated to be 20-25 years of age, raising the possibility that there was considerable variation in the age at emigration. Further research is needed on male elephant dispersal and how this life history trait affects the development of behavior.

Female African elephants remain in the natal herd and the excretions from the standardized samples elicited the same level of chemosensory responses from every age class of females. The static nature of female chemosensory responses could represent a baseline level of interest to stimuli from a juvenile female. The chemical signals emitted by an unrelated juvenile female may not warrant high levels of investigation. Elephants are believed to derive information on the age and kinship of conspecifics from signals in excretions and secretions (Buss et al. 1976; Rasmussen 1995). The messages from the orphaned juvenile female could have indicated her lack of competitive ability and kinship, thus affecting the rate at which her excretions were investigated. Juvenile females had the greatest proportion of elephants that performed chemosensory responses to the samples in Part II, but the similarity of sex and age class to Enkarsis did not produce the predicted highest rate of responses. Unlike for females, age class affected the rate of chemosensory responses for males with adults performing chemosensory responses more often than calves. Calves may use chemosensory behaviors to obtain information about their environment, but adult males are likely to perform these behaviors more often as they seek mates.

There was an insufficient number of trunk tip touches for statistical analyses, but the results suggest that the different social environments of males and females affect this chemosensory behavior. Among males, the transition from trunk tip touches to the mouth by calves to the genitals by subadults and adults indicates that the age classes may differ in the types of chemical signals sought. Chemical signals from the breath are generally associated with information about the identity of conspecifics and food stuffs (Douglas-Hamilton 1972; Lee & Moss 1999), but they are believed to advertise sexual status along with signals from the genitals (Moss 1983; Rasmussen & Wittemyer 2002). Trunk tip touches to similar aged conspecifics by males and to calves by females further supports the idea that across age classes, the chemosensory behaviors follow sexually dimorphic patterns. After dispersal, males commonly live solitary lives or associate with other males (Lee & Moss 1999) and do not display parental care, so tactile interactions with younger elephants may be absent. Subadult females are known to be allomothers (Lee 1987) and may direct their trunk touches towards younger member of their groups. Although previous studies on the recipients of trunk investigatory behaviors have been hindered by the lack of data (Bagley 2004; Loizi 2004), Merte (2006) found that the rate of trunk tip touches and the region of the body touched were affected by age class and relatedness between offspring and family members. A concentration on trunk tip touches could yield answers to questions concerning the impact of social interactions on chemosensory behaviors.

Elephants displayed developmental patterns and sex differences in the performance of certain state behaviors. Mud was utilized by elephants of every age class, but the behaviors used to attain this resource differed across age classes. For both sexes, wallowing was seen most often among calves and mudding was observed mainly in older individuals. Poorly developed motor skills for the youngest elephants and weight constraints for older elephants could affect the performance of these behaviors. Muscles necessary for the siphoning and expulsion of mud may not be fully developed in young calves. A greater mobility of the trunk could produce the various mudding techniques seen in older elephants (see Appendix E). Wallowing may substitute for mudding because it is relatively easier to perform and distributes mud over the body of young elephants. Holekamp and Smale (1998) found that the development pattern of escape behaviors in the spotted hyena (*Crocuta crocuta*) was affected by an increasing body size. During the development of an elephant, certain behaviors may become costly and alternatives develop to replace the prior behaviors while maintaining the same function.

The chemosensory repertoire was larger in Part II by one behavior. This slight increase was considered to be biologically trivial. Statistical comparisons between Part I and Part II were not made because of the differences in sample size and some units of measurement (e.g. rates). Loizi (2004) too had difficulty comparing data from wild and captive studies. The rapid nature of sample investigation during bioassays in natural habitats makes it challenging to estimate durations. A technique that records rates of chemosensory responses based on the elephants' proximity to the stimuli would make possible comparisons between captive and wild studies.

Bioassays were conducted primarily to elicit chemosensory responses to a standard stimulus of which the sources was known. Previous studies on chemosensory behaviors of elephants in their natural habitats have yielded relatively low frequencies of chemosensory responses (Loizi 2004; Bagley 2004; Merte 2006). The bioassays in this study were used to increase the likelihood of observing chemosensory responses so that developmental pathways could be detected. Johnston (2000) states that bioassays that use investigative behaviors (e.g. flehmen or sniff) for demonstrating the function of signals incur pitfalls because animals can investigate the same signal for different reasons. It is likely that the motivation for a calf to investigate a pile of feces is different from that of a male towards the same stimulus. This study did not seek to explain the underlying mechanisms causing differences in the performance of chemosensory behaviors, and it acknowledges the multitude of reasons why the age classes may differ from one another. The main goal was to see whether the chemosensory responses followed sexually dimorphic developmental patterns. Conducting bioassays with large mammals in nature can be difficult, but this study utilized a bioassay protocol that was successful in eliciting chemosensory responses. Future studies can benefit from the current methodology to facilitate the search for mammalian chemical signals in elephants and the approach may be applicable to a range of mammals.

The use of age estimations based on a range of possible ages could result in a misclassification of individuals. Elephants that are on the fringes of two age classes (e.g. 4-5 or 9-10 year old) pose problems for categorization into a distinct developmental stage. Only two focal elephants were considered borderline between the calf and juvenile age classes and all subadults and adults were identified confidently as belonging in either age class. The exclusion of the two fringe focal elephants did not alter the results. A more precise age estimation scheme would likely produce a clearer developmental pattern.

Among African elephants, numerous measures of chemosensory responses yielded sexually dimorphic developmental patterns. Age class and sex affected whether an elephant would perform chemosensory behaviors and how often the main chemosensory responses would occur. For these variables, sex differences occurred either first or only among subadults: the developmental stage when the social environments and reproductive opportunities of males and females begin to differ. Adult-like levels of chemosensory behaviors were found earlier among females than among males. The pattern of chemosensory responses to a standard stimulus across age classes was different for males and females. In the African elephant, a species where the sexes display divergent lifestyles as adults, the differential developmental of chemosensory behaviors may prepare each sex for its adult life.

Table 1. Ethogram used to record behaviors by African elephants during continuous focal observations at Ndarakwai Ranch (September 2004 - June2005)

Non-investigatory behaviors	
Penis motions	
Belly hit	Unsheathed penis arches upward and contacts the underside of the torso in a rapid motion; sometimes called an erection
Penis drop	The penis emerges and hangs down from the penis sheath
Penis pull	The penis is retracted back into the penis sheath
State behaviors	
Drink	Uptake of water into trunk and transferred inside mouth
Mud	Use of the trunk to distribute mud over areas of the body
Stand	Lack of locomotion; no change in the spatial positioning of elephant
Walk	Movement forward at a slow pace
Wallow	Repetitive rolling motion of the body in mud/water
Investigatory behaviors	
Accessory trunk behaviors*	
Blow	Forceful exhalations of air through the trunk; usually after investigating a stimulus
Dig	Use of the trunk tip to displace substrate
Pinch	Both fingers of the trunk tip of the trunk are placed together
Rub	After placing entire trunk tip on a stimulus, the trunk is moved in a circular motion
Trunk flick	Quick waves forward and/or backward, of the trunk tip; can occur while trunk tip is pinched
Trunk wriggle	The bottom half of the trunk takes on a coiled configuration

Table 1. (cont.)

Chemosensory behaviors	
Check*	Touching substrate/substance with tip of trunk (either finger)
Flehmen*	Tip of trunk contacts directly any potentially stimulating secretion or excretion; trunk tip is curled toward mouth and inserted into a small recess in the dorsal anterior part of mouth
Horizontal sniff	Either the distal end or the entire trunk is elevated above and parallel to the ground and pointed away from the elephant
Periscope sniff	The entire trunk is elevated and in a S-shape curve; the trunk tip is above the level of the head and pointed forward
Place*	Distal end of trunk is placed flat on a substrate/substance
Sniff*	Distal end of the trunk hovers over substrate/substance without contact
Trunk tip touches	Physical contact between the distal end of the trunk with any area on the body of a conspecifics

*Defined with criteria used by Schulte & Rasmussen 1999b, Loizi 2004 and Bagley 2004, Schulte et al. 2005. See also Schulte 2006.

Table 2. The distribution of the range of ages (years) in which all focal elephants were categorized, Ndarakwai Ranch (September 2004 - June 2005.

	Calves					Juveniles			
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9
Males	4	8	5	2	1	9	4	5	2
Females	3	10	7	2	1	3	4	5	9

	Subadults		Adults				
	10-14	15-19	20-24	20-34	25-39	35-50	40-60
Males	10	10	17	X	7	X	2
Females	7	13	X	14	X	6	X

X = no focal elephants qualified for this range of ages.

Table 3. The mean (±SE) bout durations (min) for three state behaviors performed by elephants while at a waterhole, Ndarakwai Ranch (September 2004 - June 2005). Data include zeros.

Behavior	Males	Females	Main difference(s)
I. Drinking[a]			
Calves (0-4yrs)	0.93±0.27	0.68±0.16	-Adult females drank longer than adult males (Table 4, I)
Juveniles (5-9yrs)	0.97±0.25	0.75±0.14	
Subadults (10-19yrs)	0.67±0.21	1.05±0.27	
Adults (>19yrs)	0.49±0.17	1.41±0.19	
II. Standing			
Calves	0.68±0.12	0.59±0.13	-No significant differences.
Juveniles	0.90±0.24	0.63±0.12	
Subadults	0.77±0.18	0.69±0.11	
Adults	1.04±0.20	0.78±0.14	
III. Walking[b]			
Calves	0.59±0.08	0.77±0.10	-Within females, calves had longer bouts of walking than did adults (Table 4, III)
Juveniles	0.53±0.06	0.60±0.05	
Subadults	0.52±0.06	0.59±0.09	
Adults	0.51±0.08	0.50±0.10	

[a] One adult male was considered an outlier because he was suspected to be ill.

[b] One adult male was considered an outlier because he arrived directly after human activity at the waterhole.

Table 4. Statistical values from various group comparisons for four state behaviors, Ndarakwai Ranch (September 2004 - June 2005).

State Behavior	Statistical test	*N*	df	Statistic	*P*-value ($\alpha = 0.05$)
I. Drinking					
Sex[a]:	2-way ANOVA		1	$F_{1,161} = 0.17$	0.91
Age class:			3	$F_{3,161} = 2.03$	0.15
Interaction:			3	$F_{3,161} = 3.59$	0.01
Adult males-adult females:	Tukey HSD				0.03
II. Mudding					
Age class:	-Kruskal-Wallis	170	3	$H = 14.64$	0.002
Calves-juveniles:	-*a posteriori* Mann-Whitney *U* tests	Calves:43 Juveniles:41		$U = 613.50$	0.01
Calves-subadults:		Calves:43 Subadults:40		$U = 495.50$	0.008
Calves-adults:		Calves:43 Adults:46		$U = 705.50$	0.01
III. Walking					
Within females Calves-adults:	-1-way ANOVA		3	$F_{3,76} = 3.55$	0.02
	-Tukey HSD				0.01
IV. Wallowing					
Age class:	-Kruskal-Wallis	170	3	$H = 24.24$	<0.001
Calves-subadults:	-*a posteriori* Mann-Whitney *U* tests	Calves:43 Subadults:40		$U = 628.50$	0.01
Calves-adults:		Calves:43 Adults:46		$U = 520.00$	<0.001
Juvenile-adults:		Juveniles:41 Adults:46		$U = 658.00$	<0.001
Subadults-adults		Subadults:40 Adults:46		$U = 749.00$	0.01

α for all non-parametric post hoc comparisons was modified using a sequential Bonferroni method.

[a] One adult male was considered an outlier because he was suspected to be ill..

[b] One adult male was considered an outlier because he arrived directly after human activity at the waterhole.

Table 5. The test statistics and *P*-values from group comparisons of the proportion of focal elephants that performed chemosensory behaviors and the rate of chemosensory behaviors, Ndarakwai Ranch (September 2004 - June 2005).

Parameter	Statistical test	*N*	df	Statistic	*P*-value (α = 0.05)
All Chemosensory Responses					
Proportion of elephants responding					
I. To stimuli of elephant origin (e.g. conspecifics, feces or urine)					
a) Between subadult males and subadult females	X^2		1	9.38	0.002
b) Between adult males and adult females	X^2		1	4.06	0.04
Mean rate					
II.	2-way ANOVA				
Sex:			1	$F_{1,162} = 3.61$	0.06
Age class:			3	$F_{3,162} = 1.41$	0.24
Interaction:			3	$F_{3,162} = 0.60$	0.61
III. Across age classes within sex	1-way ANOVA				
Males:			3	$F_{3,83} = 1.15$	0.33
Females:			3	$F_{3,80} = 0.70$	0.55
Sniff, Check, Place and Flehmen (SCPF) Responses					
Proportion of elephants responding					
IV. Between males and females	X^2		1	6.82	0.009
V. Between subadult males and females	X^2		1	6.19	0.01
VI. Between adult males and females	X^2		1	3.56	0.06
Mean rate					
VII.					
Sex:	2-way ANOVA		1	$F_{1,162} = 4.32$	0.04
Age class:			3	$F_{3,162} = 1.83$	0.14
Interaction:			3	$F_{3,162} = 0.70$	0.55
VIII. Between subadult males and females	*t*-test	Males :20 Females:20	44	t = -2.20	0.03

Table 6. The mean (±SE) relative proportion of three chemosensory behavior categories for focal elephants that performed chemosensory behaviors, Ndarakwai Ranch (September 2004 - June 2005). Data include zeros.

Chemosensory behavior	Males	Females
SCPF		
Calves (0-4yrs)	0.30±0.12	0.32±0.15
Juveniles (5-9yrs)	0.30±0.11	0.25±0.10
Subadults (10-19yrs)	0.45±0.13	0.09±0.09
Adults (>19yrs)	0.56±0.09	0.51±0.15
Raised sniffs		
Calves	0.63±0.14	0.68±0.14
Juveniles	0.67±0.12	0.60±0.12
Subadults	0.37±0.12	0.82±0.12
Adults	0.29±0.09	0.37±0.14
Accessory trunk		
Calves	0.07±0.04	0
Juveniles	0.03±0.02	0.15±0.08
Subadults	0.18±0.09	0.09±0.09
Adults	0.15±0.07	0.12±0.07

SCPF=sniffs, checks, places and flehmens; Raised sniffs= horizontal and periscope sniffs; Accessory trunk= rubs, trunk wriggles and flicks, pinches and blows.
Sex differences were found in the mean proportion of SCPF and raised sniffs among subadults (Table 7, I & III).

Table 7. The statistical details from group comparisons of the relative proportion of chemosensory behaviors, Ndarakwai Ranch (September 2004 - June 2005).

Parameter	Statistical test	*N*	df	Statistic	*P*-value (α = 0.05)
Sniff, Check, Place and Flehmen (SCPF) Responses					
I. Between subadult males and females	*t*-test	Males:12 Females:9	19	*t* = -2.19	0.04
Raised Sniff Responses					
II. Across age class within males*	1-way ANOVA		3	$F_{3,54} = 3.05$	0.04
Juveniles-adults:	Tukey HSD				0.05
III. Between subadult males and females	*t*-test	Males:12 Females:9	19	*t* = 2.57	0.02

Table 8. The mean (±SE) proportion of the trunk touches to seven body regions of conspecifics per age class and sex of focal elephants that performed trunk touches, Ndarakwai Ranch (September 2004 - June 2005).

	N	Anal	Body	Ears	Hind leg	Genitals	Mouth	Nipples	Total # of trunk touches
C-M	8	0.13 ±0.13	0.13 ±0.13	0	0.06 ±0.06	0.06 ±0.06	0.38 ±0.18	0.25 ±0.16	9
C-F	6	0	0	0.08 ±0.08	0.17 ±0.17	0.33 ±0.21	0.25 ±0.17	0.17 ±0.17	8
J-M	3	0	0	0	0.67 ±0.33	0	0.33 ±0.33	0	3
J-F	1	0	0	0	0	1.00	0	0	1
S-M	5	0	0	0.20 ±0.20	0	0.60 ±0.24	0.20 ±0.20	0	9
S-F	3	0	0	0	0.17 ±0.17	0.17 ±0.17	0.67 ±0.33	0	3
A-M	7	0	0	0	0.08 ±0.05	0.60 ±0.15	0.27 ±0.15	0.04 ±0.04	20

No focal adult females were observed to perform trunk touches. C = calves (0-4yrs), J = juveniles (5-9yrs), S = subadults (10-19yrs), A = adults (>19yrs), M = males, F=females.

Table 9. The mean (±SE) proportion of trunk touches to four age classes of conspecifics per age class and sex of focal elephants that performed trunk touches, Ndarakwai Ranch (September 2004 - June 2005).

	N	Calves	Juveniles	Subadults	Adults	# of elephants touched
C-M	8	0.50±0.19	0	0.13±0.13	0.38±0.18	8
C-F	6	0.50±0.22	0.17±0.17	0.17±0.17	0.17±0.17	6
J-M	3	0.33±0.33	0	0.67±0.33	0	3
J-F	1	1.00	0	0	0	1
S-M	5	0	0.20±0.20	0.40±0.24	0.40±0.24	5
S-F	3	0.67±0.33	0	0.33±0.33	0	3
A-M	7	0	0	0.29±0.18	0.71±0.18	7

No focal adult females were observed to perform trunk touches. C = calves (0-4yrs), J = juveniles (5-9yrs), S = subadults (10-19yrs), A = adults (>19yrs), M = males, F = females.

Table 10. The distribution of the range of ages (years) in which all focal elephants that came into proximity of bioassay samples were categorized, Ndarakwai Ranch (September 2004 - June 2005).

	Calves					Juveniles			
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9
Males	0	8	6	1	2	2	10	5	3
Females	1	3	7	0	0	4	6	1	3

	Subadults		Adults				
	10-14	15-19	20-24	20-34	25-39	35-50	40-60
Males	7	8	20	X	4	X	1
Females	9	5	X	21	X	4	X

X = no focal elephants qualified for this range of ages.

