Spring 2007

# Chemical Signaling and Resource Use by African Elephants (Loxodonta Africana)

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**Recommended Citation**

Napora, Erek Stephen, "Chemical Signaling and Resource Use by African Elephants (Loxodonta Africana)" (2007). *Electronic Theses and Dissertations*. 715.
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# CHEMICAL SIGNALING AND RESOURCE USE BY AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*)

by

EREK S. NAPORA

(Under the Direction of Bruce A. Schulte)

## ABSTRACT

In polygynous, sexually dimorphic species like the African elephant, *Loxodonta africana*, resource distribution influences female dispersion, while the location of females shapes male dispersion. Human constriction of viable habitat has affected elephant movements and impact. Elephants travel in matriarchal family groups, as single males or bachelor groups often looking for receptive females, and in mixed associations. Waterholes serve to meet the physical needs of elephants and as areas for information exchange, especially for males in search of females. When widely spaced, waterholes may be impacted heavily by elephants. I examined elephant use of a permanent waterhole to determine 1) the factors associated with elephant presence by group type, 2) behavioral differences between pre- and post-puberty male and female elephants, and 3) the impact of elephants on the woody vegetation at a privately owned protected area, Ndarakwai Ranch, Tanzania. Diurnal scans for elephants were conducted hourly from October 2004 – April 2006. Focal animal observations were made from June – October 2005. Elephant damage to woody vegetation was assessed from September 2005 – June 2006. In the long-wet season, elephant sightings were not correlated with the temperature. In the long-dry season, sightings of family and mixed groups were correlated with temperature, but male sightings were associated with female presence. Post-puberty male elephants first came to the waterhole after other groups and investigated their surroundings more than other elephants. Almost all woody vegetation surrounding the waterhole was impacted by elephants to varying degrees. The benefits resulting from permanent water sources must be weighed against the impact that elephants have on the habitat.

INDEX WORDS: Chemosensory, Woody Vegetation Damage, *Loxodonta africana*, Resource Use, Sexual Dimorphism, Tanzania, Waterhole

# CHEMICAL SIGNALING AND RESOURCE USE BY AFRICAN ELEPHANTS
# (*LOXODONTA AFRICANA*)

by

ERECK S. NAPORA

B.S., WARREN WILSON COLLEGE, 2003

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

MASTER OF SCIENCE

STATESBORO, GEORGIA

2007

# CHEMICAL SIGNALING AND RESOURCE USE BY AFRICAN ELEPHANTS
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EREK S. NAPORA

| | |
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Electronic Version Approved:
May 2007

# ACKNOWLEDGMENTS

First, I thank Dr. Bruce A. Schulte for all of his valuable input, support, and guidance; this study would not have been possible without him. I also express my appreciation for the input given by my committee members, Dr. Chandler and Dr. Leege. Thank you to all the faculty and graduate students at Georgia Southern University who assisted me throughout this process. Dr. Alan Harvey provided assistance when just the right program was needed.

Approval from the Tanzanian Wildlife Research Institute and the Commission for Science and Technology made this study possible. I would like to thank Peter and Margot Jones for allowing me access to Ndarakwai Ranch. The assistance and support of everyone at Ndarakwai Ranch were an important factor in the success of this project. Dhaval Vyas was invaluable in getting my research started. Thanks to Stacie Castelda for continuing the research. Many people assisted me in collecting data, Lance McBrayer, Julie Sergi, Matthew Groover, Meg Harper, and especially Megan Cadwallader. I also want to thank my family for all of their support throughout my research and writing process.

Funding for this project was provided by the National Science Foundation, Award No. IBN-0217062. The Georgia Southern University Academic Excellence Award also provided financial assistance. Vertebrate research was approved by the IACUC committee at Georgia Southern University No. I05015.

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# CHAPTER I

# CHEMICAL SIGNALING AND WATERHOLE USE BY THE SEXUALLY DIMORPHIC AFRICAN ELEPHANT (*LOXODONTA AFRICANA)*

## Abstract

African elephants, *Loxodonta africana*, are a polygynous, sexually dimorphic species. Females reside in close-knit family groups of related females. Male elephants seek out and compete for sexually receptive females, often traveling long distances alone or in bachelor groups. Mixed associations of one or more adult males with matriarchal groups are likely when a receptive female is located. Chemical signals are used by both sexes to indicate sexual state. Male elephants may search for females, or signs of their presence, in areas with a high probability of female use, while avoiding costly encounters with other males. Hence, male behavior may differ from females at waterholes because males are searching for signs of receptive females or male competitors. The purpose of this study was 1) to examine factors associated with elephant presence at a permanent waterhole according to elephant group type and 2) to compare waterhole use between pre-puberty and post-puberty male and female elephants. Sightings were conducted from 09-17:00 h, October 2004 – April 2006, at the only permanent waterhole within a 15 km radius at Ndarakwai Ranch in northern Tanzania. Focal animal observations were made from June – October, 2006. In the long-dry season, cow/calf and mixed groups presence was associated with ambient temperature, while male only sightings were associated with cow/calf groups. On days with multiple group type occurrences, male elephants arrived at the waterhole after both other groups. The proportion of post-puberty male elephants that performed chemosensory behaviors was greater than that of post-puberty females and pre-puberty elephants. These males also exhibited higher rates of chemosensory behaviors. Female presence was associated with environmental factors while male presence correlated with female location. The observed behavioral differences between the sexes reflect the different mating strategies within this sexually dimorphic species.

INDEX WORDS: Chemosensory, *Loxodonta africana*, Resource Use, Sexual Dimorphism, Tanzania, Waterhole

## Introduction

Communication is the transfer of information from a sender to a receiver (Wyatt 2003; Dugatkin 2004). Animals use various modes of communication, including visual, auditory, tactile, and chemical (Langbauer 2000; Rosenthal and Ryan 2000**;** Begg et al. 2003; Liebal et al. 2004). For terrestrial mammals, chemical signals provide several advantages over other modes of communication. Chemical signals can work in the dark, are energy efficient, do not require large amounts of material, and they can last for extended periods, transmitting information into the future (Müller-Schwarze 1999). As such, chemical signals can be an important source of information about the social world for many animals (Kappeler 1998; Johnston 2003; Park et al. 2004; Schulte et al. 2005).

One of the most common uses of chemical signaling is for mate selection (Kappeler 1998; Schulte and Rasmussen 1999; Park et al. 2004). Chemical signals that are used for intraspecific communication are termed pheromones (Karlson and Lüscher 1959; Wyatt 2003). Pheromones are usually tightly linked to an animal's physiological condition and can serve as reliable signals of physiological condition. As reliable signals, pheromones can be used to assess the suitability of a potential mate (Rich and Hurst 1998). Pheromones are an effective manner of mate assessment for animals in which the sexes are spatially segregated throughout much of the year, such as African elephants, *Loxodonta africana* (Poole 1996; Rasmussen and Schulte 1999).

African elephants are a polygynous, sexually dimorphic species. Females remain in their family group, a highly social environment, throughout their lives to raise offspring; whereas, males leave their natal herd around the onset of puberty, forming loose bonds with other males and searching for potential mates (Douglas-Hamilton and

Douglas-Hamilton 1975; Poole and Moss 1989; Poole 1994). These adult roles are reflected in developmental differences in behaviors prior to puberty (around 10 years of age) in both females and males when in the same natal environment (Lee 1986; Meyer 2006). By the onset of puberty, adult roles have emerged and dimorphic behaviors are observed between the sexes (Sukumar 2003; Merte 2006; Vyas 2006).

Among sexually dimorphic, polygynous species, females are typically the sole providers of parental care, as seen in the African elephant (Clutton-Brock et al. 1982; Lee and Moss 1986). Female African elephants become sexually active around 10-13 years old and remain in their natal group throughout their lives (Moss 2001). Female elephants have a relatively short fertile period (2-6 days) within a long estrous cycle (16-18 weeks) (Moss 1983). They also have a long inter-birth period and may be in estrus only once every 3-5 years (Moss 1983; Moss 2001). The average female has four offspring over the course of her lifetime (Moss 2001). Because of the high parental investment, long inter-birth period, and low average lifetime reproductive output, female success is highly dependent on the successful rearing of each offspring.

In polygynous species, male reproductive success can be highly variable, depending on the ability of a male to access sexually receptive females (Clutton-Brock et al. 1983; Pellegrini 2004). Male African elephants begin to disperse from the natal group at the onset of puberty (Lee and Moss 1999). At this point, they are physically capable of reproducing but are generally not successful until they are around 25 years old because of intrasexual competition and female choice (Moss 1983; Poole 1987, 1989a, b; Hollister-Smith 2005). To obtain access to a receptive female, adult males must be able to find her at the appropriate time and to compete successfully for her.

Asian (*Elephas maximus*) and African elephants use pheromones to communicate their sexual state. Elephant females have two distinct phases in their reproductive cycle, a follicular (approaching ovulation) and a luteal (post-ovulation) phase. The main chemosensory behaviors that elephants used with regards to sexual pheromones are sniff, check, place, and flehmen (Schulte and Rasmussen 1999). The performance of these behaviors, particularly check, place, and flehmen is an indication of interest towards a signal (Hollister-Smith 2005, Bagley et al. 2006). By using these chemosensory investigations, adult male elephants are able to discern between follicular phase and luteal phase signals from conspecific female elephant urine, but do so using different urinary signals (Rasmussen et al. 1996; Bagley et al. 2006). Using different urinary cues than male Asian elephants, females are able to distinguish follicular and luteal phases of other females, but their ability depends on the sexual state of the receiver (Slade et al. 2003). Female African elephants were unable to discern between follicular and luteal phases from unfamiliar conspecific female elephant urine (Meyer 2006). However, female African elephants may be using genital secretions to intrasexually signal their reproductive state (Meyer 2006).

Male elephants also use chemical signaling to communicate their physiological and reproductive state. Adult males annually enter a period of musth, a rut like state characterized by heightened aggression towards other males, high levels of association with females, roving behavior and extended periods of urine dribbling and temporal gland secretions (Poole 1987; Stokke and du Toit 2002). Non-musth male elephants may range widely to avoid contact with musth bulls (Stokke and du Toit 2002) and younger males can detect and avoid musth bulls and their secretions (Poole 1989a; Rasmussen and

Krishnamurthy 2000). Asian female elephants show heightened levels of chemosensory behaviors towards urine of a male in musth as opposed to non-musth (Schulte and Rasmussen 1999). Among African elephants, reproductively successful males were ten times more likely to be in musth than non-musth (Hollister-Smith 2005). However, non-musth bulls are able to successfully reproduce at a low frequency (Hollister-Smith 2005). The ability to communicate with chemical signals in Asian and African elephants is widespread within and between the sexes with the signal relevance depending on the identity and physiological state of the sender and the receiver.

In order for male and female elephants to communicate their physiological state, they must be able to transmit that information to the appropriate receiver. Elephants use infrasonic vocalizations and chemical signaling for long-distance communication (Poole and Moss 1989; Rasmussen and Schulte 1998; Langbauer 2000). Each mode has its benefits and limitations. Vocalizations, especially infrasonic ones, can travel long distances in a short duration and evoke immediate responses; however, they are ephemeral unless energy is invested in regular output. Chemical signals may be relatively inexpensive energetically and long-lasting, but they are degraded by sun and washed away by precipitation. Their localized distribution also may make detection challenging. A means to increase the likelihood of signal reception may be to visit areas with a high probability of encountering conspecifics and their chemical signals in the form of excretions and secretions.

Waterholes, especially in rainfall-limited areas, provide a common gathering area for many small and large mammals and as such, urine and feces are often present in abundance (Weir and Davison 1965; Ayeni 1975a, b; Ritter and Bednekoff 1995).

African elephants visit waterholes and have frequently been observed investigating potential signal sources such as conspecifics, urine and feces (Loizi 2004; Bagley 2004; Schulte et al. 2005; Merte 2006; Meyer 2006; Vyas 2006). Elephant dispersion, and thus the likelihood of encountering members of the opposite sex, is influenced by the availability of water (Stokke and du Toit 2002). Many parts of African elephant's range experience distinct seasons, typified by the occurrence of rainfall. In wet seasons, when rainfall is abundant and nutritious grasses are plentiful, elephants of all group types were found from 4-7 km from permanent water (Stokke and du Toit 2002). However, in dry seasons, as rainfall is scarce and forage becomes less palatable, female family groups and mixed elephant groups (female groups with adult male present) were found in proximity to permanent water (< 4 km) (Stokke and du Toit 2002). Male elephants that were not with female groups were found significantly farther from permanent water than the other two groups (10 – 12 km) (Stokke and du Toit 2002).

The differences in elephant presence near permanent water may be related to the needs of each group type. In general, smaller individuals require less total water than larger individuals, but they experience higher rates of water loss and are more susceptible to temperature extremes (Peters 1983). For elephants, female groups include calves and juveniles, potentially restricting group movement when temperatures are high and water sources are widely separated. Male elephants require a greater total amount of water, but they are less vulnerable to temperature extremes and have lower rates of water loss than smaller individuals (Peters 1983). Male elephants are less susceptible to environmental pressures, but are dependent on locating and competing for access to reproductively viable females. Permanent water sources, such as some waterholes, may provide an ideal location for male elephants to contact female elephants or their signals and to proclaim their own sexual state.

This study quantified waterhole use by pre- and post-puberty male and female elephants. The first objective was to determine if there were temporal differences in waterhole use between post-puberty males and females. Specifically, I examined whether post-puberty male elephants visited the waterhole to a greater extent when post-puberty females (in the forms of cow/calf groups and mixed associations of female groups and adult males) were present or when fresh signals had been deposited. I predicted that post-puberty male African elephants would use the waterhole as a potential information point and would visit the waterhole at times with at times when female or mixed groups were present or after these groups would be likely to visit. The second objective was to assess sex and age class differences in behavior at the waterhole. I predicted that males and females of both age categories (pre- and post-puberty) would use the waterhole similarly to meet their physiological needs, e.g., drinking and mudding. I also predicted that post-puberty males would perform higher rates of chemosensory behaviors than females at the waterhole. Males use chemosensory behaviors to gather information about the presence of conspecifics and their sexual state. Females also use chemosensory behaviors and may benefit from being able to detect the sexual state of others, but they do not need to search out familiar conspecifics. Females are generally in close proximity to other females in their family group and post-puberty males will search and find them.

## Methods

### Study site

This study was conducted at Ndarakwai Ranch, a part of the Kilimanjaro Conservancy, in northern Tanzania. Ndarakwai Ranch is a 4300 ha protected area, privately owned by Peter and Margo Jones. Prior to 1964, German and English colonists used the area for agriculture and cattle grazing (P. Jones pers. comm.). After Tanzanian Independence, Tanzania Breweries bought Ndarakwai and continued sporadic agriculture and cattle grazing. In 1995, the Jones leased Ndarakwai for 99 years, using it as a camp for photographic tourism. Ndarakwai is guarded from poachers and inappropriate land use by a staff of 15 rangers.

