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THE RELATIONSHIP OF HERPETOFAUNAL COMMUNITY COMPOSITION TO AN ELEPHANT (*LOXODONTA AFRICANA*) MODIFIED SAVANNA WOODLAND OF NORTHERN TANZANIA, AND BIOASSAYS WITH AFRICAN ELEPHANTS

by

NABIL A. NASSERI

(Under the Direction of Bruce A. Schulte)

ABSTRACT

Herpetofauna diversity and richness were compared in areas that varied in the degree of elephant impact on the woody vegetation (Acacia spp.). The study was conducted at Ndarakwai Ranch in northeastern Tanzania. Elephants moving between three National Parks in Kenya and Tanzania visit this property. From August 2007 to March 2008, we erected drift fences and pitfall traps to sample herpetofaunal community and examined species richness and diversity within the damaged areas and in an exclusion plot. I captured 143 individuals comprising 13 species of reptiles in the order Sauria and nine species of anurans. Areas of heavy damage yielded higher species richness than the exclusion plot. Species diversity did not differ between damaged areas and the exclusion plot. Frogs were more abundant in areas of high damage; in contrast, toads were found in lower abundance in the high damaged areas then the exclusion plot. The results support the idea that elephants have a positive influence on herpetofaunal species by creating habitat complexity by modifying the woodland area. In addition to this study, bioassays were conducted on three chemical compounds (cyclohexanone, 2-decanone and 2-nonanone) that could possibly be elephant pheromones. The compounds were tested from August 2007 – April 2008. The compounds were not significantly bioactive, but did yield some interesting results.

INDEX WORDS: African elephant, *Loxodonta africana*, Herpetofauna, Savanna, Diversity, Richness, Amphibians, Reptiles, Tanzania, Ecosystem Engineers, Habitat Modification, Cyclohexanone, 2-Decanone, 2-Nonanone

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B.A. TEXAS A&M - CORPUS CHRISTI, 2006

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

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TABLE OF CONTENTS

ACKNOWLEDGMENTS	5
LIST OF TABLES	7
LIST OF FIGURES	9
RESEARCH OVERVIEW	11
CHAPTER 1: A DESCRIPTION OF THE HERPETOFAUNAL COMMUNITY SAVANNA WOODLAND OF NORTHERN TANZANIA	IN A
ABSTRACT	13
INTRODUCTION	
METHODS	
RESULTS	
DISCUSSION	
REFERENCES	
CHAPTER 2: THE IMPACT OF AFRICAN ELEPHANTS (<i>LOXODONTA AFRI</i> HERPETOFAUNA SPECIES RICHNESS AND DIVERSITY IN A SAVANNA OF NORTHERN TANZANIA	'CANA) ON WOODLAND 46
ABSTRACT	
INTRODUCTION	
METHODS	
RESULTS	
DISCUSSION	
REFERENCES	64
APPENDIX A	

LIST OF TABLES

Table 1.1. Classification of elephant damage to the vegetation (Napora 2007) in drift fence areasat Ndarakwai Ranch, Tanzania from August 2007 – March 2008.28
Table 1.2. Number of individuals of each herpetofaunal species captured at Ndarakwai Ranch,Tanzania from August 2007 – March 2008.29
Table 1.3. Average snout – vent length (SVL) and tail length of herpetofauna captured atNdarakwai Ranch, Tanzania from August 2007 – March 2008.30
Table 1. 4. Reptile species (Class Reptilia) expected to be sampled based on guide books, and if sampled then by what method at Ndarakwai Ranch, Tanzania. (DF = drift fences; $N = 11$) (OS = opportunistic sampling; $N = 17$) (X = not observed; $N = 14$)
Table 1. 5. Species of reptiles (Class Reptilia) observed at Amboseli National Park. The species list was obtained from the National Museum of Kenya database. Seventeen species of reptiles were observed both at Amboseli N.P. and Ndarakwai Ranch (denoted with *)
Table 1. 6.Species of reptiles (Class Reptilia) observed at Arusha National Park. The specieslist was obtained from Razzetti and Msuya 2002. Eleven species of reptiles were observed bothat Arusha N.P. and Ndrakwai Ranch (denoted by *)
Table 2.1. Simpson's diversity index for herpetofaunal species and species richness based on damage level at Ndarakwai Ranch, Tanzania from August 2007 – March 2008
Table 2.2. Dunnett's test comparing the mean (± S.E.) herpetofauna species richness of damagesites to the control site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (*indicates statistical significance)
Table 2.3. Proportion of Sauria species captured within each damage site from August 2007 –March 2008 at Ndarakwai Ranch, Tanzania.71
Table 2.4. Proportion of Anura species captured within each damage site from August 2007 –March 2008 at Ndarakwai Ranch, Tanzania.72
Table 2.5. Dunnett's test comparing the mean (± S.E.) toad abundance of damage sites to the control site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (* indicates statistical significance).73
Table 2.6. Dunnett's test comparing the mean (± S.E.) frog abundance of damage sites to the control site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (* indicates statistical significance)

Table 2.7. Dunnett's test comparing the mean (\pm S.E.) frog species richness of damage sites to the control site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (* indicates	0
statistical significance)	. 75
Table 2.8. Non-parametric analog to Dunnett's test comparing the mean (\pm S.E.) frog Simpson Species Diversity Index of damage sites to the control site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (* indicates statistical significance) (SR = Sum of Ranks)	n's n . 76
Table 2.9. Abundance of frogs and toads captured at Ndarakwai Ranch, Tanzania from Augus 2007 – March 2008.	st . 77
Table 2.10. Trapping days ¹ of each damage site for each month (August 2007 – March 2008 ²) Ndarakwai Ranch, Tanzania.) at . 78

LIST OF FIGURES

Figure 1.1. A. Location of Ndarakwai Ranch in relation to three national parks (map courtesy of Google Maps 2000) B. Map of Ndarakwai Ranch (Spelled Endarakwai Reserve). Note Pafiki
Farm (enclosed by electric fence). C. Map displaying trapping location within Ndarakwai Ranch, Tanzania (H = High Damage; M = Medium Damage; L = Low Damage; C = Control) (Numbers indicate trap number: See Table 2.1, 2.5 and 2.6) *Tree densities were based on visual estimates.
Figure 1.2. Drift fence placed in one the damage categories showing how the drift fence bisects the middle of the pitfall allowing for captures on either end at Ndarakwai Ranch, Tanzania from August 2007 – March 2008
Figure 1.3. Funnel traps located on each side of the drift fence at Ndarakwai Ranch, Tanzania from August 2007 – March 2008
Figure 1.4. Cumulative abundance of herpetofauna captured daily at Ndarakwai Ranch, Tanzania from August 2007 – March 2008
Figure 1.5. Cumulative number of new herpetofauna species captured monthly at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (no trapping occurred from December 2007 – January 2008 due to an increase in elephants)
Figure 1.6. Cumulative number of new species of herpetofauna captured daily at Ndarakwai Ranch, Tanzania from August 2007 – March 2008
Figure 1.7. Photograph of <i>L. laterimaculatus</i> specimen captured at Ndarakwai Ranch, Tanzania on 27 October 2008
Figure 1.8. Photograph of <i>L. picturatus</i> specimen captured at Ndarakwai Ranch, Tanzania on 27 November, 2008
Figure 1.9. Photograph of <i>T. brevicollis</i> specimen captured at Ndarakwai Ranch, Tanzania on 1 October 2008
Figure 1.10. Photograph of <i>P. sudanensis</i> feeding on a large <i>T. brevicollis</i> at Ndarakwai Ranch, Tanzania on 15 March 2008
Figure 1.11. Photograph of <i>L. kilimensis</i> specimen captured at Ndarakwai Ranch, Tanzania on 21 October 2008
Figure 2.1. Mean (± SE) herpetofauna species abundance based on damage site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008

Figure 2.2. Mean (± SE) herpetofauna species richness based on damage site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.	80
Figure 2.3. Mean (± SE) herpetofauna Simpson's Species Diversity Index based on damage sit at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.	te 81
Figure 2.4. Mean (± SE) toad and frog abundance by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.	82
Figure 2.5. Mean (± SE) toad and frog species richness by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.	83
Figure 2.6. Mean (± SE) toad and frog Simpson's Species Diversity Index by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.	84
Figure 2.7. Mean (± SE) skink and non-skink abundance by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.	85
Figure 2.8. Mean (± SE) skink and non-skink species richness by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.	86
Figure 2.9. Mean (± SE) skink and non-skink Simpson's Species Diversity Index by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008	87

RESEARCH OVERVIEW

I conducted research in north Tanzania from May 2007 – May 2008 at Ndarakwai Ranch. My research was comprised of my two main projects as well as continuing data collection for several ongoing projects. My two main projects are the basis of this thesis; however, this section is dedicated to outlining the additional projects on which I worked.

In 2004, Mr. Dhaval Vyas, a previous graduate student, began two long-term projects. One was conducting mammal and bird biodiversity scans at the waterhole and the other was performing Elephant Movement Scans (EMS). Mr. Vyas operationally sectioned the waterhole into four quadrants with five boundary zones (Vyas 2006). The four quadrants were established by cross-sectioning the waterhole using the four cardinal directions. The quadrants are labeled as: Northeast (NE), Northwest (NW), Southeast (SE), and Southwest (SW). The five zones were demarcated by a determined distance (meters) from the edge of the waterhole: Zone 0 (Z0) = waterhole, Zone 1 (Z1) = 10 m, Zone 2 (Z2) = 25 m, Zone 3 (Z3) = 100 m and Zone 4 (Z4) = 400 m. Mammal and bird biodiversity scans were conducted every hour from 0900 h to 1700 h each day or whatever part of the day I was at the platform by the waterhole. Before scans began, abiotic factors were recorded: temperature in the sun and the shade, sunny/overcast, windy/breezy/none. Scans began in Z0 of SW quadrant moving out to Z4 then moving to the next quadrant clockwise. In addition to species counts, state behaviors for each species were recorded (i.e. locomoting, feeding, idle, and drinking). In addition to hourly biodiversity scans, every quarter hour EMS were performed. From the observation deck, I would scan the property west to east for elephants. Hills and other markers were used to state the location of elephants. Elephant numbers and state behaviors were recorded.

Mr. Erek Napora began his research at Ndarakwai Ranch in 2005 and continued the biodiversity scans and the EMS. Mr. Napora also started a long-term vegetation monitoring project. This project focused on elephant damage to vegetation around Ndarakwai Ranch (Napora 2007). Mr. Napora set up 40 vegetation belt transects, with 20 transects in the open savanna ecosystem, which was labeled the *Acacia mellifera* Plot and 20 transects in the savanna woodland ecosystem, called the *Acacia tortilis* Plot. He tagged 1,300 trees in the two sites. The goal of the project was to assess and record any new damage or growth/rejuvenation every three months. A score of 1 - 6 were given to trees based on their damage, where 1 represented no damage and 6 represented an uprooted and dead tree. If tree tags were removed or lost, then the tree was retagged with aluminum tags.

In 2006, Ms. Stacie Castelda continued the long-term projects, but also added another component to the vegetation assessments. Ms. Castelda created a 50 m line transect that bisected the vegetation belt transect to record elephant dung (Castelda 2008). Dung counts can be used to assess elephant densities in an area, but she also was interested in decomposition rates. All dung within a meter of the transect was recorded by counting the number of boluses present, whether the boluses were in a pile or a line, and the circumference. Ms. Castelda also created an ageing scale. Dung within the transect was then marked with paint to tract decomposition and to distinguish new and old dung. Dung counts and decomposition rates also were recorded around the waterhole and the locations were marked on a map.

I continued these projects as best I could while still performing my research. However, due to time and energy needed for keeping my drift fence and traps functional, coupled with duties at the waterhole, I was unable to continue the dung assessments.

A DESCRIPTION OF THE HERPETOFAUNAL COMMUNITY IN A SAVANNA WOODLAND OF NORTHERN TANZANIA

CHAPTER 1

ABSTRACT

When compared to mammals and birds, very little is known of the distribution and ecology of the reptile and amphibians (herpetofauna) species of Tanzania. Most of the sampling has occurred within rainforest ecosystems and mountain ranges with relatively little surveys done in savanna woodlands. Tanzania has 366 herpetofaunal species and over a quarter (26.2%) are endemic to Tanzania but relatively little is known about community composition in specific habitats. With the increase in human population and affiliated decrease in habitat an understanding of their distribution and abundance is important. The objective of the current study was to describe the herpetofaunal community in a northern Tanzania savanna woodland dominated by Acacia tortilis. The study was conducted from August 2007 - March 2008 at Ndarakwai Ranch, a 4,300 ha privately owned property consisting of mixed savanna woodland and open savanna habitat located in the Kilimanjaro District of northern Tanzania. The herpetofaunal community was sampled using drift fences with pitfall traps and by performing observational scans. I captured 143 individuals comprising 13 species of reptiles in the order Sauria and nine species of anurans within my trap locations. I also observed another six species of Sauria, two chelonian species and 11 species of snakes through opportunist sampling.

INTRODUCTION

Little is known about the zoogeography, distribution and ecology of reptile and amphibian (herpetofauna) species in East Africa because of the scarcity of collected specimens and surveys (Spawls et al. 2002; Malonza et al. 2006; Jackson and Blackburn 2007; Menegon et al. 2008). The majority of sampling that has been carried out in Tanzania has been in tropical rain forest or the Eastern Arc Mountain range (Vonesh 1998; Vonesh 2001; Loader et al. 2004). Although savanna woodlands make up the majority of Tanzania's subtropical forest cover (Homewood and Brockington 1999) very few herpetofaunal surveys have occurred within savanna woodlands. Savanna woodlands consist of medium to large deciduous trees that have more or less a canopy of touching trees with a thin woody understory and a ground layer of herbaceous grasses (Frost et al. 1986; Skarpe 1992; Bullock et al. 1995).