Table 11. The number of days the three types of bioassay samples were placed in each of the four sections of the waterhole and the proportion of these days when elephants were recorded in proximity to the type of sample, Ndarakwai Ranch (September 2004 - June 2005).

	Feces		Urine		Vanilla Extract	
Section	# of days sample was placed	Proportion of days with elephants in proximity	# of days sample was placed	Proportion of days with elephants in proximity	# of days sample was placed	Proportion of days with elephants in proximity
NE	16	0.12	32	0.19	29	0
NW	31	0.03	29	0.21	34	0
SE	36	0.03	27	0.07	27	0.04
SW	46	0.09	41	0.44	39	0.02

Table 12. Mean (±SE) rate (Freq/proximity) of chemosensory responses of all focal elephants to the placed urine and feces of a juvenile female elephant that was placed in four sections around a waterhole, Ndarakwai Ranch (September 2004 - June 2005). Data include zeros.

Stimulus*		Section**			
Feces	Urine	NE	NW	SE	SW
1.06±0.41	3.04±0.33	1.53±0.46	1.79±0.52	0.75±0.75	3.28±0.39

*Mann-Whitney U test: $U = 1047$, $N_1 = 31$, $N_2 = 109$, $P = 0.001$.

**Kruskal-Wallis: $H_3 = 11.43$, $P = 0.01$. No pair-wise differences were found after adjusting the p-value using a sequential Bonferroni method.

Table 13. Statistical details of the proportion of elephants that came near placed samples around a waterhole, Ndarakwai Ranch (September 2004 - June 2005).

	X^2	df	*P*-value*(α=0.05)
Males			
I. Across age classes	13.03	3	0.005
a) Calves-Juveniles	0.09	1	0.76
b) Calves-Subadults	2.94	1	0.09
c) Calves-Adults	10.13	1	0.001
d) Juveniles-Subadults	2.23	1	0.13
e) Juveniles-Adults	9.13	1	0.002
f) Subadults-Adults	2.05	1	0.15
Females			
II. Across age classes	1.74	3	0.63

*Sequential Bonferroni adjusted *P*-values for pair-wise tests.

Table 14. Statistical details of the proportion of elephants that performed chemosensory behaviors to placed samples around a waterhole, Ndarakwai Ranch (September 2004 - June 2005).

	X^2	df	*P*-value*(α=0.05)
Across age classes			
I. Males	8.24	3	0.04
a) Calves-Juveniles	3.02	1	0.08
b) Calves-Subadults	3.86	1	0.04
c) Calves-Adults	8.09	1	0.004
d) Juveniles-Subadults	0.08	1	0.78
e) Juveniles-Adults	1.00	1	0.32
f) Subadults-Adults	0.44	1	0. 50
II. Females	2.93	3	0.40
Between sexes			
I. Calf males-Calf females	1.03	1	0.31
II. Juvenile males-Juvenile females	0.76	1	0.38
III. Subadult males-Subadult females	0.17	1	0.68
IV. Adult males-Adult females	4.34	1	0.04

*Sequential Bonferroni adjusted *P*-values for post hoc pair-wise tests.

Table 15. Statistical details of age class comparisons among and between males and females in the mean rate of and mean number of different chemosensory behaviors, Ndarakwai Ranch (September 2004 - June 2005).

Parameter	df	*F*/*t*	*P*-value (α=0.05)
Rate of chemosensory behaviors			
I. Age class: Males*	3,74	2.98	0.04
II. Age class: Females	3,60	0.05	0.98
III. Calf males-calf females	26	0.82	0.42
IV. Juvenile males-Juvenile females	32	0.50	0.61
V. Subadult males-Subadult females	27	0.04	0.97
VI. Adult males-Adult females	49	-1.78	0.08
Number of different chemosensory behaviors**			
VII. Age class: Males	3,41	0.12	0.94
VIII. Age class: Females	3,27	0.78	0.51
IX. Calf males-calf females	6	-0.36	0.73
X. Juvenile males-Juvenile females	17	-1.42	0.17
XI. Subadult males-Subadult females	15	-0.90	0.39
XII. Adult males-Adult females	30	-1.06	0.29

**a posteriori* Tukey-HSD showed that adults had a higher rate than did calves, $P < 0.05$.
**Does not include zeros.

Table 16. The mean (±SE) proportion of four main chemosensory responses to the placed urine and feces of a juvenile female African elephant per age class and sex of focal elephants, Ndarakwai Ranch (September 2004 - June 2005).

Sex & Age class	Sniff	Check	Place	Flehmen	TOTAL	*N**
Males						
Calf	0.50±0.08	0.16±0.11	0.10±0.10	0	0.76	4
Juvenile	0.68±0.09	0.10±0.04	0.05±0.03	0	0.82	10
Subadult	0.52±0.08	0.19±0.09	0	0.09±0.04	0.81	10
Adult	0.67±0.06	0.10±0.03	0.06±0.03	0.01±0.01	0.84	21
Females						
Calf	0.50±0.16	0.30±0.18	0	0	0.80	4
Juvenile	0.78±0.10	0.09±0.06	0	0	0.87	9
Subadult	0.57±0.09	0.11±0.08	0	0	0.68	7
Adult	0.71±0.08	0.07±0.03	0.01±0.01	0	0.80	11

*The number of elephants per age class that performed SCPF.

Table 17. The mean (±SE) proportion of six less common chemosensory responses (Accessory trunk behaviors) to the placed urine and feces of a juvenile female African elephant per age class and sex of focal elephants, Ndarakwai Ranch (September 2004 - June 2005).

Sex & Age class	Blow	Dig	Periscope	Pinch	Trunk Flick	Trunk Wriggle	TOTAL	*N**
Males								
Calf	0.10± 0.10	0	0	0.03± 0.03	0.03± 0.03	0.08± 0.08	0.24	3
Juvenile	0.05± 0.04	0	0.01± 0.01	0.04± 0.02	0.03± 0.02	0.05± 0.05	0.18	6
Subadult	0.03± 0.03	0	0	0.01± 0.01	0.08± 0.06	0.08± 0.05	0.19	5
Adult	0.03± 0.02	0	0	0.02± 0.02	0.08± 0.03	0.02± 0.01	0.16	13
Females								
Calf	0.03± 0.03	0.13± 0.13	0	0	0.05± 0.03	0	0.20	3
Juvenile	0	0	0	0.03± 0.03	0.08± 0.06	0.02± 0.02	0.13	3
Subadult	0.07± 0.07	0.02± 0.02	0	0	0.23± 0.12	0	0.32	4
Adult	0.03± 0.03	0	0	0.05± 0.05	0.11± 0.06	0.02± 0.02	0.20	6

*The number of elephants per age class that performed Accessory trunk behaviors.

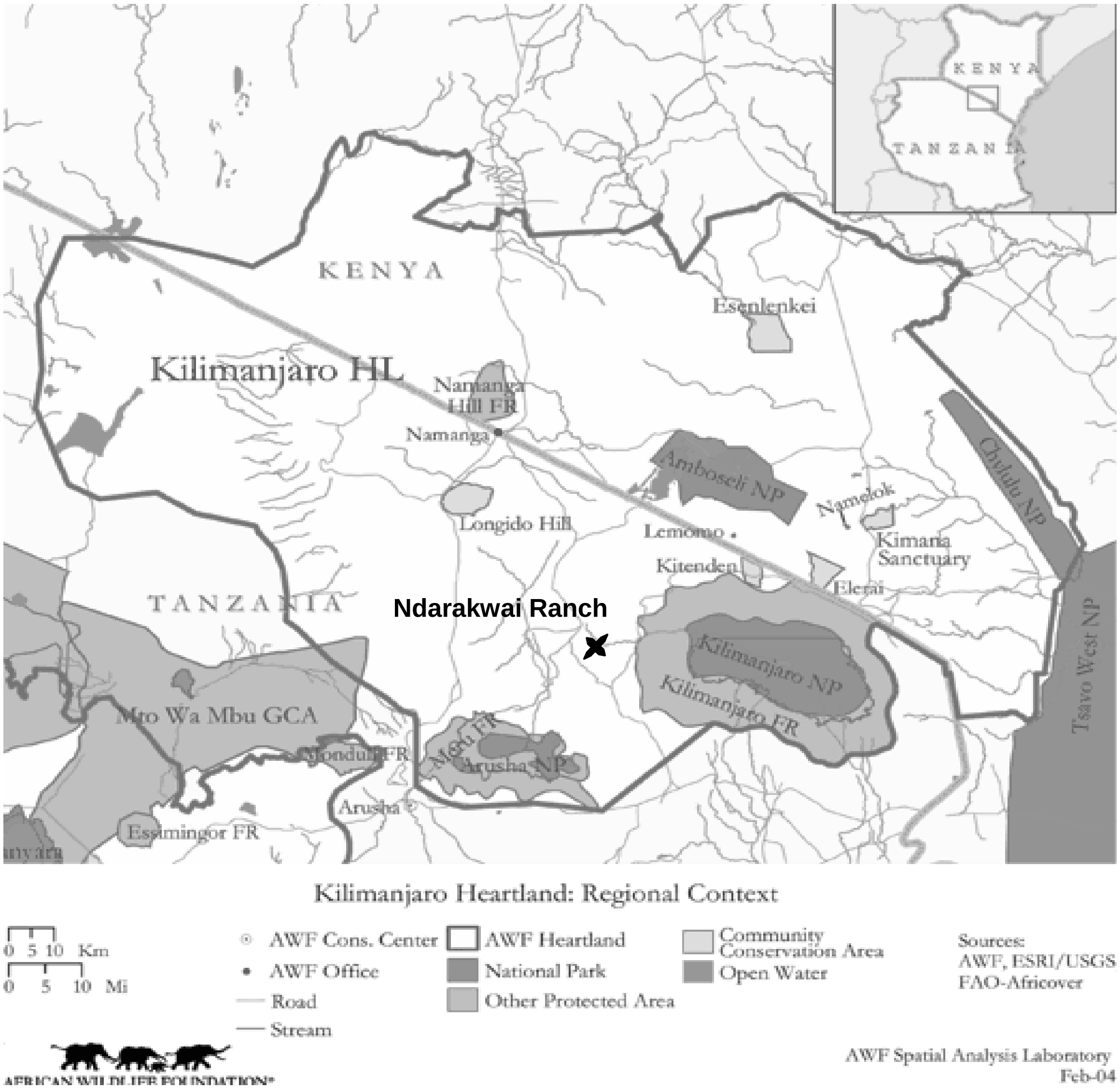

Figure 1. Map of the north-central border between Kenya and Tanzania. Ndarakwai Ranch (ca. 4300 ha) is marked with an "X" (AWF Spatial Analysis Laboratory 2004).

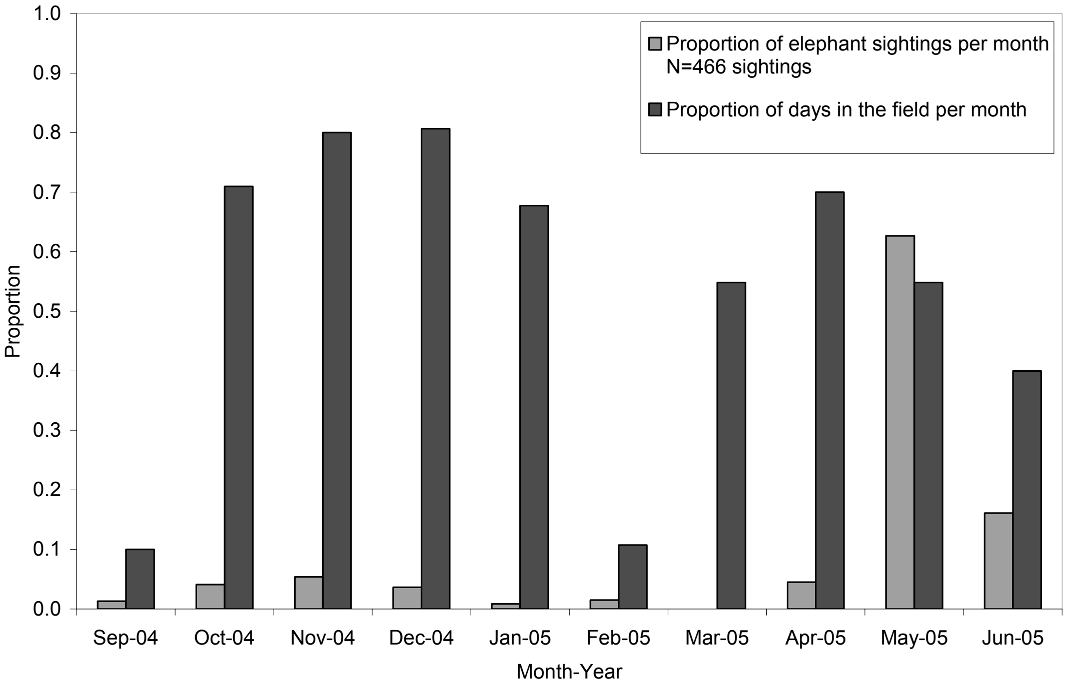

Figure 2. The proportion of elephant sightings per month and the proportion of days spent in the field, Ndarakwai Ranch (September 2004 - June 2005).

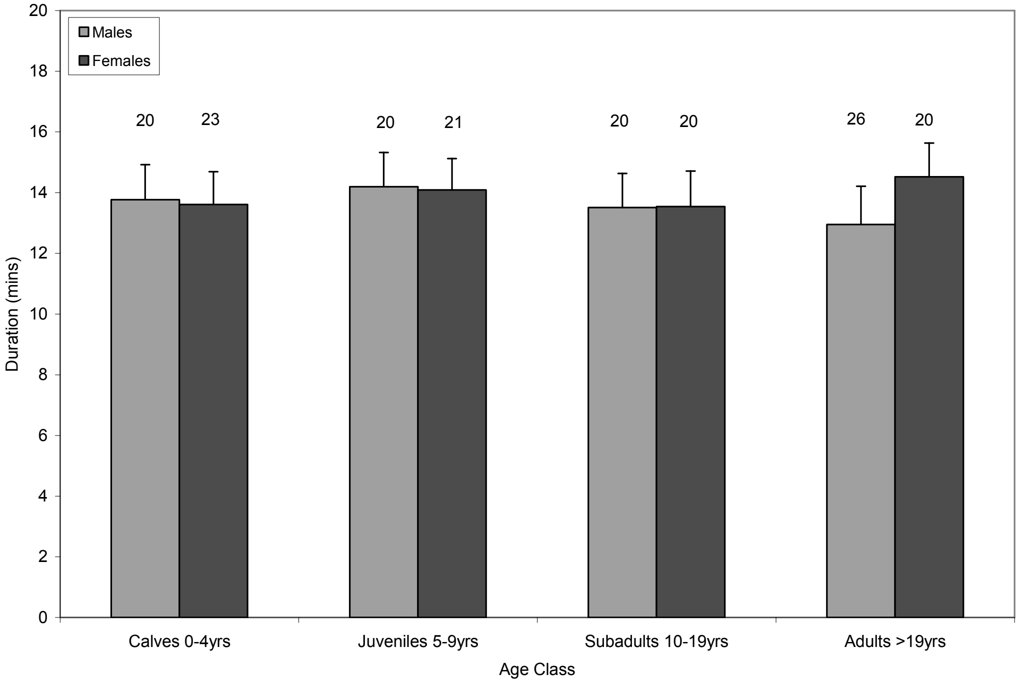

Figure 3. The mean (+SE) focal length (min) per age class for males and females at Ndarakwai Ranch (September 2004 - June 2005). Durations are based on the time the focal elephant was visible; "not visible" periods were not included. Sample sizes are shown above the bars. No significant differences were found.

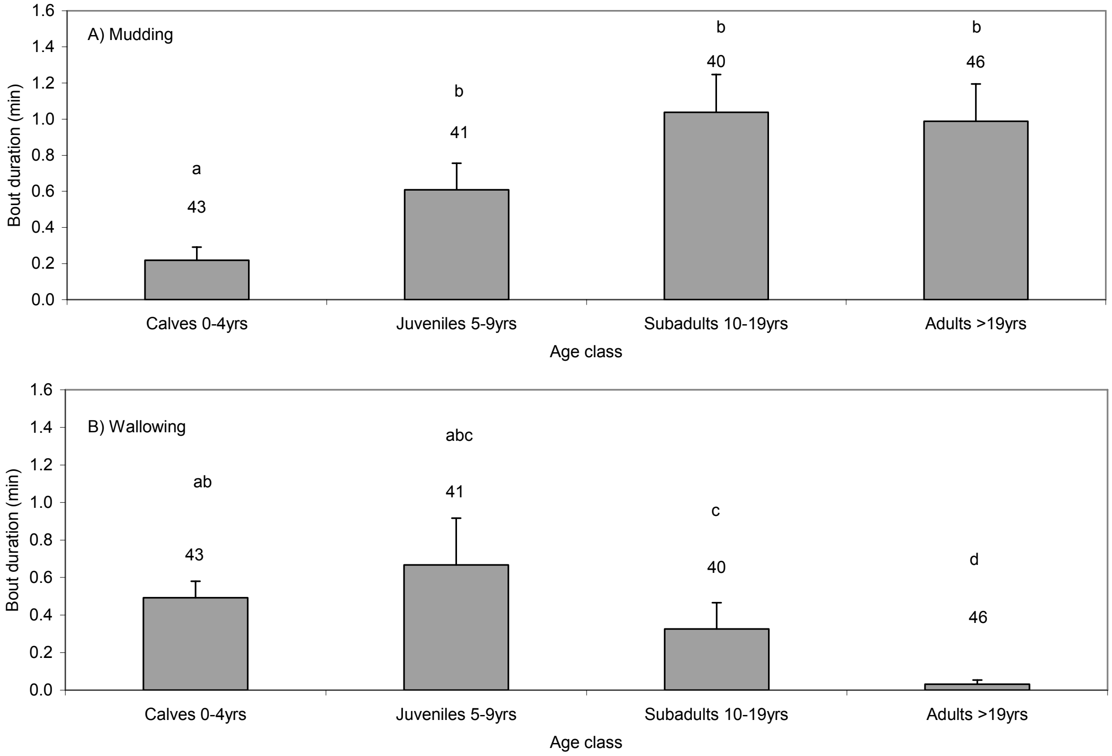

Figure 4. The mean (+SE) durations (min) for A) wallowing and B) mudding bouts across age classes of focal elephants, Ndarakwai Ranch (Sep. 2004-Jun. 2005). Sample sizes are shown above the bars. Different letters indicate differences between age classes at *P* = 0.05 (Table 4, II & IV). Data include zeros and outliers.