Ndarakwai is in proximity to Kilimanjaro and Arusha National Parks in Tanzania and Amboseli National Park in Kenya (Figure 1.1). This area typically experiences short (November and December) and long (March – May) wet seasons separated by dry periods (Moss 2001). Ndarakwai is bordered on two sides by the Ngare Nairobi River, which is dry for most of the year. Other water sources at Ndarakwai are several small water furrows that ultimately end at a manmade and maintained 4000 $m^2$ waterhole. This waterhole is the only permanent water source available for wildlife within a 15 km radius and is an important resource for animals in the area (R. Kosianga, Ndarakwai Ranch manager, pers. comm.). At least 26 different cow/calf groups made up of 229 elephants and 39 males $\geq$ 20 years old were sighted at the waterhole.

## Temporal waterhole use

All observations were made using a pair of Konica Minolta 8 x 42 binoculars at the manmade waterhole. Elephants were habituated to human presence at the observation tower as long as observers maintained a low profile.

Data for elephant temporal use were collected from October 2004-April 2006. These data were collected by Dhaval Vyas (previous MSc. researcher) from October 2004-June 2005 and by Erek Napora from July 2005-April 2006. (Inter-observer reliability was found to be 95-100%). Hourly scans of elephants in proximity (0-300 meters) to the waterhole were conducted for 5 minutes at the start of the hour from 09:00 until 17:00 hrs. These scans covered 75% of potential daylight hours available. By observing most of the daylight and all afternoon hours, we hoped to observe the greatest number of elephants, as this is when temperatures are the highest. Each hour, the number of elephants, their location at the waterhole, and the group composition (cow/calf, male only, and mixed) were recorded. Cow/calf groups were comprised of post-pubescent female(s) and her/their offspring. Male groups consisted of post-puberty males only, either solitary or in groups. Mixed groups were cow/calf groups with at least one post-puberty male $\geq$ 20 years old present.

The 19-month sampling period was divided into four seasons based on the occurrence of rain. Months with rainfall on more than 10% of days were classified as wet. The four seasons were short-wet (September – December 2004, November – December 2005), short-dry (January – February 2004, 2005), long-wet (March – May 2005, March – April 2006), and long-dry (June – October 2005). The seasonal classification in this study is similar to that used by researchers at Amboseli National

Park (Moss 2001). The only difference between this classification and the Amboseli classification is the slightly longer short-wet season in 2004 and the shorter long-wet season in 2006 (this is because the study ended in April 2006).

**Behavioral observations**

From July – October 2005 during the long-dry season, I conducted focal animal observations (Martin and Bateson 1993) of elephants at the waterhole. I randomly selected females and males in two age classes, pre-puberty (0-9 years) and post-puberty (10+ years), and then chose a focal animal haphazardly without replacement. Animals were aged and sexed based on morphological traits, such as body size, shoulder height, and tusk length and wear (Moss 1996). The average focal duration was 15.3 ± 0.4 minutes (Table 1.1), and the duration of focal observations did not differ by age class or sex (age class: $H_{1,97} = 0.167$, $p > 0.05$; sex: $H_{1,97:} = 1.77$, $p > 0.05$).

All observed behaviors were categorized as either state or event behaviors (Martin and Bateson 1993). State behaviors were behaviors that had a measurable duration (≥5 sec) and event behaviors were instantaneous or nearly so (<5 sec). Mudding and wallowing behaviors were combined into mudding/wallowing as a behavior that indicates the application of mud to the body. The event behaviors were categorized as chemosensory behaviors, where the focal elephant's trunk performed any chemosensory behavior (Table 1.2).

**Data analysis**

For the long-wet and the long-dry seasons, Pearson's Product-Moment correlations were used to examine the association between the proportion of sightings for each group type over the course of the day and the correlation between the proportion of sightings for each group type and the mean temperature at each sighting. In both seasons, all proportions and mean temperatures were normally distributed. On days with multiple group types present, a matched pairs comparison of the time of first arrival and the mean time of arrival was made. Descriptive statistics are presented as overall percentages or as mean ± standard error.

For data that did not meet assumptions of normality, I transformed the data and if this was unsuccessful in achieving normality, then I performed non-parametric analyses. Non-parametric two-way analysis of variance was conducted on the average ranks of proportion data (Sokal and Rohlf 1995). The rate of chemosensory behaviors was not normally distributed. I log-transformed the mean rate of chemosensory behaviors and the assumptions of normality and equal variance were met. I then performed a two-way ANOVA to test the effect of age and sex. The influence of age class, sex, and response (if they performed the behavior or not) on the proportion of individuals performing chemosensory behaviors were examined with a 3-way contingency table. If a significant interaction between all three factors was encountered, I made separate 2-way tests of independence between sex and response for each age category (Sokal and Rohlf 1995). JMP IN 4.0.4 (SAS Institute 2000) for Windows operating systems was used for all statistical analyses, except for 3-way contingency analysis. Three-way contingency analysis was made using a Microsoft excel program following the formula from Sokal and Rohlf (1995), created by Dr. A. Harvey.

## Results

### Seasonal distribution of elephant scans

Elephant presence at the waterhole varied seasonally. Of scans with elephants present, more elephants were observed in the long-wet season, 29.5 ± 2.5 per scan, compared to the long-dry season, 16.2 ± 1.0 per scan; however, elephants were observed in a greater percentage of scans during the long-dry season. Twenty-six percent of all scans in the long-dry season (n = 665) had elephants present, significantly greater than the 15% of scans with elephants in the long-wet season (n = 639), which was greater than percentage of scans in the short-wet (n = 663) and short-dry seasons (n = 391), 7% and 4% respectively (Table 1.3). Of the 334 scans where elephants were observed, over 80% took place in long-dry and long-wet seasons (Table 1.4).

### Distribution of elephant sightings within long-wet and long dry seasons

Multiple elephant groups were often sighted during the same scan, of these elephant group sightings, 88% occurred in the long-wet and long-dry seasons. Among all sightings in the long-wet and long-dry seasons (n = 669), 34% were of cow/calf groups, 52% were of mixed groups, and 14% were of male groups. During long-wet season, the arrival of elephants at the waterhole was greatest in the early afternoon hours (Figure 1.2a), while during the long-dry season, arrival times shifted to later in the afternoon (Figure 1.2b). In the long wet season, the proportion of male sightings at each hourly period was significantly correlated with the proportion of cow/calf sightings ($N = 9$, $r = 0.90$, $p < 0.01$) and the proportion of mixed sightings ($N = 9$, $r = 0.72$, $p = 0.03$). The proportion of cow/calf sightings and mixed sightings had the same pattern of association, but the correlation was not significant ($N = 9$, $r = 0.65$, $p = 0.06$). In the long-dry season, the proportion of cow/calf sightings across the day was significantly correlated with the proportion of male sightings ($N = 9$, $r = 0.69$, $p = 0.04$) and mixed sightings ($N = 9$, $r =$

0.80, p = 0.01). The proportion of male sightings and mixed sightings over the course of the day were not significantly correlated (N = 9, r = 0.58, p = 0.10).

In the long-wet season, the mean temperature during sightings of cow/calf, male, or mixed groups was not associated with the proportions of sightings of each group type (cow/calf: N = 9, r = 0.47, p = 0.20; mixed: N = 9, r = 0.38, p = 0.32; male: N = 9, r = 0.14, p = 0.71) (Figure 1.3a-c). In the long-dry season, both group types with females and calves, cow/calf and mixed groups, showed significant associations with the proportion of sightings at the waterhole and the mean temperature (cow/calf: N = 9, r = 0.77, p = 0.01; mixed: N = 9, r = 0.74, p = 0.02) (Figure 1.4a, b). The mean temperature at sightings for male groups was not associated with the proportion of the sightings of males (N = 9, r = -0.43, p = 0.43) (Figure 1.4c).

### Days with multiple group types observed

Multiple groups of elephants were sighted in 48% of the 334 scans with elephants. On days when multiple group types were sighted, the first male groups were sighted over 1 hour later in the day than the first cow/calf or mixed groups. On days with male groups and cow/calf groups, the mean time of sighting the first male group was 13:41 ± 00:21 hrs, 1 hour after the mean time of sighting the first cow/calf group at 12:37 ± 00:21 hrs (Table 1.5, a). On days with male groups and mixed groups, the mean time of sighting the first male group was 13:36 ± 00:22 hrs, significantly later than the mean time of sighting the first mixed group at 12:19 ± 00:22 (Table 1.5, b). The mean time of sighting the first cow/calf group and the first mixed group was only minutes apart and not significantly different (Table 1.5, c).

## State behaviors

The four most common behaviors (drinking, mudding/wallowing, standing, and walking) accounted for over 90% of mean observation time for both age classes and sexes (Table 1.6). Post-puberty males spent 23 ± 4% of observation time mudding/wallowing, greater than all other age and sex classes ($H_{1,97} = 4.31$, $p < 0.05$) (Table 1.6). Pre-puberty females and males and post-puberty females spent similar proportions of time drinking (0.39 ± 0.04, 0.36 ± 0.04, and 0.34 ± 0.04 respectively) compared to post-puberty males (0.24 ± 0.05), but the proportion of time drinking did not significantly differ by age class or sex (age class: $H_{1,97} = 3.54$, $p > 0.05$; sex $H_{1,97} = 2.01$ $p > 0.05$).

The four major state behaviors can be categorized as behaviors where the trunk was not able to investigate (drinking and mudding/wallowing) and behaviors where the trunk was able to investigate (walking and standing) the surroundings. The mean proportion of observation time in state behaviors in which the trunk was available to investigate its environment showed no significant differences between age or sex (age class: $H_{1,97} = 0.27$, $p > 0.05$; sex: $H_{1,97} = 1.41$ $p > 0.05$) (Figure 1.5). Hence, any differences in chemosensory behaviors by age class or sex cannot be explained by the time available to perform these behaviors.

## Chemosensory events

A total of 208 chemosensory events were observed being performed by 49 different elephants (Figure 1.6). The performance of chemosensory behaviors depended on the age and sex of individuals. Among post-puberty elephants, males had much higher mean rates of chemosensory behaviors than females, while pre-puberty elephants showed no sex difference ($F_{1,45} = 7.94$ $p < 0.01$) (Figure 1.7).

In examining the proportion of individuals in each age class and sex that performed the sniff behavior and the proportion of individuals in each age class and sex that performed check, place, or flehmen (CPF), a significant interaction was evident between age class, sex, and response (Table 1.7a, b). For the sniff behavior and CPF, the proportion of pre-puberty elephants performing the behaviors was similar between the sexes (sniff: females = 6/25, males = 4/24; CPF: females = 5/25, males = 5/24) (Table 1.7c, d). The proportion of post-puberty male elephants that performed the sniff behavior and CPF was significantly greater than the proportion of post-puberty female elephants (sniff: females = 3/34, males = 13/18; CPF: females = 2/34, males = 13/18 (Table 1.7e, f). For raised sniffs, a significant interaction between age class, sex, and response was not found (Table 1.7g). However, within age class the proportion of males and females that performed raised sniffs differed significantly (Table 1.7h). Pre-puberty elephants showed no difference between the sexes (females = 9/25, males = 9/24), while a greater proportion of post-puberty males than post-puberty females performed raised sniffs (females = 8/34, males = 11/18) (Table 1.7i, j).

## Discussion

African elephants displayed distinct seasonal differences in their occurrence at the only permanent waterhole at Ndarakwai Ranch. Over 88% of elephant sightings occurred in the long-wet and long-dry seasons. Of these sightings, 86% were of groups with post-puberty females and their offspring (cow/calf and mixed) and 14% were of male groups. Within the long-wet and long-dry seasons, post-puberty male groups and groups with female elephants differed in their occurrence at the waterhole and in factors associated with their occurrence. In each season, the proportion of elephant sightings over the course of the day varied in their association with other group types and with the temperature at sightings. These differences in association reflect the physiological and reproductive differences that group members in each group type exhibit.

In the long-wet season, the proportion of male group sightings from 09-1700 hrs was correlated with both cow/calf and mixed groups. During wet seasons, as grasses grow in increasing quality and quantity, elephants aggregate and group size increases, possibly facilitating inter-group communication (Moss and Poole 1983). Male elephants are often found associating with these large female aggregations, as large female aggregations ease the task of mate assessment for males. Competition between males for access to females is typically only during mid-estrus (Poole 1989) and within large female aggregations there may be several females in estrus, reducing competition over a single female. As might be expected based on the abundant resources, particularly water, elephant sightings at the Ndarakwai waterhole were not significantly associated with temperature.

In contrast, during the long-dry season the proportion of both cow/calf and mixed group sightings were positively correlated with temperature. The quality and quantity of forage declines during dry seasons, and elephants are more widely dispersed according to group type (Moss and Poole 1983; Owen-Smith 1988; Sukumar 2003; Osborn 2004). Stokke and du Toit (2002) showed that cow/calf and mixed groups were found close to permanent water, while males ranged farther from water sources. The difference between the association of temperature and occurrence at a waterhole by group type may be related to the presence of younger individuals.

Smaller individuals experience a higher rate of water loss than larger individuals and are more susceptible to temperature extremes (Peters 1983). Because of the needs of the smaller individuals within their groups, cow/calf and mixed groups are limited in the distance that they can travel from water and by the frequency with which they need to come to the waterhole (Stokke and du Toit 2002; Conybeare 2004). Therefore, cow/calf and mixed groups occurrence at water sources may be associated with ambient temperature as shown in the current study. However, temperature can be expected to have less of an influence on male groups because of their lower rate of water turnover and lower vulnerability to thermal stress from extreme temperatures (Peters 1983). The current study showed no association between the proportion of male sightings and temperature, supporting this prediction.

In the long-dry season, the proportion of male group sightings was not correlated with the temperature, but was associated with the proportion of cow/calf sightings. In many species where males do not provide parental care, male dispersion depends on the location of females (Krebs and Davies 1993). In African elephants, male dispersion is influenced by female location (Poole and Moss 1989) and by the presence of other males (Stokke and du Toit 2002). The interactions between males and females and between individual males can be influenced by the state of musth (Poole 1989a, b; Hollister-Smith 2005). The condition of musth is signaled by a distinct posture, temporal gland secretions and urine dribbling and is a reliable signal of physical condition (Poole 1987, 1989a). Female elephants prefer musth over non-musth males as mates (Hollister-Smith

2005). Contacts with older musth males can suppress musth in younger males, and non-musth males show avoidance behaviors towards secretions of musth males (Slotow et al. 2000; Stokke and du Toit 2002). Male elephants must balance their need to find females with the potential negative consequences of encountering musth males.

One way for male elephants to detect female signals, while avoiding possible male conflict, is by investigating chemical signals left by both sexes. On days when male groups and cow/calf or mixed groups were sighted, single males or male only groups first came to the waterhole approximately one hour after either group type. This may enable them to encounter fresh excretions from other elephants. Elephant excretions can provide valuable information about the sex and reproductive state (Rasmussen and Schulte 1998; Langbauer 2000; Rasmussen 2006; Schulte 2006). To obtain potential information conveyed by signal sources, elephants use chemosensory trunk behaviors.

At the waterhole, elephants exhibited sexual dimorphism in the performance of chemosensory behaviors. Chemosensory behaviors are used by elephants to gather information from their surroundings and are often performed towards elephant excretions (Schulte and Rasmussen 1999; Hollister-Smith 2005; Bagley et al. 2006; Vyas 2006). In this study, all age and sex classes had similar amounts of time available for the trunk to investigate the surroundings. However, post-puberty males performed chemosensory behaviors at a much higher rate than post-puberty females and pre-puberty elephants. The higher rate of any chemosensory behavior indicates that post-puberty male elephants are more frequently investigating their surroundings, possibly searching for information from conspecifics.

