

# SEED PROTECTION THROUGH DISPERSAL BY AFRICAN SAVANNAH ELEPHANTS (*LOXODONTA AFRICANA AFRICANA*) IN NORTHERN TANZANIA

By Bradley R. Spanbauer

Seed dispersal by animals is important for maintaining healthy populations of many tree species. The Janzen-Connell hypothesis, states that trees are under selective pressures to have their seeds dispersed away from the parent plant and into an environment more suitable for growth. Seeds typically do not survive underneath the parent plant for a myriad of reasons, including light and nutrient limitations, and excessive predation. Large-seeded tree species are especially affected by these factors because their seeds cannot be dispersed by abiotic factors, such as wind. Trees with large seeds that can only be effectively dispersed by large-bodied animals are referred to as megafaunal syndrome species. African forest elephant disperser effectiveness has been well studied. African savannah elephants may fill a similar niche, although experimental data are few. African savannah elephants have been suggested as critical seed dispersers, and may be the only remaining organisms capable of effectively dispersing seeds of megafaunal syndrome species.

I examined the effectiveness of savannah elephant dung as a protective barrier for three tree species: *Acacia tortilis*, *Tamarindus indica*, and *Balanites aegyptiaca*. Experimental treatments were established to measure the effect of dung in protecting passed seeds. I also addressed the Janzen-Connell model. I predicted that seeds in dung and seeds away from the parent tree would experience less infestation than fresh seeds. Simple linear regression was used to determine daily removal and infestation rates. Two-way analysis of variance was used to compare time in days and treatment and their interaction. Multiple comparisons using a Tukey's test of honest significant differences were made to check for true differences between paired treatments from the ANOVA. Finally, loglinear analysis was used to test for differences among infestation of seeds at different distances from adult conspecific trees.

In January 2013, ants or termites in Experiment 1 likely removed passed seeds in dung. Fresh seeds experienced similar levels of removal. Chi-square analysis of data supported my hypothesis and revealed differences in beetle emergence between passed and fresh seeds. In support of my prediction, in October 2013, seeds in dung experienced less beetle infestation than fresh seeds in Experiment 2. Seeds at distances greater than five meters experienced less beetle infestation than seeds underneath conspecific trees in Experiment 3. This study was the first to experimentally address post-dispersal seed fate for megafaunal syndrome species by savannah elephants. It creates a link between disperser effectiveness of forest and savannah elephants, and provides foundation for further examining savannah elephants as seed dispersers of megafaunal syndrome species.

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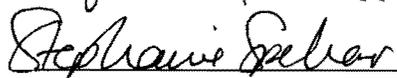
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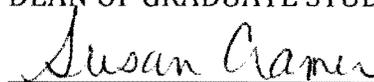
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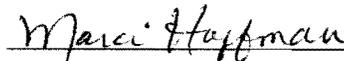
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## TABLE OF CONTENTS

	Page
LIST OF TABLES.....	iv
LIST OF FIGURES.....	v
INTRODUCTION.....	1
CHAPTER I SEED PROTECTION THROUGH DISPERSAL BY AFRICAN SAVANNAH ELEPHANTS (LOXODONTA AFRICANA AFRICANA) IN NORTHERN TANZANIA.....	10
Abstract.....	10
Introduction.....	12
Methods.....	15
Study Area.....	15
Sampling Procedures.....	16
Data analysis.....	18
Results.....	18
Discussion.....	20
Acknowledgements.....	25
CONCLUSION.....	27
REFERENCES.....	39

## LIST OF TABLES

		Page
Table 1	Experimental treatment groups and numbers of seeds per treatment for Experiment 1 and Experiment 2.....	32
Table 2	Experimental treatments and number of seeds per treatment for <i>Balanites aegyptiaca</i> experiments.....	33
Table 3	Analysis of variance results for <i>A. tortilis</i> experiments.....	34
Table 4	Results of Tukey's HSD test for <i>A. tortilis</i> experiments.....	35
Table 5	Analysis of variance results for <i>T. indica</i> experiments.....	36
Table 6	Results of Tukey's HSD test for <i>T. indica</i> experiments.....	37
Table 7	Results of loglinear analysis of variance for <i>Balanites aegyptiaca</i> experiments.....	38