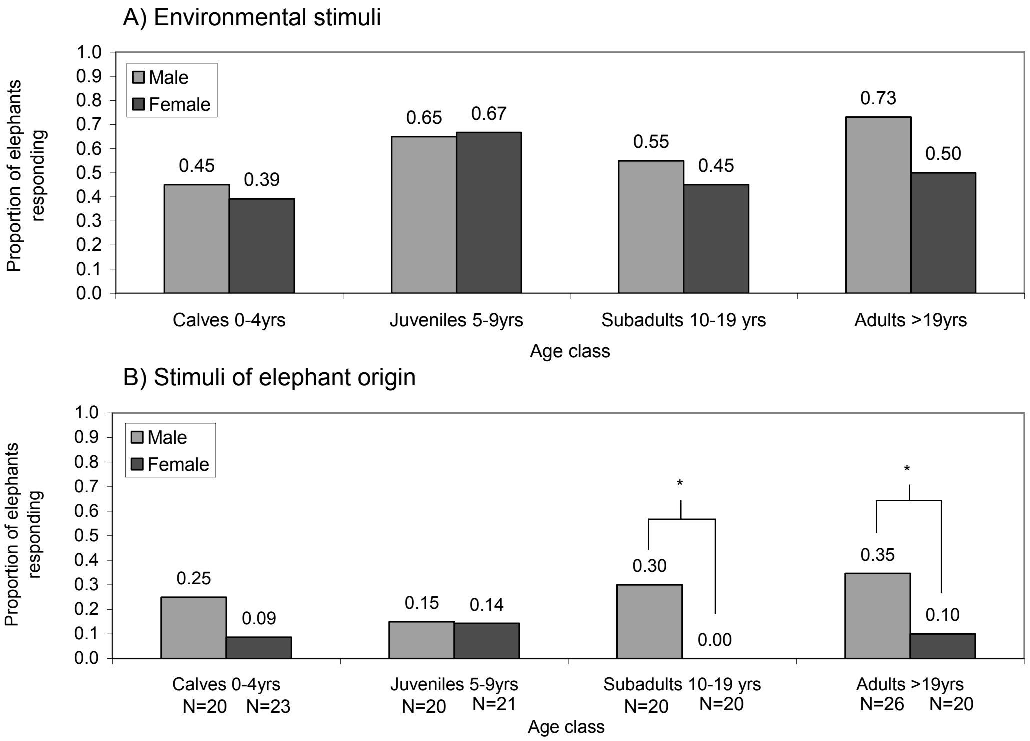

Figure 5. The proportion of focal elephants per age class and sex that performed chemosensory responses to A) environmental stimuli (e.g. substrate) and B) stimuli of elephant origin (e.g. conspecifics, feces or urine), Ndarakwai Ranch (September 2004 - June 2006). Sample sizes for both are A & B shown below the x-axis of B. $^*P < 0.05$, See Table 5, Ia-b.

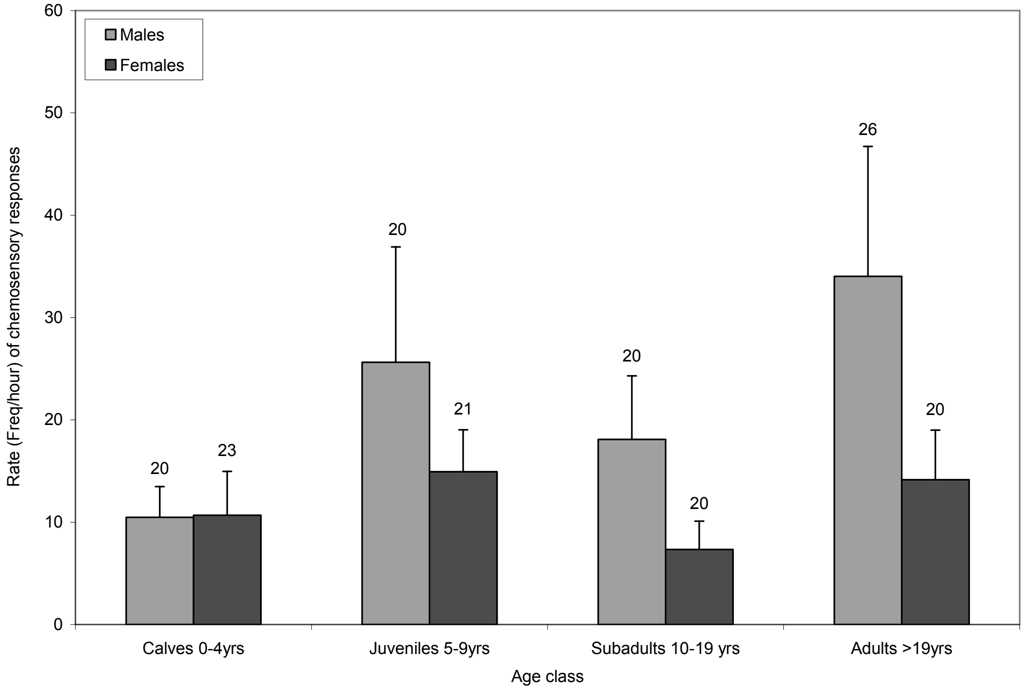

Figure 6. The mean (+SE) rate (Freq/hour) of all chemosensory responses to any type of stimulus per age class and sex of all focal elephants, Ndarakwai Ranch (September 2004 - June 2005). Sample sizes are shown above the bars. No significant differences were found (Table 5, II). Data include zeros.

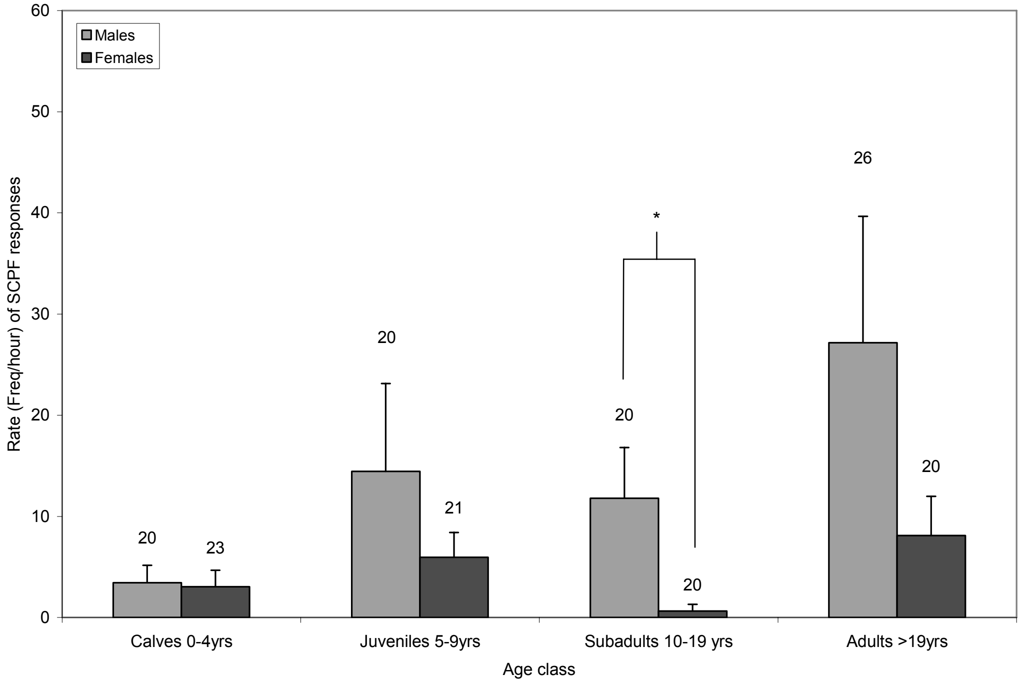

Figure 7. The mean (+SE) rate (Freq/hour) of sniff, check, place and flehmen (SCPF) responses to any type of stimulus per age class and sex of focal elephants, Ndarakwai Ranch (September 2004-June 2005). Samples sizes are shown above the bars. Males had a higher rate than females with significant sex differences occurring between subadult males subadult females (Table 5, VII - VIII). Data include zeros.

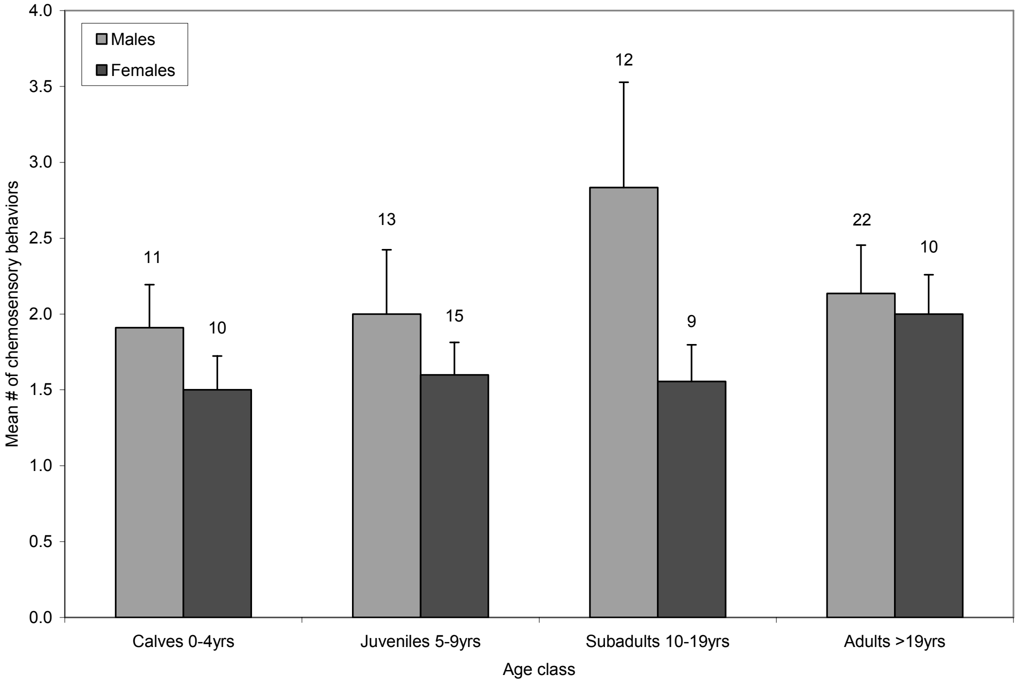

Figure 8. The mean (+SE) number of different chemosensory behaviors performed per age class and sex of all focal elephants, Ndarakwai Ranch (September 2004-June 2005). Sample sizes are shown above the bars. Males had a significantly larger repertoire size than did females (1-way ANOVA: age class: $F_{3,94} = 0.63$, $P = 0.59$; sex: $F_{1,94} = 4.02$, $P = 0.05$; interaction: $F_{3,94} = 0.75$, $P = 0.52$). Data do not include zeros.

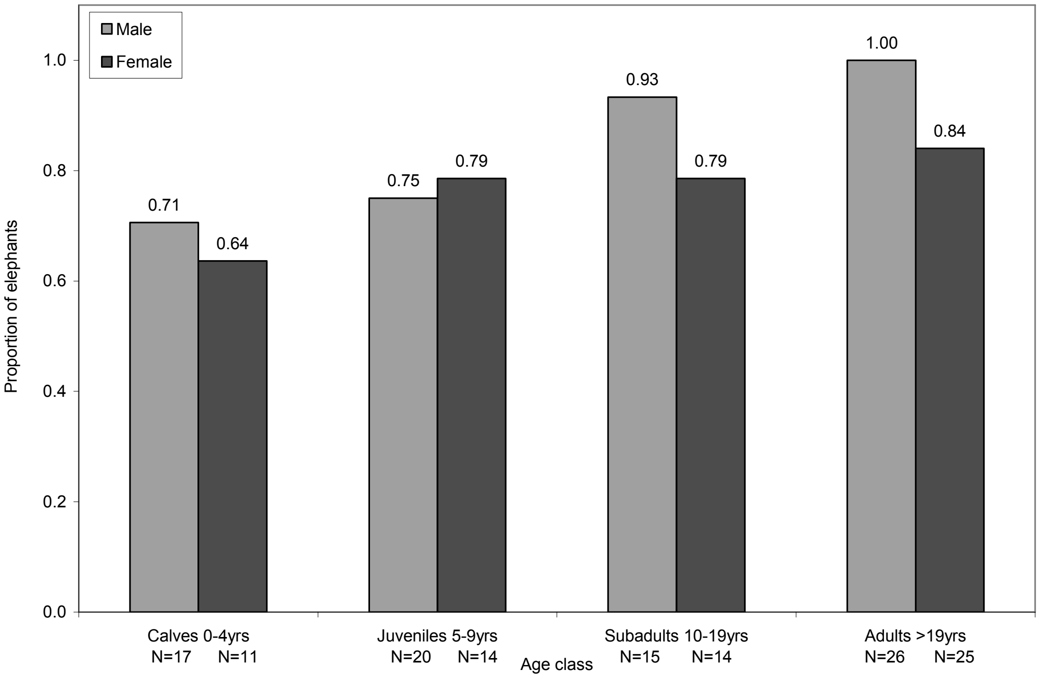

Figure 9. The proportion of elephants, which came in proximity (within one body length) of a sample, that came near (within one trunk length of) a sample, Ndarakwai Ranch (September 2004 - June 2005). The number of elephants per age class and sex that came in proximity is shown on the x-axis. There were significant differences between adult males and calf and juvenile males (Table 13, Ic & Ie).

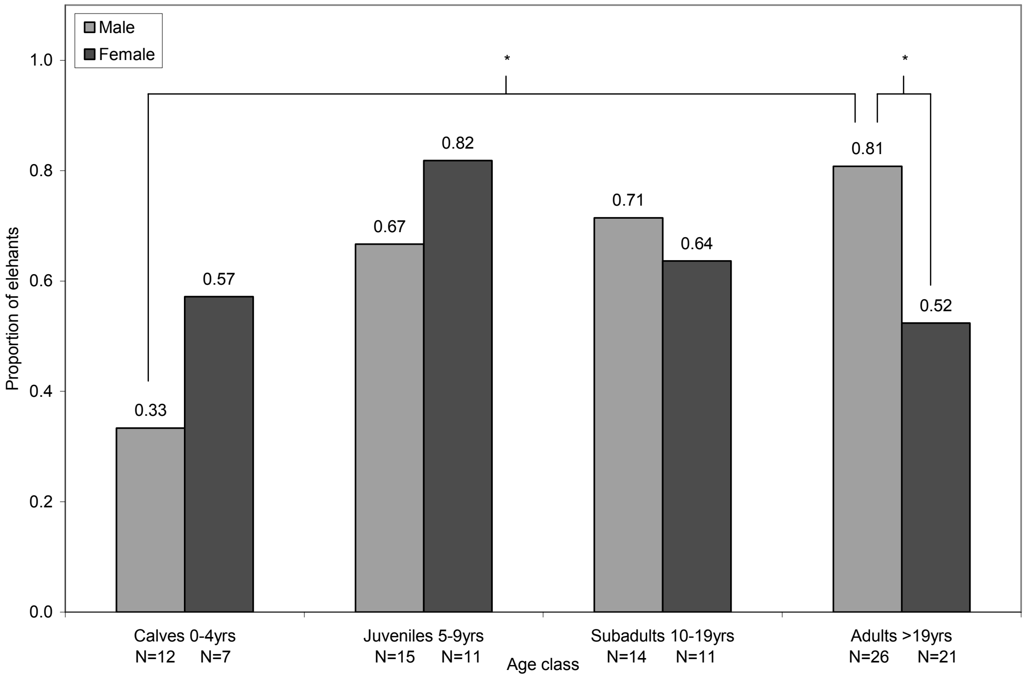

Figure 10. The proportion of elephants, which came near (within one trunk length of) the samples, that performed chemosensory behaviors to the placed urine and feces of a juvenile female elephant, Ndarakwai Ranch (September 2004 - June 2005). The number of elephants per age class and sex that came near samples is shown on the x-axis. $^*P <$ 0.05, See Table 14 Ic & IV.

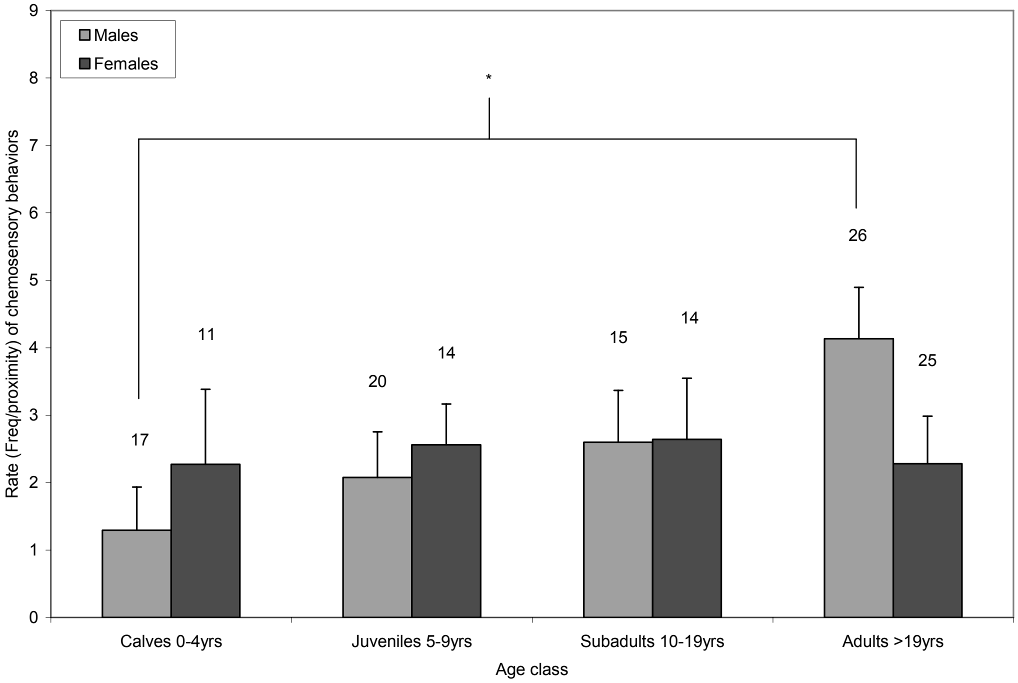

Figure 11. The mean (+SE) rate (Freq/proximity) of chemosensory responses of all focal elephants to the placed urine and feces of a juvenile female elephant, Ndarakwai Ranch (September 2004 - June 2005). Sample sizes are shown above bars. * $P < 0.05$, see Table 15, I. Data include zeros.