The chemosensory behaviors performed by elephants in this study differ in function. Raised sniffing behaviors are used for initial investigations of the surroundings and to determine the direction from which scents are coming (Merte 2006; Rasmussen 2006). The four primary chemosensory behaviors that elephants perform are sniff, check, place, and flehmen (Schulte and Rasmussen 1999). These behaviors have been used in many studies to gauge the level of interest elephants may have towards potential elephant signal sources (for example, Hollister-Smith 2005, Bagley et al. 2006, Meyer 2006, Vyas 2006). Sniff may be the only behavior necessary to provide an elephant with adequate information (Rasmussen and Schulte 1998, Schulte et al. 2005). However, particularly with signals that may contain possible pheromones, flehmens generally preceded by check and/or place behaviors are used to transfer potential signals to the vomeronasal organ (Rasmussen and Schulte 1998, Rasmussen 2006). Elephants use chemosensory behaviors, particularly those linked to the vomeronasal system (check, place, and flehmen), to identify and determine the sexual state and status of other elephants (Rasmussen 2006).

Among post-puberty elephants, the proportion of individuals that performed check, place, or flehmen was much greater in males than in females; while among pre-puberty elephants, this proportion was relatively low and did not vary between the sexes (Table 1.7). It is likely that for behaviors that assist in identifying an individual’s sexual state and status, the benefits are greater for post-puberty males to investigate their environment than any other age or sex class. Among sexually dimorphic species, males must locate females and then compete for access to them, while also attempting to avoid harmful encounters with other males (Clutton-Brock et al. 1982). However, the low proportion of post-puberty females performing chemosensory behaviors may indicate that they do not need to search for the opposite sex; males will come to them. The only chemosensory behavior in which there was not an age, sex, and response interaction was that of raised sniff. Post-puberty females performed raised sniffs more than any other chemosensory behavior, but still less than the proportion of post-puberty males. Of all behaviors observed, this appeared to be the least discriminatory; it may assist elephants to gather information on the presence and location of conspecifics (Rasmussen 2006). To communicate sexual status between group members, female elephants may rely on other signal sources, such as genital secretions, which are directly contacted by group members (Meyer 2006). Because females remain in their family group throughout their lives (Moss 2001), they have the opportunity to contact each other throughout the day and may not need to investigate the waterhole for elephant signals to the same degree as males.

The differences between male and female elephants' adult roles were reflected in the results of this study. These results indicate that the waterhole is being used by both sexes to meet their differing requirements. Females require that the greater needs of young offspring be met. Female success is influenced by their ability to successfully raise each offspring and access to critical resources is necessary for this. Male elephants also must fulfill their physiological requirements, but they may do so when they are also able to search for signals relating to conspecifics. Alternatively, male elephants may follow female elephants everywhere, lagging behind them to assess potential mates while avoiding direct encounters with superior competitors. In this scenario, waterholes may not be special information centers (Ward and Zahavi 1973). This hypothesis could be tested by observing chemosensory behaviors some distance from waterholes to examine how male and female investigatory patterns differ from each other and from their behavior at waterholes. Nevertheless, the current study supports the hypothesis that waterholes at least serve as one information source used by post-puberty male elephants to find and accurately identify the sexual state of conspecifics. In areas where permanent water is a limited resource, waterholes may provide an arena for intraspecific communication that is especially critical for the reproductive success of post-puberty male elephants.

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# CHAPTER II

# AFRICAN ELEPHANT, *LOXODONTA AFRICANA*, IMPACT ON WOODY VEGETATION SURROUNDING A PERMANENT WATERHOLE IN A PROTECTED AREA

## Abstract

African elephant, *Loxodonta africana*, populations are beginning to recover from heavy poaching pressures in the 1970s and 1980s. In East Africa, both elephant and human populations are increasing, restricting elephants to smaller habitats. As elephant home range and their ability to disperse are constrained, the potential for elephants to damage their habitat increases. Within a habitat, the abundance and location of water sources are often the most important factors influencing elephant damage to woody vegetation. This study assessed elephant impact on woody vegetation within a privately owned protected area in northern Tanzania. Damage to woody vegetation was monitored in two sampling plots that differed in their most common species, *Acacia tortilis* and *A. mellifera*, respectively. Twenty permanent transects of varying size within 2 km of a permanent waterhole were placed in each plot. Damage was assessed three times from September, 2005 – June, 2006. Over 95% of the woody vegetation was damaged by elephants. The severity of damage varied according to species type. Distance from the waterhole only had an effect on the proportion of individuals with elephant damage in the *A. tortilis* plot. The proportion of woody vegetation with new elephant damage was not associated with counts of elephants sighted in the area during the three months before tree damage was assessed. Because elephants may be heavily influenced by water, it was predicted that damage from elephants would be widespread in proximity to the only permanent waterhole within a protected area; this was supported by the results of this study. Waterholes are an important resource for elephants and can be a tourism focal point. However, the management of protected areas may need to consider the impact elephants have on the habitat surrounding isolated, permanent water sources.

INDEX WORDS: *Acacia mellifera, Acacia tortilis*, Woody Vegetation Damage, *Loxodonta africana*, Tanzania, Waterhole

## Introduction

Over much of the 1970s and into the 1980s in Eastern Africa, populations of the African elephant, *Loxodonta africana*, declined because of poaching (Douglas-Hamilton 1987, Barnes & Kapela 1991). In the past 20 years, the reduction of poaching has facilitated an increase or stabilization in elephant numbers (Blanc et al. 2007); during the same time, the human population has increased 3% per year (World Bank Basic Data Table 2007). Human population growth and the associated loss and fragmentation of habitats are now the chief threats facing elephants in Eastern Africa (Blanc et al 2007). An increase in human settlement often leads to greater habitat fragmentation, which can influence the distribution of elephants (Blom et al. 2004).

African elephants have been affected by human pressures and land-use decisions. Historically, rainfall was the limiting factor of African elephant distribution, but human influences now play a greater role in determining range (Osborn 2004a). In some areas elephants have changed their habitat preferences in response to increased human disturbances, particularly poaching (De Boer et al. 2000). In many regions, elephant populations are no longer able to move freely within their former range (Owen-Smith 1988).

Human management of elephant populations has become necessary and will most likely determine the fate of elephants and their environment (Kangwana 1995, Waithaka 1997, O'Connell-Rodwell et al. 2000). Elephant populations often are restricted to protected areas such as national parks, preserves and private game ranches, reducing or eliminating travel to new habitats (Waithaka 1997, Osborn 2002). The compression of elephant populations within protected areas can alter habitat structure, deplete resources, and lower biological diversity (Dublin et al. 1990, Cumming et al. 1997, Waithaka 1997, Osborn, 2002, Western & Maitumo 2004). Within protected areas, riverine habitats are often disproportionately impacted by elephants (Osborn 2002).

Elephant distribution also is influenced by natural factors, such as the spatial and seasonal distribution of resources. The two most important resources for elephants are forage and water. Elephants have absolute daily nutrient requirements three times greater than any other terrestrial animal (Owen-Smith 1988). To meet these requirements, elephants tend to switch foraging strategies seasonally, grazing protein rich grasses in wet seasons and browsing woody vegetation in dry seasons as grasses decline in nutritional value (Owen-Smith 1988, Sukumar 2003, Osborn 2004b). Because elephants drink nearly every day and experience seasonal differences in the maximum distance they are able to travel from permanent water sources (Stokke & du Toit 2002, Conybeare 2004), the distribution of permanent water sources influences the impact elephants have on vegetation (Conybeare 2004, O'Connor et al. 2007).

Tanzania has one of the highest proportions of protected wild areas in the world and 25% of all known and probable African elephants (Blanc et al. 2007). The large percentage of elephants makes Tanzania a critical site for balancing the conservation of elephants with the impact they have on their environment. The growing needs of the burgeoning human population in Tanzania (World Bank Basic Data Table 2007) will further compress elephants into protected areas, limiting their ability to disperse and intensifying the impact they have on their habitat. The objective of this study was to quantify elephant damage to woody vegetation, according to species and in relation to distance from the water source, around the only permanent water source at Ndarakwai

Ranch, a privately owned, unfenced protected area in Northern Tanzania. Waterholes serve as congregation points for elephants, and during visits to the waterhole they may rest and browse nearby (Napora 2007). I predicted that damage to trees would be high close to the waterhole. If Ndarakwai serves as a protective refuge and a reliable oasis, then damage to the woody vegetation may be pervasive, showing little variation in the region of the waterhole.

## Methods

### Study site

This study was conducted at Ndarakwai Ranch, a part of the Kilimanjaro Conservancy, in northern Tanzania. Ndarakwai Ranch is a 4300 ha protected area, privately owned by Peter and Margo Jones. Prior to 1964, German and English colonists used the area for agriculture and cattle grazing (P. Jones pers. comm.). After Tanzanian Independence, Tanzania Breweries bought Ndarakwai and continued sporadic agriculture and cattle grazing. Prior to 1995, wildlife was only infrequently observed at Ndarakwai because human activities, such as cutting forest for charcoal and unregulated wildlife hunting were common (P. Jones pers. comm.). In 1995, the Jones leased Ndarakwai for 99 years, using it as a camp for photographic tourism. They hired a staff of 15 rangers to guard the area from poachers and inappropriate land use.

Ndarakwai is in proximity to Kilimanjaro and Arusha National Parks in Tanzania and Amboseli National Park in Kenya (Figure 1.1). This area typically experiences a short (November & December) and long (March – May) wet season interspersed by dry periods (Moss 2001, Napora 2007). Ndarakwai is bordered on two sides by the Ngare Nairobi River, which is dry for most of the year. Other water sources at Ndarakwai are several small water furrows that ultimately end at a manmade and maintained 4000 $m^2$ waterhole. This is the only permanent waterhole available to wildlife within a 15 km radius (R. Kosianga, Ndarakwai Ranch manager, pers. comm.) and it serves as an important resource for animals in the area. Elephants exhibit seasonal use of the waterhole (Vyas 2006, Napora 2007).

**Data collection**

Two sampling plots were placed in proximity to the waterhole and delimited by natural features; a seasonal river and a 50 to 400 m wide treeless grassy area formed the borders of the first sampling area and the same grassy area, a large hill, and rocky outcroppings formed the border of the second sampling area (Figure 2.1). In the first sampling plot (AT plot), the most abundant species was *Acacia tortilis*, in the second sampling plot (AM plot) the most common species was *A. mellifera* (Table 2.1). In each plot, I randomly placed 20 permanent transects (Lindsay 1996). Each plot was sampled three times. The AT plot was sampled from September 19 – 24 and October 10, 2005, January 4 – 18, 2006, and April 4 – 15, 2006. The AM plot was sampled on October 27 – November 7, 2005, February 12 – 21, 2006, and June 10 – 16, 2006.

Each transect was 54 meters wide and had a varying length depending on the density of the most abundant woody vegetation species in that plot (Figure 2.2). The area of transects ranged from 540 – 4050 $m^2$. To obtain a large sample size, each transect comprised at least 20 individuals of the most common woody plant species ≥ 2m (*A. tortilis* in the AT plot and *A. mellifera* in the AM plot) (Lindsay 1996). For each individual ≥ 0.5m, the species, height (to nearest meter), and GPS coordinates were recorded (Noad & Birnie 1989, Lindsay 1996, van Wyk & van Wyk 1997, Calenge et al.

2002). Individuals were then placed in damage categories adapted from Calenge et al. 2002 (Table 2.2). To identify elephant damage accurately, I observed mammals of several species such as elephants, giraffes (*Giraffa cameloparadalis*), and impala (*Aepyceros melampus*) feeding on woody vegetation in proximity to the permanent waterhole. After the individuals departed, I examined the damaged areas. Elephants had easily differentiated foraging style from other mammals because of their destructive nature. Even light foraging consisted of the tearing off of branches, while other animal species removed foliage only.

In June and July 2006 a second researcher, Stacie Castelda and I examined all individuals for the presence of foliage. To examine the validity of the damage categories, I compared the proportion of woody vegetation placed in each overall damage category and whether or not foliage was present. Among all woody vegetation, 91% with low damage, 65% with moderate damage, and only 10% with severe damage had foliage present (Figure 2.3). The significant decrease in proportion of trees with foliage across the three damage categories supported the damage classification scheme ($G = 321.91$, $df = 2$, $p < 0.0001$).

**Data analysis**

The mean proportion of individuals per transect for each plot, species, and damage category were compared using non-parametric analyses. The mean proportion of individuals damaged across sampling periods was analyzed using Friedman’s test for randomized blocks (Sokal & Rohlf 1995). If two groups were compared, a Mann-Whitney non-parametric test was conducted and the Z – score approximation were reported. If more than two groups were compared, a Kruskal-Wallis ANOVA was used and the H – value was reported. The third sampling period provided the most precise estimate of elephant damage by the end of the study and all analyses on damage were made with the data from the third sampling period with the exception of the comparison between sampling periods. The relationship between the distance from the waterhole (m) and if a woody plant individual was damaged or not was analyzed using logistic regression. All trees were placed in categories of damaged or undamaged. The relationship between the distance from the waterhole (m) and if a damaged woody plant individual had severe or not severe (low or moderate) damage also was analyzed. JMP IN 4.0.4 (SAS Institute 2000) for Windows operating systems was used for all statistical analyses ($\alpha = 0.05$). Descriptive statistics presented include mean ± standard error.

## Results

In both plots, there were 1299 individuals of 9 different species of woody vegetation (Table 2.1). In the AT plot, the mean transect size was $2100 \pm 216$ $m^2$, significantly greater than the mean transect size of $1236 \pm 104$ $m^2$ in the AM plot ($t_{38} = 3.60$, $p < 0.001$). The difference in transect size indicates that the dominant species in the AT plot, *A. tortilis*, was less dense than the dominant species in the AM plot, *A. mellifera*.

In the AT plot, *A. tortilis* and A. *mellifera* comprised over 97% of all trees sampled. Because of the small number of individuals (n = 19), the four other species located in plot were excluded from further analyses. In the AM plot, 77% of the trees were *A. mellifera*, 10% were *Balanites aegyptiaca*, and 13% were six other species that I combined and analyzed together.

### Elephant damage across sampling periods

By the last sampling period, 96 ± 1% of the woody vegetation in both plots was damaged by elephants. In the AT plot, the mean proportion of woody vegetation with any damage increased in each sampling period (Count= 20; $\chi^2 = 23.70$, $p < 0.0001$), and approached significance in the AM plot (Count = 20; $\chi^2 = 5.63$, $p = 0.06$) (Figure 2.4).

### Overall elephant damage

Both plots showed high percentages of elephant damage. In the AT plot, 94 ± 2% of woody vegetation had elephant damage, significantly less than the 97 ± 1% of woody vegetation with elephant damage in the AM plot (Count AT plot = 20, AM plot = 20, Z = -3.01, p = 0.003). In the AT plot, 99.8 ± 0.2% of *A. mellifera* were damaged, significantly greater than the 90.5 ± 2% of *A. tortilis* damaged (Count *A. tortilis* = 20, *A. mellifera* = 20, Z = -4.96, p = <0.0001). In the AM plot, 100% of *A. mellifera*, 89 ± 4% of *B. aegyptiaca*, and 90 ± 6% of other species were damaged. Overall, the percentage of individuals damaged in each category was significantly different (H = 8.17, df = 2, p = 0.02). The only significant difference between pair-wise comparisons between species in the percentage of individuals with elephant damage was between *A. mellifera* and *B. aegyptiaca* (Count *A. mellifera* = 20, *B. aegyptiaca* = 16, Z = -2.92, p = 0.004). The difference in the percentage of *A. mellifera* and other six species damaged was nearly significant (Count *A. mellifera* = 20, Other = 17, Z = -1.90, p = 0.06) and no difference between *B. aegyptiaca* and other species was found (Count *B. aegyptiaca* = 16, Other = 17, Z = -1.01, p = 0.31).