Tanzania is classified as a megadiversity nation with 310 species of mammals, 1016 species of birds, 245 species of reptiles and 121 amphibian species with reasonably high endemism (13 mammals, 13 birds, 56 reptiles and 40 amphibians) (World Resource Institute 1995; Shemwetta and Kideghesho 2000). Compared to other vertebrate species studied in East Africa, herpetofauna species have received the least amount of attention (Vonesh 1998). With over a quarter (26.2%) of the herpetofaunal species endemic to Tanzania, an understanding of their distribution and abundance is important especially with the increase in human population and concomitant decrease in habitat. Inventories have focused on national parks (Moehlman et al. 1995), however, determining the species composition outside of parks also is important for conservation and management planning (Weber et al. 2001).

Northern Tanzania is comprised primarily of dry savanna with an elevation between 1,200 m to 2,400 m (Spawls et al. 2002). This region contains numerous parks, including Serengeti National Park, Lake Manyara National Park, Tarangire National Park, the Masai

Steppe, Arusha National Park and Mt. Kilimanjaro National Park. Spawls et al. (2002) and Channing and Howell (2006) have provided estimated distribution ranges of species in this region; however, due to an increase in villages and towns their true distributions are unknown.

The objective of the current study was to describe the herpetofaunal community in a northern Tanzania savanna woodland dominated by *Acacia tortilis*. Guidebooks provide general range information for many species of amphibians and reptiles in north Tanzania, but very few studies have been conducted that report the composition of the herpetofauna outside of the national parks within this region and in the common habitat of a savanna woodland.

METHODS

Study Site

The study was conducted at Ndarakwai Ranch, which is located in the Kilimanjaro District of northern Tanzania in the Sita District (S03°00.663' E37°00.113'). This part of Tanzania experiences a bimodal seasonal pattern with a short wet and dry season and a long wet and dry season (Castelda 2008). Ndarakwai Ranch is approximately 4,300 ha consisting of mixed savanna woodland and open savanna habitat and located between three national parks: Amboseli National Park in Kenya to the north, Mt. Kilimanjaro National Park to the east and Arusha National Park to the south (Vyas 2006; Napora 2007) (Fig. 1.1A). Prior to Tanzanian independence in 1961, Ndarakwai Ranch belonged to German and then English colonials. Once Tanzania regained independence, the area was taken over by Tanzania Breweries Ltd. and was used for agriculture and by pastoralist (Vyas 2006). Tanzania Breweries Ltd. eventually abandoned the land and the area was taken over by squatters (Peter Jones per. comm.). In 1994, Peter Jones leased out the land and created Ndarakwai Ranch and turned the land into a privately owned, semi-protected unfenced conservation area. The only fenced part of Ndarakwai Ranch is

Rafiki Farm (Fig. 1.1B). Rafiki is a 250 ha area on Ndarakwai Ranch that has been fenced to exclude most megafauna since 1998. Agriculture and livestock grazing also are not permitted in Rafiki. Rafiki was originally created to be used as a rehabilitation area for injured or orphaned wildlife. Previous to and during the study, the only large herbivore in Rafiki was an orphaned eight year old elephant. The orphaned elephant was not a permanent resident but was allowed into Rafiki during the day for a couple hours. Rafiki also contained a few homes for employees of Ndarakwai Ranch. On the southern end of the ranch, there is a permanent 4,300 m² manmade waterhole. The waterhole is at times the only water source for 15 km (Napora 2007). The waterhole is fed by a diversion from the Ngare Nairobi River and it attracts a diverse array of wildlife throughout the year (Vyas 2006).

From August 2007 to March 2008, herpetofaunal identity and abundance were recorded at Ndarakwai Ranch in wooded areas where the trees had varying degrees of impact by elephants (Table 1.1). The area is a mixed woodland habitat primarily composed of *Acacia tortilis* and *A. mellifera* with *A. tortilis* being the dominant species (Napora 2007). In order to make sure captures were not influenced by tree species, all 12 drift fences were placed in areas where the only tree species was *A. tortilis*.

Capturing Method

Non-lethal herpetofaunal traps and opportunistic observation were used to sample the herpetofaunal community. Opportunistic observations were carried out by scanning the ground and surrounding vegetation while walking around Ndarakwai Ranch, primarily between my residence, Kasablanca, and the waterhole (approximately 1.9 km) (Fig. 1.1C). The herpetofaunal community was sampled using drift fences with pitfalls and funnel traps. Drift fences were 10 m

long and 0.5 m high. Drift fences were constructed using plastic sheeting and wooden stakes. The stakes were attached at the beginning of the plastic sheeting and at 2 m intervals. The base of the plastic sheeting was buried 20 cm in the soil. Buckets (20 L) were buried at each end of the drift fence between the first and second stake to serve as pitfalls. The lip of the bucket was flush with the ground. The drift fence ran over the middle of the buckets allowing for capture on either side of the drift fence (Fig. 1.2). Holes were made at the bottom of the buckets as well as on the sides to allow rainwater to drain out. In addition, leaf litter and twigs were placed in the buckets to provide refuge for captured individuals. Twenty-four pitfall traps and 120 m of drift fence were used in the study.

Funnel traps constructed from mosquito wire or window screening (Gaskell 2007) were placed on both sides of the drift fence (Fig. 1.3). The funnel traps were placed at the midpoint of the drift fence between the two pitfalls. Cardboard sheets were leaned against the fence and over the funnel traps to provide shelter from the sun. Funnel traps were very ineffective. I also initially attempted to set sticky and cloth traps in trees, these sticky and cloth traps were laborintensive and were never successful. Opportunistic visual sampling was carried out when approaching trap locations. All captured individuals were placed in collection bags and morphological measurements taken at the research station. The next day, individuals were returned and released 15 m due west of the drift fence from which they were captured.

Data Collection

Because of the high traffic of large mammals that traveled through the area, drift fences were destroyed occasionally and needed repair. Pitfalls were closed until a new drift fence was installed. For two months, from December 2007 – January 2008, a large number of elephants

were present at Ndarakwai Ranch and trapping was not feasible, so the traps were closed. When traps were opened, they were checked on a daily basis. There were 1,976 trapping days (number of pitfalls open times number of trapping days); due to the ineffectiveness of funnel traps, they were not used in the calculation of trapping days.

Using field guides, captured herpetofauna were identified to the lowest taxonomic level possible (Spawls et al. 2002; Bauer 2003; Channing and Howell 2006), cataloged and photographed. There is debate as to the correct taxonomy for the "typical skinks." Guidebooks use both the genus *Mabuya* and *Trachylepis* (Spawls et al. 2002; Branch 2005), with the most current literature classifying them as *Trachylepis* (Bauer 2003; Malonza et al. 2006), and I followed this nomenclature. A hand ruler was used to measure snout to vent length (SVL) (mm) and from vent to tip of tail (mm) (Simmons 2002). Notes were made on tail re-growth if tails were broken. A hand held PescolaTM spring scale (30 g and 60 g) was used to measure mass (g). Captured specimens were uniquely marked (toe-clipped and marked with non-toxic paint) following accepted standard methods to identify recaptures (Clark 1971; Howard 1978; Dodd 1993; Johnson 2005; Winne et al. 2006).

RESULTS

Herpetofaunal Community Characteristics

From August 2007 to March 2008, 141 herpetofaunal individuals were captured in pitfalls and funnel traps, and two individuals were obtained by visual observation and opportunistic sampling within the trapping areas. There were 1,976 trap days yielding a trap success of 7.2%. The 143 captured individuals were comprised of 13 species of saurians and nine species of anurans (Table 1.2). With only one major break in December and January, sampling was continued throughout the study period (Fig. 1.4). With the advent of rains in

October individuals from new species were captured (Fig. 1.5). Individuals from new species were still being captured at the end of the study (Fig.1.6). In addition to herpetofauna being sampled within the trapping locations, there were an extra six species of saurians, two chelonian species and 11 species of snakes sampled through opportunistic sampling outside of the trapping locations. However, these additional 19 species were not included in the analysis only those sampled within the trap locations.

The majority of herpetofaunal species sampled in this study were expected to be found based on distribution maps (Spawls et al. 2002). However, four species (two species of geckos and two species of skinks) were observed in this study for which there were no or only sporadic records in this region. The side-spotted dwarf gecko (*Lygodactylus laterimaculatus*) is an East African endemic with records only from Voi and the Taita Hills in Kenya and around Moshi, Tanzania (distance from Ndarakwai Ranch: 170 km, 150 km and 60 km, respectively) (Fig. 1.7). The typical length of an adult from this species is 50 - 70 mm (Spawls et al. 2002); the individual I captured had an SVL of 27 mm with a total length of 52 mm (Table 1.3).

The white-headed dwarf gecko (*Lygodactylus picturatus*) is another endemic East African dwarf gecko that is similar to *L. laterimaculatus*. Only one specimen of *L. picturatus* was captured in my traps, but they were prominent on the sisal plants (*Agave sisalana*) around Ndarakwai Ranch (Fig. 1.8). The specimen captured had an SVL of 31 mm and a total length of 64 mm (Table 1.3).

The short-necked skink (*Trachylepis brevicollis*) is a large, robust skink with an typical total length of 180 - 260 mm and a maximum length of 320 mm (Fig. 1.9). Once again, only one specimen was captured in my traps, but I observed several killed on the side of a road and

witnessed a northern striped-bellied sand snake (*Psammophis sudanensis*) feeding on one (Fig. 1.10). The individual captured had an SVL of 151 mm and a total length of 303 mm (Table 1.3).

The last species of note is the Kilimanjaro five-toed skink (*Leptosiaphos kilimensis*), which is found in the Usambara and Uluguru Mountain Range (distance from Ndarakwai Ranch is approximately 200 km and 400 km, respectively) (Fig. 1.11). This is a small fossorial skink with a typical total length of 100 - 150 mm (50 to 70% of total length is from the tail). The only individual captured had a SVL of 34 mm and a total length of 55 mm (Table 1.3), but the tail had been broken off.

DISCUSSION

The objective of this study was to describe the herpetofaunal community within an *Acacia* dominated woodland in northern Tanzania. Solely based on distribution maps from the most recent guidebooks, this region is represented by 21 different species of saurians and 19 species of anurans (Spawls et al. 2002; Channing and Howell 2006). In the present study, I sampled nine of the 21 species of saurians, representing 42.9% of the expected species of saurians (Table 1.4). However, I did sample four species that were not expected to be found in this area.

Of the four unexpected species sampled, two species are in the genus *Lygodactylus* and both are endemic to East Africa. *Lygodactylus* species are unique geckos in that they are diurnal and most are territorial, living in small colonies where there is one dominant male with several females and juvenile males (Spawls et al. 2002). Very little is known of the behavior or natural history of *L. laterimaculatus*. I only captured one specimen within my trap sites, but there was a colony of 4 - 5 individuals inhabiting a large mammal observation deck at a waterhole. My observations suggest that they are more crepuscular than diurnal as the only time I observed these geckos was at dusk, unless it was raining. In addition, the specimen I captured was feeding on a line of ants at the bottom of an *A. tortilis* tree. *Lygodactylus picturatus* is a much more common species found along low elevation (ca. 500 m) coastal woodlands from Kenya to northeastern Tanzania (Spawls et al. 2002). *L. picturatus* is on the IUCN near threatened list, but their actual distribution and abundance is unclear due to confusion over taxonomy. They were very common on sisal plants. Sisal is not a native plant species, but it was introduced to Tanzania as a cash crop in 1893 (Sabea 2001). The plants were used to make rope and were grown all over Tanzania. This may explain how it was introduced at Ndarakwai Ranch. *L. picturatus* and *L. laterimaculatus* are arboreal species so the sampling method used here was not appropriate to capture these species and they may be more abundant on the surrounding vegetation.

Range extensions were documented for two species of skinks. *Trachylepis brevicollis* is a large robust skink common throughout Kenya into eastern Uganda and up through North Africa. However, there are sporadic records from three sites in north-central Tanzania (Spawls et al. 2002). They are largely terrestrial and use burrows and fallen logs as refugia. The specimen captured was in an area of heavy elephant damage where a large tree was uprooted with a lot of downed logs and possible burrow sites. The Kilimanjaro five-toed skink (*L. kilimensis*) is a crepuscular species found in the leaf litter of rain forests (Usambara and Uluguru Mountains in Tanzania) and in the highlands of Kenya (Taita Hills) (Spawls et al. 2002). The lone specimen from the present study was captured in an area of low tree damage. The canopy cover and higher leaf litter levels found in savanna locations with less disturbance by large ungulates and other megafauna (Sankaran and Augustine 2004; Pringle 2008) may provide habitat similar to that of the rainforests and highlands.

In addition to the four previously discussed species there were 13 species sampled within my study site; however, I failed to sample 12 species that were expected to be in the study area. Five of the species I did not sample were arboreal species. Hence, I abandoned arboreal traps. I did observe four of these arboreal species through opportunistic sampling while walking around Ndarakwai Ranch, so they were present in the area (Table 1.4). The seven other species expected to be found were terrestrial species. I observed two of these species not within my trap locations at Ndarakwai Ranch. One species I did not observe is recorded to be nocturnal but also non-active during dry periods and only emerges during the rainy season (*Holodactylus africanus*) (Spawls et al. 2002). Three species (*Pachydactylus turneri*, *Cordylus beraduccii* and *Gerrhosaurus major*) that I did not observe inhabit rock outcrops, which were not present within my study area; the other species was *G. nigrolineatus* a shy, secretive plated lizard that is rarely seen (Spawls et al. 2002).