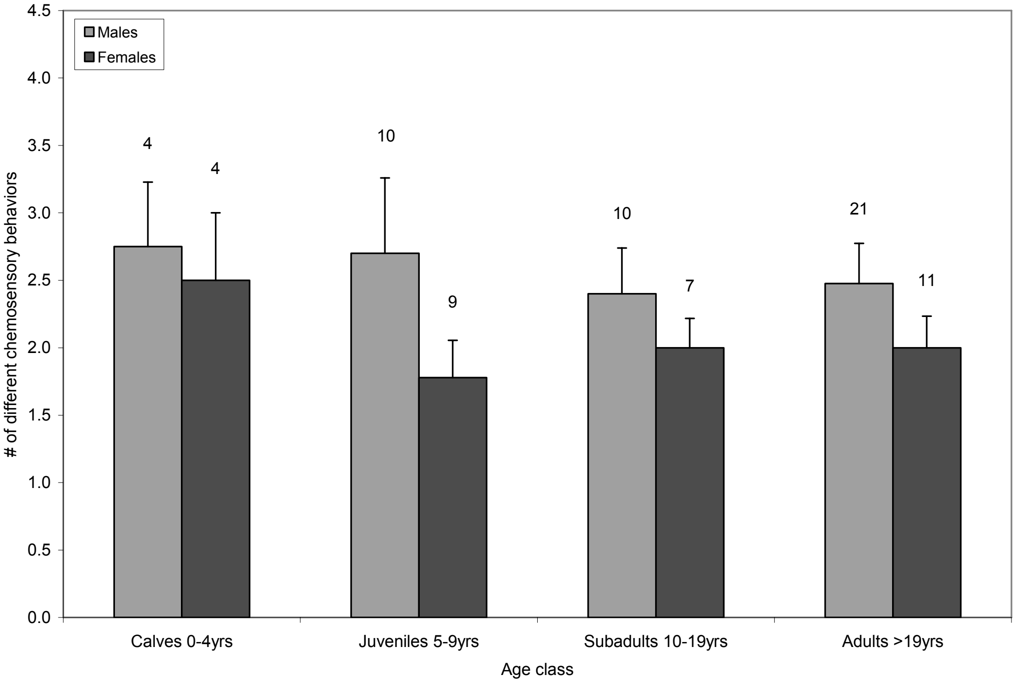

Figure 12. The mean (+SE) number of different chemosensory behaviors performed by all focal elephants to the placed urine and feces of a juvenile female elephant, Ndarakwai Ranch (September 2004 - June 2005). Sample sizes are shown above the bars. Data do not include zeros.

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APPENDIX A

MAP OF THE PERMANENT WATERHOLE AT NDARAKWAI RANCH, TANZANIA

Overhead view of the 4,300 m^2 waterhole showing zones 0-2 and the four sections, Ndarakwai Ranch, Tanzania. The observation platform is marked by the arrow in the NE section. The widths of zones were as follows: Zone 0 = waterhole; Zone 1=10 m; Zone 2 = 25 m; Zone 3 = 100 m; Zone 4 = 300 m. Zones 3 and 4 are not shown. Zone 3 was not assessed in the SW section and zone 4 was not assessed in the SE and SW sections because forest cover limited visibility. All bioassay samples were placed in zone 1 and each of the six sites is marked with a circle.

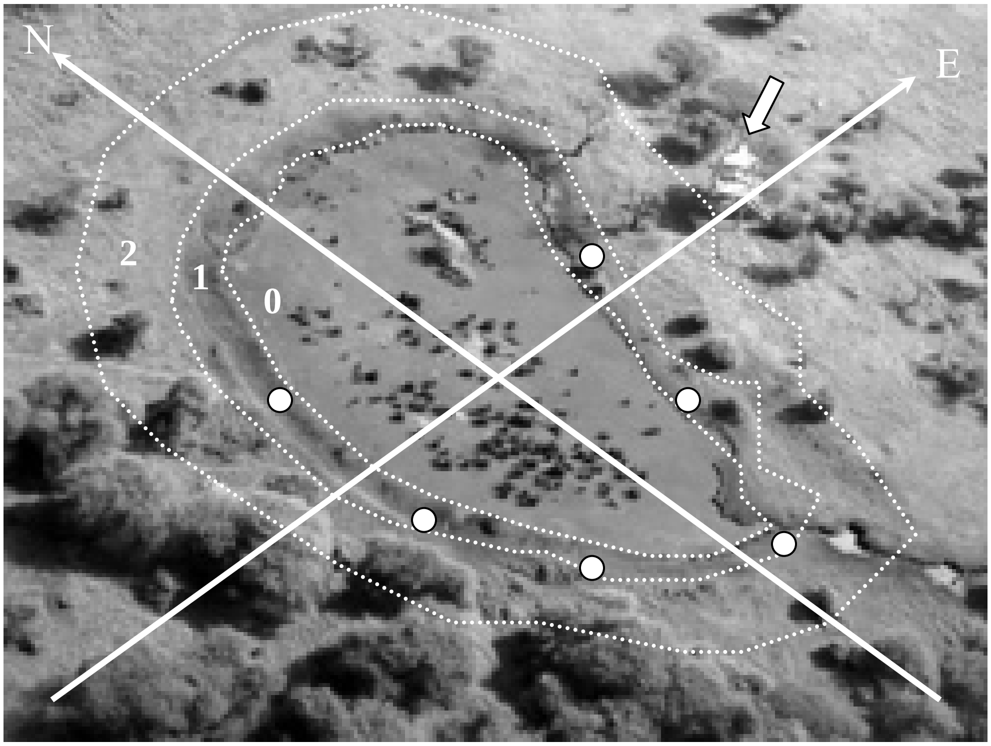

Figure A.1. Overhead view of the 4,300 m^2 waterhole showing zones 0-2 and the four sections, Ndarakwai Ranch, Tanzania (September 2004 - June 2005). Author and date of photo unknown.

APPENDIX B

SPECIES OF WOODY VEGETATION AT NDARAKWAI RANCH

List of woody vegetation at Ndarakwai Ranch, Tanzania. Species that are found at the waterhole are in bold.

Table B.1. List of plant species identified at Ndarakwai Ranch (September 2004 - June 2005).

Family	Common name	Scientific name
Anacardiaceae	Muthikeyo	*Rhus vulgaris*
Bignoniaceae	African tulip tree	*Spathodea campanulata*
Bignoniaceae	jacaranda	*Jacaranda mimosifolia*
Bignoniaceae	yellow trumpet tree	*Tecoma stans*
Boraginaceae	**large-leaf cordia**	*Cordia africana*
Boraginaceae	sandpaper cordia	*Cordia ovalis*
Burseraceae	common corkwood	*Commiphora pyracanthoides*
Burseraceae	hairy corkwood	*Commiphora africana*
Cactaceae	prickly pear	*Opuntia vulgaris*
Capparidaceae	**wooly caper bush**	*Capparis tomentosa*
Casuarinaceae	Australian beefwood	*Casuarina cunninghamia*
Euphorbiaceae	bridelia	*Bridelia micrantha*
Euphorbiaceae	-	*Euphorbia bussei*
Euphorbiaceae	tree euphorbia	*Euphorbia candelabrum*
Leguminosae	East African labumum	*Calpurnia aurea*
Leguminosae	**flat-top acacia**	*Acacia abyssinica*
Leguminosae	**black-thorn acacia**	*Acacia mellifera*
Leguminosae	red-thorn acacia	*Acacia lahai*
Leguminosae	**umbrella acacia**	*Acacia tortilis*
Leguminosae	whistling-thorn acacia	*Acacia drepanolobium*
Leguminosae	**yellow-fever tree**	*Acacia xanthophloea*
Proteaceae	silly Oak	*Grevilla robusta*
Zygophyllaceae (Balanitaceae)	desert date	*Balanites aaegyptiaca*

Species were identified using dichotomous keys from Noad and Birnie (1989) and van Wyk and van Wyk (1997).
Vouchers were not collected from any of these species.

REFERENCES FOR APPENDIX B

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van Wyk, B. & van Wyk, P. 1997. *Field Guide to Trees of Southern African.* Cape Town: Struik Publishers.

APPENDIX C

AVIAN AND MAMMALIAN SPECIES

Table includes the number of different birds and mammals seen at the waterhole from September 2004 to June 2005 at Ndarakwai Ranch, Tanzania. The general diets of each species of bird are based on the type of food (e.g. animal or plant) that the species is known to eat primarily. Bold letters indicate that the species was not seen at the waterhole, but elsewhere on Ndarakwai Ranch.

Table C.1. List of bird species and their general diets, Ndarakwai Ranch (September 2004 - June 2005).

Family	Bird Species	Scientific Name	Diet
Accipitridae	African harrier-hawk	*Polyboroides t. typus*	carnivore
Accipitridae	augur buzzard	*Buteo a. augur*	carnivore
Accipitridae	eastern pale chanting goshawk	*Melierax poliopterus*	carnivore
Accipitridae	gabar goshawk	*Micronisus gabar aequatorius*	carnivore
Accipitridae	hooded vulture	*Necrosyrtes monachus pileatus*	carnivore
Accipitridae	little sparrowhawk	*Accipiter m. minullus*	carnivore
Accipitridae	Montagu's harrier	*Circus pygargus*	carnivore
Accipitridae	pallid harrier	*Circus macrourus*	carnivore
Accipitridae	secretary bird	*Sagittarius serpentarius*	carnivore
Accipitridae	tawny eagle	*Aquila r. rapax*	carnivore
Accipitridae	? vulture		carnivore
Alcedinidae	brown-hooded kingfisher	*Halcyon albiventris orientalis*	carnivore
Alcedinidae	striped kingfisher	*Halcyon c. chelicuti*	carnivore
Anatidae	spur-winged goose	*Plectropterus g. gambensis*	herbivore
Ardeidae	black heron	*Egretta ardesiaca*	carnivore
Ardeidae	dwarf bittern	*Ixobrychus sturmii*	carnivore
Ardeidae	grey heron	*Ardea c. cinerea*	carnivore
Bucerotidae	African grey hornbill	*Tockus nasutus*	carnivore
Bucerotidae	Von der Decken's hornbill	*Tockus deckeni*	carnivore

Appendix C. (cont.)

Family	Bird Species	Scientific Name	Diet
Bucorvidae	southern ground hornbill	*Bucorvus leadbeateri*	carnivore
Charadriidae	blacksmith plovers	*Vanellus armatus*	insectivore
Charadriidae	crowned plover	*Vanellus c. coronatus*	insectivore
Ciconiidae	marabou stork	*Leptoptilos crumeniferus*	carnivore
Ciconiidae	white stork	*Ciconia c. ciconia*	carnivore
Ciconiidae	yellow billed stork	*Mycteria ibis*	carnivore
Coliidae	blue-naped mousebird	*Urocolius macrourus pulcher*	herbivore
Columbidae	African green pigeon	*Treron calva gibberifrons*	frugivore
Columbidae	emerald-spotted wood dove	*Turtur chalcospilos*	omnivore
Columbidae	laughing dove	*Streptopelia s. senegalensis*	granivore
Columbidae	namaqua doves	*Oena c. capensis*	granivore
Columbidae	ring-necked dove	*Streptopelia capicola somalica*	granivore
Columbidae	speckled pigeon	*Columba g. guinea*	granivore
Coraciidae	lilac-breasted roller	*Coracias caudata*	carnivore
Corvidae	pied crow	*Corvus albus*	omnivore
Corvidae	white-naped raven	*Corvus albicollis*	omnivore
Cuculidae	white-browed coucal	*Centropus s. superciliosus*	carnivore
Dicruridae	common drongo	*Dicrurus a. adsimilis*	insectivore
Estrildidae	African firefinch	*Lagonosticta rubricata hildebrandti*	granivore
Estrildidae	black and white mannikin	*Lonchura bicolor*	granivore
Estrildidae	black-faced waxbill	*Estrilda erythronotus delamerei*	granivore
Estrildidae	cut-throat finch	*Amadina fasciata alexanderi*	granivore
Estrildidae	purple grenadier	*Uraeginthus ianthinogaster*	granivore
Estrildidae	red-cheeked cordon-bleu	*Uraeginthus b. bengalus*	granivore
Falconidae	common kestrel	*Falco tinnunculus*	carnivore
Falconidae	falcon	*Falco sp.*	carnivore
Falconidae	lesser kestrel	*Falco naumanni*	carnivore
Fringillidae	white-bellied canary	*Serinus dorsostriatus*	granivore
Laniidae	long-tailed fiscal shrike	*Lanius cabanisi*	carnivore
Laniidae	red-backed shrike	*Lanius collurio*	carnivore
Laniidae	red-tailed shrike	*Lanius isabellinus*	carnivore

Appendix C. (cont.)

Family	Bird Species	Scientific Name	Diet
Laniidae	shrike sp.	*Lanius sp.*	carnivore
Malaconotidae	brubru	*Nilaus afer minor*	carnivore
Meleagrididae	helmeted guineafowl	*Numida meleagris*	insectivore
Meropidae	bee-eater	*Merops sp.*	insectivore
Motacillidae	African pied wagtail	*Motacilla aguimp vidua*	insectivore
Muscicapidae	African dusky flycatcher	*Muscicapa adusta interposita*	insectivore
Musophagidae	white-bellied go-away bird	*Corythaixoides leucogaster*	herbivore
Nectariniidae	eastern violet-backed sunbird	*Anthreptes orientalis*	omnivore
Nectariniidae	long-tailed sunbird	*Nectarinia sp.*	omnivore
Nectariniidae	scarlett chested sunbird	*Nectarinia senegalensis lamperti*	omnivore
Nectariniidae	? sunbird		omnivore
Oriolidae	black-headed oriole	*Oriolus larvatus rolleti*	insectivore
Otididae	kori bustard	*Ardeotis kori*	omnivore
Passeridae	chestnut sparrow	*Passer eminibey*	granivore
Passeridae	grey-capped social weaver	*Pseudonigrita arnaudi*	granivore
Passeridae	grey-headed sparrow	*Passer griseus*	granivore
Passeridae	rufous sparrow	*Passer r. rufocinctus*	omnivore
Pelecanidae	white pelican	*Pelecanus erythrorhynchus*	carnivore
Phasianidae	crested francolin	*Francolinus sephaena*	omnivore
Phasianidae	yellow-necked spurfowl	*Francolinus leucoscepus*	herbivore
Phoeniculidae	Abyssinian scimitarbill	*Rhinopomastus minor cabanisi*	insectivore
Phoeniculidae	green wood-hoopoe	*Phoeniculus purpureus*	insectivore
Picidae	bearded woodpecker	*Dendropicos namaquus schoensis*	insectivore
Picidae	cardinal woodpecker	*Dendropicos fuscescens*	insectivore
Picidae	Nubian woodpecker	*Campethera nubica*	insectivore
Platysteiridae	batis	*Batis sp.*	insectivore
Ploceidae	black-necked weaver	*Ploceus melanogaster stephanophorus*	granivore
Ploceidae	chestnut weaver	*Ploceus r. rubiginosus*	granivore
Ploceidae	grosbeak-weaver	*Amblyospiza albifrons melanota*	granivore
Ploceidae	red-billed buffalo weaver	*Bubalornis niger intermedius*	granivore
Ploceidae	vitelline masked weaver	*Ploceus velatus uluensis*	granivore

Appendix C. (cont.)

Family	Bird Species	Scientific Name	Diet
Ploceidae	white-headed buffalo weaver	*Dinemellia dinemelli boehmi*	granivore
Psittacidae	Fischer's lovebirds	*Agapornis fischeri*	granivore
Pteroclididae	black-faced sandgrouse	*Pterocles decoratus*	granivore
Pycnonotidae	common bulbul	*Pycnonotus barbatus*	omnivore
Rallidae	black crake	*Amaurornis flavirostris*	carnivore
Rallidae	common moorhen	*Gallinula chloropus meridionalis*	omnivore
Ramphastidae	red and yellow barbet	*Trachyphonus erythrocephalus*	omnivore
Rostratulidae	greater painted-snipe	*Rostratula b. benghalensis*	omnivore
Scolopacidae	common greenshank	*Tringa nebularia*	insectivore
Scolopacidae	common redshank	*Tringa totanus ussuriensis*	carnivore
Scolopacidae	common snipe	*Gallinago g. gallinago*	insectivore
Scolopacidae	little stint	*Calidris minuta*	insectivore
Scolopacidae	? sandpiper		insectivore
Scolopacidae	wood sandpiper	*Tringa glareola*	insectivore
Scopidae	hamerkop	*Scopus u. umbretta*	carnivore
Strigidae	pearl-spotted owlet	*Glaucidium perlatum licua*	carnivore
Struthionidae	common ostrich	*Struthio camelus massaicus*	omnivore
Sturnidae	Hildebrandt's starling	*Lamprotornis hildebrandti*	omnivore
Sturnidae	red-billed oxpecker	*Buphagus erythrohynchus*	insectivore
Sturnidae	? starling		omnivore
Sturnidae	superb starling	*Lamprotornis superbus*	omnivore
Sturnidae	wattled starling	*Creatophora cinerea*	omnivore
Sylviidae	banded parisoma	*Parisoma boehmi*	insectivore
Sylviidae	buff-bellied warbler	*Phyllolais pulchella*	granivore
Sylviidae	cisticola	*Cisticola sp.*	granivore
Sylviidae	red-faced crombec	*Sylvietta whytii jacksoni*	insectivore
Sylviidae	yellow bellied eremomela	*Eremomela icteropygialis*	insectivore
Threskiornithidae	hadada ibis	*Bostrychia hagedash brevirostris*	insectivore
Threskiornithidae	sacred ibis	*Threskiornis a. aethiopicus*	carnivore
Upupidae	hoopoe	*Upupa epops*	carnivore
Viduidae	paradise whydah	*Vidua paradisaea*	granivore

Appendix C. (cont.)