## LIST OF FIGURES

		Page
Figure 1	Intact, potentially viable seeds of <i>Acacia tortilis</i> remaining over time for Experiment 1 in January 2013.....	30
Figure 2	Intact, potentially viable seeds of <i>Tamarindus indica</i> remaining over time for Experiment 2 in October 2013.....	31

## Introduction

Seed dispersal mechanisms are a critical component of plant life histories and have shaped ecosystems around the world (Campos-Arceiz and Blake 2011). The study of the processes surrounding animal-dispersed seeds is of critical importance in tropical ecology for understanding and ensuring the stability and integrity of tropical ecosystems (Janzen 1970, Janzen and Martin 1982), which are among the most diverse and species-rich ecosystems on Earth. Harms et al. (2000) stated that seed dispersal by animals does indeed increase forest diversity, and it is through such processes that these ecosystems are maintained naturally. Understanding seed dispersal mechanisms is important for expanding ecological knowledge, especially concerning the tropics. Still, from a conservation perspective, maintaining these tropical biodiversity “hotspots” is of great importance in promoting global ecosystem integrity (Myers et al. 2000).

Janzen (1970) and Connell (1971) developed a model for understanding the evolution of seed dispersal. The aptly named Janzen-Connell hypothesis states that trees are under selective pressures to have their seeds dispersed away from the parent plant and into an environment more suitable for growth. Beneath the parent tree, seeds are more likely to be negatively affected by density-dependent factors (e.g., competition for nutrients and light) deriving from the parent tree and its

offspring. In addition, seeds on or underneath the parent tree may fall victim to seed predators and pathogens. Seeds underneath the parent plant are contained in ripening fruits and are concentrated under the tree and may be easily detected by seed predators. Supporting the Janzen-Connell model is the observation that for tropical trees, few or no seedlings survive beneath the parent tree due to factors that cause mortality, such as seed and seedling predators and pathogens; it is only outside of or away from these effects that seeds and seedlings can survive (Mucunguzi 1995, Cochrane 2003, Or and Ward 2003, Campos-Arceiz and Blake 2011). By consuming and transporting seeds, animal seed dispersers help many tree species, especially in the tropics, maintain healthy, viable populations and reduce the devastating likelihood of seed predation.

Bruchid beetles are common seed predators in the tropics, especially among *Acacia* spp. (Miller 1993, 1995, Mucunguzi 1995, Or and Ward 2003). When seeds have fully developed, bruchid eggs are oviposited on seedpods still attached to the tree or that have fallen to the ground. The larvae hatch and bore into the seed and consume the embryo, rendering it inviable (Mucunguzi 1995), although this is not absolute (Coe and Coe 1987). The larvae will remain in the seed, develop, and emerge as adults. Bruchid beetles can have an enormous impact on seed crop survival. Or and Ward (2003) stated that for seeds that have not been ingested by a vertebrate, infestation by bruchid beetles can range from 25.3-99% of seeds.

While there are numerous animal seed dispersers across the tropics, from birds to primates and rodents to ungulates, the effectiveness of such dispersers must be studied. Disperser effectiveness, or the contribution a disperser makes to plant fitness (Schupp 1993), varies. Cochrane (2003) highlighted three components of disperser effectiveness: the quantity or proportion of available seeds that are reliably handled by the frugivore, the quality of handling or probability that a handled seed is dispersed in a condition to germinate, and the quality of deposition or probability that a seed is deposited in a site suitable for long-term establishment. If a seed disperser is truly effective, it should be able to consume and pass intact, viable seeds and deposit them in an environment that is better suited for germination with greater survival probability than underneath the parent plant. Each component is important to seed survival and tree recruitment, but not all dispersers are equally effective. Many animals that are often considered seed dispersers are also seed predators and perhaps vice versa. The African elephant (*Loxodonta africana*) destroys much vegetation in its ecosystems; for example, they topple and consume entire trees to satiate themselves. While this could be detrimental to tree populations, the clearing of entire trees by elephants may enhance populations of some species. In pulling down a tree, elephants may be opening up gaps for new individuals to establish themselves, acting as a player in the processes of succession and tree recruitment. By consuming such a large

amount of vegetation from trees, elephants consume numerous seeds, which are then deposited elsewhere after passing through the gut.