## Elephant damage categories

In each plot, the mean proportion of individuals in each damage class depended on the woody vegetation species (AT plot: $H_{4,150} = 34.17$, $p < 0.0001$; AM plot: $H_{2,119} = 33.84$, $p < 0.0001$). In the AT plot, *A. tortilis* had a greater mean proportion of individuals with low damage and severe damage and a lower proportion of moderate damage than *A. mellifera* (Figure 2.5a). In the AM plot, *B. aegyptiaca* had the greatest proportion of individuals with low damage, followed by *A. mellifera* and other species (Figure 2.5b). *Acacia mellifera* and other species had similar mean proportions of individuals with moderate damage as each other, but greater than *B. aegyptiaca*. Other species had the greatest proportion of individuals with severe damage, followed by *A. mellifera*, and lastly *B. aegyptiaca*.

*Acacia mellifera*, the only species frequently encountered in both plots, had similar damage patterns in each plot (Figure 2.5, compare the white bars). The proportion of individuals significantly differed in each damage class ($H_{2,114} = 6.88$, $p < 0.05$), but not between plots ($H_{1,114} = 0.70$, $p > 0.05$).

## Elephant damage and distance from waterhole

The range of distances from the waterhole for the woody plants sampled was 83–1252 meters in the AT plot and from 320 – 1722 meters in the AM plot. For both plots combined, distance from the waterhole was not able to explain whether an individual woody plant was damaged or undamaged ($r^2 = 0.001$, N = 1299, $p = 0.41$, slope = -0.0002), but this was different from each individual plot. In the AT plot, as distance from the waterhole increased, the probability of an individual woody plant being damaged decreased significantly, but distance explained only a small portion of the variation ($r^2 =$

0.034, N = 715, $p < 0.001$, slope = -0.0014). When each species in the AT plot (*A. tortilis* and *A. mellifera*) was analyzed individually, the probability of an individual *A. tortilis* being damaged decreased significantly ($r^2 = 0.024$, N = 429, p = 0.01, slope = -0.0011) and the probability of an individual *A. mellifera* being damaged did not change as distance increased ($r^2 = 0.011$, N = 267, p = 0.67, slope = -0.0012). In the AM plot, similar to the AT plot, as distance from the waterhole increased, the probability of an individual woody plant being damaged decreased significantly, but distance explained only a small portion of the variation ($r^2 = 0.084$, N = 584, p = 0.005, slope = -0.0035). Because there were no undamaged *A. mellifera* and only 1 undamaged other species, logistic regression was not able to be performed. The probability of *Balanites aegyptiaca* being damaged was not explained by the distance from the waterhole ($r^2 = 0.021$, N = 61, p = 0.30, slope = -0.0015).

Of damaged individuals, I examined the probability that a woody plant would have severe damage or not have severe damage (low or moderate damage). In the plots combined, the overall increase in woody vegetation that was not severely damaged was low as distance from the waterhole increased ($r^2 = 0.009$, N = 1241, p = 0.034, slope = 0.0006). Overall, for the two plots and the species within each plot, distance from the waterhole did not explain a significant amount of variation in whether an individual was damaged severely (all $p > 0.05$).

## Discussion

Elephants damaged over 95 % of all woody vegetation sampled within 2 km of the only permanent water source within a 15 km radius. Elephant damage to the woody vegetation varied by species. *A. mellifera* and other species found in small numbers had the greatest proportion of damaged individuals, followed by *A. tortilis* and then *B. aegyptiaca*. *A. tortilis* and *B. aegyptiaca* had the greatest proportions of individuals in the low damage category, while the greatest proportion of damage to *A. mellifera* and other species was moderate. None of the species had more than 15% of their individuals damaged severely. The distance of woody vegetation from the waterhole explained a small amount of the variation between damaged and undamaged individuals and between severely damaged and not severely damaged individuals.

The impact that elephants have on woody vegetation can depend on the species of woody vegetation and the severity of damage (Conybeare 2004). Only one of the species in this study, *Acacia tortilis*, has had elephant impact reported in other studies. MacGregor and O'Connor (2004) found that there was a lag of 2-3 years between the heavy use of *A. tortilis* and the death of an individual. *A. tortilis* does not coppice well and responds poorly to severe and moderate damage. Twenty-one percent (92/439) of *A. tortilis* did not have foliage present and may be dying. If *A. tortilis* at Ndarakwai respond similarly to those studied by MacGregor and O'Connor (2004) in South Africa, individuals that were classified as having moderate damage (another 9% (40/439)) may be at risk of dying. The ability of *A. mellifera* to respond to elephant damage has not been established, but 29% (207/714) of *A. mellifera* did not have foliage and may be dying. If they responded similarly to *A. tortilis*, another 39% (279/714) in the moderate damage category may be at risk.

O'Connor et al. (2007) identified 11 conditions that predict if a woody vegetation species is likely to be extirpated from a small reserve by elephants. Of these 11 conditions, species at Ndarakwai meets at least five of them: (a) the terrain lacks topographic refuges; (b) there are no absolute and only weak partial refuges from elephant because distance from water is not a foraging constraint; (c) the reserve is located in a semi-arid region that experiences variable grass production, hence heightened utilization of woody material occurs; (d) the species lacks a coppicing ability (possibly *A. tortilis* only); (e) the species is highly used.

This study showed that elephant damage to woody vegetation was widespread within both sampling plots. The waterhole at Ndarakwai experiences a high number of elephant group sightings over much of the year (Napora 2007). However, the distance that woody vegetation was from the waterhole only explained a very small amount of the variation between individuals that were damaged or not damaged. Within this area, < 2 km from the waterhole, there is no refuge for woody vegetation from elephant damage. Little of the variation in the severity of elephant damage to woody plant individuals was explained by distance from the waterhole.

Calenge et al. (2002) found that elephant damage was patchily distributed and concentrated around permanent water sources. The concentration of damage allowed individual woody plants that were located far from permanent water to face little threat from elephants. Elephant use of the Ndarakwai waterhole and the surrounding areas might lead to concentrated damage, allowing woody species farther from water to persevere, as seen in other areas (see O'Connor et al. 2007). Ndarakwai is a protected area used for photographic tourism and the opportunity to observe elephants at the waterhole is a major draw (Jones pers. comm.). Elephants benefit from the artificially maintained water source, using it to meet physiological needs and possibly to facilitate communication between the sexes (Napora 2007). Reserve managers must balance the potential of high vegetation damage in some areas, particularly around water sources, with the potential benefits these water sources hold.

The investigation of elephant damage to woody vegetation surrounding the only permanent waterhole at Ndarakwai is continuing. Our research group hopes to answer questions regarding the seasonality of elephant damage with regards to elephant presence at the waterhole. We are also investigating how the different levels of elephant damage to woody vegetation may impact the distribution of herpetofauna. With additional information on elephant visitation rates, number and patterns as well as continued monitoring of the woody vegetation, we hope to examine further the influence of elephant presence at the waterhole on the surrounding environment.

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Table 1.1. Mean observation duration (± SE) and sample size of continuous focal observations of pre-puberty (0-9 y) and post-puberty (≥10 y) elephants, Ndarakwai Ranch (July - October 2005).

| **Sex** | **Age Class** | **Sample size** | **Mean observation duration[1] ± SE (min)** |
|---|---|---|---|
| Female | Pre-Puberty | 25 | 14.1 ± 0.7 |
| Female | Post-Puberty | 34 | 16.1 ± 1.0 |
| Male | Pre-Puberty | 24 | 15.6 ± 0.7 |
| Male | Post-Puberty | 18 | 15.6 ± 1.0 |
| Total | | 101 | 15.3 ± 0.4 |

[1] The mean observation duration is the duration of visible focal time; it does not include "not visible."

Table 1.2. Ethogram used to record African elephant behaviors observed at Ndarakwai Ranch, (July – October, 2005).

| **State behaviors** | |
|---|---|
| Defecate | Release of feces from the anus |
| Drink | Uptake of water into trunk and placed into the mouth |
| Dust | Using a foot or trunk to place dirt on the body |
| Eat | Placing food into the mouth with the trunk |
| Mudding/ Wallowing | Applying mud over areas of the body with either the trunk or by repetitive rolling of the body in mud/water |
| Not visible | Focal animal unable to be seen |
| Other | Behavior not defined in the ethogram |
| Stand | Lack of locomotion; no change in the spatial positioning of elephant |
| Suckle | Mouth on nipple of post-puberty female or nipple placed in mouth of pre-puberty elephant |
| Urinate | Release of urine from vagina or penis |
| Walk | Movement forward at a slow pace |
| **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 |

Based on Schulte and Rasmussen 1999, Schulte 2006, Vyas 2006.

Table 1.3. Statistical analyses of hourly scans and elephant presence at the waterhole by season, Ndarakwai Ranch (October 2004 – April 2006)[1].

| **Comparison** | **Test** | **D.F.** | **Statistic** | **p-value*** |
|---|---|---|---|---|
| *Elephant presence during hourly scans* | 2-Way Contingency Table | 3 | G = 135.4 | <0.01 |
| Season[1]: | | | | |
| LD & LW: | a posteriori G-tests | 1 | G = 20.3 | <0.01[a] |
| LD & SD: | | 1 | G = 90.0 | <0.01[a] |
| LD & SW: | | 1 | G = 90.6 | <0.01[a] |
| LW & SD: | | 1 | G = 30.0 | <0.01[a] |
| LW & SW: | | 1 | G = 21.3 | <0.01[a] |
| SD & SW: | | 1 | G = 2.7 | 0.10[a] |

[1] Season: LD = long-dry, LW = long-wet, SD = short-dry, SW = short-wet (see page 7 for definition of seasons).

* $\alpha = 0.05$

[a] Indicates p-values that have been corrected using the Hochberg adjustment.

Table 1.4. The seasonal distribution of hourly scans with elephants observed across all seasons, Ndarakwai Ranch (October 2004 – April 2006).

| **Season** | **Total scans** | **Scans w/ elephants (N)** | **Proportion of scans w/ elephants** |
|---|---:|---:|---:|
| SW | 663 | 47 | 0.14 |
| SD | 391 | 18 | 0.05 |
| LW | 639 | 96 | 0.29 |
| LD | 665 | 173 | 0.52 |
| Total | | 334 | 1 |

[1] Season: SW = short-wet, SD = short-dry, LW = long-wet, LD = long-dry (see page 7 for definition of seasons).

Table 1.5. Statistical analyses of the time of elephant sightings on dates when multiple group types were observed, Ndarakwai Ranch (October 2004 – April 2006).

| **Comparison** | **Mean Time (± SE)** | **Test** | **N** | **D.F.** | **Statistic** | **p-value*** |
|---|---|---|---|---|---|---|
| *Time of first sighting* | | | | | | |
| a. Male | 13:41 (00:21) | Matched | 37 | 36 | t = 2.64 | 0.01 |
| Cow/Calf: | 12:37 (00:21) | Pairs | | | | |
| b. Male: | 13:36 (00:22) | | 32 | 31 | t = 3.45 | <0.01 |
| Mixed: | 12:19 (00:22) | | | | | |
| c. Cow/Calf: | 12:46 (00:19) | | 54 | 53 | t = 0.43 | 0.67 |
| Mixed: | 12:37 (00:18) | | | | | |

* $\alpha = 0.05$

Table 1.6. The mean (± SE) proportion of observation time spent performing the four most prevalent state behaviors, Ndarakwai Ranch (July – October 2005).

| | | **Mean proportion of observation time(± SE)** | |
|---|---|---|---|
| **Behavior** | **Age class** | **Female** | **Male** |
| Drinking | Pre-Puberty | 0.39 ± 0.04 | 0.36 ± 0.04 |
| | Post-Puberty | 0.34 ± 0.04 | 0.24 ± 0.05 |
| Mudding / Wallowing[1] | Pre-Puberty | 0.13 ± 0.05 | 0.09 ± 0.03 |
| | Post-Puberty | 0.11 ± 0.02 | 0.23 ± 0.04* |
| Standing | Pre-Puberty | 0.19 ± 0.04 | 0.24 ± 0.05 |
| | Post-Puberty | 0.27 ± 0.03 | 0.20 ± 0.04 |
| Walking | Pre-Puberty | 0.23 ± 0.03 | 0.24 ± 0.03 |
| | Post-Puberty | 0.20 ± 0.03 | 0.25 ± 0.03 |
| Total | Pre-Puberty | 0.94 ± 0.02 | 0.93 ± 0.02 |
| | Post-Puberty | 0.92 ± 0.02 | 0.91 ± 0.02 |

*Indicates significant difference between female and male, $p<0.05$.

[1] Mudding and wallowing proportions were combined.

Sample size: Pre-Puberty (Female: 25, Male: 24), Post-Puberty (Female: 34, Male: 18)

Table 1.7. The statistical analysis of the proportion of individuals in each age and sex category that performed chemosensory behaviors, Ndarakwai Ranch (July – October 2005).

| Behavior | Comparison | Analysis | G | df | p-value |
|---|---|---|---|---|---|
| Sniff | a. Overall interaction | 3-way contingency table | 13.41 | 1 | <0.001 |
| | c. Pre-puberty: females vs. males | Goodness of fit | 0.41 | 1 | 0.52 |
| | e. Post-puberty: females vs. males | Goodness of fit | 22.63 | 1 | <0.001 |
| CPF | b. Overall interaction | 3-way contingency table | 11.59 | 1 | <0.001 |
| | d. Pre-puberty: females vs. males | Goodness of fit | 0.005 | 1 | 0.94 |
| | f. Post-puberty: females vs. males | | 26.0 | 1 | <0.001 |
| Raised sniff | g. Overall interaction | 3-way contingency table | 3.33 | 1 | 0.07 |
| | h. Age class | 3-way contingency table | 7.13 | 2 | 0.03 |
| | i. Pre-puberty: females vs. males | Goodness of fit | 0.01 | 1 | 0.93 |
| | j. Post-puberty: females vs. males | Goodness of fit | 7.11 | 1 | 0.008 |

Table 2.1. The species and number of trees present in two woody vegetation sampling plots in proximity to a permanent waterhole, Ndarakwai Ranch (September 2005 – June 2006).

| **Species** | **AT Plot** | **AM Plot** | **Total** |
|---|---|---|---|
| *Acacia mellifera* | 267 | 447 | 714 |
| *A. tortilis* | 429 | 10 | 439 |
| *Balanites aegyptiaca* | 10 | 60 | 70 |
| *Cordia ovalis* | 3 | 34 | 37 |
| One unidentified sp. | 0 | 17 | 17 |
| *Commiphora africana* | 4 | 7 | 11 |
| *A. drepanolobium* | 0 | 8 | 8 |
| *A. xanthophloea* | 2 | 0 | 2 |
| *Euphorbia candelabrum* | 0 | 1 | 1 |
| Total | 715 | 584 | 1299 |

In AM plot, the six species other than *A. mellifera* or *B. aegyptiaca* were combined into the category "other" for analysis.