Family	Bird Species	Scientific Name	Diet
Viduidae	pin-tailed whydah	*Vidua macroura*	granivore
Viduidae	straw-tailed whydah	*Vidua fischeri*	granivore
	? duck/grebe		herbivore
	? ground bird (maybe francolin)		
	? small finch/sparrow		granivore

Species were identified from Zimmerman et al. (1996).
Diets were derived from Perrins & Harrison (1979) and Zimmerman et al. (1996).
? indicates that the species of bird was unknown.

Table C.2. Species of wild and domestic mammals observed at Ndarakwai Ranch, Tanzania (September 2004 - June 2005).

Family	Wild Species	Species Name
Bovidae	buffalo	*Syncerus caffer*
Bovidae	bush duiker	*Sylvicapra grimmia*
Bovidae	bushbuck	*Tragelaphus scriptus*
Bovidae	common waterbuck	*Kobus e. ellipsiprymnus*
Bovidae	eland	*Tragelaphus (Taurotragus) oryx*
Bovidae	grant's gazelle	*Gazella granti*
Bovidae	impala	*Aepyceros melampus*
Bovidae	Kirk's dikdik	*Madoqua kirkii*
Bovidae	reedbuck	*Redunca redunca*
Bovidae	thomson's gazelle	*Gazella thomsonii*
Bovidae	wildebeest	*Connochaetes taurinus*
Canidae	black-backed jackal	*Canis mesomelas*
Cercopithecidae	black and white colobus	*Colobus guereza*
Cercopithecidae	blue monkey	*Cercopithecus mitis*
Cercopithecidae	olive baboon	*Papio cynocephalus*
Cercopithecidae	vervet monkey	*Cercopithecus aethiops*
Elephantidae	elephant	*Loxodonta africana*
Equidae	zebra	*Equus burchellii*
Felidae	cheetah	*Acinonyx jubatus*
Giraffidae	giraffe	*Giraffa cameloparadalis*
Herpestidae	banded mongoose	*Mungos mungo*
Herpestidae	marsh mongoose	*Atilax paludinosus*
Herpestidae	slender mongoose	*Herpestes sanguineus*
Hyaenidae	spotted hyena	*Crocuta crocuta*
Hyaenidae	striped hyena	*Hyaena hyaena*
Hystricidae	porcupine	*Hystrix africaeaustralis*
Suidae	warthog	*Phacochoerus africanus*
	Domestic Species	
Bovidae	cow	*Bos* sp.
Bovidae	goat	*Capra hircus*
Bovidae	sheep	*Ovis* sp.

Species were identified from Kingdon (1997).

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APPENDIX D

CRITERIA FOR AGE ESTIMATIONS OF AFRICAN ELEPHANTS

Age classes of African elephants at Ndarakwai Ranch (September 2004 - June 2005) based on known ages and on descriptions of height, tusk size, body and social descriptions published by Moss (1996, 2001).

Table D.1. The morphological descriptions of elephants in four age classes, Ndarakwai Ranch, Tanzania (September 2004 – June 2005).

Age class and specific age (years old)	Height	Ca. Tusk length and description	Body and social description
Calves			
<1	shoulder reaches elbow of adult female	none	body usually visibly hairy
1	shoulder slightly taller than breast-level of adult female	none	head and ears in proportion with body
2	reaches armpit of adult female	may begin to show (2 cm)	trunk looks more in proportion
3	reaches lower ear of adult female	5-7 cm	decreased suckling
4	reaches anal flap of adult female	15-18 cm	suckling drastically reduced
Juveniles			
5	1/4 size of adult	20-23 cm	Males: begin to spar, time spent with mother reduced Females: allomother younger calves
6	shoulder taller than middle ear of adult female	22 cm	tusks begin to turn outward
7	shoulder at level of eye of adult female	22 cm; began to splay out, males have thicker tusks	look more like a small adult Males: have heavier bodies
8	overall size 1/2 of adult female	25-30 cm	
9	overall size 3/4 of adult female	27 cm	males are larger than females of same age and spend less time with family; females more integrated into family

Appendix D. (cont.)

Age class and specific age (years old)	Height	Ca. Tusk length and description	Body and social description
Subadults			
10-15	Males: overall size 3/4 of adult female	27 cm; Males: tusk circumference greater than that of females Females: thin splayed tusks	Males: larger than females of same age; spending less time with family Females: more square in body shape than adult females
15-19	Males: taller than adult females but small compared to older males	Females: tusks began to converge, straighten, or become asymmetrical	Males: same height as adult females over 40 years old
Adults			
>19	Males: shoulder height still increasing, taller than largest females	tusks thick at lip	Males: taller than adult females, head broadens, body heavy set Females: back has lengthened so that body appears long

APPENDIX E

MUDDING BEHAVIORS

A qualitative assessment of the age classes of elephants that were likely to be observed performing various mudding behaviors (see Table 1 for description of mudding behavior), Ndarakwai Ranch (September 2004 - June 2005).

Table E.1. Four distinct behaviors patterns used by elephants in four age classes to distribute mud over the body, Ndarakwai Ranch (September 2004 – June 2005).

	Calves 0-4yrs	Juveniles 5-9yrs	Subadults 10-19yrs	Adults >19yrs
Mud toss on sides	Yes; erratic trunk movements, very little of body area covered with mud	Yes	Yes	Yes
Mud toss on head	No	No	Yes	Yes; mainly by males
Mud spray	No; infrequently by older calves	Yes; more likely by older juveniles	Yes	Yes
Mud swab	No	No	Yes; mainly by males	Yes; mainly by males

APPENDIX F

TEMPORAL CHANGES IN THE OCCURRENCE, BEHAVIOR AND CONTRASPECIFIC ASSOCIATIONS OF AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*) AT A WATERHOLE ON NDARAKWAI RANCH, TANZANIA

OBJECTIVES

The primary objective of this study was to determine the seasonal and diurnal temporal changes (hourly) in the occurrence of elephants at an artificial waterhole. Few facts were known about the elephant population under study, so the goal was to learn how and what features of elephant visits changed across time. Seasonal and temporal changes in the number of elephant sightings, group composition and behavior were examined. I hypothesized that elephant occurrence at the waterhole was dependent on rainfall. Elephant sightings at the waterhole were predicted to increase during the dry season and decrease during the wet season. For changes in group composition, I predicted that cow/calf groups would be the most commonly sighted group type and that there would be an increase in the occurrence of males following wet seasons. Elephants were predicted to show elevations in feeding and drinking behaviors following the wet season and during the early morning and late afternoon hours. The second objective was to determine the pattern of waterhole visits by other species. I examined the interspecific associations at the waterhole to see which species were most commonly together with elephants. Competition between large mammals was expected to affect a low level of co-occurrence between elephants and other large herbivores. The seeds and invertebrates found in elephant dung provide resources for granivorous and insectivorous birds that will have a higher co-occurrence with elephants than will other types of birds.

METHODS

Study Site

Details of the study site are the same as those in Part I (see pp.23-25).

The man-made waterhole and a surrounding area were sampled from September 2004-June 2005. Data from July 2005-October 2005 were collected by a second observer (E. Napora) and were reliable with the previous data based on one month of simultaneous sampling and interobserver reliability checking at the waterhole in June 2005. The presence of mammalian and avian fauna (Appendix C) was recorded on an hourly basis using scan sampling methods (Lehner 1996). The waterhole was partitioned into four sections and four zones (Appendix A). A high density of trees reduced visibility and limited the SE section to zone 3 and SW section to zone 2. Where possible, section and zone boundaries were distinguished using natural landmarks (e.g. roads and bushes).

Data Collection

Data on the measurable amount (e.g. milliliters) of precipitation were not available. The criterion used to distinguish wet seasons from dry seasons was based on the number of days rainfall was recorded without consideration of the amount of rainfall. Ten percent was used as the criterion for defining wet season because it was during these months that rain fell when I was not in the field; therefore the actual proportion of days with rainfall for these months was higher than 0.10. Wet seasons were composed of consecutive months in which the proportion of rain days per month equaled or exceeded 0.10. Dry seasons were composed of all other months. The length of a wet season was based on the number of months that met or exceeded the 0.10 criterion: Long Wet =

September-December (2004), Short Dry = January-February (2005), Short Wet = March-May (2005) and Long Dry = June-October (2005).

The proportion of elephant sightings per season was calculated from the total number of elephant sightings from September 2004 to October 2005. Since the majority of elephant sightings occurred in one month (May), the proportion of group types sighted and the proportion of state behaviors recorded per month were calculated from the total number of elephant sightings for each month. Mammals and bird species sightings from 900h to 1700h were used for the time of day analyses because the number of scans during this period accounted for over 95% of the total number scans. Sunrise varied between 600h and 700h and sunset between 1800h and 1900h over the study period. Mean temperatures (°C) per month and per hour were calculated from the daily temperatures and from the temperatures for the particular hour, respectively, from September 2004 to October 2005. Proportions for the time of day analyses were from the total number elephant sightings per group type or state behavior (within category variation) and the total number of elephant sightings per month (among category variation). The identity of individual elephants or other species was not recorded, so information on the number of different individuals is not presented.

Bird species were grouped into six categories based on their general diet: carnivores, frugivores, granivores, herbivores, insectivores, and omnivores (Perrins and Harrison 1979; Zimmerman et al. 1996). Diet was chosen as a grouping variable because it expected to vary with season and to be affected by elephants.

An association or co-occurrence index was used to measure the instances when two species were at the waterhole at the same time. Only sightings of species in zones 0-

2 from 900h to 1700h were analyzed since animals in these zones were reasoned to be within visual distance of one another. The Simple Ratio (Cairns & Schwager 1987; Ginsberg & Young 1992) was applied to derive the co-occurrence indices (Appendix G).

Data Analysis

JMP IN 4.0.4 (SAS Institute 2000) for Windows operating systems was used for all statistical analyses. If data on proportions did not meet normality assumptions, an arcsine transformation was performed. One-way ANOVA and ANCOVA with number of scans and temperature as covariates were used to compare number of sightings across seasons. Spearman rank correlation was used to determine the relationship between variables.

SUMMARY

The first objective was to describe the seasonal and temporal patterns of elephant visits.

Seasonal Patterns:

[NOTE: Statistical analyses were conducted only for 1)]

1) Elephant sightings at the waterhole did vary depending on season and time of day. This result was apparent even when the effects of sampling effort (number of scans) and temperature were held constant (ANCOVA: sampling effort, $F_{3,116}=18.05$, $p<0.001$ and temperature, $F_{3,111}=15.34$, $p<0.001$). Elephants were sighted more in the Short Wet season than in any other season (Fig. F.1). Although the peak in the proportion of elephant sightings occurred in May (292/742 sightings, 39.4%) during the Short Wet (March-May 2005) season, the proportion elephant sightings during the Long Dry season (June

2005-October 2005; 351/742 sightings, 47.3%) were greater than those of the months prior to May 2005 (Fig. F.2). Elephant visits to the waterhole did display seasonal patterns.

2) Among group types, mixed groups of elephants were the most common group type sighted per month (Figs. F.3 & F.4). Elephants were sighted often in cow/calf groups, and there was an increase in the proportion of cow/calf groups out of all elephants sighted from June 2005-October 2005 (Long Dry). Males were observed more often with females than alone or in bull groups and the proportion of solitary male or bull group sightings did not show seasonal patterns.

3) Drinking and eating did not follow the predicted patterns. Drinking was observed less often in the Short Dry season (January-February 2005) than in the other three seasons (Fig. F.5). The waterhole was full of water during this season, but other sources of water (e.g. peripheral water holes) may have attracted elephants. Elephants were rarely seen eating at the waterhole. Locomotion (e.g. walking or running) or stationary were the most common states in which elephants were observed, although seasonal patterns were absent.

Temporal Patterns:

[NOTE: Statistical analyses were conducted only for 1)]

1) From 900h to 1400h, the temperature gradually increased and the proportion of elephant sightings also increased from 900h to 1300h. Temperature and proportion of elephant sightings were strongly correlated (Fig. F.6).

Elephants were most commonly sighted at 1300h (130/742 sightings 17.5%) and 1500h (130/742 sightings, 17.5%), thus providing evidence for a temporal pattern of waterhole visits.

2) Bull, calf/cow and mixed groups sightings were most common at 1300h and 1500h, and solitary elephants were sighted mainly at 1500h (Fig. F.7). The morning and late afternoon hours were when cow/calf groups were the most common group type sighted, but temporal patterns were not evident in any of the group types (Fig. F.8).

3) Drinking and feeding behaviors were not common during the morning or late afternoon hours. Sightings of all behaviors followed a similar pattern as that of elephant sightings from 900h to 1700h (Fig. F.9). At 900h, when the mean temperature was cool, 63% (12/19 sightings) of all state behaviors observed were of elephants in locomotion (Fig. F.10). After 900h, the probability of observing a specific behavior stayed fairly constant with locomoting and stationary composing over 70% of all behaviors. Elephant behaviors did not seem to be affected by time of day.

The second objective was to measure the seasonal and temporal changes in the waterhole visits of other species and to examine how often elephants were at the waterhole at with contraspecifics.

Mammal and Bird Sightings:

1) Baboon, eland, impala, vervet monkey and warthog were sighted relatively more often before May, the month during which elephants were the species most often seen (Fig. F.11). Zebra sightings too were low during May, but

increased thereafter. Carnivorous and herbivorous birds were sighted more often before the Long Dry season (June 2005-October 2005) and granivorous bird sightings also were greatest during this period (Fig. F.12). Seasonal patterns in the mammal and bird sightings suggest that some species are increasing their visits to the waterhole before and after the peak in elephant sightings.

2) From 900h to 1700h, impala and vervet monkey sightings were more common before 1200h and zebra tended to be seen more than other species in the late afternoon hours (Fig. F.13). Among birds, granivores were the most often sighted birds from 900h to 1400h, and the relative proportion of herbivore and insectivore sightings increased slightly after 1400h (Fig. F.14). Few species showed a temporal pattern as obvious as that of elephants, and the probability of observing most species of mammal was the same across times of day.

3) For the interspecific relationships at the waterhole, elephants had a low probability of being seen with other mammals (Table F.1). Birds had a higher co-occurrence with elephants than did mammals, and granivorous birds were observed the most often when elephants were present (Table F.2). The low levels of co-occurrence between elephants and other species may be dependent on the differential times of the season or day that these species visited the waterhole. Whether there was active avoidance of elephants by other species cannot be determined from this dataset.

Table F.1. The percent co-occurrence between mammal species at the waterhole using the Simple Ratio method (see Appendix G), Ndarakwai Ranch (September 2004 - October 2005).

	elephant	baboon	eland	impala	vervet monkey	warthog	waterbuck	zebra
elephant	-	0.02	0.00	0.01	0.01	0.04	0.01	0.02
baboon	-	-	0.01	0.08	0.01	0.05	0.04	0.02
eland	-	-	-	0.01	0.00	0.01	0.00	0.04
impala	-	-	-	-	0.06	0.04	0.05	0.05
vervet monkey	-	-	-	-	-	0.01	0.01	0.04
warthog	-	-	-	-	-	-	0.06	0.04
waterbuck	-	-	-	-	-	-	-	0.04
zebra	-	-	-	-	-	-	-	-

Table F.2. The percent co-occurrence between categories of birds based on general diet and elephants at the waterhole using the Simple Ratio method (see Appendix G) Ndarakwai Ranch (September 2004 - October 2005).

	elephant	carnivore	frugivore	granivore	herbivore	insectivore	omnivore
elephant	-	0.06	0.02	0.09	0.05	0.07	0.02
carnivore	-	-	0.04	0.28	0.26	0.24	0.10
frugivore	-	-	-	0.04	0.02	0.04	0.02
granivore	-	-	-	-	0.20	0.26	0.09
herbivore	-	-	-	-	-	0.17	0.09
insectivore	-	-	-	-	-	-	0.08
omnivore	-	-	-	-	-	-	-

Table F.3. The number of sightings of four elephant group types at a waterhole per month, Ndarakwai Ranch (September 2004 - October 2005).

Month-Year	Bull	Cow/calf	Mixed	Solitary	Grand Total
September-04	0	3	3	0	6
October-04	1	0	17	1	19
November-04	0	7	18	0	25
December-04	1	4	6	6	17
January-05	0	2	2	0	4
February-05	0	0	7	0	7
April-05	3	8	8	2	21
May-05	13	75	174	30	292
June-05	1	16	51	7	75
July-05	1	44	60	23	128
August-05	0	22	20	3	45
September-05	0	33	3	2	38
October-05	6	27	31	1	65
Grand Total	26	241	400	75	742

Definitions of group types provided on page 13.

Table F.4. The number of sightings of seven state behaviors that elephants could be observed performing at a waterhole per month, Ndarakwai Ranch (September 2004 - October 2005).