The distribution maps of anurans used in this study only provided information on where the species were known to occur, i.e. valid specimen voucher, and not where the species actually may occur (Channing and Howell 2006). Therefore, I am using these distribution maps very conservatively and only as a reference. Based on this information, 19 species of anurans could be expected within my study sites. I sampled a total of nine species of anurans, with one species that I could not identify, which I am currently in contact with Dr. Kim Howell on obtaining a positive identification. I sampled 47.4% of the expected species found within my study area. Since I only sampled terrestrial habitats, I missed on sampling any of the strictly aquatic species.

I captured two species that are aquatic, *X. victorianus* and the mascarene ridged frog (*Ptychadena mascareniensis*). Both of these species were captured after heavy rains, so they may have left their water source in search of new breeding grounds or food. African clawed

frogs use permanent water sources during the dry seasons, but as the heavy rains approach they disperse looking for ephemeral breeding pools where breeding conditions may be improved (Channing and Howell 2006), i.e. less current from a rushing stream due to flooding. *P. mascareniensis* feeds on an array of insects, especially winged ants and termites. As the rains begin, termites begin to disperse in swarms to establish new colonies (Dial and Vaughan 1987; Korb and Linsenmair 2001). I only captured two specimens of *P. mascareniensis*; however, they were both after rains and in areas of high tree damage. Dispersal morphs of termites may be targeting dead wood to set up new colonies, and their congregation may attract mascarene ridged frogs. Mascarene ridged frogs also are preyed upon by a number of bird species and tend to flee from water into undergrowth (Channing and Howell 2006). When foraging far away from their territory, areas of heavy damage would provide necessary refuge.

This study documented 22 species of herpetofauna including four rare species. In addition, six species of saurians, 11 species of serpents and two chelonian species were observed at Ndarakwai Ranch increasing the total to 41 species of herpetofauna, 32 reptile species (Table 1.4) and nine species of amphibians. However, there may be more species here then observed, since I was still sampling new species at the end of my research (Fig. 1.6). Within a 4,300 ha area, I sampled a relatively small area focusing primarily on terrestrial species. Aquatic and arboreal species were not sampled efficiently. Yet, the species recorded here are important because they inhabit an area that is surrounded by villages. With human populations increasing and contributing to habitat loss, knowing the distribution of these species, especially outside of national parks or reserves, is crucial for management activities. As an example, there are 32 species of reptiles at Ndarakwai Ranch, which is slightly more than Amboseli N.P. (25 species; National Museum of Kenya; Table 1.5) and Arusha N.P. (26 species; Razzetti and Msuya 2002;

Table 1.6) (observed species only). Ndarakwai Ranch seems to be managed effectively, and there is now a base for future studies to compare if land practices or climatic factors change.

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Damage Category	Operational Definition
Low	No damage to main trunk and with minimal damage to branches and
2011	foliage
Medium	Damage to main trunk (not pushed over) and greater than 50% of
Wiedrum	branches and foliage damaged
High	Main trunk pushed over and/or uprooted

Table 1.1. Classification of elephant damage to the vegetation (Napora 2007) in drift fence areas at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.

Order	Family	Species	High	Medium	Low	Control
REPTILIA						
Sauria	Agamidae	Agama agama	1	1		
Sauria	Gerrhosauridae	Gerrhosaurus				1
		flavigularis				1
Sauria	Gekkonidae	Hemidactylus	2	1	3	
a :	0.11 .1	squamulatus	_	-	-	
Sauria	Gekkonidae	Lygodactylus			1	
Courie	Californidaa	laterimaculatus				
Sauria	Gerkonidae	Lygoaaciyius	1			
Sauria	Lacertidae	piciuraius Latasia				
Sauria	Lacentidae	longicuadata	1	4		3
Sauria	Scincidae	Lentosianhos				
Suuriu	Semerade	kilimensis			1	
Sauria	Scincidae	Lvgosoma afrum	2	1	1	1
Sauria	Scincidae	Lygosoma	-	2		2
		sundevalli	I	2		2
Sauria	Scincidae	Trachylepis	1			
		brevicollis	1			
Sauria	Scincidae	Trachylepis		1	1	
		striata		1	1	
Sauria	Scincidae	Trachylepis varia	1	2	4	
Sauria	Scincidae	Panaspis	6	3	1	9
		wahlbergii		-	-	
		Total	16	15	12	16
AMPHIBIA			-	1.5	-	10
Anura	Butonidae	Bufo gutturalis	5	17	2	12
Anura	Buionidae	Bufo xeros	2	3	2	4
Anura	Ranidae	Cacosternum sp.	1			
Allula	Kalliuae	riychuuenu mascaronionsis	2			
Anura	Ranidae	Tomonterna				
Allula	Kallitat	tandvi	2	1		
Anura	Hyperoliidae	Kassina				
7 mara	nyperonnaae	senegalensis	6	3	1	1
Anura	Hvperoliidae	Leptopelis				
) [bocagii	1			
Anura	Pipidae	Xenopus	7		7	
		victorianus	/		/	
Anura	Unknown	Unknown	1			
		Total	25	24	17	17

Table 1.2. Number of individuals of each herpetofaunal species captured at Ndarakwai Ranch,Tanzania from August 2007 – March 2008.

Species	$SVL \pm S.E. (mm)$	Tail Length (mm)
Sauria		
Agama agama	75.0	100.0
Gerrhosaurus flavigularis	141.0	345.0
Hemidactylus squamulatus	41.0 (± 4.0)	16.4 (± 4.2)
Lygodactylus laterimaculatus*	27.0	25.0
Lygodactylus picturatus*	31.0	33.0
Latasia longicuadata	83.1 (± 2.2)	181.1 (± 20.5)
Leptosiaphos kilimensis*	34.0	21.0
Lygosoma afrum	85.0 (± 13.5)	45.4 (± 11.9)
Lygosoma sundevalli	93.2 (± 17.0)	50.2 (± 5.8)
Trachylepis brevicollis*	151.0	152.0
Trachylepis striata	68.0 (± 30.0)	81.0 (± 71.0)
Trachylepis varia	46.8 (± 3.6)	42.33 (± 13.9)
Panaspis wahlbergii	$38.9 (\pm 0.9)$	35.9 (± 3.9)
Anura		
Bufo gutturalis	$60.7 (\pm 4.6)$	
Bufo xeros	$65.0(\pm 3.9)$	
Cacosternum sp.	18.0	
Ptychadena mascareniensis**		
Tomopterna tandyi	40.3 (± 4.2)	
Kassina senegalensis	$41.6 (\pm 1.2)$	
Leptopelis bocagii	49.0	
Xenopus victorianus	61.5 (± 3.8)	
Unknown	15.0	

Table 1.3. Average snout – vent length (SVL) and tail length of herpetofauna captured at Ndarakwai Ranch, Tanzania from August 2007 – March 2008. -

* denotes rare species** denotes dead specimen

<u> </u>		~	
Order	Family	Species	Observed
Sauria	Agamidae	Agama agama	DF
Sauria	Gekkonidae	Hemidactylus brooki	OS
Sauria	Gekkonidae	Hemidactylus mabouia	OS
Sauria	Gekkonidae	Hemidactylus squamulatus	DF
Sauria	Gekkonidae	Holodactylus africanus	Х
Sauria	Gekkonidae	Lygodactylus capensis	OS
Sauria	Gekkonidae	Lygodactylus laterimaculatus	OS
Sauria	Gekkonidae	Lygodactylus picturatus	DF
Sauria	Gekkonidae	Pachydactylus turneri	Х
Sauria	Gekkonidae	Pachydactylus tuberculosus	Х
Sauria	Scincidae	Leptosiaphos kilimensis	DF
Sauria	Scincidae	Lygosoma afrum	DF
Sauria	Scincidae	Lygosoma sundevalli	DF
Sauria	Scincidae	Panaspis wahlbergii	DF
Sauria	Scincidae	Trachylepis brevicollis	DF
Sauria	Scincidae	Trachylepis planifrons	OS
Sauria	Scincidae	Trachylepis striata	DF
Sauria	Scincidae	Trachylepis varia	DF
Sauria	Lacertidae	Cordylus beraduccii	Х
Sauria	Lacertidae	Heliobolus spekii	OS
Sauria	Lacertidae	Latasia longicuadata	DF
Sauria	Lacertidae	Nucrus boulengeri	OS
Sauria	Gerrhosauridae	Gerrhosaurus flavigularis	DF
Sauria	Gerrhosauridae	Gerrhosaurus major	Х
Sauria	Gerrhosauridae	Gerrhosaurus nigrolineatus	Х
Serpentes	Boidae	Python natalensis	OS
Serpentes	Colubridae	Crotaphopeltis hotamboeia	Х
Serpentes	Colubridae	Dasypeltis scabra	Х
Serpentes	Colubridae	Dispholidus typus	Х
Serpentes	Colubridae	Lamprophis fuliginosus	OS
Serpentes	Colubridae	Philothamnus battersbyi	OS
Serpentes	Colubridae	Philothamnus semivariegatus	Х
Serpentes	Colubridae	Prosymna stuhlmanni	Х
Serpentes	Colubridae	Psammophis mossambicus	OS
Serpentes	Colubridae	Psammophis sudanensis	OS
Serpentes	Colubridae	Rhamphiophis rostratus	OS
Serpentes	Colubridae	Telescopus semiannulatus	Х
Serpentes	Elapsoidea	Dendroaspis polylepis	OS
Serpentes	Elapsoidea	Naja haje	OS
Serpentes	Elapsoidea	Naja nigricollis	OS
Serpentes	Leptotyphlopidae	Leptotyphlops scutifrons	DF
Serpentes	Typhlopidae	Typhlops lineolatus	Х

Table 1. 4. Reptile species (Class Reptilia) expected to be sampled based on guide books, and if sampled then by what method at Ndarakwai Ranch, Tanzania. (DF = drift fences; N = 11) (OS = opportunistic sampling; N = 17) (X = not observed; N = 14).

Table 1. 4 Continued Reptile species (Class Reptilia) expected to be sampled based on guide books, and if sampled then by what method at Ndarakwai Ranch, Tanzania. (DF = drift fences; N = 11) (OS = opportunistic sampling; N = 17) (X = not observed; N = 14).

Order	Family	Species	Observed	
Serpentes	Viperidae	Bitis arietans	OS	
Testudines	Pelomedusidae	Pelomedusa subrufa	OS	
Testudines	Testudinidae	Geochelone pardalis	OS	
Testudines	Testudinidae	Kinixys spekii	Х	

Order	Family	Species
Sauria	Agamidae	Agama agama*
Sauria	Chamaeleonidae	Chamaeleo roperi
Sauria	Gekkonidae	Hemidactylus brooki*
Sauria	Gekkonidae	Hemidactylus mabouia*
Sauria	Gekkonidae	Hemidactylus squamulatus*
Sauria	Gekkonidae	Hemidactylus platycephalus
Sauria	Scincidae	Lygosoma sundevalli
Sauria	Scincidae	Trachylepis brevicollis*
Sauria	Scincidae	Trachylepis varia*
Sauria	Lacertidae	Heliobolus spekii*
Sauria	Lacertidae	Latasia longicuadata*
Sauria	Gerrhosauridae	Gerrhosaurus flavigularis*
Serpentes	Atractaspididae	Aparallactus jacksoni
Serpentes	Colubridae	Dispholidus typus
Serpentes	Colubridae	Lamprophis fuliginosus*
Serpentes	Colubridae	Lycophidion capense
Serpentes	Colubridae	Philothamnus battersbyi*
Serpentes	Colubridae	Psammophis angolensis
Serpentes	Colubridae	Psammophis mossambicus*
Serpentes	Colubridae	Psammophis sudanensis*
Serpentes	Elapsoidea	Dendroaspis polylepis*
Serpentes	Elapsoidea	Naja haje*
Serpentes	Elapsoidea	Naja nigricollis*
Serpentes	Elapsoidea	Naja pallid
Serpentes	Leptotyphlopidae	Leptotyphlops scutifrons*

Table 1.5. Species of reptiles (Class Reptilia) observed at Amboseli National Park. The species list was obtained from the National Museum of Kenya database. Seventeen species of reptiles were observed both at Amboseli N.P. and Ndarakwai Ranch (denoted with *).

Order	Family	Species
Sauria	Agamidae	Agama agama*
Sauria	Chamaeleonidae	Bradypodion tavetanum
Sauria	Chamaeleonidae	Chamaeleo gracilis
Sauria	Gekkonidae	Pachydactylus mabouia
Sauria	Gekkonidae	Pachydactylus turneri
Sauria	Scincidae	Lygosoma afrum*
Sauria	Scincidae	Panaspis wahlbergii*
Sauria	Scincidae	Trachylepis striata*
Sauria	Scincidae	Trachylepis varia*
Sauria	Lacertidae	Adolfus jacksoni
Sauria	Lacertidae	Nucrus boulengeri*
Serpentes	Atractaspididae	Atractaspis bibronii
Serpentes	Boidae	Python natalensis*
Serpentes	Colubridae	Crotaphopeltis hotamboeia
Serpentes	Colubridae	Dasypeltis scabra
Serpentes	Colubridae	Duberria lutrix
Serpentes	Colubridae	Lamprophis fuliginosus*
Serpentes	Colubridae	Lycophidion capense
Serpentes	Colubridae	Natriciteres olivacea
Serpentes	Colubridae	Thelotornis capensis
Serpentes	Elapsoidea	Dendroaspis angusticeps
Serpentes	Elapsoidea	Elapsoidea loveridgei
Serpentes	Elapsoidea	Naja haje*
Serpentes	Leptotyphlopidae	Leptotyphlops scutifrons*
Serpentes	Viperidae	Bitis arietans*
Testudines	Testudinidae	Geochelone pardalis

Table 1. 6. Species of reptiles (Class Reptilia) observed at Arusha National Park. The species list was obtained from Razzetti and Msuya 2002. Eleven species of reptiles were observed both at Arusha N.P. and Ndarakwai Ranch (denoted by *).