Table 2.2. The classification of elephant damage to woody vegetation in two sampling plots at Ndarakwai Ranch, Tanzania (September 2005 – June 2006).

| **Description of elephant damage** | **Damage category** |
|---|---|
| 1. No damage | None |
| 2. Some damaged branches | Low |
| 3. One or more main branches broken (but not all) or significant part of the crown (≥50%) browsed | Low |
| 4. All branches broken at some point, or completely browsed | Moderate |
| 5. Pushed over or all main stem(s) broken | Severe |
| 6. Uprooted | Severe |

Adapted from Calenge et al. 2002.

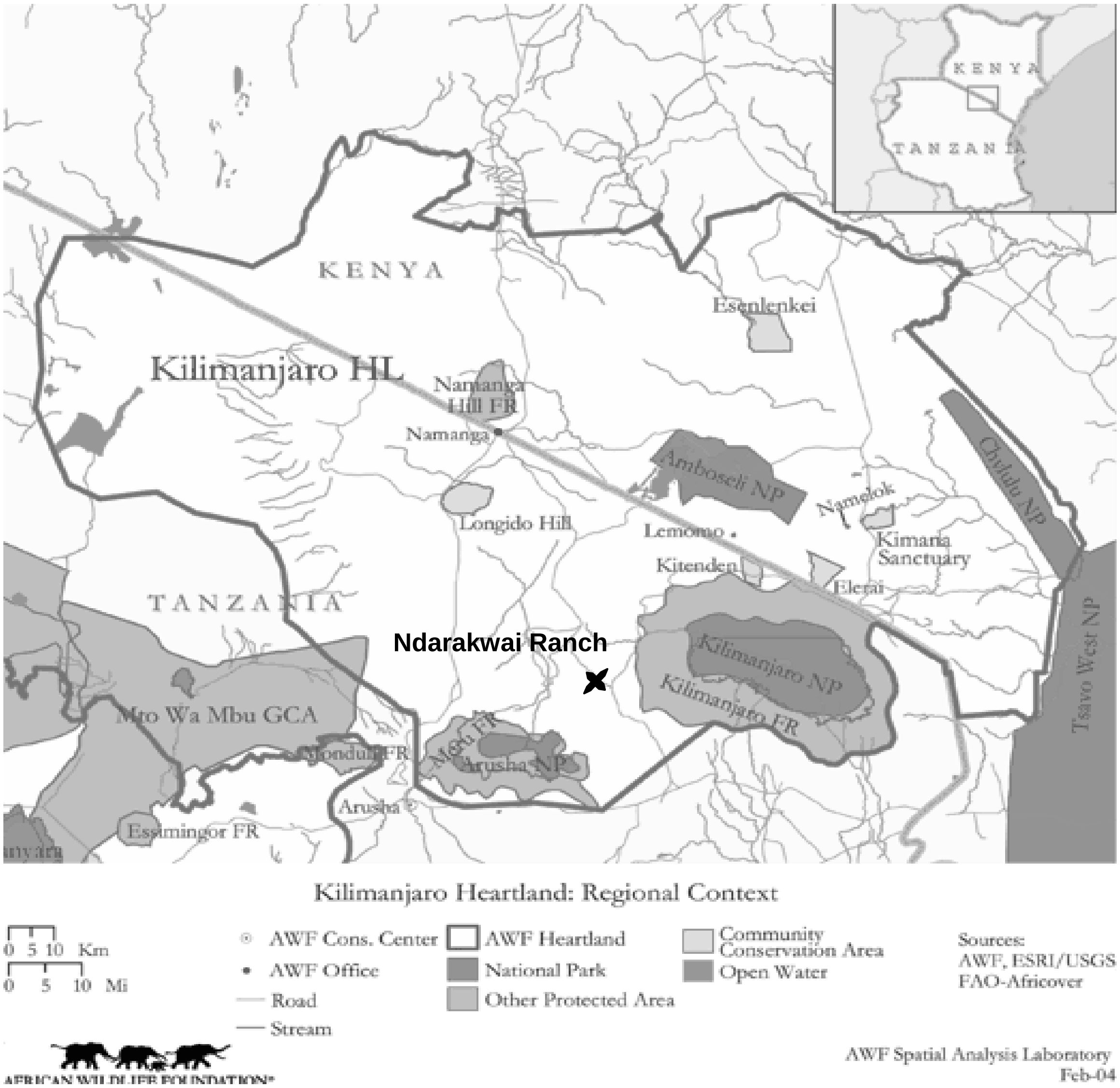


Figure 1.1. Map of the north-central border between Kenya and Tanzania. Ndarakwai Ranch (ca. 4300 ha) is marked with an "X" (AWF Spatial Analysis Laboratory 2004).

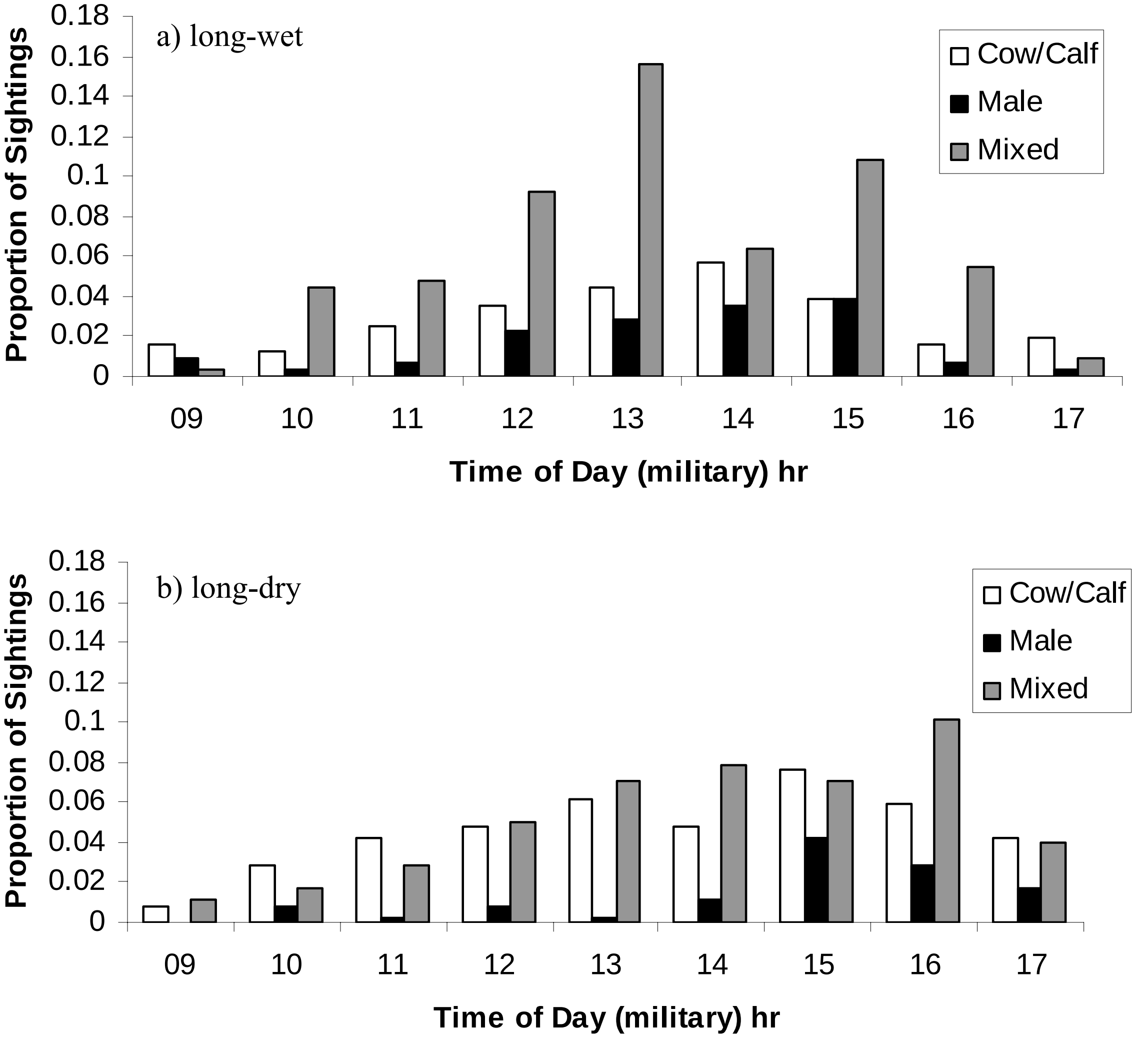
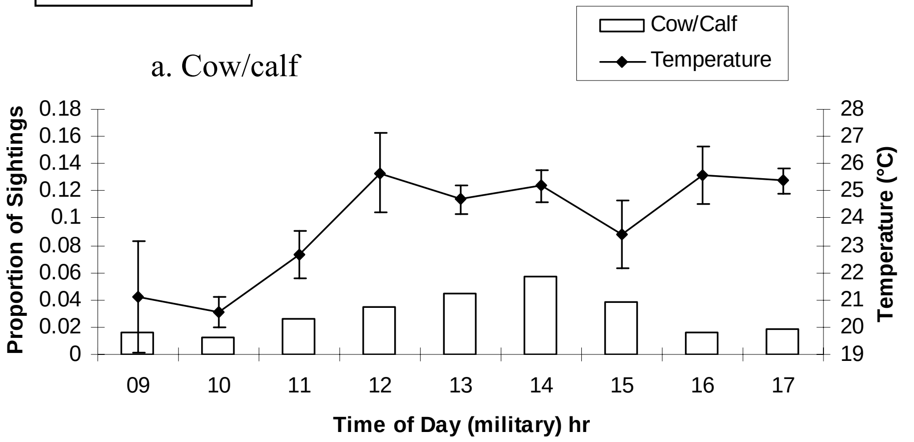


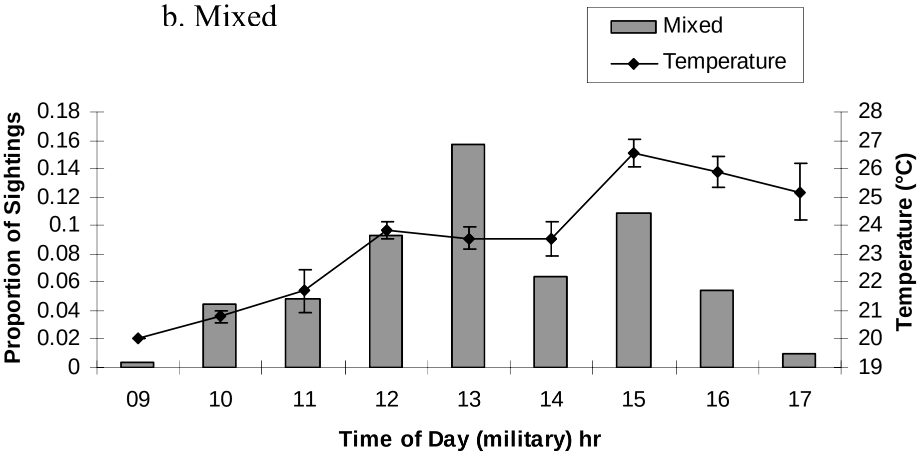
Figure 1.2. The proportion of elephant group sightings in the long-wet and long-dry seasons from 09:00 – 17:00 hrs, Ndarakwai Ranch (April – May, June – October 2005, March – April 2006). a) Long-wet: The proportion of male sightings was significantly correlated with the proportion of cow/calf and mixed sightings. b) Long-dry: The proportion of cow/calf sightings was significantly correlated with the proportion of male and mixed sightings. The proportion of male sightings and mixed sightings were not significantly correlated.

## Long-Wet

a. Cow/calf



b. Mixed



c. Male

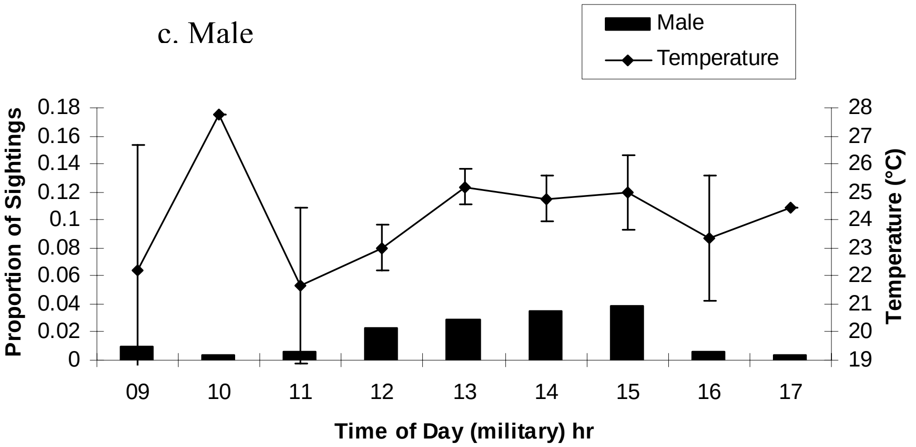


Figure 1.3. The proportion of elephant sightings for each group type (a. cow/calf, b. male, and c. mixed) and the mean temperature at the time of sightings for each group type 09:00 – 17:00 hrs during the long-wet season, Ndarakwai Ranch (April – May 2005, March – April 2006). There were no significant correlations between the proportion of sightings and the mean temperature for any of the group types. Temperature points without error bars represent the temperature measured during a single sighting.