Month-Year	drinking	eating	interacting	locomoting	mudding	stationary	wallowing	Grand Total
Sep-04	2	1	0	1	0	2	0	6
Oct-04	2	2	0	7	0	8	0	19
Nov-04	4	1	0	11	0	9	0	25
Dec-04	6	1	0	8	0	2	0	17
Jan-05	0	1	0	3	0	0	0	4
Feb-05	0	1	0	2	0	4	0	7
Apr-05	1	0	0	18	0	2	0	21
May-05	30	13	1	101	17	119	11	292
Jun-05	13	3	4	26	1	27	1	75
Jul-05	11	6	0	59	1	50	1	128
Aug-05	3	0	0	24	0	18	0	45
Sep-05	5	1	0	11	0	21	0	38
Oct-05	19	9	0	25	0	12	0	65
Grand Total	96	39	5	296	19	274	13	742

See Table 1 for definitions of behaviors.

Table F.5. The number of sightings of four elephant group types at a waterhole per hour from 900h to 1700h, Ndarakwai Ranch (September 2004 - October 2005).

Time	Bull	Cow/calf	Mixed	Solitary	Grand Total
9:00	1	9	6	3	19
10:00	3	15	29	3	50
11:00	1	23	34	4	62
12:00	1	31	57	10	99
13:00	5	37	82	6	130
14:00	4	34	52	13	103
15:00	5	39	64	22	130
16:00	1	26	55	11	93
17:00	5	26	21	4	56
Grand Total	26	240	400	76	742

Definitions of group types provided on page 13.

Table F.6. The number of sightings of seven state behaviors that elephants could be observed performing at a waterhole from 900h to 1700h, Ndarakwai Ranch (September 2004 - October 2005).

Time	drinking	eating	interacting	locomoting	mudding	stationary	wallowing	Grand Total
9:00	4	1	0	12	0	2	0	19
10:00	6	7	0	16	1	20	0	50
11:00	6	5	0	28	1	21	1	62
12:00	11	2	1	39	3	39	4	99
13:00	17	9	2	44	6	50	2	130
14:00	16	5	1	40	0	40	1	103
15:00	20	6	0	50	6	43	5	130
16:00	9	2	1	41	2	38	0	93
17:00	7	2	0	26	0	21	0	56
Grand Total	96	39	5	296	19	274	13	742

See Table 1 for definitions of behaviors.

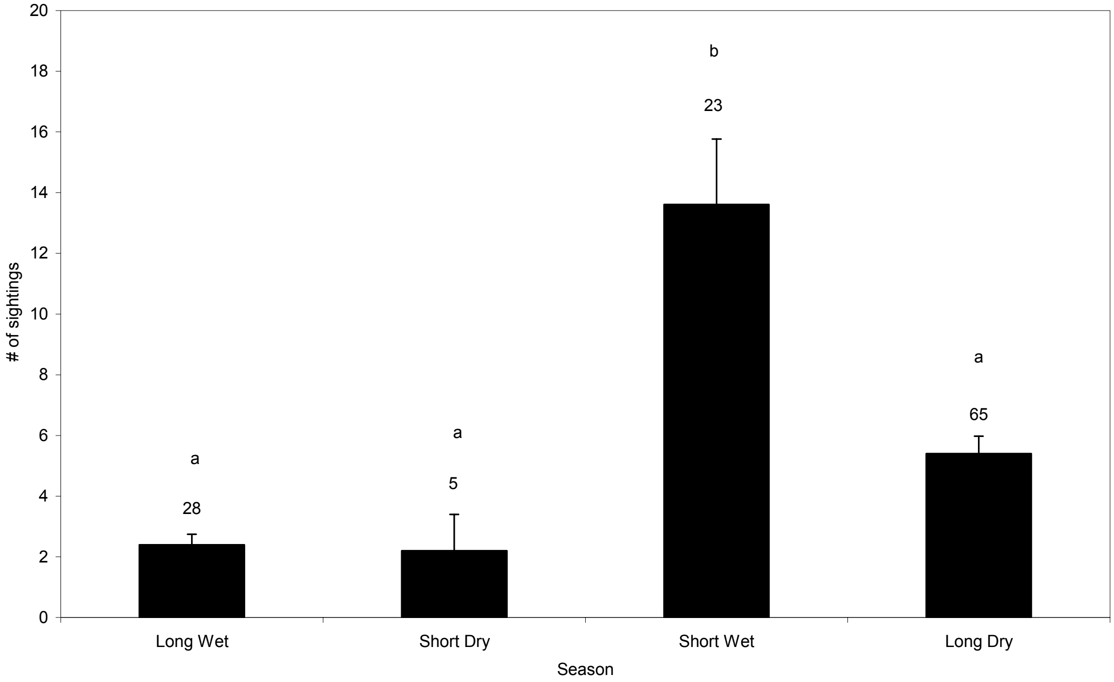

Figure F.1. The mean (+SE) number of elephant sightings at a waterhole per season: Long Wet = September - December, Short Dry = January - February, Short Wet = March -May and Long Dry = June - October; Ndarakwai Ranch (September 2004 - October 2005). The number of days elephants were sighted is shown in each bar. Different letters indicate significant differences between seasons. (1-way ANOVA $F_{3,117} = 18.07$, $P < 0.001$; Tukey HSD $P < 0.05$).

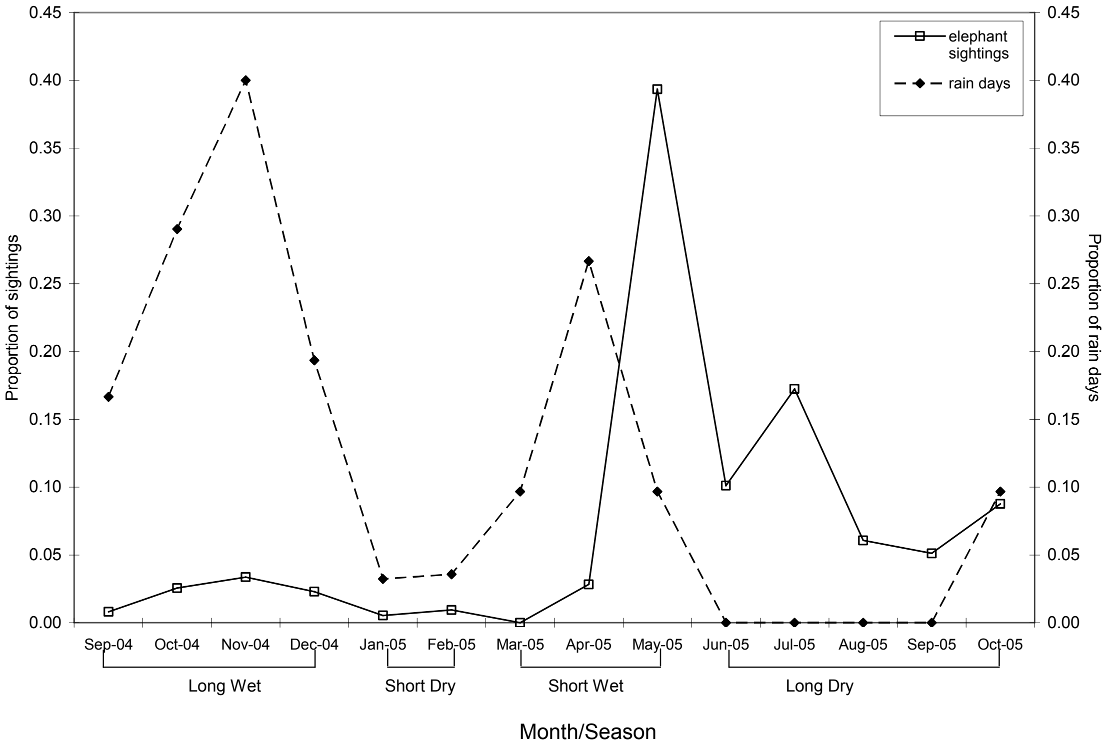

Figure F.2. The proportion of elephant sightings per month at a waterhole from September 2004 - October 2005 at Ndarakwai Ranch, Tanzania. Rainfall was recorded in 10% of the days for the months in the wet seasons. No elephants were sighted in March.

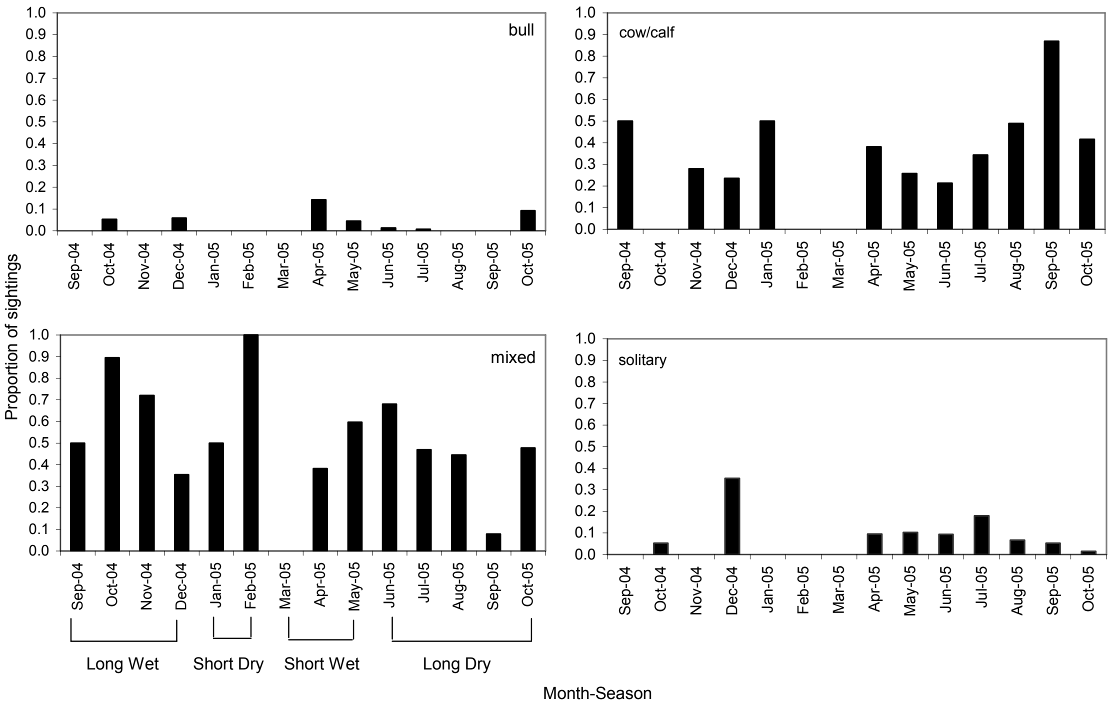

Figure F.3. The proportion of sightings of four elephant group types at a waterhole from September 2004 - October 2005 at Ndarakwai Ranch, Tanzania. Rainfall was recorded in 10% of the days for the months in the wet seasons. Proportions were calculated from the number of elephant sightings per month (Table F.3). No elephants were sighted in March 2005.

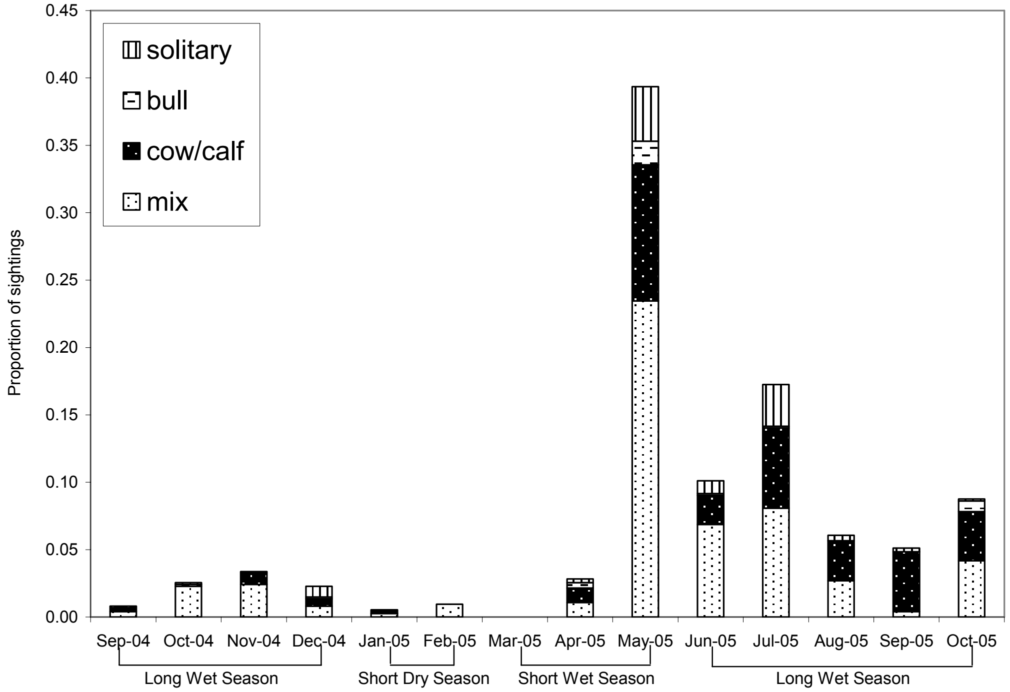

Figure F.4. The proportion of sightings of four elephant group types at a waterhole from September 2004 - October 2005 at Ndarakwai Ranch, Tanzania. Rainfall was recorded in 10% of the days for the months in the wet seasons. Proportions were calculated from the total number of elephant sightings (Table F.3). No elephants were sighted in March 2005.

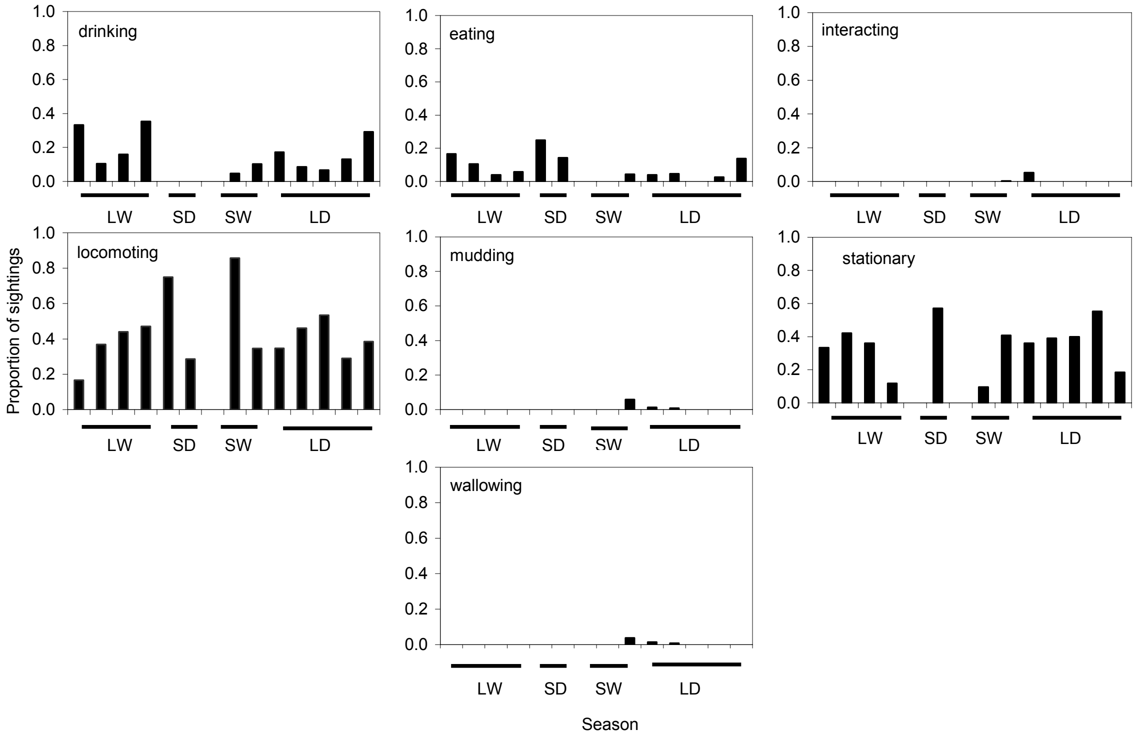

Figure F.5. The proportion of sighting seven state behaviors that elephants were observed performing at a waterhole, Ndarakwai Ranch (September 2004 - October 2005). LW = Long Wet season (September 2004 - December 2004), SD = Short Dry season (January 2005 - February 2005), SW = Short Wet season (March 2005 - May 2005), LD = Long Dry season (June 2005 - October 2005). Proportions were calculated from the total number of elephant sightings per month (Table F.4). No elephants were sighted in March.