B.



C.

Figure 1.1. A. Location of Ndarakwai Ranch in relation to three national parks (map courtesy of Google Maps 2009). B. Map of Ndarakwai Ranch (Spelled Endarakwai Reserve). Note Rafiki Farm (enclosed by electric fence). C. Map displaying trapping location within Ndarakwai Ranch, Tanzania (H = High Damage; M = Medium Damage; L = Low Damage; C = Control) (Numbers indicate trap number: See Table 2.1, 2.5 and 2.6) *Tree densities were based on visual estimates.


Figure 1.2. Drift fence placed in one the damage categories showing how the drift fence bisects the middle of the pitfall allowing for captures on either end at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 1.3. Funnel traps located on each side of the drift fence at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 1.4. Cumulative abundance of herpetofauna captured daily at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 1.5. Cumulative number of new herpetofauna species captured monthly at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (no trapping occurred from December 2007 – January 2008 due to an increase in elephants).



Figure 1.6. Cumulative number of new species of herpetofauna captured daily at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 1.7. Photograph of *L. laterimaculatus* specimen captured at Ndarakwai Ranch, Tanzania on 27 October 2008.



Figure 1.8. Photograph of *L. picturatus* specimen captured at Ndarakwai Ranch, Tanzania on 27 November, 2008.



Figure 1.9. Photograph of *T. brevicollis* specimen captured at Ndarakwai Ranch, Tanzania on 1 October 2008.



Figure 1.10. Photograph of *P. sudanensis* feeding on a large *T. brevicollis* at Ndarakwai Ranch, Tanzania on 15 March 2008.



Figure 1.11. Photograph of *L. kilimensis* specimen captured at Ndarakwai Ranch, Tanzania on 21 October 2008.

THE IMPACT OF AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*) ON HERPETOFAUNA SPECIES RICHNESS AND DIVERSITY IN A SAVANNA WOODLAND OF NORTHERN TANZANIA

CHAPTER 2

ABSTRACT

Ecosystem engineers create and maintain ecosystems through physically changing living or non-living materials from one state to another. In Africa, no other animal fulfills this role like the African elephant. Elephants remove dominant hardy vegetation replacing it with quick growing vegetation, transforming dense woodlands into open grasslands. However, very little is known of the relationship between modified habitats and the species composition within them. The objective of the present study was to sample the reptile and amphibian (herpetofaunal) community within an Acacia habitat that varied in the degree of elephant impact in northern Tanzania. If elephant foraging was only modifying but not degrading or enriching the habitat, then herpetofauna species abundance, richness and diversity were predicted to be similar in elephant damaged and elephant excluded areas. My study was conducted at Ndarakwai Ranch in northeastern Tanzania. Elephants moving between three National Parks in Kenya and Tanzania visit this property. In August 2007 to March 2008, drift fences and pitfall traps were placed to sample the herpetofaunal species richness and diversity within high, medium and low elephant damaged areas and in an exclusion plot. Areas of heavy damage yielded higher species richness than the exclusion plot. Species diversity did not differ between the damaged areas and the exclusion plot. Frogs were more abundant in areas of high damage; in contrast, toads were found the least in high damage areas. The results support the idea that elephants have a positive influence on herpetofaunal species by creating habitat complexity through modifying the woodland area.

INTRODUCTION

Elephants are considered ecosystem engineers in that they create and maintain ecosystems through physically changing living or non-living materials from one state to another (Jones et al. 1994, Jones et al. 1997). Elephant browsing strategies involve bark stripping, breaking major branches and uprooting trees to feed on the top foliage. Elephants remove dominant hardy vegetation replacing it with quick growing vegetation, thereby transforming dense woodlands into open grasslands (Laws 1970; Owen-Smith 1987; Dublin et al. 1990; du Toit and Cumming 1999; Shannon et al. 2006). Elephants generally browse on woody trees, such as Acacia (*Acacia* spp.), marula (*Scelerocarya birrea*), mopane (*Colophospermum mopane*) and baobabs (*Adansonia digitata*) (Jachmann 1989; Lewis 1991; Omondi et al. 2004). Elephants may feed as they pass through an area without stopping or remain within the area and feed continuously (Western 1989; Stuart-Hill 1992). Feeding bouts of this nature create a mosaic of altered habitats.

The rejuvenation of vegetation is stunted when elephants are prevented from migrating between forage areas and this can lead to permanent, potentially degraded alterations in the landscape (Birkett and Stevens-Wood 2005; de Beer et al. 2006). On the other hand, elephants encourage succession in areas that have reached a climax and help control bush encroachment (Meik et al. 2002). The effects elephants have on vegetation have been studied extensively (Clutton-Brock and Guiness 1987; Illius and Gordon 1987; Sukumar and Gadgil 1988; Stokke and du Toit 2002; Osborn and Parker 2003; Ntumi et al. 2005; Shannon et al. 2006). However, research is limited on whether elephants are degrading or enriching habitats for other vertebrate species in the habitat (Herremans 1995; Cumming and Brock 1997; Pringle 2008).

In some cases, vertebrates are used to assess habitat quality or otherwise monitor ecosystem conditions, but precautions are necessary to ensure that the species selected are viable indicators (Landres et al. 1988). Recently, the arboreal Kenyan dwarf gecko (*Lygodactylus keniensis*) was found to select habitats that became physically more complex as a result of elephant activity, i.e., refugia were created by elephants stripping bark and splintering branches (Pringle 2008). In a study by Friend and Cellier (1990), feral pigs and buffalo increased microhabitats for amphibians and to lesser extent reptiles by expanding ephemeral waterholes through wallowing. Amphibians are sensitive to environmental changes in terrestrial and aquatic habitats because of their life history characteristics and permeable skin (Waddle 2006). Hence, they are touted as useful indicators of ecosystem status.

The objective of the present study was to sample the reptile and amphibian (herpetofaunal) community within an *Acacia* habitat that varied in the degree of elephant impact in northern Tanzania. If elephant foraging was degrading the habitat, then herpetofauna species abundance, diversity and richness were predicted to be higher in areas with lower elephant impact. Conversely, if elephant activities enriched the habitat, then the herpetofauna would show higher levels in one or more of these measures. These hypotheses were examined by evaluating the overall herpetofaunal community composition, and then assessing amphibian, toads (*Bufo* spp.) and frogs (non-*Bufo* spp.), and reptile, non-skinks (non-Scincidae) and skinks (Scincidae), abundance, richness and diversity. These groups were considered separately because of their different natural histories and habitat preferences.

METHODS Study Site

From August 2007 to March 2008, herpetofaunal composition and abundance were recorded at a control plot, Rafiki Farm, and a disturbed open woodland savanna area near the waterhole at Ndarakwai Ranch (See Methods in Chapter 1). In the control area, the most prevalent tree species is *Acacia tortilis*. The disturbed area was unfenced and located where elephants traversed regularly and caused damage to vegetation (Napora 2007). The area is a mixed woodland habitat primarily composed of *A. tortilis* and *A. mellifera* with *A. tortilis* being the dominant species (Napora 2007). The control area is a woodland habitat composed of *A. tortilis* and *A. mellifera* with *A. tortilis* being the dominant species (Napora 2007). The control area is a woodland habitat composed of *A. tortilis* and *A. mellifera* that has been fenced off to exclude large herbivores, such as zebra (*Equus burchellii*), eland (*Taurotragus oryx*), elephant, Cape buffalo (*Syncerus caffer*) and giraffe (*Giraffa cameloparadalis*), although the last two species were not very common on Ndarakwai Ranch.

Trap Location

The majority of the vegetation in the open disturbed area had some major branches broken off and more than 50% of the canopy had been lost because of elephant feeding (Napora 2007). With 90% of the vegetation in this condition, a random selection of trap locations was not possible. Therefore, locations were selected based on specific guidelines detailing levels of habitat damage (Table 1.1).

In order to make sure captures were not influenced by tree species, all drift fences were placed in areas where the only tree species was *A. tortilis*. I sampled three different locations within the control area and three locations within each damage category of high, medium and

low, yielding 12 sampling locations (three trap arrays/damage site) (Fig. 1.1C). Modified guidelines set by Napora (2007) were used to classify the damage sites (Table 1.1).

Capturing Method

Within the two sites, the open disturbed area and the exclusion area (Rafiki, henceforth called the control), sampling was conducted using non-lethal herpetofaunal traps and opportunistic observation (see Methods Ch.1). The herpetofaunal community was sampled using drift fences with pitfalls and funnel traps. Drift fences were 10 m long and 0.5 m high. Drift fences were constructed using plastic sheeting and wooden stakes. The stakes were attached at the beginning of the plastic sheeting and in 2 m intervals along its length (10 m). The base of the plastic sheeting was buried 20 cm deep and covered with soil and smoothed out. Buckets (20 L) were used as pitfall traps. Pitfalls were buried at each end of the drift fence between the first and second stake. The buckets were buried so that the lip of the bucket was flush with the ground. The drift fence ran over the middle of the buckets allowing for capture on either side of the drift fence (Fig. 1.2). Holes were made at the bottom of the buckets as well as on the sides to allow water to drain out. In addition, some leaf litter and twigs were placed in the buckets to provide refuge for captured individuals. A total of 24 pitfall traps and 120 m of drift fence were used.

Funnel traps constructed from mosquito wire or window screening (Gaskell 2007) were placed on both sides of the drift fence (Fig. 1.3). The funnel traps were placed at the midpoint of the drift fence between the two pitfalls. Cardboard sheets were leaned against the fence and over the funnel traps to provide shelter from the sun. Opportunistic sampling was carried out when approaching trap locations. All captured individuals were placed in collection bags and returned

to the research station for morphological measurements. Individuals were released within 24 hours 15 m due west of the drift fence from which they were captured.

Data Collection

Because of the high traffic of large mammals that traveled through the disturbed area, drift fences were destroyed occasionally and often needed repair. Pitfalls were closed until a new drift fence was installed. For two months, from December 2007 – January 2008, a large number of elephants were present at Ndarakwai Ranch and trapping was not feasible, so the traps were closed. When traps were open, they were checked on a daily basis.

Using field guides, captured herpetofauna were identified to the lowest taxonomic level possible (Spawls et al. 2002; Bauer 2003; Channing and Howell 2006), cataloged and photographed. There is debate as to the correct taxonomy for the "typical skinks". Guidebooks use both the genus *Mabuya* and *Trachylepis* (Spawls et al. 2002; Branch 2005); however, current literature classifies them as *Trachylepis* (Bauer 2003; Malonza et al. 2006), which is used here. A hand ruler was used to measure snout to vent length (SVL) (mm) and from vent to tip of tail (mm) (Simmons 2002). Notes were made on tail re-growth or if tails were broken. Hand held Pescola[™] spring scales (30 g and 60 g) were used to measure mass (g). Captured specimens were uniquely marked (toe-clipped and marked with non-toxic paint) following accepted standard methods to identify recaptures (Clark 1971; Howard 1978; Dodd 1993; Johnson 2005; Winne et al. 2006).

Statistical Analysis

Species Richness

Species richness was the total number of species captured within a location. Mean species richness calculations that met the assumptions of equal variance and normality were analyzed using a one-way analysis of variance (ANOVA) to test for variation between locations. If there was variation, then the different damaged sites were compared to the control with a post hoc Dunnett's test. Assumptions that could not be met were tested using the Kruskal-Wallis test, which is a non-parametric analog of an ANOVA (Sokal and Rohlf 1995). A non-parametric equivalent of a Dunnett's test to compare damaged areas to the control was used (Zar 1984).

This was done by calculating the q statistic:

$$q = (R_A - R_B) / S.E.$$

where R_A is the Sum of Ranks of a group and R_B is the Sum of Ranks of the control area. The Sum of Ranks for each damage area was calculated and compared to the control area.

I tested species richness of all herpetofaunal species by damage sites, then compared species richness of skinks (Scincidae), non-skinks (non-Scincidae), toads (*Bufu* spp.) and frogs (non-*Bufo* spp.) across damage sites independently.

Species Abundances

Species abundances were calculated as total number of individuals captured within a trap location. I analyzed the difference in mean abundance of all herpetofaunal species, skinks, nonskinks, toads and frogs between the trapping locations. The data that met the assumptions were analyzed using a one-way ANOVA and if there was a significant difference due to damage site, then the damage sites were compared to the control with Dunnett's test (Sokal and Rohlf 1995). Data not meeting assumptions were analyzed using the Kruskal-Wallis test and differences between sites were tested with the non-parametric analog of Dunnett's test. This was tested to determine if a certain type of herpetofauna use habitats that differ in the degree of modification by elephants.

Species Diversity

Species diversity within each trap location was calculated using Simpson's Species diversity index:

$$\mathbf{D} = 1 \cdot \Sigma \left[n_i (n_i \cdot 1) / N(N \cdot 1) \right],$$

where n_i is the number of individuals of species *i* captured at the location and *N* is the total number of individuals captured at the location. The species indexes that met the assumptions were tested with an one-way ANOVA followed by Dunnett's test to compared the different areas to the control. Data that did not meet the statistical assumptions of equal variance and normality and could not be corrected with transformation were analyzed with a Kruskal-Wallis test, subsequently followed by the non-parametric analog of the Dunnett's test (Sokal and Rohlf 1995; Zar 1984). Therefore, I compared the mean Simpson species diversity indexes of herpetofauna, skinks, non-skinks, toads and frogs across each trapping location.