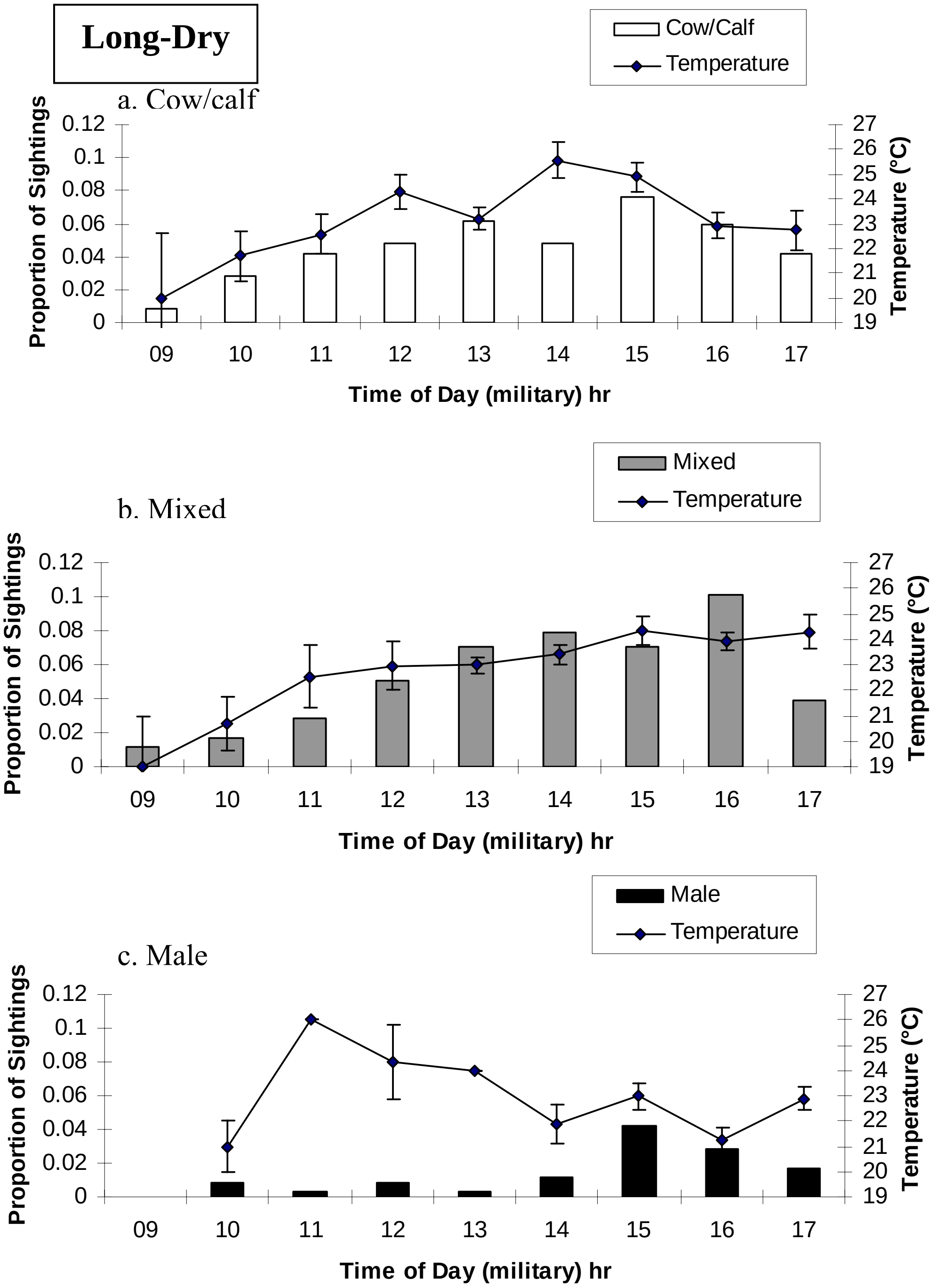


Figure 1.4. The proportion of all elephant sightings for each group type (a. cow/calf, b. male, and c. mixed) and the mean temperature of sightings 09:00 – 17:00 hrs during the long-dry season, Ndarakwai Ranch (June – October 2005). The proportion of sightings for cow/calf and mixed groups were significantly correlated with the mean temperature at sightings, but male groups were not. Temperature points without error bars represent the temperature measured during a single sighting.

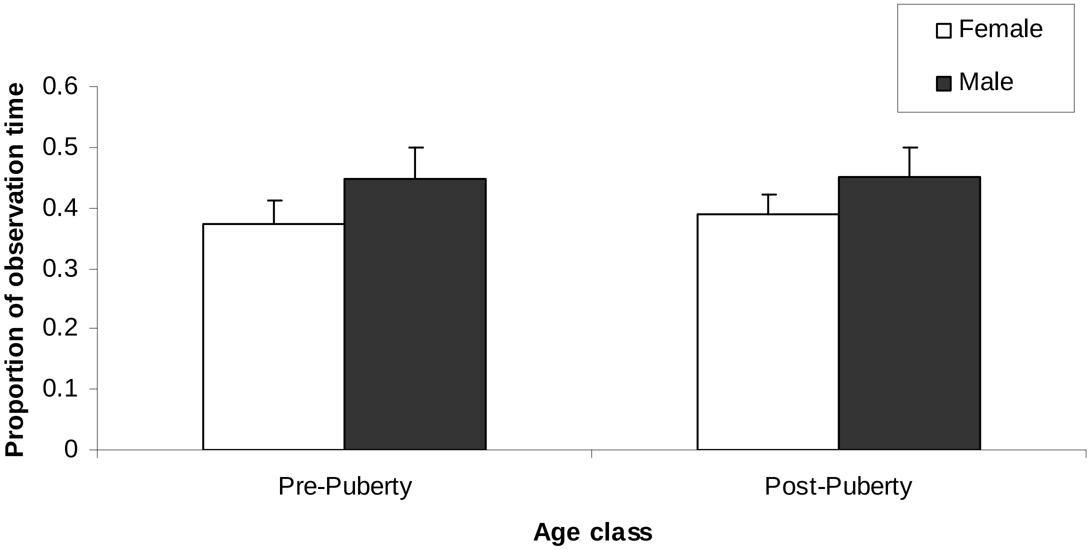


Figure 1.5. The mean proportion of observation time that an elephant's trunk was able to investigate the environment, Ndarakwai Ranch (July – October 2005). The proportion of time available to investigate the environment was similar across age class and sex.

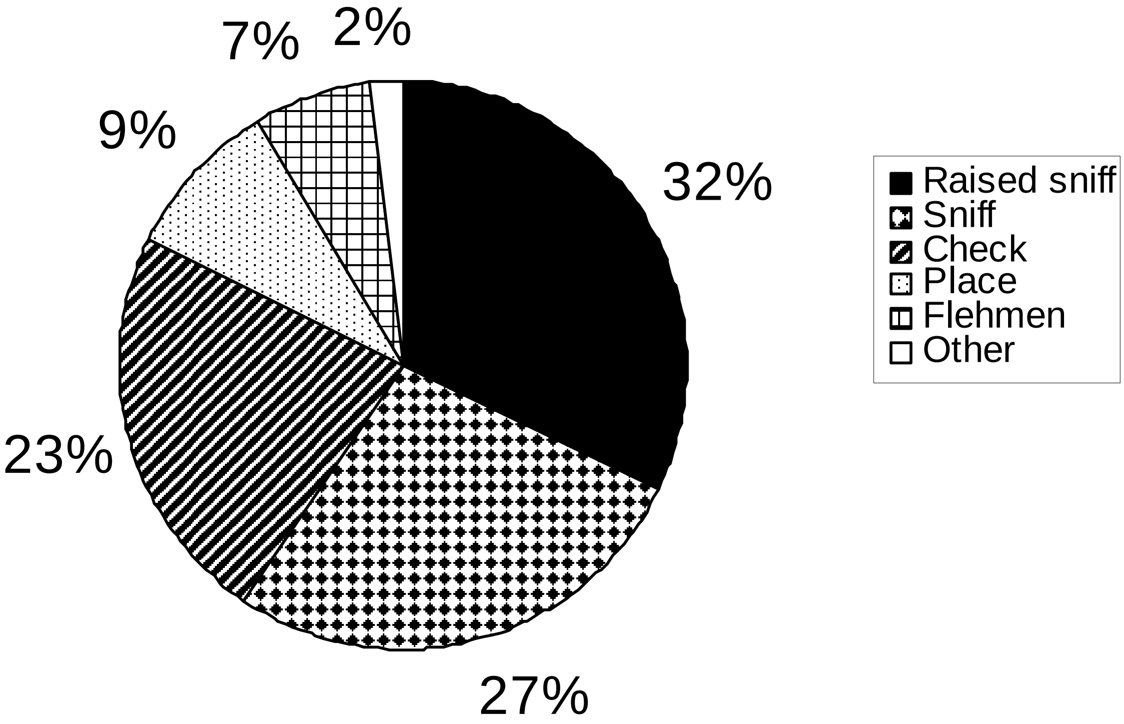


Figure 1.6. The percentage of chemosensory events in each behavioral category, Ndarakwai Ranch (June – October 2005). A total of 208 chemosensory events were performed by 49 different elephants.

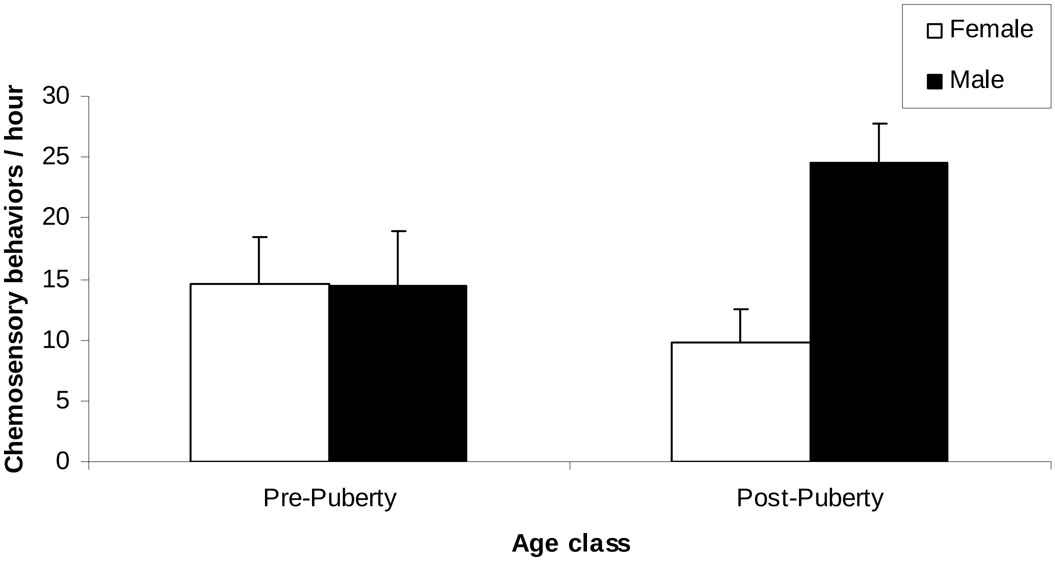


Figure 1.7. The mean rate of all chemosensory behaviors per hour by age class and sex, Ndarakwai Ranch (July 2005 – October 2005). A significant interaction was found between age class and sex ($F_{1,45} = 7.94$ $p < 0.01$).
Sample size: Pre-Puberty Female = 11, Male = 12; Post-Puberty Female = 10, Male = 16.

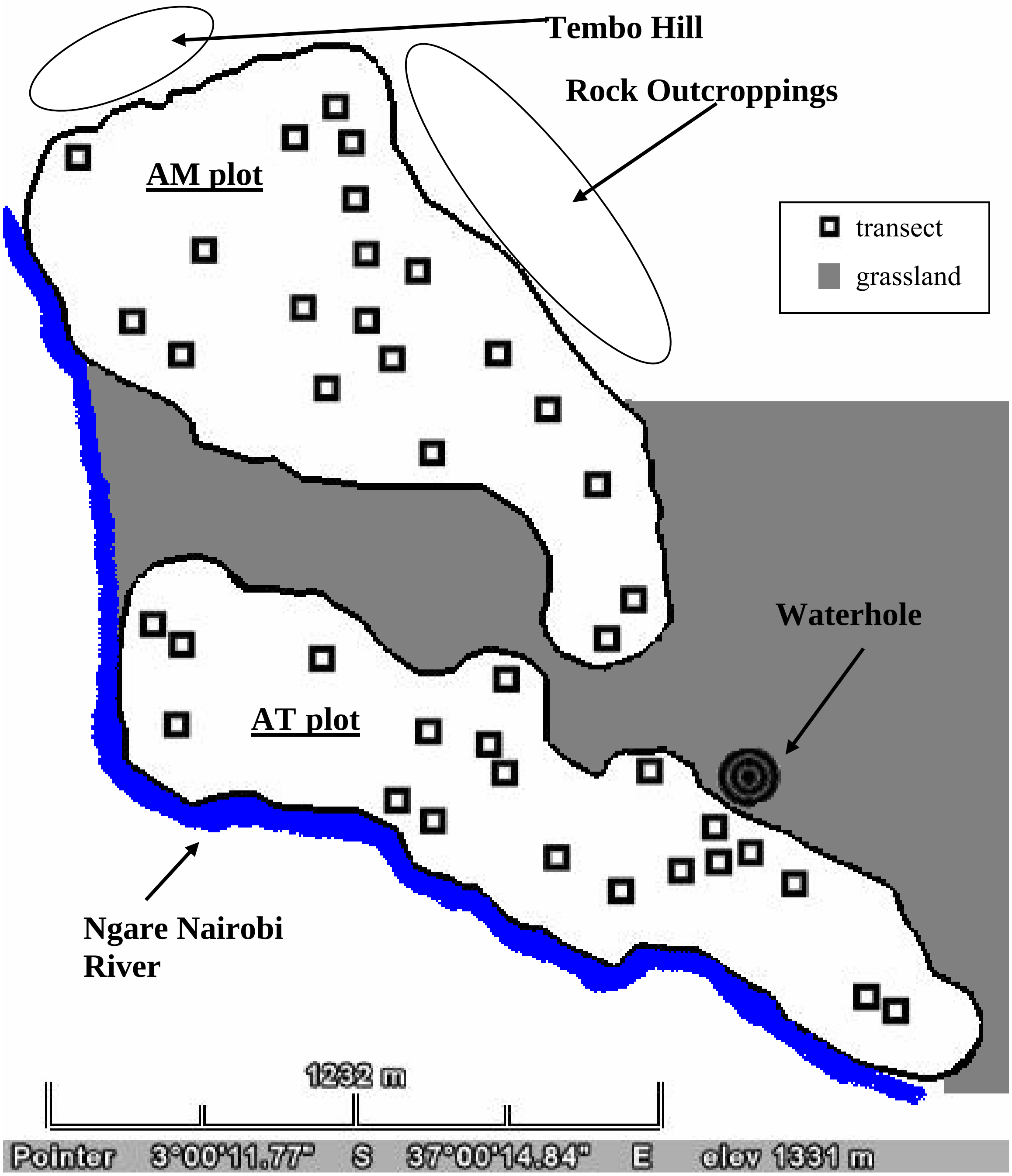


Figure 2.1. The location of the two sampling plots (AT and AM) and the 20 transects within each sampling plot with regards to the permanent waterhole, Ndarakwai Ranch (September 2005 – June 2006) (Google Earth 2007). The distance separating the AT and AM plot ranged from 50 to 400 meters.

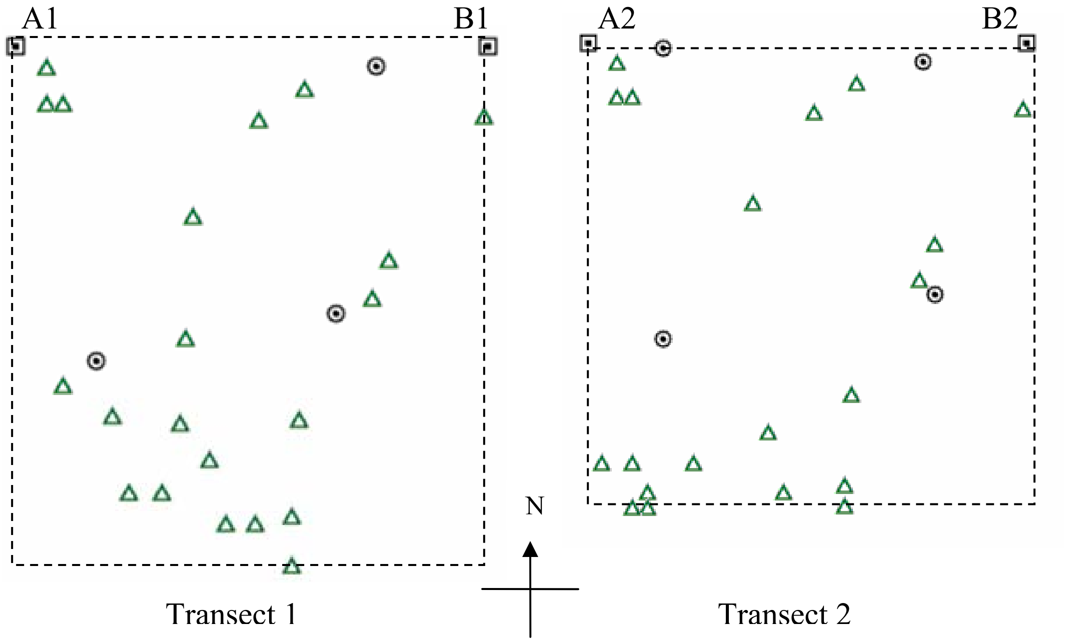


Figure 2.2. Transects from the AT plot, illustrating the transect design, Ndarakwai Ranch (September 2005 – June 2006). The width of both transects was the same 54 meters (between A and B). All trees ≥ 0.5m tall falling between the Northwest and Northeast corners and to the South were counted (*Acacia tortilis* are represented by triangles and *A. mellifera* by circles, other species were not encountered in these transects). The Southern boundary is the line where the 20th individual ≥ 2m tall was encountered. Any other individuals falling along that line also were included. In this example, the length of transect 1 is 77 meters, greater than the width of transect 2 because 20 individuals ≥ 2m tall were encountered farther South in transect 1 than 20 individuals in transect 2.