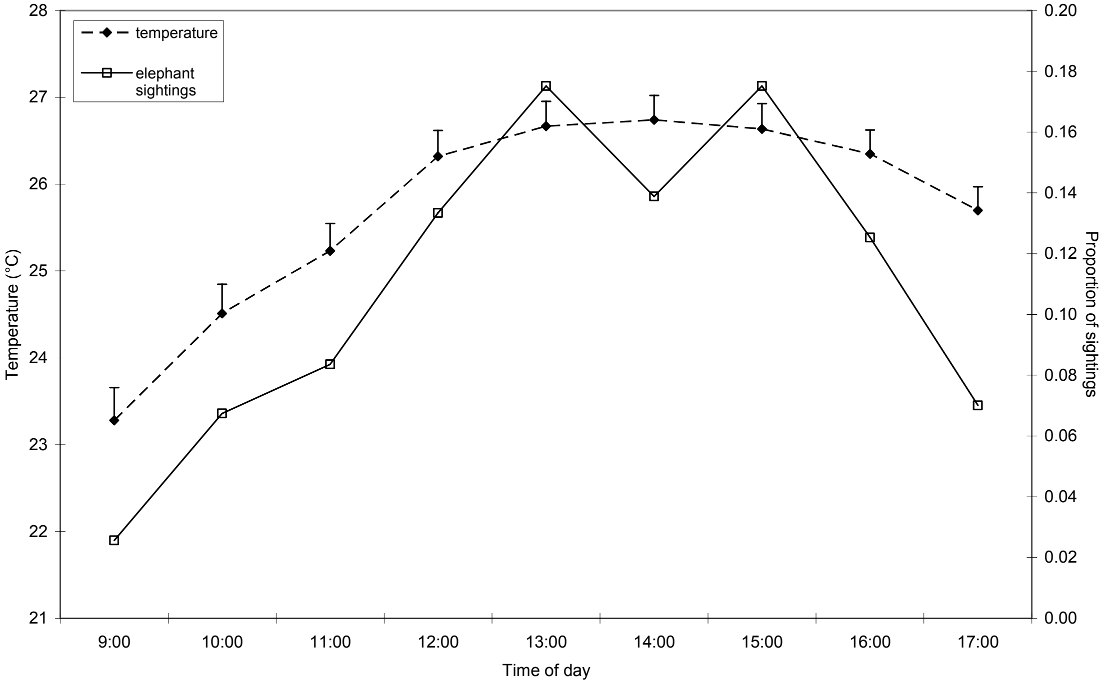

Figure F.6. The proportion of elephant sightings and the mean (+SE) temperature (°C) at a waterhole from 900h to 1700h, Ndarakwai Ranch (September 2004 - October 2005). The proportion of elephant sightings were strongly correlated with the temperature (Spearman rank correlation: $r_s = 0.91$, $N = 9$, $P < 0.001$).

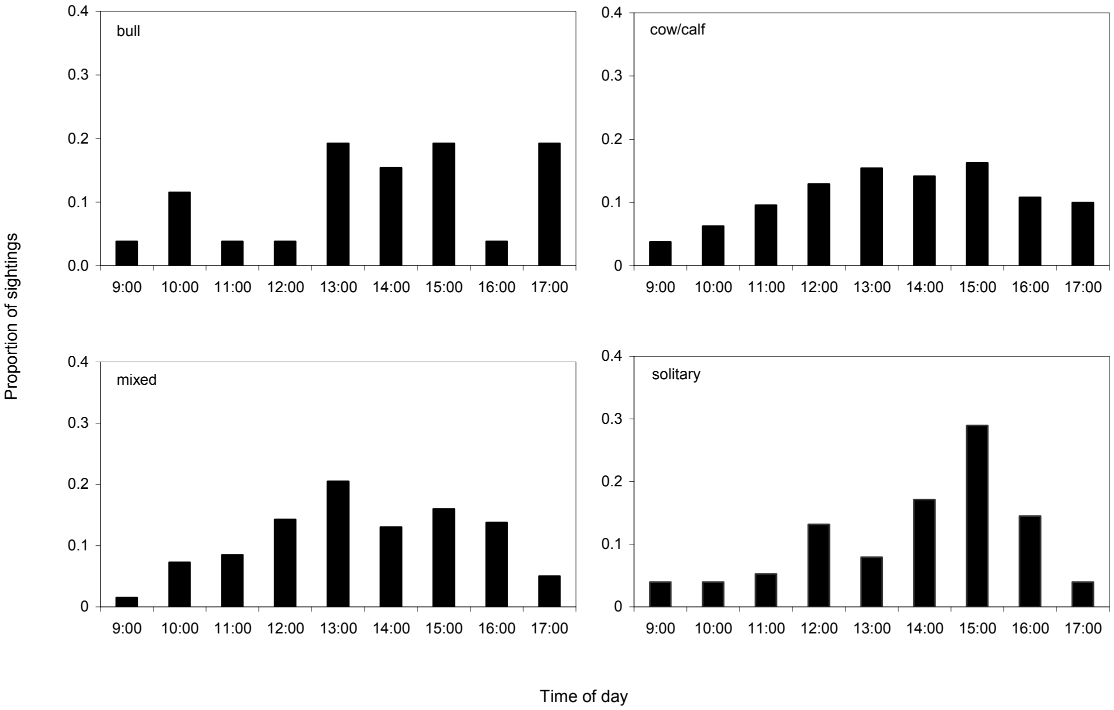

Figure F.7. The proportion of sightings of four elephant group types from 900h to 1700h at a waterhole from September 2004 - October 2005, Ndarakwai Ranch, Tanzania. Proportions were calculated from the total number of elephant sightings within each group type (Table F.5).

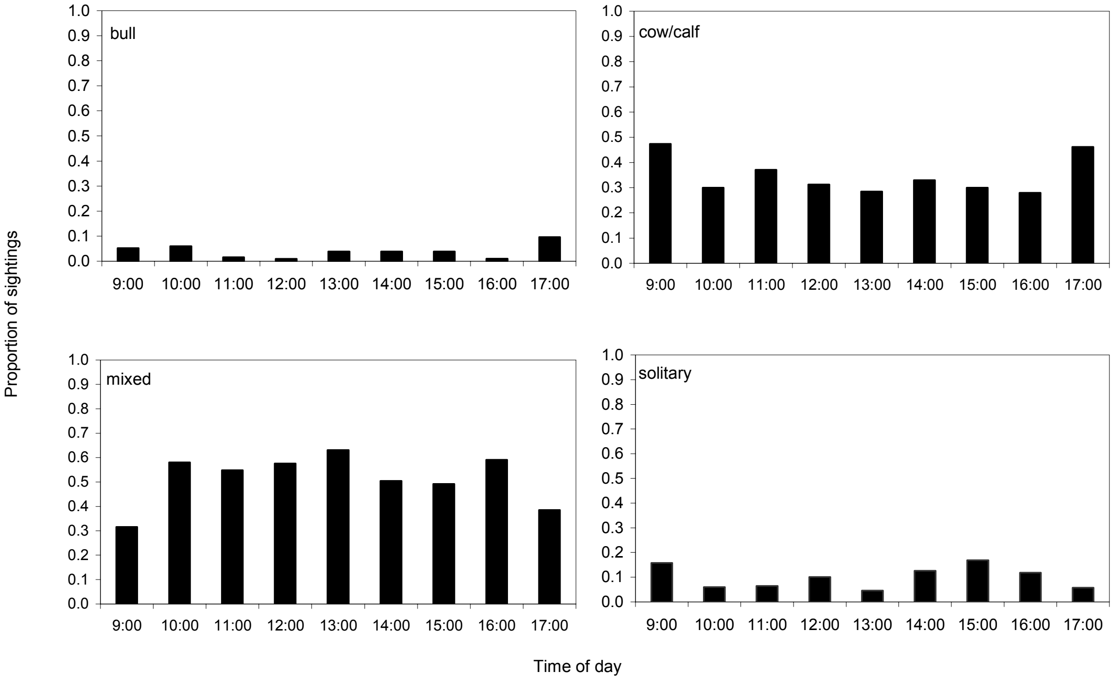

Figure F.8. The proportion of sightings of four elephant group types from 900h to 1700h at a waterhole from September 2004 - October 2005, Ndarakwai Ranch, Tanzania. Proportions were calculated from the total number of elephant sightings per hour (Table F.5).

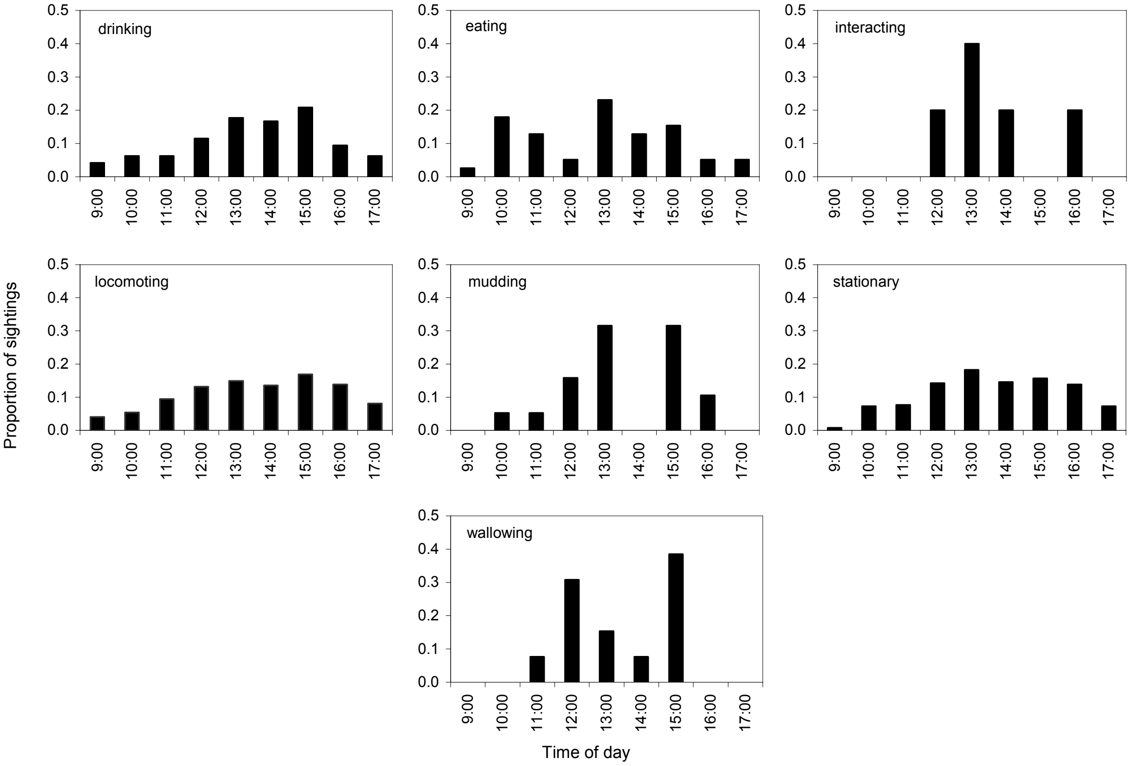

Figure F.9. The proportion of elephant sightings during which elephants were observed in seven state behaviors at a waterhole from 900h to 1700h, Ndarakwai Ranch (September 2004 - October 2005). Proportions were calculated from the total number of elephant sightings within each state behavior (Table F.6).

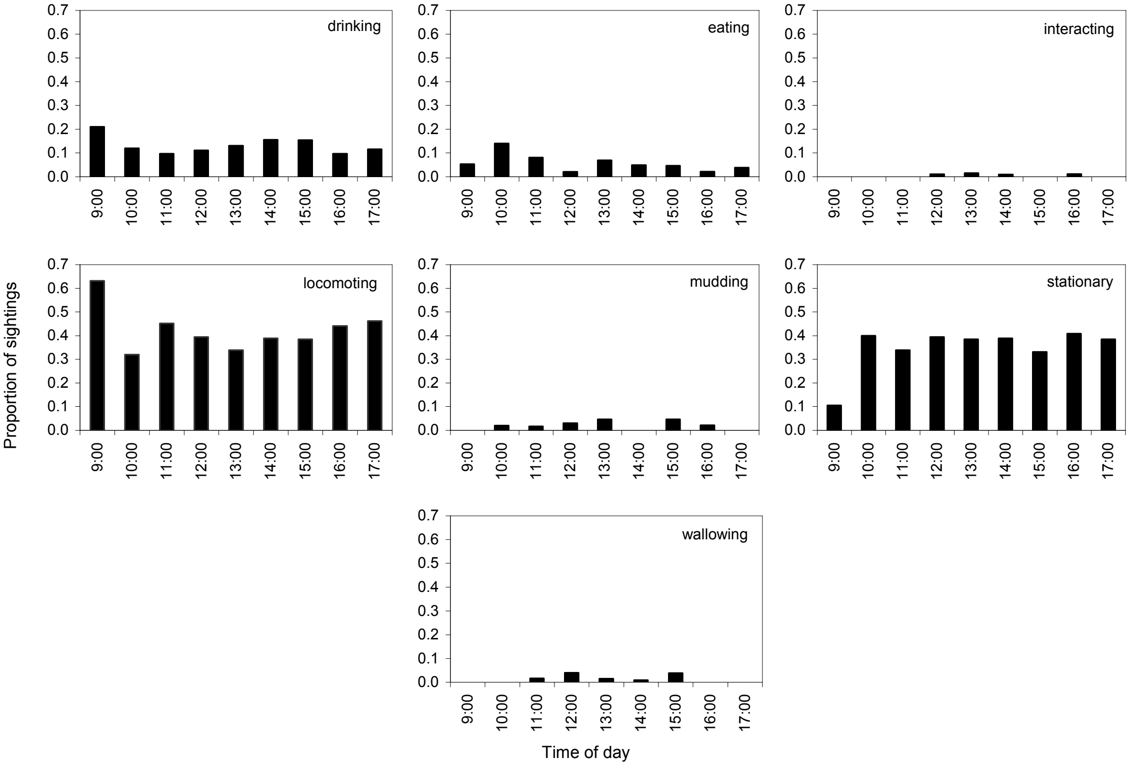

Figure F.10. The proportion of elephant sightings during which elephants were observed in seven state behaviors at a waterhole from 900h to 1700h, Ndarakwai Ranch (September 2004 - October 2005). Proportions were calculated from the total number of elephant sightings per hour (Table F.6).

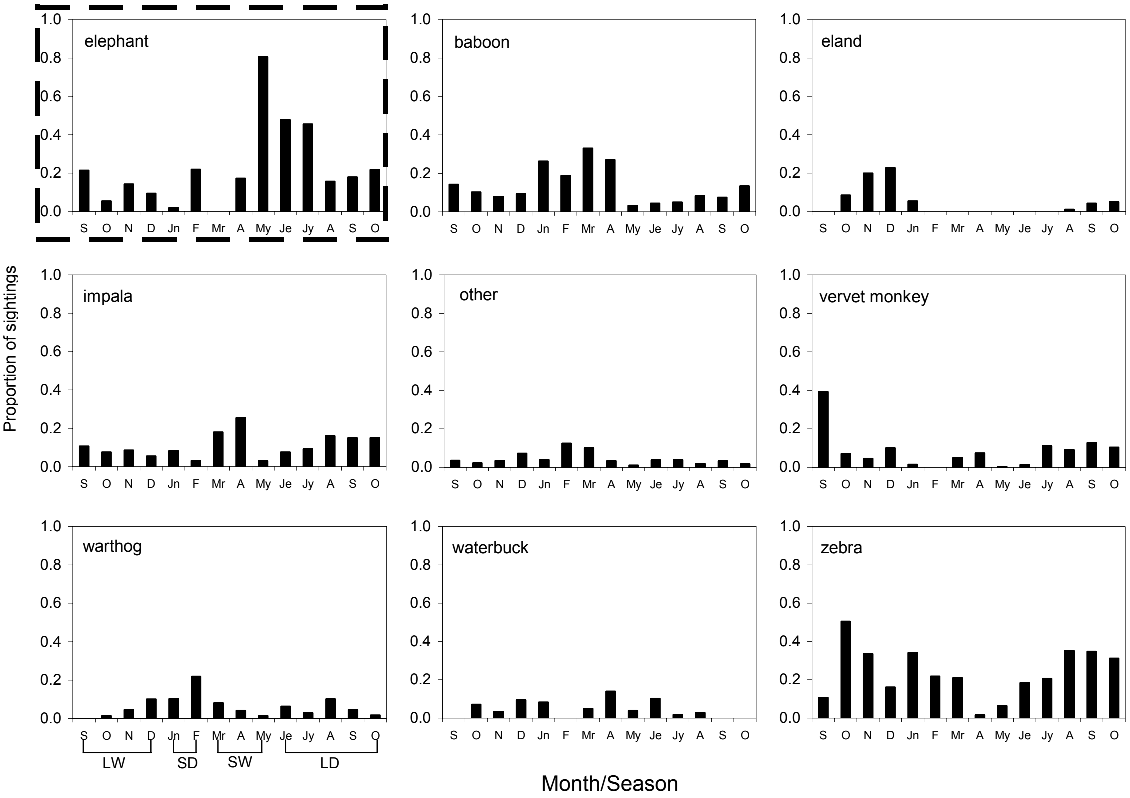

Figure F.11. The relative proportion of sighting various species of mammals at a waterhole per month, Ndarakwai Ranch (September 2004 - October 2005). Dikdiks, banded mongoose, wildebeests, giraffes, slender mongoose and blue monkeys were lumped into Other because of the low frequency of sighting these species. Proportions were calculated from the total number of mammal sightings per month. Dashed lines are used to facilitate comparisons between elephants and other mammal species.

S = September, O = October, N = November, D = December, Jn = January, F = February, Mr = March, A = April, My = May, Je = June, Jy = July, A = August.

LW = Long Wet season (September 2004 - December 2004), SD = Short Dry season (January 2005 - February 2005), SW = Short Wet season (March 2005 - May 2005), LD = Long Dry season (June 2005 - October 2005).