All statistical analyses were tested to a 95% confidence limit ($\alpha = 0.05$) using JMP 7.0.1 (SAS Institute 2007) for the Macintosh operating system. All descriptive statistics are displayed as mean (\pm S.E.). Only reptiles within the order Sauria and amphibians within the order Anura were analyzed. Snakes were not considered in the analysis due to a lack of captures since traps were not designed to capture snakes.

RESULTS Herpetofauna Measures as Related to Elephant Impact on the Vegetation

Herpetofauna Species Richness and Diversity

The mean abundance of herpetofauna individuals captured did not significantly differ between damage sites (ANOVA: $F_{3,8} = 0.65$, P = 0.61) (Table 1.2; Fig. 2.1). Species richness also did not differ significantly between damage areas, but there was a trend towards higher richness in high damage areas ($F_{3,8} = 3.18$, P = 0.08) (Table 2.1; Fig. 2.2). The Dunnett's test showed that high damage areas were found to have significantly higher species richness than the control (P = 0.05; Table 2.2). Medium and low damaged areas when compared to the control had similar species richness (Table 2.2). Across the damage sites the Simpson's Species Diversity Index were similar (Kruskal-Wallis $H_3 = 4.44$, P = 0.22) (Table 2.1; Fig. 2.3).

A total of 18 different herpetofaunal species were sampled in areas of high elephant damage. There were nine saurian species and nine anuran species. Wahlberg's snake-eyed skinks (*Panaspis wahlbergii*) accounted for 37.5% of all captured saurians in areas of high damage (Table 2.3). The Lake Victoria clawed frog (*Xenopus victorianus*), the Senegal kassina (*Kassina senegalensis*) and the guttural toad (*Bufo gutturalis*) were the most abundant anurans in areas of high damage (27%, 23% and 19% respectively) (Table 2.4).

Medium damage areas were comprised of 12 species of herpetofauna. Nine species of saurians were captured as compared to four species of anurans (Table 1.2). The southern long-tailed lizard (*Latasia longicuadata*) was the most abundant saurian captured, composing 27% of all captured individuals (Table 2.3). *B. gutturalis* accounted for 17 of the 24 anuran specimens captured (Table 2.4).

Areas of low damage had 11 species sampled (7 saurians; 4 anurans). The variable skink (*Trachylepis varia*) accounted for 33% and the Nyika gecko (*Hemidactylus squamulatus*) accounted for 25% of the individuals captured (Table 2.3). *B. gutturalis* and *X. victorianus* were the most abundant species of anurans in low damage areas. A total of 17 individual anurans were captured and 82% of sampled individuals belonged to *B. gutturalis* (41%) and *X. victorianus* (41%) (Table 2.4).

The control site had the lowest species richness with only eight species sampled. There were five saurian species and three anuran species. Fifty-six percent of the saurians sampled in the control area were *P. wahlbergii* (Table 2.3). In the control site, *B. gutturalis* was the most abundant species of anurans sampled. *B. gutturalis* accounted for 71% of all captured anurans (Table 2.4).

Amphibian Composition Across Damage Sites

Frogs (non-*Bufo* spp.) sampled within the study sites were comprised of six different species in three different families (Table 1.2). *K. senegalensis* and *X. victorianus* were the only two species of frogs that were captured in areas other than high damage. *K. senegalensis* was the only species to be captured in every damage category, with higher prevalence in high (N = 6) and medium (N = 3) damage areas. Only two species of toads were sampled in this study (Table 1.2). Both species were found within all the damage categories. However, *B. gutturalis* (N = 41) was almost four times more abundant than *B. xeros* (N = 11). Seventy percent of *B. gutturalis* individuals were captured in areas of medium damage areas and in the control; similarly, 60% of the *B. xeros* specimens were sampled in medium damage areas and in the control area (Table 2.4). In addition, toads were significantly larger than frogs (F $_{1,65} = 6.86$, P = 0.01) within all damage

sites. The average length of all toad species was 61.9 ± 3.5 mm, while the average SVL of all frog species was 49.2 ± 3.1 mm (Table 1.3).

Damage site had a significant effect on toad abundances but not on frog abundances, though there was a trend ($F_{3,8} = 6.65$, P = 0.01; $F_{3,8} = 3.07$. P = 0.09, respectively) (Fig. 2.4). Toad abundances were significantly lower in areas of high damage as compared to the control (P = 0.04; Table 2.5); conversely, frogs were significantly more abundant in the heavy damaged sites then the control (P = 0.05; Table 2.6). Two species of toads (*B. gutturalis* and *B. xeros*) were captured; therefore, no difference was detected in species richness between damage sites $(H_3 = 2.75, P = 0.43; Fig. 2.5)$. Seven species of frogs were captured between the different trapping sites with the majority being sampled in heavy damage areas (Table 1.2). Frog species richness significantly differed between the damage areas ($F_{3,8} = 6.46$, P = 0.02) with species richness being the highest in high damage areas as compared to the control (P = 0.01; Table 2.7). The Simpson's Species Diversity Index of toads was not affected by damage sites ($F_{3,8} = 0.44$, P = 0.73; Fig. 2.6); whereas, the Simpson's Index for frogs was significantly different between the damage sites ($H_3 = 9.31$, P = 0.03). When compared to the control site, the high damage site had the highest Index score (Table 2.8). Table 2.9 provides a complete reference to mean abundances of frogs and toads captured in each trap location at Ndarakwai Ranch.

Saurian Composition Across Damage Sites

Seven species of skinks (Scincidae) and six species of non-skinks (non-Scincidae) that comprised four families were sampled within the different damage sites (Table 1.2). The saurian fauna was distributed similarly throughout the damage sites. *Lygosoma afrum* and *Panaspis wahlbergii* were the only two species captured within all three damage sites and the control area. Mean skink and non-skink abundances did not differ significantly across damage sites ($F_{3,8} = 0.35$, P = 0.79; $F_{3,8} = 0.23$, P = 0.87, respectively) (Fig. 2.7) nor did species richness ($F_{3,8} = 0.31$, P = 0.82; $F_{3,8} = 0.41$, P = 0.75, respectively) (Fig. 2.8). Simpson's Species Diversity Index for skinks and non-skinks also was not significantly different across the damage areas ($H_3 = 2.46$, P = 0.48; $F_{3,8} = 0.76$, P = 0.55, respectively) (Fig. 2.9).

DISCUSSION Herpetofaunal Richness and Diversity

The objective of the present study was to examine the relationship between the herpetofaunal communities within an *Acacia* habitat that varied in the degree of elephant impact. Compared to the control area from which elephants and other megafauna were excluded, elephant modified areas had no negative effect on herpetofaunal abundance (Fig. 2.1), species richness (Fig. 2.2) or diversity (Fig. 2.3). Species richness however was found to be greater in areas of high vegetation damage as compared to the control area (Table 2.2). This may be due to the increase in habitat complexity (Crooks 2002; Friend and Cellier 1990; Kretzer and Cully Jr. 2001; Pringle 2008) caused by elephants.

Habitat selection is not a random process; it is based on appropriate habitat characteristics for that particular organism (Goldsbrough et al. 2006). In herpetofaunal species, viable refuge availability is the primary driving force in habitat selection (Toft 1985; Meik et al. 2002; Pringle 2008). Broken branches and uprooted trees provide coarse woody debris, which herpetofauna use as refugia, hunting areas and breeding grounds (Greenberg 2001). In addition, the craters and mounds created by uprooted trees form habitats for numerous organisms, some of which may be food sources for reptiles and amphibians (Guo 1996; Olff and Ritchie 1998).

Prey abundance and type is a secondary factor in habitat selection by herpetofauna (Toft 1985; Meik et al. 2002; McCauley et al. 2006; Pringle et al. 2006). A majority of the species captured within the study sites are strict insectivores with the exception of *T. brevicollis*, *T. varia*, *B. gutturalis* and *B. xeros*, which also may feed on larger prey such as other frogs, lizards and even small rodents (Spawls et al. 2002; Channing and Howell 2006). Foraging behavior could play a role in habitat selection. The southern long-tailed lizard (*L. longicuadata*) was the most abundant in areas of medium damage. *L. longicuadata* is a sit-and-wait forager that depends on speed for capturing prey. Individuals wait under brush in the shade and when a potential prey species comes along; they dash out, grab the insect and sprint back to their refuge. In areas of heavy damage, sprinting to capture prey would be difficult because of the many obstacles created by the woody debris; whereas, foraging in areas of low damage would leave them without the appropriate refuge. However, in medium damage areas, they have fewer obstacles, can sprint freely and still have adequate refugia.

Arthropods and other invertebrates also may be targeting areas of heavy damage to use for feeding and nesting, since damaged trees are not able to deter insects as effectively (Larsson et al. 1983; Harmon et al. 1986). Therefore, an abundance and diversity of prey may be attracting these different species of herpetofauna. With an increase in potential habitat and prey, competition for these resources may be reduced as compared to the control where resources may be at a minimum.

Nine of the 22 species sampled in this study were anurans. Damage levels had an effect on toad abundances, with toads being scarcer in high damage sites as compared to the control (Table 2.5); there was a trend that damage levels may affect frog abundances. Frogs were more abundant in areas of high damage than in control area (Table 2.6). The increased complexity of the habitat creates new niches and habitat for a diverse array of frog species to use as compared to the control area (Fig. 2.5 and Fig. 2.6). Craters and coarse woody debris created by up-rooted and broken trees are beneficial to frogs because of the increased availability of elevated perches for calling, the augmented number of refuges against predators and desiccation, and the enhanced foraging resources. Amphibians depend on vocalizations to attract conspecific mates and habitat characteristics may affect the effectiveness of their calls (Penna and Solis 1996). The frog species captured in this study call for mates from perches; whereas, the toad species captured do not use perches for calling (Channing and Howell 2006). A high abundance of woody debris will diminish the quality of calls coming from the substrate and therefore be disadvantageous to toads.

Toads and frogs also use their respective habitats in different ways to avoid desiccation. Toads tend to make use of 'forms', shallow depressions in the soil, to absorb moisture (Schwarzkopf and Alford 1996; Griffin and Case 2001). Frogs may prefer high amounts of coarse woody debris because decaying coarse woody debris has greater water holding qualities (Jaeger 1980; Owens et al. 2008) and can protect against desiccation.

Damaged areas also may induce different feeding gradients and form a type of resource partitioning between frogs and toads (Toft 1985). Predators target prey relative to their body size; therefore, toads will target larger prey than frogs (Scharf et al. 2000). The toad species within this study feed primarily on beetles and arachnids, spiders and scorpions, but *B. gutturalis* also will feed on small lizard and frogs (Channing and Howell 2006). The majority of frog species with the exception of *X. victorianus* tend to feed on smaller insects such as ants and termites. When compared to the control, toads were significantly less abundant in high damage areas (Table 2.5). This may be because abundant coarse woody debris associated with high

damage areas might pose as obstacles for foraging and locomotion thereby deterring toads from inhabiting such an area (Whiles and Grubaugh 1993). With smaller prey and more obstacles, the cost-benefit ratio is not favorable to the larger toads in areas of heavy damage, but poise favorable foraging habitat for the smaller frogs. Dung beetles were found in lower densities in areas of dense vegetation structure because it was believed to impede their flying, dung searching and dung rolling (Steenkamp and Chown 1996; Crooks 2002).

Hotspots and Anomalies

Several trap sites had captures that did not follow any trend or were not similar to the other trap locations within the same damage class. When inspecting for species richness and diversity the two trap sites within the medium damage class had similar Simpson Diversity Index and species richness scores; however, the third trap location was much lower (Table 2.1). Trap location may explain the difference. This third drift fence was placed in a small patch of medium damaged trees that was isolated from the woodland area by an open grass field (Fig.1.1C). Nevertheless, the site was selected because it was the only patch that was a still an acceptable distance away from the nearest drift fence.

There was a similar situation in the high damage area for frog and toad abundances (Table 2.5). Two trap areas had very similar abundances but the third location had only one-third of the captured individuals as the other two sites. This area was located in more open space than the other two (Fig. 1.1C). In addition, this area had fewer trap days because it was the last trap installed initially and after periods in which traps were closed. Hence, the lower sampling effort may account for the reduced captures here (Table 2.10).

When examining the abundances between frogs and toads there was a noticeable hotspot

at the third trap area in the low damage trees (Table 2.9). Seven of the eight frogs were captured at this site and all were *X. victorianus*. Compared to other traps in the low damage area, the pitfall traps at this drift fence were flooded more often, which indicates the trap location was at a lower elevation and held more water and such an area is more likely to have aquatic species move through the area than a drier, more elevated region.

An interesting factor in this study was the small number of recaptures and specimens observed. Of the 143 individual specimens captured, marked and released, only two *L*. *longicuadata* individuals were recaptured. Captured individuals were released 15 m due west of the drift fence in areas of suitable habitat. I also only observed two specimens (*L*. *laterimaculatus* and *A. agama*) through opportunistic sampling within my trapping sites. This was probably due to the time at which I checked traps. Since I had duties at the observation platform, I did not check traps until 10:00 or 11:00 h by which time some species may have already fed or been active and returned to their refuge for the warmest past of the day (McBrayer per. comm.).

Long-term Implications

This study provides some evidence that the exclusion of elephants would likely lead to lower species richness of herpetofauna due to a reduction in habitat complexity. The local herpetofaunal community in this savanna woodland shows a positive relationship in terms of species richness to tree damage by free ranging elephants. The elephants in this region are capable of moving from one area to another creating a mosaic of modified habitats. These modified habitats are capable of producing habitats for herpetofauna species that tend to be generalist when selecting habitat but also provide habitat for more sensitive species like frogs.