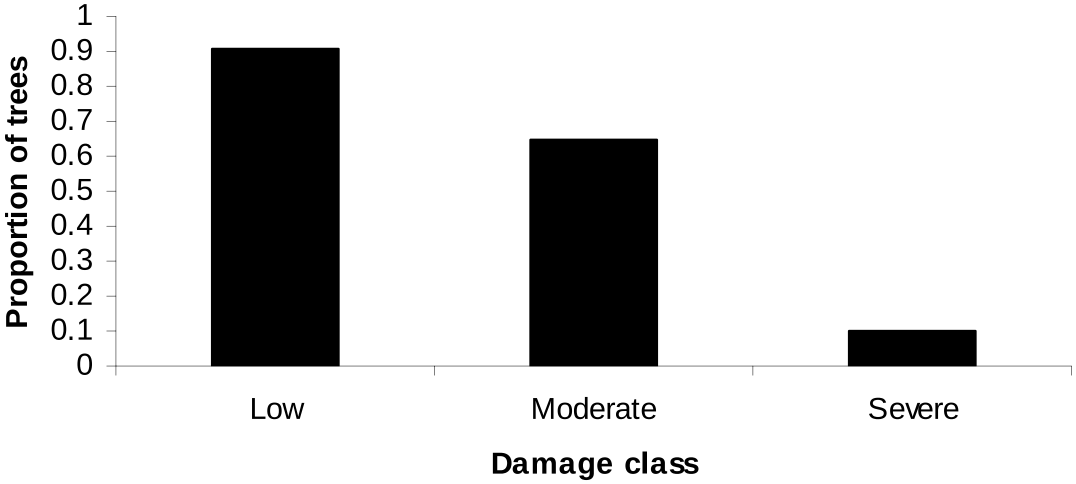


Figure 2.3. The proportion of all woody vegetation in each damage class with foliage present at the end of the study, Ndarakwai Ranch (June and July, 2006). (N: Low = 596, Moderate = 542, Severe = 107).

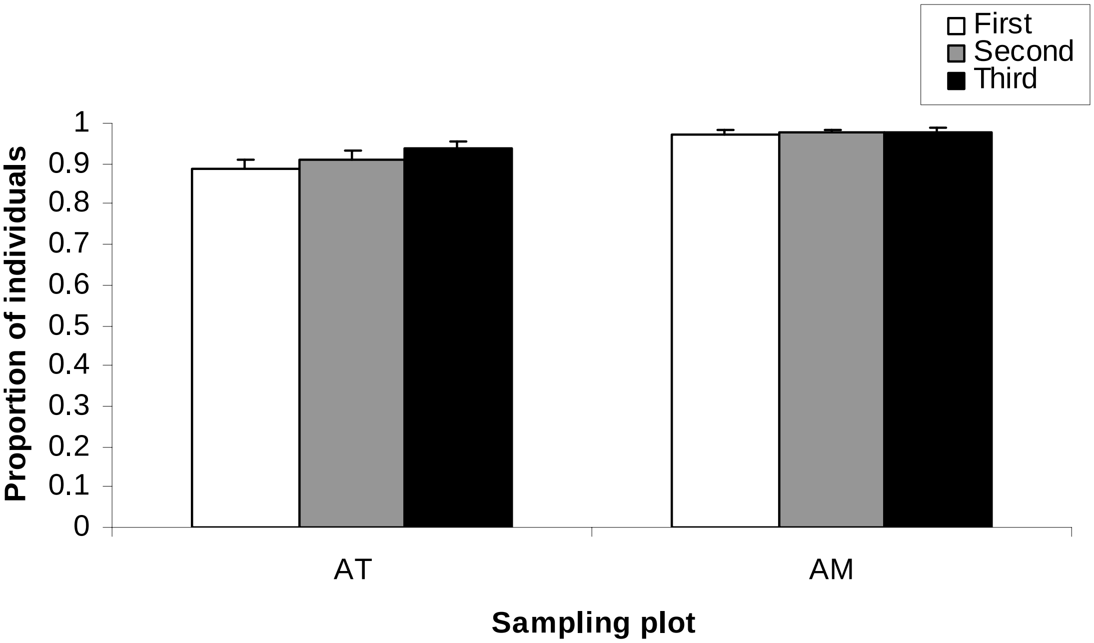
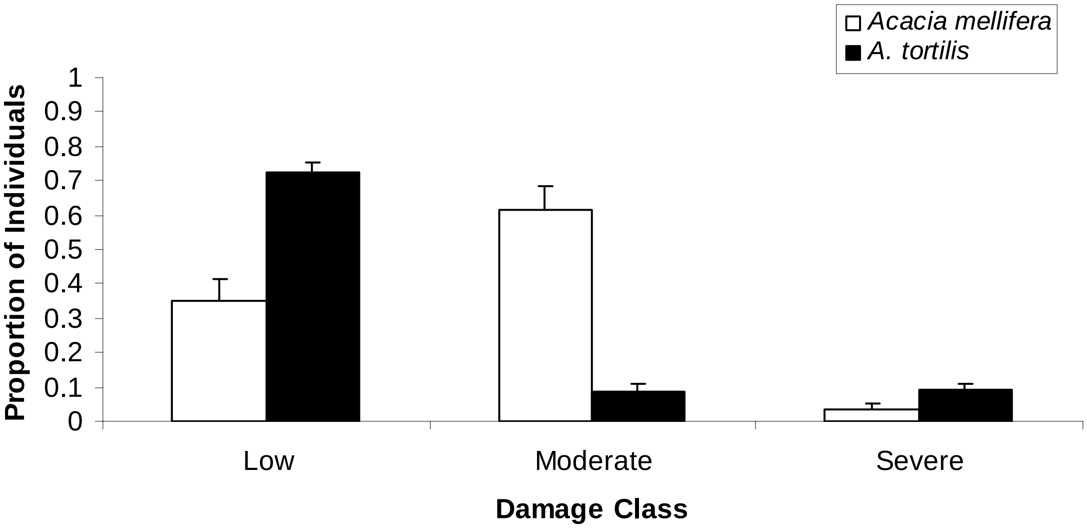


Figure 2.4. The mean proportion (±SE) of individuals with any elephant damage in the AT plot and AM plot for each of the three sampling periods, Ndarakwai Ranch (September 2005 – June 2006). The proportion of trees with elephant damage was significantly different across the sampling periods for the AT plot, but not for AM plot.

a) AT Plot



b) AM Plot

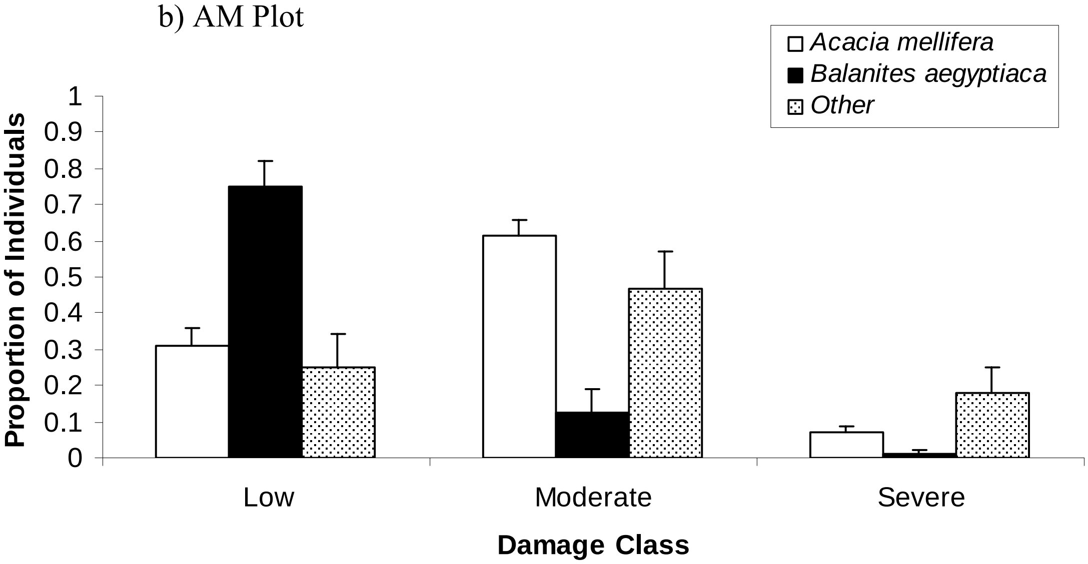


Figure 2.5. The mean (±SE) proportion of individuals in the three damage classes for the two most common species in the AT plot and the two most common species and other species in the AM plot, Ndarakwai Ranch (September 2005 – June 2006).

# Appendix A

## RATE OF POST-PUBERTY MALE ELEPHANT CHEMOSENSORY BEHAVIOR AT NDARAKWAI RANCH, TANZANIA

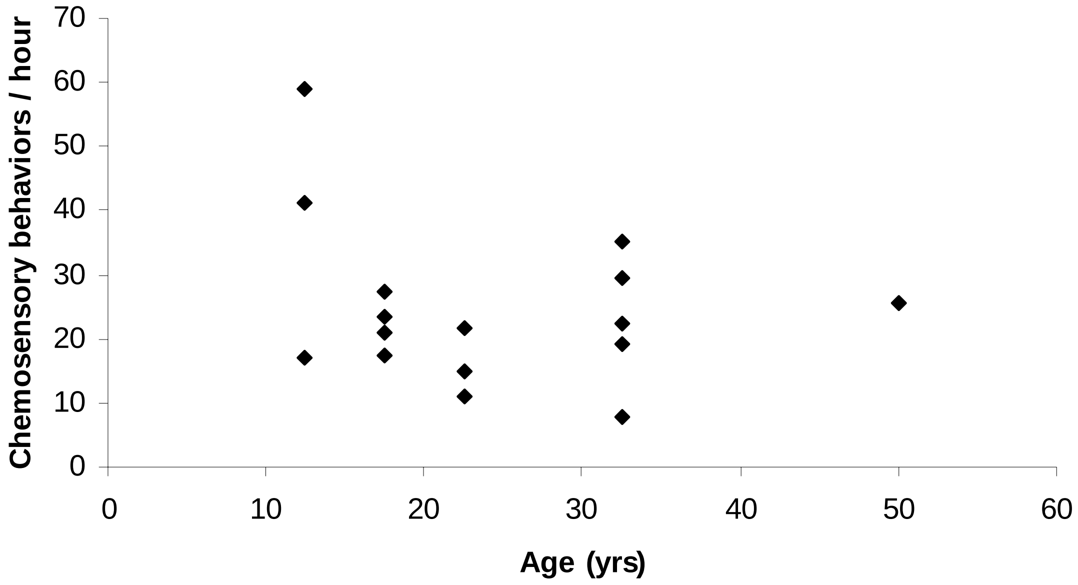


Figure A.1. The rate of chemosensory behaviors per hour and the age of focal elephant for all males that performed any chemosensory behaviors, Ndarakwai Ranch (July 2005 – October 2005).

# Appendix B

## ADDITIONAL WOODY VEGETATION ANALYSES

### Elephant damage and distance from waterhole

Methods followed those in Chapter II (page 41). These data were not included in Chapter II to analyze the relationship between elephant damage to vegetation and transect distance from the waterhole because logistic regression was performed using each individual tree.

The mean transect distance from the waterhole in the AT plot was 543 ± 88 meters ($N = 20$), while in the AM plot it was 1207 ± 79 meters ($N = 20$), and overall it was 875 ± 79 meters ($N = 40$). The range of transect distances was from 110 – 1250 meters in the AT plot and from 410 – 1850 meters in the AM plot. For both plots, transect distance from the waterhole did not have a significant effect on the proportion of all trees with any damage ($F_{1,38} = 0.14$, $p = 0.71$) (Figure B.1), but this was not constant for each plot. In the AT plot, as distance from the waterhole increased, the proportion of all species with any elephant damage increased ($r^2 = 0.26$, $F_{1,18} = 6.34$, $p = 0.02$) (Figure B.2). However, when each species was analyzed individually, the distance from the waterhole had no effect on the proportion of any damage (all $p > 0.05$). In the AM plot there was no relationship between the distance from the waterhole and the proportion of all trees with any damage ($r^2 = 0.13$, $F_{1,18} = 2.61$, $p = 0.12$) (Figure B.3), or between the distance from the waterhole and any damage for each species (all $p > 0.05$).

In the AT plot there were 40 *A. tortilis*, 3 *B. aegyptiaca*, and 1 *A. mellifera* and in the AM plot there were 11 *B. aegyptiaca* and 3 other species that were undamaged. The average distance of these undamaged individuals was significantly greater than the average distance of transects in the AM plot ($t_{32} = 2.38$, $p = 0.02$), but this relationship was not significant for woody vegetation in the AT plot ($t_{64} = 1.02$, $p = 0.29$) or when the two plots were combined ($t_{96} = 0.23$, $p = 0.82$) (Figure B.4).

**New elephant damage and elephant sightings at the waterhole**

Methods followed those in Chapter II (page 41) with the following addition: A distinction was made between old and new elephant foraging to examine difference in elephant damage between sampling periods. The age of the damage (i.e. old or new) was estimated based on the color of the damaged area. I monitored woody vegetation with known damage dates and the new damage color faded after about 3 months. If both old and new damage was present, I recorded the overall tree damage category and the category of the new damage. New damage could equal the overall damage category or be placed in a lower category.

The proportion of individuals with new elephant damage in each of the three sampling periods was not significantly affected by the number of elephants sighted at the waterhole in the three months before the sampling period (all $p > 0.05$) (Table B.1). A trend was evident in the AT plot for a greater proportion of any new damage as elephant sightings per day increased, but it was not significant ($r^2 = 0.07$, $F_{1,1} = 0.14$, $p = 0.78$) (Figure B.5). These results are likely influenced the low number of sampling periods ($n = 3$). Data were not analyzed for the AM plot because elephant numbers were only available before two sampling periods.