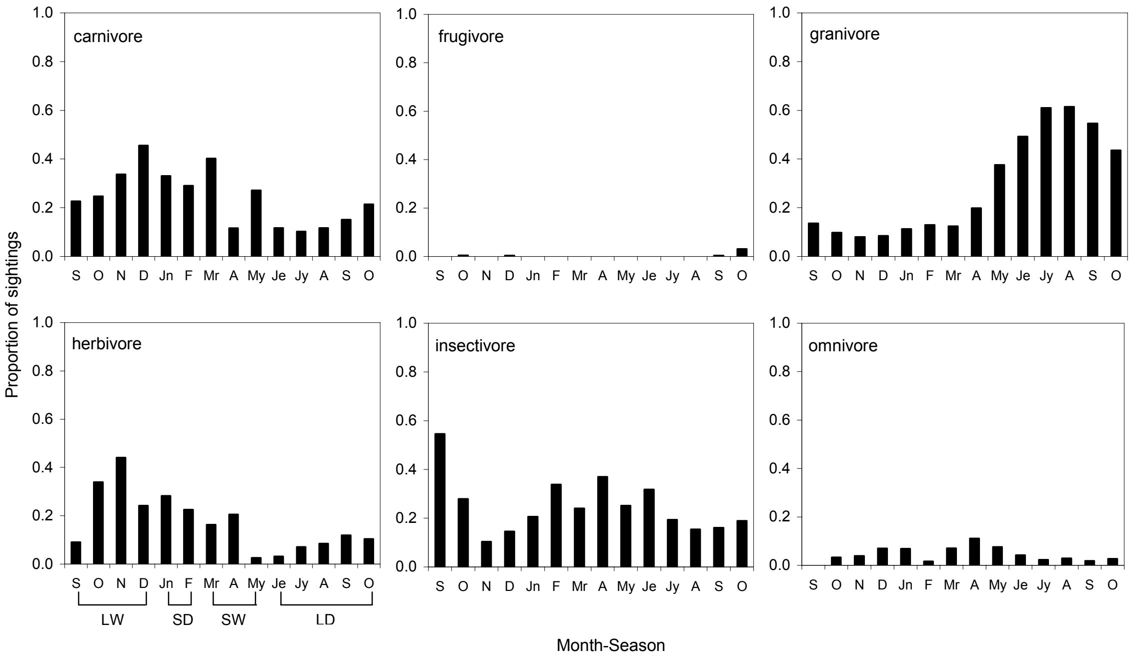

Figure F.12. The relative proportion of sighting various categories of birds, based on general diet, at a waterhole per month, Ndarakwai Ranch (September 2004 - October 2005). Proportions were calculated from the total number of bird sightings per month. S = September, O = October, N = November, D = December, Jn = January, F = February, Mr = March, A = April, My = May, Je = June, Jy = July, A = August. LW = Long Wet season (September 2004 - December 2004), SD = Short Dry season (January 2005 - February 2005), SW = Short Wet season (March 2005 - May 2005), LD = Long Dry season (June 2005 - October 2005).

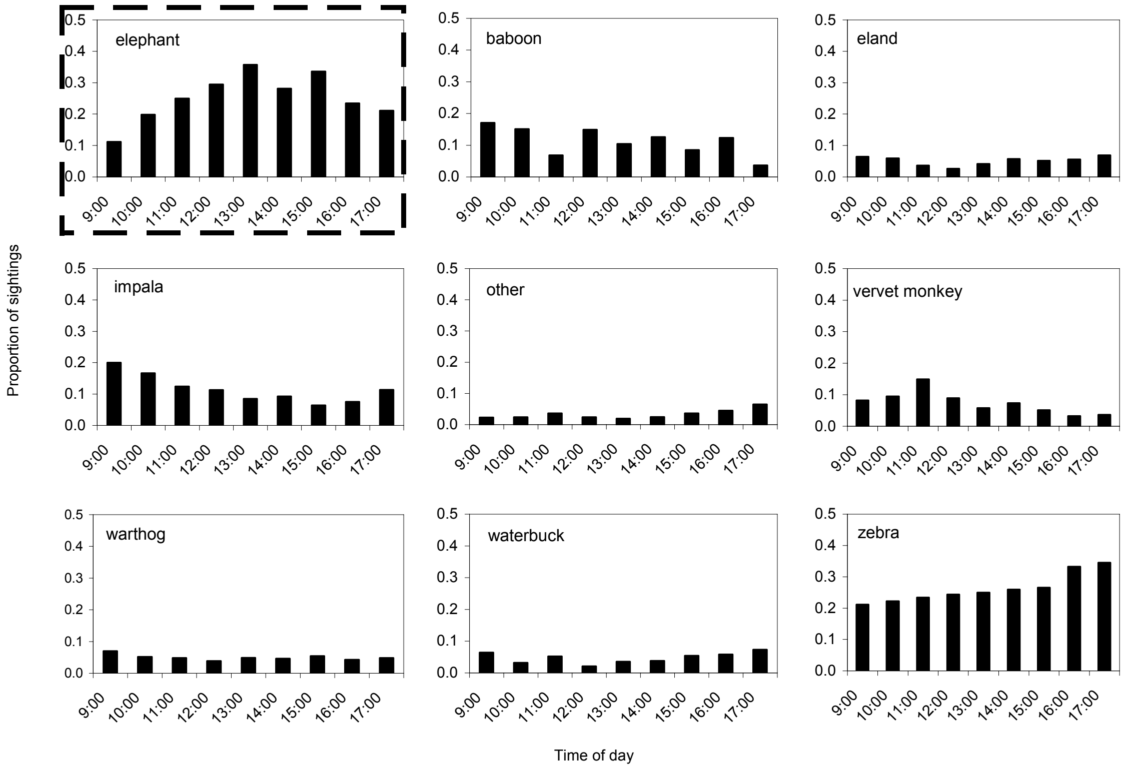

Figure F.13. The relative proportion of sighting various species of mammals at a waterhole from 900h-1700h, Ndarakwai Ranch (September 2004 - October 2005). Dik-diks, banded mongoose, wildebeests, giraffes, slender mongoose and blue monkeys were lumped into Other because of the low frequency of sighting these species. Proportions were calculated from the total number of mammal sightings per hour. Dashed lines are used to facilitate comparisons between elephants and other mammal species.

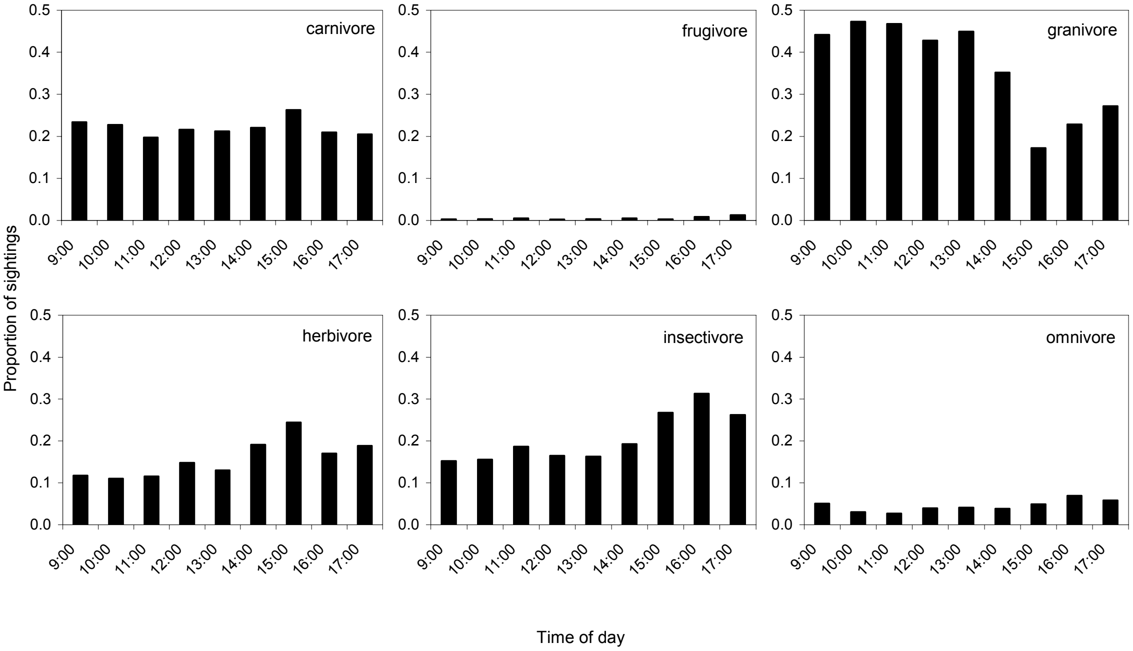

Figure F.14. The relative proportion of sighting various categories of birds, based on general diet, at a waterhole from 900h-1700h, Ndarakwai Ranch (September 2004 - October 2005). Proportions were calculated from the total number of bird sightings per hour.

REFERENCES FOR APPENDIX F

Cairns, S.J. & Schwager, S.J. 1987. A comparison of association indices. *Animal Behaviour*, **35**, 1454-1469.

Ginsberg, J.R. & Young, T.P. 1992. Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, **44**, 377-379.

APPENDIX G

SIMPLE RATIO

The Simple Ratio method (Cairns & Schwager 1987; Ginsberg & Young 1992) was used to derive co-occurrence indices. It involves dividing the number of sightings of species A and B together (x) by the difference between the total number of observation periods (N) and the number of observation periods when neither A nor B are observed (D):

$$\frac{x}{N - D}$$

Another method used to calculate co-occurrence for species A involved dividing the total number times species A was sighted with species B (x_a) by the number sightings for species A (N_a):

$$\frac{x_a}{N_a}$$

Unlike the Simple Ratio, the co-occurrence value for species A with species B will not equal the co-occurrence value for species B with species A if the number of sightings for the two species was different.

This study used the Simple Ratio because it was based on the number of times when both species were sighted at the waterhole out of the total number of observations. A co-occurrence value from the second method would be based on only the presence of one of the two species.

APPENDIX H

ELEPHANT COW/CALF GROUPS AND ADULT MALES

These tables show the names and the number of individuals and the age class composition in the different cow/calf groups of elephants and the names of the adult males seen at the waterhole at Ndarakwai Ranch, Tanzania, from September 2004 to June 2005. The number of individuals per group excludes adult males and is based on the mode of the number of individuals per sighting. The system of naming individual and elephant groups began as an arbitrary process that involved naming an elephant based on the date or time and the first letter of the month it was observed. This system proved inadequate and a new system was created that identified individuals based on Kiswahili nouns and adjectives. A recent modification of the latter method involves naming groups after specific Tanzanian tribal dialects, of which ca. 120 exist, and using words within a dialect to name individuals within the group.

Table H.1. Names and age class composition of cow/calf groups observed at Ndarakwai Ranch, (September 2004 -June 2005).

Group name*	# of elephants**	A-F	S-F	S-M	S-?	J-F	J-M	J -?	C-F	C-M	C-?
03S (Mbeya)	8	2	2	1		1	1		1		
105	9	3	1				2		3		
Baridi	7	1	2			1	1				2
Bila & 16A	14	4	2				1				4
Curly	12	3		1			1				
Daycare	9	3	1					1			4
Dent's	13	3	2				1				3
Duo	9	1								1	

Appendix H (cont.)

Group name*	# of elephants**	A-F	S-F	S-M	S-?	J-F	J-M	J -?	C-F	C-M	C-?
LongLefty (Kushoto)	5	1	1			1	1			1	
LongTusk	10	4		1				4			1
M Group	10	1	3				1		1		
MojaMrefu	5	2	1			1	1				
Moustache	7	2	1				2				2
Mrefu	10	3									
NchiniJuu	8	3					2			1	1
Nubby	9	3	1					3			2
Pie (Kipenyoo)	7	1	2					3			3
Pinda & MojaTu	13	3	2						2	1	
Rags (Rufiji)	6	1	1			1			1	1	1
Solo A-F (Iringa)	8	2	1			2	1				2
Tano	8	2	3								3
Upepo	9	4	1				1				3
Vunja	12	1									
Waka	8	2			2			1			3
Uvimbe	11	2	3					2			4
06A	2	1							1		
Swali	unknown	1									
Mwezi	unknown	1									
Matuta	unknown	1									
Total = 26	229	61	30	3	2	7	16	14	9	5	38

*Group names were based on numerous variables: name of the largest female, date and month seen (e.g. 06A = August 6) and Kiswahili words.
**Determined by the mode of the number of elephants seen per sighting.
? = sex of individual unknown.
C = calves (0-4yrs), J = juveniles (5-9yrs), S = subadults (10-19yrs), A = adults (>19yrs), M = males, F = females.

Table H.2. List of 44 adult males and their range of possible ages (years), Ndarakwai Ranch (September 2004 - June 2005). Names in bold are males that were focal animals.

Name*	Age (yrs)	Name	Age (yrs)	Name	Age (yrs)
01O	20-25	**03D**	25-40	**Baunsa**	40-60
05M	20-25	09A	25-40	**Kifaru**	40-60
06J	20-25	**12M**	25-40	Mkuki	40-60
06M	20-25	**Bukoba**	25-40		
11O	20-25	Dodoma	25-40		
17M	20-25	Kobe	25-40		
19O	20-25	Komanda	25-40		
22N	20-25	**Mafia**	25-40		
25A	20-25	**Muheza**	25-40		
28F	20-25	**Neupe**	25-40		
35N	20-25	Nusu	25-40		
44S	20-25	**Pua Nene**	25-40		
59D	20-25	Risasi	25-40		
94S	20-25	Rombo	25-40		
Bado Fupi	20-25	Tatu	25-40		
Camo	20-25				
Em	20-25				
Kisu	20-25				
Korof	20-25				
Meno Kulia	20-25				
Mskio	20-25				
Ruka	20-25				
Sinya	20-25				
Solo	20-25				
Sungura	20-25				
Tango	20-25				

*Group names were based numerous variables: name of the largest female, date and month seen (e.g. 06A = August 6) and Kiswahili words.

APPENDIX I

SUMMARY TABLES

Summary of the results of all dependent variables from Parts I and II.

Table I.1. Summary of chemosensory results from Part I, Ndarakwai Ranch (September 2004 - June 2005).

PART I - SEXUALLY DIMORPHIC DEVELOPMENTAL PATTERNS OF CHEMOSENSORY RESPONSES TO NATURALLY EXISTING STIMULI				
Chemosensory Responses				
		Significant result(s)		
Dependent variable	Hypothesis	Sexual dimorphism	Age class differences within sex	Figure & table reference(s)
Proportion of focal elephants that performed chemosensory responses to environmental stimuli	The changes in the social environment across age classes and the differential opportunities for reproduction between males and females lead to sex differences in the development of chemosensory behaviors	None	None	Fig. 5; Table 5, Ia-b
Proportion of focal elephants that performed chemosensory responses to stimuli of elephant origin	See above	Yes: Greater proportion of subadult and adult males than subadult and adult females	None	Fig. 5; Table 5, Ia-b
Rate of all chemosensory responses	See above	None, but males were close to having a higher rate than females	None	Fig. 6; Table 5, II

Appendix I (cont.)

Dependent variable	Hypothesis	Significant result(s)		Figure & table reference(s)
		Sexual dimorphism	Age class differences within sex	
Rate of sniff, check, place and flehmen (SCPF)	See above	Yes: Subadult males had a higher SCPF rate than that of females; SCPF rate of adult males was almost higher than that of females	None	Fig. 7; Table 5, VII-VIII
Rate of raised sniffs	See above	None	None	In text pg.33
Repertoire size	Repertoire size changes as elephants gained experience about their environment	Yes: Males had a larger repertoire size than females	None	Fig. 8
Repertoire composition	Repertoire composition changes as elephants gained experience about their environment	Yes: Sex differences in proportion of SCPF and raised sniff responses among subadults; only males performed flehmen	Yes: Juvenile males had a greater proportion of raised sniffs than did adults	Tables 6 & 7

Appendix I (cont.)

Table I.2. Summary of trunk tip touch results from Part I, Ndarakwai Ranch (September 2004 - June 2005).

PART I - SEXUALLY DIMORPHIC DEVELOPMENTAL PATTERNS OF CHEMOSENSORY RESPONSES TO NATURALLY EXISTING STIMULI				
Trunk Tip Touches				
		Significant result(s)		
Dependent variable	Hypothesis	Sexual dimorphism	Age class differences within sex	Figure & table reference(s)
Trunk tip touches to body regions	The changes in the social environment across age classes and the differential opportunities for reproduction between males and females lead to sex differences in the development of chemosensory behaviors	Not applicable[a]	Not applicable[a]	In text pg. 36
Trunk trip touches to conspecifics	See above	Not applicable[a]	Not applicable[a]	In text pg. 36

[a] Not enough data for statistical analyses.

Appendix I (cont.)

Table I.3. Summary of mean bout durations of state behaviors from Part I, Ndarakwai Ranch (September 2004 - June 2005).

PART I - SEXUALLY DIMORPHIC DEVELOPMENTAL PATTERNS OF CHEMOSENSORY RESPONSES TO NATURALLY EXISTING STIMULI				
State Behaviors				
		Significant result(s)		
Dependent variable	Hypothesis	Sexual dimorphism	Age class differences	Figure & table reference(s)
Drinking	The changes in the social environment across age classes and the differential opportunities for reproduction between males and females lead to sex differences in the performance of state behaviors	Yes: Females had longer drinking bouts	None	Table 3, I; Table 4, I
Walking	See above	None	Yes: Female calves had longer walking bouts	Table 3, III; Table 4, III
Mudding	See above	None	Yes: Duration of mudding bouts was lowest among calves	Fig. 4; Table 4, II
Wallowing	See above	None	Yes: Duration of wallowing bouts was greater among calves, juveniles and subadults than among adults.	Fig. 4; Table 4, IV
Standing	See above			Table 3
Water activities	Time spent performing water activities affects rate of chemosensory behaviors	None, but males came close to having a negative relationship	None	In text pg. 31

Appendix I (cont.)

Table I.4. Summary of chemosensory results from Part II, Ndarakwai Ranch (September 2004 – June 2005).

PART II - SEXUALLY DIMORPHIC DEVELOPMENTAL PATTERNS OF CHEMOSENSORY RESPONSES TO STANDARD STIMULI

Dependent variable	Hypothesis	Significant result(s)		Figure & table reference(s)
		Sexual Dimorphism	Age class differences within sex	
Proportion of elephants that came near samples	The changes in the social environment across age classes and the differential opportunities for reproduction between males and females lead to sex differences in the development of chemosensory behaviors	None	Yes: Greater proportion of adult males than calf and juvenile males	Fig. 9; Table 13, Ic & Ie
Proportion of elephants that did chemosensory responses to samples	See above	Yes: Greater proportion of adult males	Yes: Greater proportion of adult males than calf males	Fig. 10; Table, 14 Ic & IV
Rate of chemosensory	See above	None	Yes: Greater rate among adult males than calf males	Fig. 11; Table 15, I
Repertoire size	Repertoire size changes as elephants gained experience about their environment	None	None	Fig. 12; Table 15, VII-XII
Repertoire composition	Repertoire composition changes as elephants gained experience about their environment	None, but of focal animals only males were observed to perform flehmen	None	Table 16 & 17