More research is needed to determine the full impact elephants have on their ecosystems. Arboreal species needed to be sampled more effectively in modified areas. The saurian species sampled in this study were typically terrestrial and damage levels had no effect on either abundance or richness (Fig. 2.7 and Fig. 2.8), but damage levels may affect arboreal saurian species. In addition, habitat structures should be systematically quantified, i.e. coarse woody debris, ground cover and canopy cover, and analyzed. Furthermore, the invertebrate fauna within the modified areas need to be sampled to test the hypothesis that prey availability is a driving source in habitat selection for these species. This may even include looking at ant absence from damaged *A. tortilis* that may allow invertebrates to come in and feed on the damaged tree.

Savanna ecosystems hold some of the world's largest diversity of mammals and microecosystems (du Toit and Cumming 1999). The creation and rejuvenation of these diverse ecosystems are aided by elephants as the resident ecosystem engineers. With the suppression or removal of elephants, the savanna ecosystem is subsequently turning into over-grown thickets with loss of viable food sources and habitats (Meik et al. 2002). Prior to the inception of Ndarakwai Ranch, the area was used by the Tanzania Breweries Ltd. for agriculture and cattle grazing (Vyas 2006). In 1995, when Ndarakwai Ranch was established by Peter and Margot Jones as a semi-protected area, the first wildlife to appear was elephants (Peter Jones per. comm.). Gradually over the years, more wildlife began to appear and the landscape began to transform back to original savanna. Fourteen years later, over 90% of the vegetation on Ndarakwai Ranch has been modified by elephants (Napora 2007), but there are over 115 species of birds, 30 species of mammals (Vyas 2006; Castelda 2008; per. observ.), and 42 species of herpetofauna. When comparing areas with ecosystem engineers to areas without them over a

long spatial scale, areas with ecosystem engineers have a more diverse habitat, a greater abundance of resources and higher species diversity (Jones et al. 1997). Ecosystems that are moderately modified overtime have increased habitat complexity and support a higher diversity of animals due to more microhabitats available for reproduction, foraging and refugia (MacArthur and MacArthur 1961; Pianka 1966; Pianka 1967; Hadden and Westbrooke 1996; Crooks 2002).

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Damage Site	Simpson's Diversity Index	Species Richness	
High 1	0.86	9	
High 2	0.90	9	
High 3	0.96	8	
Mean (± SE)	0.91 (± 0.03)	8.7 (± 0.33)	
Medium 1	0.78	6	
Medium 2	0.89	8	
Medium 3	0.52	3	
Mean (± SE)	0.73 (± 0.11)	5.7 (± 1.5)	
Low 1	0.80	4	
Low 2	0.86	5	
Low 3	0.84	8	
Mean (± SE)	0.83 (± 0.02)	5.7 (± 1.2)	
Control 1	0.87	5	
Control 2	0.78	5	
Control 3	0.75	4	
Mean (± SE)	0.80 (± 0.04)	4.67 (± 0.33)	

Table 2.1. Simpson's diversity index for herpetofaunal species and species richness based on damage level at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.

Table 2.2. Dunnett's test comparing the mean (\pm S.E.) herpetofauna species richness of damage sites to the control site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (* indicates statistical significance).

Damage Site	Abs (Dif) - LSD	P = value
High	0.04	0.05*
Medium	-2.96	0.81
Low	-2.96	0.81

	Damage Site				
Species	High	Medium	Low	Control	
Agama agama	1/16	1/18	0/18	0/15	
Gerrhosaurus flavigularis	0/16	0/18	0/18	1/15	
Hemidactylus squamulatus	2/16	1/18	3/18	0/15	
Latasia longicuadata	1/16	7/18	0/18	2/15	
Leptosiaphos kilimensis	0/16	0/18	1/18	0/15	
Lygodactylus laterimaculatus	0/16	0/18	1/18	0/15	
Lygodactylus picturatus	1/16	0/18	0/18	0/15	
Lygosoma afrum	2/16	1/18	1/18	1/15	
Lygosoma sundevalli	1/16	2/18	0/18	2/15	
Panaspis wahlbergii	6/16	3/18	1/18	9/15	
Trachylepis brevicollis	1/16	0/18	0/18	0/15	
Trachylepis striata	0/16	1/18	1/18	0/15	
Trachylepis varia	1/16	2/18	4/18	0/15	

Table 2.3. Proportion of Sauria species captured within each damage site from August 2007 – March 2008 at Ndarakwai Ranch, Tanzania.
Species	High	Medium	Low	Control
Bufo gutturalis	5/26	17/24	7/17	12/17
Bufo xeros	2/26	3/24	2/17	4/17
Cacosternum spp.	1/26	0/24	0/17	0/17
Kassina senegalensis	6/26	3/24	1/17	1/17
Leptopelis bocagii	1/26	0/24	0/17	0/17
Ptychadena mascareniensis	2/26	0/24	0/17	0/17
Tomopterna tandyi	2/26	1/24	0/17	0/17
Xenopus victorianus	7/26	0/24	7/17	0/17

Table 2.4. Proportion of Anura species captured within each damage site from August 2007 – March 2008 at Ndarakwai Ranch, Tanzania.

Damage Site	Abs (Dif) - LSD	P = value
High	0.02	0.04*
Medium	-0.53	0.71
Low	-0.17	0.13

Table 2.5. Dunnett's test comparing the mean (\pm S.E.) toad abundance of damage sites to the control site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (* indicates statistical significance).

Damage Site	Abs (Dif) - LSD	P = value
High	0.04	0.05*
Medium	-1.57	0.78
Low	-1.27	0.53

Table 2.6. Dunnett's test comparing the mean (\pm S.E.) frog abundance of damage sites to the control site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (* indicates statistical significance).

Table 2.7. Dunnett's test comparing the mean (\pm S.E.) frog species richness of damage sites to the control site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (* indicates statistical significance).

Damage Site	Abs (Dif) - LSD	P = value
High	0.747	0.01*
Medium	-1.59	0.92
Low	-1.25	0.64

Table 2.8. Non-parametric analog to Dunnett's test comparing the mean (\pm S.E.) frog Simpson's Species Diversity Index of damage sites to the control site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008 (* indicates statistical significance) (SR = Sum of Ranks).

Comparison	Difference	S.E.	q	Critical Value
SR _{High} - SR _{Control}	32.625	8.83	3.69	~2.06*
SR _{Medium} - SR _{Control}	0	8.83	0	~2.06
SR_{Low} - $SR_{Control}$	0.165	8.83	0.087	~2.06

Damage Site	Frogs	Toads
High 1	9	3
High 2	8	2
High 3	3	2
Mean (± SE)	6.7 (± 1.9)	$2.3 (\pm 0.3)$
Medium 1	3	10
Medium 2	1	5
Medium 3	0	5
Mean (± SE)	1.3 (± 0.9)	6.7 (± 1.7)
Low 1	1	3
Low 2	0	2
Low 3	7	4
Mean (± SE)	2.67 (± 2.2)	3 (± 0.6)
Control 1	0	5
Control 2	0	6
Control 3	1	5
Mean (± SE)	0.3 (± 0.3)	5.3 (± 0.3)

Table 2.9. Abundance of frogs and toads captured at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.

			Mo	onth			
Damage	August 2007	September 2007	October 2007	November 2007	February 2008	March 2008	Grand Total
High 1	36	24	30	34	36	30	190
High 2	28	24	30	34	22	30	168
High 3	0	12	30	34	18	30	124
Medium 1	24	24	31	34	36	30	179
Medium 2	36	24	30	34	8	30	162
Medium 3	4	24	30	34	30	30	152
Low 1	36	32	30	34	22	30	184
Low 2	14	24	31	34	26	30	159
Low 3	0	18	30	34	36	30	148
Control 1	38	24	30	34	6	30	162
Control 2	38	24	30	34	32	30	188
Control 3	38	24	30	34	4	30	160
Grand Total	292	278	362	408	276	360	1976

Table 2.10. Trapping days¹ of each damage site for each month (August 2007 – March 2008²) at Ndarakwai Ranch, Tanzania.

¹Trapping Day = # of traps open/day ²December and January traps were closed because of the abundance of elephants



Figure 2.1. Mean (\pm SE) herpetofauna species abundance based on damage site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 2.2. Mean (± SE) herpetofauna species richness based on damage site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 2.3. Mean (± SE) herpetofauna Simpson's Species Diversity Index based on damage site at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 2.4. Mean (\pm SE) toad and frog abundance by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 2.5. Mean (\pm SE) toad and frog species richness by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.

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Figure 2.6. Mean (\pm SE) toad and frog Simpson's Species Diversity Index by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 2.7. Mean (\pm SE) skink and non-skink abundance by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 2.8. Mean (\pm SE) skink and non-skink species richness by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.



Figure 2.9. Mean (± SE) skink and non-skink Simpson's Species Diversity Index by damage sites at Ndarakwai Ranch, Tanzania from August 2007 – March 2008.

BIOASSAYS OF FOUR CHEMICALS WITH AFRICAN ELEPHANTS APPENDIX A

INTRODUCTION

Male and female African elephants (*Loxodonta africana*) live in different social organizations. Females reside in groups of overlapping generations of related individuals typically led by the largest, eldest female (Poole 1989a; Archie et al. 2006). Females become physiologically capable of reproducing around the age of 10 years and may continue to reproduce for another 40 or more years (Moss 1996). As females are entering reproductive maturity, sub-adult males of the same age are beginning to disband from their natal herd, commonly traveling in loosely knit bachelor herds (Douglas-Hamilton 1972; Moss 1983; Hall-Martin 1987). Typically, African male elephants are physiologically able to reproduce by 14 years of age but socially cannot compete for females until they are at least 25 years old (Poole 1987; Poole 1989b). During this time, they travel alone or in groups with other males. Because males have unpredictable dispersal patterns and wide-ranging movements (Archie et al. 2006), interactions with reproductive receptive females require active searching.

Male elephants use visual, auditory and chemical cues to locate potential mates across expansive spatial and temporal scales. Females have a 16-week estrous cycle during which they are fertile for two to five days around ovulation (Moss 1983; Rasmussen and Schulte 1998). In addition, their lengthy gestation (approximately 22 months) and nursing of calves for several years results in an interbirth interval of three to five years. Elephants are able to locate receptive conspecifics by visual, auditory and chemosensory behaviors, such as sniff, check, place and flehmen (Schulte and Rasmussen 1999). By using such chemosensory behaviors both African and Asian (*Elephas maximus*) male elephants can differentiate between the luteal urine and

follicular urine of conspecific female elephants (Rasmussen et al. 1996; Rasmussen 2001; Bagley et al. 2006). The estrous pheromone, (Z)-7-dodecen-1-yl acetate has been identified in Asian elephants (Rasmussen et al. 1997), and the identity of an estrous pheromone in African elephants is under investigation (Goodwin et al. 2005, Castelda 2008).

In addition to being able to identify receptive conspecifics, males undergo an annual physiological phenomenon known as musth (Poole 1987, 1989a,b, 1999). Musth has a physiological effect on male elephants but also impacts social dominance. Size is correlated positively with dominance between bulls; however, regardless of size, bulls in musth are dominant over non-musth bulls (Kurt 1974; Sukumar and Gadgil 1988; Poole 1989a; Buss 1991). Musth males display elevated aggression towards other males and increased socialization with females. Outward signs of musth include urine dribbling (UD), temporal gland secretion (TGS), swollen temporal glands and a more upright posture (Eisenberg et al. 1971; Hall-Martin 1987; Poole 1987; Rasmussen et al. 1996).

The high metabolic cost of musth, e.g. loss of water during UD and TGS, makes this a form of "honest" signaling (Maynard-Smith and Price 1973; Clutton-Brock and Albon 1979). These signals, like the estrous pheromone (Z)-7-dodecen-1-yl acetate found in follicular urine of Asian elephants, provide information to conspecifics of both sexes about the physiological state of the sender. Urine dribble provides a "road map" to females in estrous to find mates (Poole 1987).

Previous studies with Asian elephants have shown that upon entering the active space of musth secretions, non-musth and subordinate males as well as luteal females will first display investigatory chemosensory behaviors, which will then generate avoidance and repulsion

behaviors (Rasmussen and Krishnamurthy 2000; Rasmussen et al. 2002; Rasmussen 2003; Rasmussen et al. 2003; Greenwood et al. 2005; Goodwin et al. 2006). These reactions support the idea that TGS of musth males are multifunctional by emitting a combination of sexual and warning pheromones that could affect male–male or male-female interactions (Rasmussen et al. 1990). In early chemical studies, temporal gland secretions in musth Asian elephants was found to be composed of more than 23 major and 16 minor compounds (Rasmussen et al. 1990); whereas, TGS of African elephants contained only 16 compounds (Rasmussen et al. 1996). However, a majority of the compounds found in African elephants also are found in Asian elephants (Goodwin et al. 2006), and more modern techniques may result in a greater number of compounds being discovered in the TGS of both species.

Previous studies conducted within our lab have focused on elephant chemosensory behaviors towards conspecifics, feces and urine (Loizi 2004; Vyas 2006; Napora 2007; Loizi et al. 2009) and others have performed bioassays to potential female sex pheromones on wild (Loizi 2004; Castelda 2008) and captive African elephants (Loizi 2004; Bagley 2004, Meyer 2006). There have been no bioassay studies done to determine potential pheromones in male African elephants. In the present study, three chemical compounds (2-decanone, 2-nonanone and cyclohexanone) that could be potential pheromones were selected based on the literature available and their presence in African elephant urine and TGS (Rasmussen et al. 1990; Perrin and Rasmussen 1994; Rasmussen et al. 1996; Rasmussen and Wittemyer 2002). There are several examples of convergent evolution between pheromones in elephants and different insects (Rasmussen et al. 1996; Rasmussen and Schulte 1998; Rasmussen et al. 2003). Over 126 species of Lepidoptera share Z7-12:AC, which is used as a sex pheromone. Surprisingly, Z7-12:AC is also an estrous pheromone in Asian elephants (Rasmussen et al. 1996, Rasmussen and Schulte

1998). Frontalin, a musth pheromone in Asian elephants, acts as an aggregation pheromone in bark beetles (*Dendroctonus tenebrans*) (Rasmussen and Schulte 1998; Rasmussen et al. 2002). Therefore, 2-decanone and 2-nonanone were selected because they act as aggregation pheromones in the olive bark beetle (*Phloeotribus scarabaeoides*) (Francke and Dettner 2005) and cyclohexanone, which is a sex attractant in *Bombyx mori* (Karlson and Butenandt 1959) and found in the early stages of musth in Asian elephants.