Table B.1. The proportion of new elephant damage for each species in the two vegetation sampling plots and the number of elephant sightings at the only permanent waterhole at Ndarakwai Ranch, Tanzania (June, 2005 – June 2006).

| **Species** | **Sampling period** | **N**[1] | **Elephant sightings**[2] | **Damage class** | | | |
|---|---|---|---|---|---|---|---|
| | | | | **Low** | **Moderate** | **Severe** | **Any** |
| Plot 1 | | | | | | | |
| *Am* | 1 | 267 | 2.35 | 0.05 | 0.08 | <0.01 | 0.14 |
| | 2 | 267 | 0.71 | 0.14 | 0.07 | 0 | 0.21 |
| | 3 | 267 | 0.20 | 0.02 | <0.01 | <0.01 | 0.03 |
| *At* | 1 | 429 | 2.35 | 0.06 | <0.01 | <0.01 | 0.07 |
| | 2 | 429 | 0.71 | 0.09 | 0 | 0.01 | 0.11 |
| | 3 | 429 | 0.20 | 0.02 | <0.01 | 0.01 | 0.03 |
| Plot 2 | | | | | | | |
| *Am* | 1 | 447 | 1.92 | 0.10 | 0.02 | 0 | 0.12 |
| | 2 | 447 | 0.18 | 0.07 | 0.03 | <0.01 | 0.11 |
| | 3 | 447 | Unk[3] | 0.13 | 0.02 | 0.01 | 0.16 |
| *Ba* | 1 | 60 | 1.92 | 0.03 | 0.02 | 0 | 0.05 |
| | 2 | 60 | 0.18 | 0 | 0 | 0 | 0 |
| | 3 | 60 | Unk[3] | 0 | 0 | 0 | 0 |
| Other | 1 | 77 | 1.92 | 0.01 | 0 | 0.01 | 0.03 |
| | 2 | 77 | 0.18 | 0.01 | 0.01 | 0 | 0.03 |
| | 3 | 77 | Unk[3] | 0.03 | 0.01 | 0.03 | 0.06 |

[1] N is the total number of individuals for each species of woody vegetation.

[2] Elephant sightings is the number of elephant sightings per day at the waterhole in the 90 days preceding the first sampling period and between sampling periods one and two and two and three. (From Napora 2007).

[3] The number of elephant sightings at the waterhole between sampling periods two and three were not recorded.

See Table 2.1 for Species and Table2.2 for definitions of damage class.

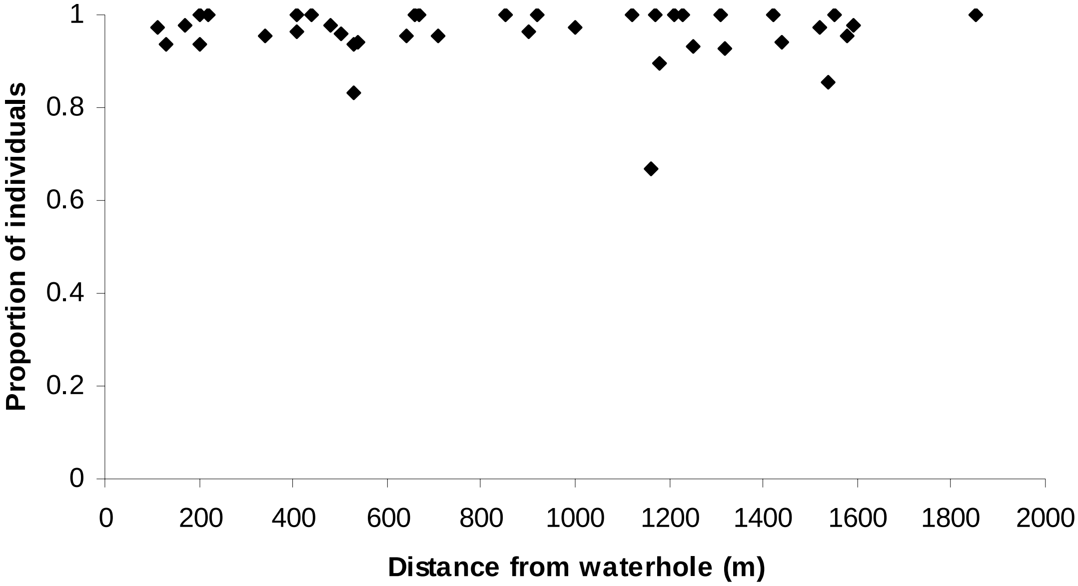


Figure B.1. The proportion of all individuals with damage and the distance from the waterhole for each transect (n = 40) and in both sampling plots, Ndarakwai Ranch (September 2005 – June 2006).

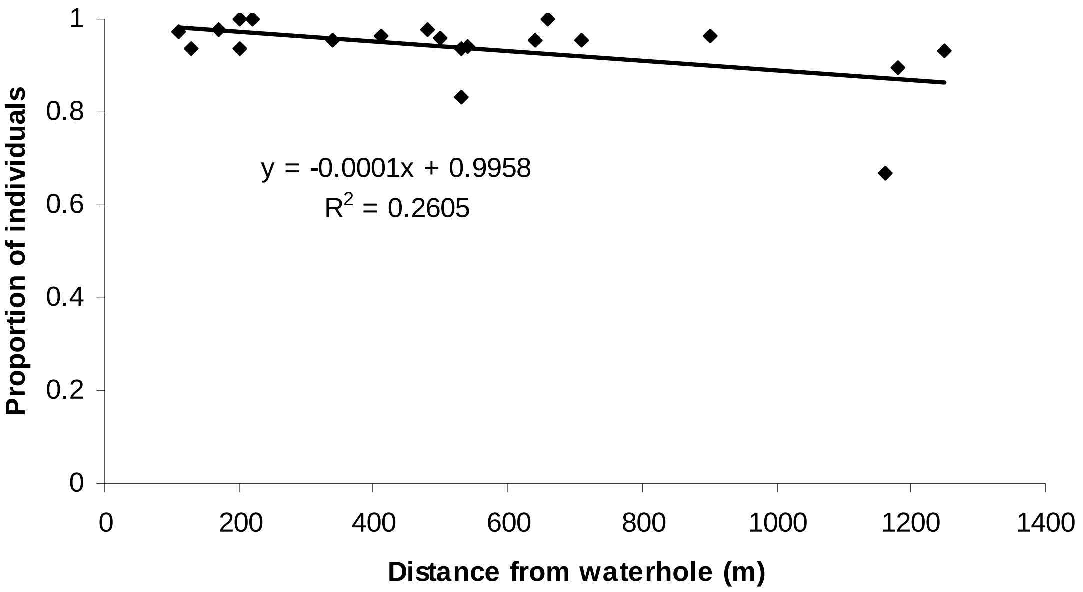


Figure B.2. The proportion of all individuals with damage and the distance from the waterhole for each transect (n = 20) and in the AT plot, Ndarakwai Ranch (September 2005 – June 2006).

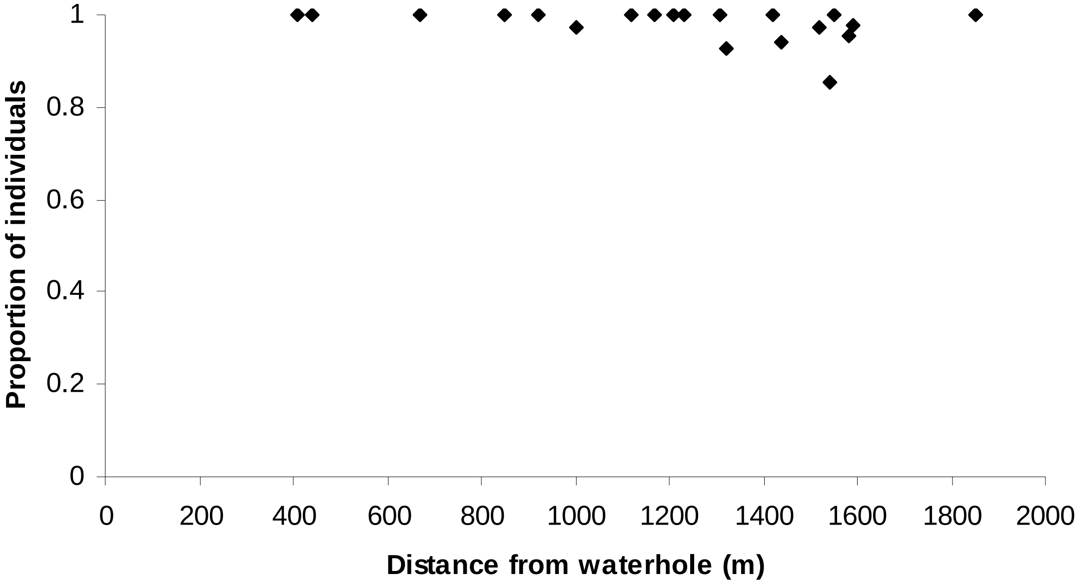


Figure B.3. The proportion of all individuals with damage and the distance from the waterhole for each transect (n = 20) and in the AM plot, Ndarakwai Ranch (September 2005 – June 2006).

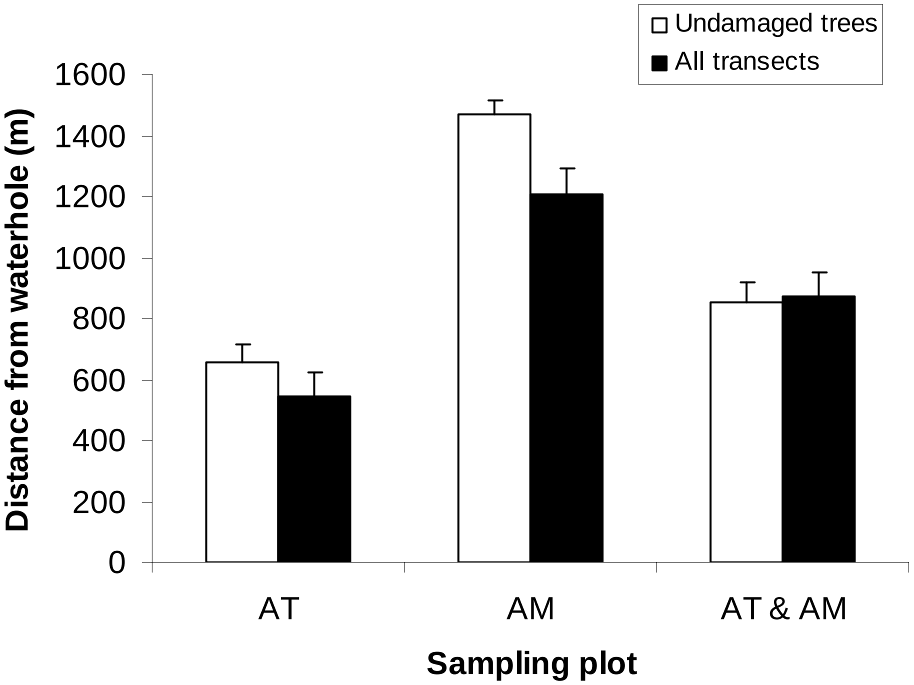


Figure B.4. The mean distance from the waterhole of undamaged trees (n = 54), and for all transects in sampling the AT plot, the AM plot, and the AT and AM plots combined, Ndarakwai Ranch (September 2005 – June 2006). The average distance of undamaged trees was significantly greater than the average distance of transects in the AM plot ($t_{32}$ = 2.38, p = 0.02). There was no significant difference in the AT plot and AM plot combined ($t_{96}$ = 0.23, p = 0.82) or in the AT plot ($t_{64}$ = 1.02, p = 0.29). (AT plot trees = 44, transects = 20; AM plot trees = 14, transects = 20).

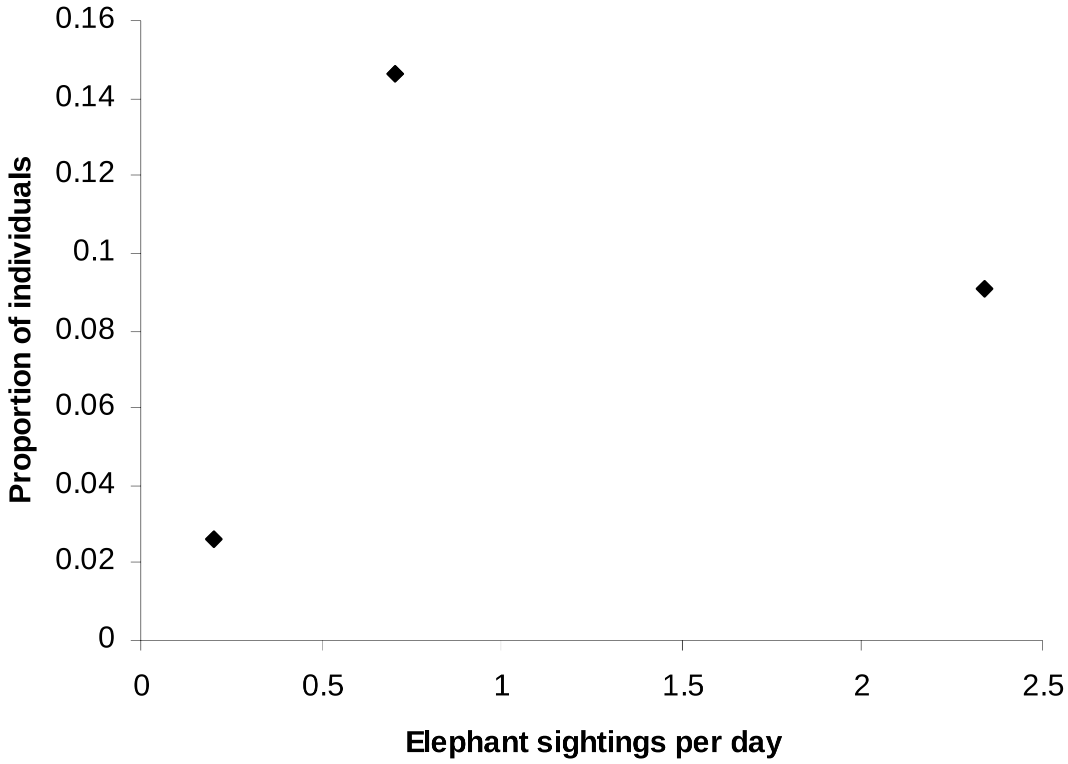


Figure B.5. The relationship between the number of elephant sightings per day at the waterhole and the proportion of individuals in the AT plot with new elephant damage, Ndarakwai Ranch (September 2005 – June 2006). The number of elephant sightings per day was from elephant occurrence at the waterhole 90 days before the first sampling period and between sampling period one and two and two and three.

# APPENDIX C

# REPRESENTATION OF TYPICAL ELEPHANT GROUP SIZE AND ENVIRONMENTAL CONDITIONS DURING THE LONG-DRY AND LONG-WET SEASONS AT NDARAKWAI RANCH, TANZANIA

Figure C.1. Representation of conditions during the long-dry season at Ndarakwai Ranch, northern Tanzania  In the long-dry season, elephants are usually found in smaller groups of close family members and forage is usually scarce (as illustrated by the small family group and brown, patchy grass in this picture).

Figure C.2. Representation of conditions during the long-dry season at Ndarakwai Ranch, northern Tanzania. In the long-wet season, elephants are usually found in large aggregations of extended family groups with adult males present and forage is usually plentiful (as illustrated by the large aggregation of elephants and the thick, greenish grass in this picture).