The objective of this study was to determine the bioactivity of these three putative compounds and whether these compounds are multifunctional in that they contain specific and different messages for females and males, e.g. male – female (attractant to females) and male – male (warning to potential competitors). If the compounds are bioactive, then individuals coming within a close proximity of the sample should have a higher proportion of investigatory behavior than when near the control. With a multifunctional sex directed stimuli, females should elicit greater chemosensory behavior toward the compound than the control; whereas, males would elicit chemosensory behaviors toward the compound but also should have a greater proportion of avoidance behaviors toward it than to the control.

METHODS

Study site

<u>Waterhole</u>

Bioassays were conducted from August 2007 – April 2008 at the permanent ca. 4,300 m² man-made waterhole at Ndarakwai Ranch (see Chapter 1 for information on Ndarakwai Ranch) (Fig. 1.1). Since 2004, over 250 elephants have been identified and catalogued photographically around the waterhole, which is fed by water diverted from the Ngare Nairobi River. A diverse array of wildlife visits the waterhole throughout the year (Vyas 2006). The vegetation around

the waterhole is comprised of mixed acacia woodland primarily *Acacia tortilis* to the west and open savanna to the northeast comprised of *A. mellifora* and *Spike sporibolous* (Napora 2007, Castelda 2008; unpublished data). A six-meter high wooden observation platform at the waterhole provided an excellent opportunity for examining behavioral patterns of elephants of various ages, sex and reproductive status without disturbing the elephants (Vyas 2006).

Bioassay Stimuli

The compounds tested were 2-nonanone, 2-decanone and cyclohexanone and a vanilla extract/water solution (our standard control). The control was a vanilla extract (10 ml) dissolved in 500 ml water. Vanilla is used as a control because it elicits low levels of chemosensory investigation from Asian and African elephants (Schulte and Rasmussen 1999; Loizi 2004; Bagley et al. 2006; Castelda 2008).

Bioassay Procedure at the Waterhole (August 2007 – April 2008)

Sample Placement

The control (vanilla solution) and one of the biological treatments (hereafter each will be called a "sample") were placed at sites around the waterhole. The samples were set 3-5 m apart (control and one experimental). When multiple sets of samples were placed around the waterhole, the sets were separated by at least 15 m. Sample sets were placed in order to increase the probability of elephants encountering the samples. Compounds were tested separately, but they were always paired with the control (Table A.1).

The selected locations were presoaked with water from the waterhole to reduce soil permeability, allowing the samples to remain at the surface for a longer period of time. This was done within the first 30 minutes of arriving at the waterhole and approximately one hour before samples were placed. Whenever possible, samples were poured when elephants were within 300 m and moving directly to the waterhole. If elephants were sauntering towards the waterhole, then the locations and samples were prepped and then placed when elephants were deliberately moving towards the waterhole. The compounds were presented in an approximation to natural concentrations of 100 µl of the chemical compound to 500 ml water (Goodwin per. comm.). On any given bioassay day, only the control and single compound in solution were placed around the waterhole; multiple experimental compounds were never tested simultaneously (Table A.1). In a previous study at Ndarakwai Ranch, Castelda (2008) tested multiple different compounds simultaneously with the control. To facilitate locating the samples from the observation tower a natural, inconspicuous marker such as dead wood and stones was placed approximately 1 m away from each sample. At the end of the day, each sample was washed away and covered using water and soil from the waterhole, and the markers were removed.

Behavioral Sampling

Behavioral observations were recorded on a Hitachi DZ-HS300A 8GB HDD (25x optical zoom) digital video recorder. The focal animal was the first elephant to move within proximity, defined as one body length distance, of the sample. Since size varies between age and sex, body length as a unit of measurement was specific to each elephant. Focal sampling with continuous sampling (Martin and Bateson 1993) continued as the elephant remained at least one body length from the sample. Once the elephant was more than one body length from the sample or not visible for three minutes, the assay was terminated. All approaches were videotaped, permitting data acquisition in situations when multiple animals approached. The use of the digital video recorder allowed for exact durations of proximity to the treatments. The video recorder also aided in identifying elephants, determining group sizes, sexing and aging the elephants. Behaviors were classified from a modified ethogram from Meyer (2006) (Table A.2).

The ages of the elephants that visit Ndarakwai Ranch are unknown. Therefore, age approximations were made using the system that Moss (1996) devised. Age estimates are made by morphological features, primarily shoulder height and tusk size (Moss 1996) (Table A.3). The four elephant age classes were defined as follows: Calf (>0-4 yrs), Juveniles (5-9 yrs), Pubescent/Sub-adults (10-14/15-19 yrs), and Adults (>19 yrs). For data analysis, I combined calf and juveniles into one group called pre-Pubescent, and sub-adults and adults into post-Pubescent. No attempt was made to analyze the data by family groups, although this may be a confound in that it is possible individuals from a related group may respond similarly.

Statistical Analysis

Analyses were performed using the data from all elephants that came within proximity (one body length) of either the experimental compound or the control. In addition, data from post-pubescent elephants that went to both the compound and the control also were analyzed separately. Proportions (number of elephants that came within proximity of the sample and performed some form of chemosensory behavior) were analyzed using Chi-square goodness of fit test. Duration (amount of time spent within one body length of the sample) and two behavior rates (all chemosensory behaviors performed per proximity and avoidance behaviors per proximity) were analyzed using student t-test and Pairwise Student t-test for post-pubescent elephants that went to both compound and control. Data that did not meet the assumptions of the parametric statistical tests were transformed and if transformation did not work then the non-parametric Wilcoxon Signed Ranks (WSR) test and Pairwise WSR were used (Sokal and Rohlf 1995). All statistical analyses were tested to a 95% confidence limit ($\alpha = 0.05$) using JMP 7.0.1 (SAS Institute 2007) for the Macintosh operating system. All descriptive statistics are displayed as mean (\pm S.E.).

RESULTS

Cyclohexanone

Cyclohexanone was bioassayed from December 2007 – April 2008 with no bioassays conducted in February 2008. Seventy-three elephants were bioassayed in this time. The proportion of chemosensory and avoidance behaviors performed by all elephants did not differ between cyclohexanone and vanilla ($x^2 = 1.47$, df = 1, P = 0.23: Fig A.1; $x^2 = 1.0$, df = 1, P = 0.32; Fig. A.2, respectively). Cyclohexanone did not elicit higher rates of chemosensory behavior than vanilla ($Z_1 = -1.24$, P = 0.21) (Fig. A.3). Cyclohexanone also did not induce greater rates of avoidance behavior than the control ($Z_1 = -1.89$, P = 0.24) (Fig. A.4). In addition, the duration of proximity to cyclohexanone was similar to that of vanilla ($Z_1 = -0.09$, P = 0.93) (Fig. A.5).

Five post-pubescent males and four post-pubescent females went to both cyclohexanone and vanilla. An identical proportion of post-pubescent females performed chemosensory behaviors to cyclohexanone as to vanilla ($x^2 = 0.00$, df = 1, P = 1.0); however, post-pubescent males had a higher proportion of chemosensory behaviors toward cyclohexanone than to vanilla ($x^2 = 5.49$, df = 1, P = 0.02) (Fig. A.6). Males also had higher proportions of avoidance behaviors toward cyclohexanone than to vanilla ($x^2 = 3.86$, df = 1, P = 0.05); whereas, females had similar proportions of avoidance behaviors to both samples ($x^2 = 0.54$, df = 1, P = 0.46) (Fig. A.7). Males did not differ in the rate of chemosensory or avoidance behaviors toward cyclohexanone and vanilla (ts = -6.5, df = 4, P = 0.13; ts = -5.0, df = 4, P = 0.13, respectively) (Fig. A.8 and A.9). Likewise, females responded similarly (t = -0.23, df = 3, P = 0.84; ts = 0.05, df = 3, P = 1.0, respectively). Females did spend a longer time within proximity to cyclohexanone than to vanilla (t = -3.86, df = 3, P = 0.03), but males spent a similar amount of time within proximity to each sample (t = -1.22, df = 4, P = 0.29) (Fig. A.10).

2-Decanone

From August – September 2007, 50 elephants were exposed to 2-decanone and vanilla. The proportion of chemosensory behaviors toward 2-decanone was very similar to that of vanilla $(x^2 = 0.01, df = 1, P = 0.92; Fig. A.11)$. However, the proportion of avoidance behaviors was significantly higher toward 2-decanone than the control $(x^2 = 5.53, df = 1, P = 0.02; Fig. A.12)$. The rate of chemosensory behaviors did not differ ($Z_1 = 0.3, P = 0.76; Fig. A.13$); whereas, elephants had a higher rate of avoidance behavior to 2-decanone than to the control ($Z_1 = -2.0, P = 0.05; Fig. A.14$). Duration spent within proximity was also similar between the two compounds ($Z_1 = -0.63, P = 0.53; Fig. A.15$).

Eighteen elephants went to both 2-decanone and vanilla; 10 were post-pubescent males and seven were post-pubescent females. Post-pubescent females and males performed similar proportions of chemosensory behaviors to 2-decanone and vanilla ($x^2 = 0.00$, df = 1, P = 1.0; $x^2 =$ 0.97, df = 1, P = 0.33, respectively) (Fig. A.16). The proportion of avoidance behaviors also was similar between 2-decanone and vanilla based on sex (females – $x^2 = 1.46$, df = 1, P = 0.23; males – $x^2 = 0.40$, df = 1, P = 0.53) (Fig. A.17). Female elephants did not differ in their rate of chemosensory and avoidance behaviors (t = -0.19, df = 6, P = 0.86; ts = -0.5, df = 6, P = 1.0, respectively). Rate of chemosensory and avoidance behavior were not different among males as well (ts = 2.5, df = 9, P = 0.5; ts = .5, df = 9, P = 1.0) (Fig. A.18 and A.19). Duration within proximity did not differ in females (t = 1.7, df = 6, P = 0.13) or males (t = -0.37, df = 9, P = 0.72) (Fig. A.20).

2-Nonanone

Bioassays were conducted on 60 elephants in November 2007. Not all elephants went to both 2-nonanone and vanilla. Forty-two elephants came within proximity of 2-nonanone and 58 elephants were within proximity to vanilla. The proportion of chemosensory behaviors performed was significantly higher toward 2-nonanone than the vanilla control ($x^2 = 5.89$, df = 1, P = 0.02; Fig. A.21). The proportion of avoidance behavior was low and not significantly different between 2-nonanone and vanilla ($x^2 = 1.58$, df = 1, P = 0.21; Fig. A.22). The rates of both chemosensory and avoidance behaviors between the compound and the control were similar ($Z_1 = 1.56$, P = 0.12; Fig. A.23; $Z_1 = 1.23$, P = 0.22; Fig. A.24, respectively). In addition, duration spent within proximity to the compound or the control did not differ ($Z_1 = 0.78$, P = 0.42; Fig. A.25).

Twenty post-pubescent males and eight post-pubescent females were sampled at 2nonanone and vanilla. Females did not have a higher proportion of chemosensory behaviors towards 2-nonanone and vanilla ($x^2 = 0.29$, df = 1, P = 0.59) and neither did males ($x^2 = 2.9$, df = 1, P = 0.09) (Fig. A.26). Proportions of avoidance behaviors also was similar between the two samples in females ($x^2 = 1.5$, df = 1, P = 0.23) and males ($x^2 = 1.4$, df = 1, P = 0.23) (Fig. A.27). Female and male elephants did not differ in the rate of performed chemosensory behaviors between 2-nonanone and vanilla (ts = -5.0, df = 7, P = 0.47; ts = 8.5, df = 19, P = 0.67, respectively) (Fig. A.28). Similarly, rate of avoidance also was similar between samples in females (ts = -0.5, df = 7, P = 1.0) and males (ts = 0.5, df = 19, P = 1.0) (Fig. A.29). Females spent a comparable amount of time within proximity of 2-nonanone and vanilla (t = 0.13, df = 7, P = 0.9) as did males (t = -1.0, df = 19, P = 0.34) (Fig. A.30).

DISCUSSION

The purpose of this study was to determine the bioactivity and functionality of three putative compounds (cyclohexanone, 2-decanone and 2-nonanone) found in secretions of male African and Asian elephants. If any of these compounds were potential pheromones, then they would elicit more chemosensory behaviors than the control used and their functionality could be inferred in part by the reactions of elephants to the placed compounds. Elephant behaviors were analyzed first without taking sex or age class into account to determine if the compound could be a pheromone in general and then data from post-pubescent elephants were analyzed to determine if responses to the compounds were specific to reproductively mature elephants.

The behavioral response of the wild elephants in this study did not support that any of the compounds bioassayed were pheromones. However, there were some interesting results. Cyclohexanone did not elicit any behavioral difference compared to the control when the responses of all the elephants were analyzed, but when only post-pubescent elephants were considered, there were a couple of intriguing outcomes. Post-pubescent males had higher proportions of chemosensory and avoidance behaviors toward cyclohexanone than to the control, but their rate of responses did not differ. Post-pubescent females responded for a longer duration toward cyclohexanone than the control. These results are suggestive of signal meaning to sexually mature elephants. Every post-pubescent male that came within proximity of cyclohexanone performed an investigatory behavior (Fig. A.6) and 80% (4 of 5) of them performed some avoidance behaviors (Fig. A.7). The low rate or response could be that once the elephant investigated cyclohexanone, the compound was identified and no further investigation was needed, especially since 80% of the elephants had a negative reaction.

However, this needs to be kept in perspective because of the small sample size of post-pubescent males sampled. Another interesting outcome was the duration that post-pubescent females spent in proximity to cyclohexanone (Fig. A.10). Post-pubescent females spent nearly four and half times more time near cyclohexanone than to vanilla, yet the proportion or rate of behaviors did not differ. Cyclohexanone may serve as a indicator signal to sexually mature females. Cyclohexanone is found in the early stages of musth in Asian elephants (Rasmussen et al. 1990) and therefore could be an signal of early musth to females. That could explain why females are not very interested in the compound, as seen with their low rate of investigation, but also not avoiding it like the males. To females this compound maybe acting as a notice but to post-pubescent males that may be competitors, this compound may be a warning that an elephant is entering musth and looking for females. Once again, however, these are interpretations made on a very small sample size.

The lack of bioactivity in 2-nonanone is the most surprising because it was the only compound found in all stages of musth in African elephants (Rasmussen et al. 1990). However, 2-decanone was of some interest because this compound elicited no form of bioactivity in post-pubescent elephants, however, the proportion and rate of chemosensory behavior was significantly higher toward 2-decanone than to the control when observing all the elephants. Fifty-seven percent of the 49 elephants that came within proximity of 2-decanone performed some form of chemosensory behavior (Fig. A.11) and 27% of those performed an avoidance behavior. In contrast, while 58% of the 24 elephants that came within proximity of vanilla performed chemosensory behavior, only one elephant (4%) performed an avoidance behavior (Fig. A.12). Although the rates of avoidance differed between 2-decanone and vanilla, interpretation is difficult because the rates were very low (Fig. A.14).

There is some evidence of bioactivity for these compounds but more assays need to be carried out. By isolating pheromones from African elephants, we can better understand not just the biology of elephants but also facilitate their conservation. These pheromones could be used to draw elephants toward protected corridors or even used to deter elephants from agricultural areas. Hence, it is worthwhile to continue studies on the identities of chemical signals that mediate intra- and intersexual interactions in African elephants.

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Compound	Control Iulian Data		Number of	Number of Elephants
Compound Control Junan Date		Juliali Date	Elephants	Assayed
2-Decanone	Vanilla	3 August 2007	14	14
2-Decanone	Vanilla	4 August 2007	19	12
2-Decanone	Vanilla	27 August 2007	31	17
2-Decanone	Vanilla	5 September 2007	7	7
2-Nonanone	Vanilla	3 October 2007	15	4
2-Nonanone	Vanilla	8 November 2007	14	11
2-Nonanone	Vanilla	26 November 2007	13	13
2-Nonanone	Vanilla	29 November 2007	16	12
2-Nonanone	Vanilla	30 November 2007	75 - 80	26
Cyclohexanone	Vanilla	1 December 2007	23	14
Cyclohexanone	Vanilla	5 January 2008	11	1*
Cyclohexanone	Vanilla	23 January 2008	7	5
Cyclohexanone	Vanilla	31 January 2008	16	9
Cyclohexanone	Vanilla	19 March 2008	1	1
Cyclohexanone	Vanilla	20 March 2008	1	1
Cyclohexanone	Vanilla	26 March 2008	14	14
Cyclohexanone	Vanilla	8 April 2008	42	30

Table A.1. Summary of days when bioassays of certain compounds were tested and the number of elephants present and number of elephants that actually came within proximity (one body length) of the compound or control.

* first elephant to come within proximity retreated leading entire group away from the waterhole

Behavior categories	Definition
and defined behaviors	
<u>Approach</u>	Presented in order of closeness to sample
Proximity	Elephant within one body length of sample.
Near	Elephant within one trunk length of sample.
Chemosensory	Presented in order of least to most discriminatory
Sniff	Nasal openings hover over sample without contact.
Check	Touch sample with tip of either finger.
Place	Entire nasal opening is placed on a sample and held momentarily.
Flehmen	Tip of trunk touches sample then placed in the VNO ducts in the
	roof of the mouth.
<u>Accessory Trunk</u>	
Blow	Performed after inspecting a sample. Air is expelled quickly from
	nasal openings of trunk; usually audible and mucus expelled
	usually visible.
Dig	Elephant used trunk tip or foot to displace ground at sample area.
Periscope sniff	Trunk is raised to air above head level and held for at least 2
	seconds.
Pinch	The two fingers of trunk pick up dirt around the sample.
Suck	Same trunk position as Place accompanied with trunk contraction;
	usually audible.
Trunk Flick	Performed after inspecting a sample. Bottom ¹ / ₄ of trunk moves up
	and down rapidly.
Wriggle	Performed after inspecting a sample. Trunk twists and then
	untwists once at a moderate pace (slower than trunk flick)
<u>Other</u>	
Dust	Elephant throws dirt from sample area on body using trunk.
Ear Wave	Ears extend out and rapidly brought back to the body.
Motionless	Elephant exhibits no behavior for at least 5 seconds.
Other	Behaviors exhibited that are not defined in ethogram.
Vocalize	Elephant vocalizes after investigating sample.

Table A.2. Ethogram to record behaviors performed by wild African male and female elephants to bioassay samples. Specific behaviors were categorized into Approach, Chemosensory, Accessory Trunk, and Other.

Ethogram compiled by Meyer (2006)

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	tusk begin to turn outward
7	shoulder at level of eye of adult female	22 cm; began to splay out, males have thicker tusk	look more like a small adult Males: have heavier bodies
8	overall size $\frac{1}{2}$ of adult female	25-30 cm	malas are larger than
9	overall size /4 of addit female	27 Cm	females are larger than females same age and spend less time with family; females more integrated into family
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 Female: more square in body shape than adult females

Table A.3. The morphological descriptions of elephants in four age classes of wild African male and female elephants (Moss, 1996)
Age class and specific age (years old)	Height	Ca. Tusk length and description	Body and social description
Subadults 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
Adult > 19	Males: shoulder height still increasing taller than largest female	Tusks thick at lip	Males: taller than adult females, head broadens, body heavy set Females: back has lengthened so that body appears long

Table A.3 Continued.



Figure A.1. Proportion of all elephants that performed chemosensory behaviors toward cyclohexanone (N = 54) and vanilla (N = 37) at Ndarakwai Ranch, Tanzania from December 2007 – April 2008 (no bioassays were conducted in February).



Figure A.2. Proportion of all elephants that performed avoidance behaviors toward cyclohexanone (N = 54) and vanilla (N = 37) at Ndarakwai Ranch, Tanzania from December 2007 – April 2008 (no bioassays were conducted in February).



Figure A.3. The mean (\pm SE) rate of chemosensory behaviors by all elephants toward cyclohexanone (N = 54) and vanilla (N = 37) at Ndarakwai Ranch, Tanzania from December 2007 – April 2008 (no bioassays were conducted in February).



Figure A.4. The mean (\pm SE) rate of avoidance behaviors by all elephants toward cyclohexanone (N = 54) and vanilla (N = 37) at Ndarakwai Ranch, Tanzania from December 2007 – April 2008 (no bioassays were conducted in February).



Figure A.5. The mean (\pm SE) duration (one body length) of all elephants within proximity to cyclohexanone (N = 54) and vanilla (N = 37) at Ndarakwai Ranch, Tanzania from December 2007 – April 2008 (no bioassays were conducted in February).



Figure A.6. Proportion of post-pubescent elephants (Females: N = 4; Males: N = 5) that performed chemosensory behaviors toward cyclohexanone and vanilla based on sex at Ndarakwai Ranch, Tanzania from December 2007 – April 2008 (no bioassays were conducted in February) (PP = Post-Pubescent).



Figure A.7. Proportion of post-pubescent elephants (Females: N = 4; Males: N = 5) that performed avoidance behaviors toward cyclohexanone and vanilla based on sex at Ndarakwai Ranch, Tanzania from December 2007 – April 2008 (no bioassays were conducted in February) (PP = Post-Pubescent).



Figure A.8. The mean (\pm SE) rate of chemosensory behavior of post-pubescent females (N = 4) and males (N = 5) towards cyclohexanone and vanilla at Ndarakwai Ranch, Tanzania from December 2007 – April 2008 (no bioassays were conducted in February) (PP = Post-Pubescent).



Figure A.9. The mean (\pm SE) rate of avoidance behavior of post-pubescent females (N = 4) and males (N = 5) towards cyclohexanone and vanilla at Ndarakwai Ranch, Tanzania from December 2007 – April 2008 (no bioassays were conducted in February) (PP = Post-Pubescent).



Figure A.10. Mean duration (\pm SE) of post-pubescent females (N = 4) and males (N = 5) within proximity (one body length) of cyclohexanone and vanilla at Ndarakwai Ranch, Tanzania from December 2007 – April 2008 (no bioassays were conducted in February) (PP = Post-Pubescent).



Figure A.11. Proportion of all elephants that performed chemosensory behaviors toward 2-decanone (N = 49) and vanilla (N = 24) at Ndarakwai Ranch, Tanzania from August 2007 – September 2007.



Figure A.12. Proportion of all elephants that performed avoidance behaviors toward 2-decanone (N = 49) and vanilla (N = 24) at Ndarakwai Ranch, Tanzania from August 2007 – September 2007.



Figure A.13. The mean (\pm SE) rate of chemosensory behaviors by all elephants toward 2-decanone (N = 49) and vanilla (N = 24) at Ndarakwai Ranch, Tanzania from August 2007 – September 2007.



Figure A.14. The mean (\pm SE) rate of avoidance behaviors by all elephants toward 2-decanone (N = 49) and vanilla (N = 24) at Ndarakwai Ranch, Tanzania from August 2007 – September 2007.



Figure A.15. The mean (\pm SE) duration of all elephants within proximity to 2-decanone (N = 49) and vanilla (N = 24) at Ndarakwai Ranch, Tanzania from August 2007 – September 2007.



Figure A.16. Proportion of post-pubescent elephants (Females: N = 7; Males: N = 10) that performed chemosensory behaviors toward 2-decanone based sex at Ndarakwai Ranch, Tanzania from August 2007 – September 2007 (PP = Post-Pubescent).



Figure A.17. Proportion of post-pubescent elephants (Females: N = 7; Males: N = 10) that performed avoidance behaviors towards 2-decanone and vanilla based on sex at Ndarakwai Ranch, Tanzania from August 2007 – September 2007 (PP = Post-Pubescent).



Figure A.18. The mean (\pm SE) rate of chemosensory behavior of post-pubescent females (N = 7) and males (N = 10) toward 2-decanone and vanilla at Ndarakwai Ranch, Tanzania from August 2007 – September 2007 (PP = Post-Pubescent).



Figure A.19. The mean (\pm SE) rate of avoidance behavior of post pubescent (N = 7) and males (N = 10) toward 2-decanone and vanilla at Ndarakwai Ranch, Tanzania from August 2007 – September 2007 (PP = Post-Pubescent).



Figure A.20. Mean (\pm SE) duration of post-pubescent (N = 7) and males (N = 10) within proximity (one body length) of 2-decanone and vanilla at Ndarakwai Ranch, Tanzania from August 2007 – September 2007 (PP = Post-Pubescent).



Figure A.21. Proportion of all elephants that performed chemosensory behaviors toward 2nonanone (N = 42) and vanilla (N = 58) at Ndarakwai Ranch, Tanzania in November 2007.



Figure A.22. Proportion of all elephants that performed avoidance behaviors toward 2-nonanone (N = 42) and vanilla (N = 58) at Ndarakwai Ranch, Tanzania in November 2007.



Figure A.23. The mean (\pm SE) rate of chemosensory behaviors by all elephants toward 2-nonanone (N = 42) and vanilla (N = 58) at Ndarakwai Ranch, Tanzania in November 2007.



Figure A.24. The mean (\pm SE) rate of avoidance behaviors by all elephants toward 2-nonanone (N = 42) and vanilla (N = 58) at Ndarakwai Ranch, Tanzania in November 2007.



Figure A.25. The mean (\pm SE) duration of all elephants within proximity to 2-nonanone (N = 41) and vanilla (N = 55) at Ndarakwai Ranch, Tanzania in November 2007.



Figure A.26. Proportion of post-pubescent elephants (Females: N = 8; Males: N = 20) that performed chemosensory behaviors toward 2-nonanone and vanilla based on sex at Ndarakwai Ranch, Tanzania in November 2007 (PP = Post-Pubescent).



Figure A.27. Proportion of post-pubescent elephants (Females: N = 8; Males: N = 20) that performed avoidance behaviors toward 2-nonanone and vanilla based sex at Ndarakwai Ranch, Tanzania in November 2007 (PP = Post-Pubescent).



Figure A.28. The mean (\pm SE) rate of chemosensory behavior of post-pubescent females (N = 8) and males (N = 20) toward 2-nonanone and vanilla at Ndarakwai Ranch, Tanzania in November 2007 (PP = Post-Pubescent).



Figure A.29. The mean (\pm SE) rate of avoidance behavior of post-pubescent females (N = 8) and males (N = 20) toward 2-nonanone and vanilla at Ndarakwai Ranch, Tanzania in November 2007 (PP = Post-Pubescent).



Figure A.30. Mean duration (\pm SE) of post-pubescent females (N = 8) and males (N = 20) within proximity (one body length) of 2-nonanone and vanilla at Ndarakwai Ranch, Tanzania in November 2007 (PP = Post-Pubescent).