Elephants in general have been suggested to be effective seed dispersers, indeed; I argue that African savannah elephants (*Loxodonta africana africana*) are perhaps one of the most effective seed dispersers on the planet. African savannah elephants are the largest extant land animal, have been indicated as key components of their ecosystems, and consume up to 150 kg of food per day (Campos-Arceiz and Blake 2011). In addition to enormous food requirements, their wide dietary breadth, large gape size, and extensive home ranges (Owen-Smith 1988) also shape their seed dispersal function. African elephants can consume and swallow many more seeds intact than other potential dispersers (Cochrane (2003) reported 99% surviving). Animal dispersers such as primates, rodents, or ungulates are much more likely to grind and crush the seeds during mastication, thereby destroying seeds. Still, some seeds do not survive chewing by elephants. The probability of a seed to survive mouth and gut treatment depends on seed size, hardness, and protection. *Tamarindus indica* seeds ingested by Asian elephants (*Elephas maximus*) showed 75% survival (Campos-Arceiz et al. 2008b). However, elephants often swallow large amounts of food whole, and thus can pass viable seeds. When an elephant consumes a seed, the seed spends up to two days (Cochrane 2003) within the digestive tract. During this time, the elephant has likely moved away from the tree and has walked a great distance before the seed reaches the end of the gastro-

intestinal tract and exits the body. Elephants have large home ranges (Campos-Arceiz and Blake 2011); thus, many viable seeds are likely transported over great distances, thereby potentially enhancing plant species diversity across a landscape. Campos-Arceiz and Blake (2011) indicate that large body size paired with long gut retention times and extensive home ranges make elephants superb dispersers.

When elephants consume seeds from adult trees, they are also providing another benefit to the tree. Seed predators, such as the aforementioned bruchid beetles, can be extremely destructive to a seed crop. Elephants intervene by consuming branches with seedpods, as well as seeds and seedpods from the ground. Several studies have suggested that seeds consumed pre-infestation and even post-infestation have the potential to survive (Coe and Coe 1987, Miller 1993, Mucunguzi 1995, Or and Ward 2003, Campos-Arceiz and Blake 2011). By consuming seeds, elephants are providing a better pathway to survival by protecting seeds from beetle larvae infestation.

Previous studies on forest elephants (*Loxodonta africana cyclotis*) highlight the importance of their role in tropical forest ecosystems. Babweteera et al. (2007) compared three habitats in Uganda, only one of which had a resident elephant population, and examined population dynamics of *Balanites wilsoniana*, a large-seeded tree species distributed across Central and West Africa. In the two habitats where forest elephants were absent, more than 80% of seedlings were found underneath an adult conspecific, whereas in Kibale National Park, which hosts an

intact forest elephant population, 40% of juvenile trees were found away from a parent tree, sometimes at distances of 80 meters from the nearest adult conspecific (Babweteera et al. 2007). Using trap cameras, Babweteera et al. (2007) concluded that only forest elephants visited fruiting *B. wilsoniana* trees. Also, *B. wilsoniana* density was higher in Kibale National Park (1.22 individuals/ha), compared to the other two habitats (0.14 individuals/ha and 0.15 individuals/ha) (Babweteera et al. 2007). Finally, Babweteera et al. (2007) noted that in Kibale National Park, more *B. wilsoniana* individuals existed in size classes between seedlings and adults (saplings and poles), compared to the other two habitats, one of which only had seedlings (besides adult individuals of *B. wilsoniana*).

Another study conducted on *B. wilsoniana* by Cochrane (2003) produced similar results. Cochrane (2003) chose 50 trees in Kibale National Park, Uganda, and compared seeds underneath the parent tree versus seeds that were dispersed away from adult *B. wilsoniana*. Underneath the parent tree, 84% of seeds were predated upon, and only 3% germinated. Elephants visited 23 of the 50 trees and consumed approximately a quarter of the marked seeds (Cochrane 2003). Cochrane (2003) also conducted germination experiments and found that seeds that passed through the elephant digestive system experienced more germination (54.9% vs. 2.9%) and reduced time to germination (82 days vs. 132 days) than those that did not pass through the elephant digestive system. Chapman et al. (1992) found similar results for germination experiments comparing passed and unpassed *B. wilsoniana* seeds in

Kibale National Park (50.9% vs. 0.7%). Nchanji and Plumptre (2003) also found similar results for several plant species in south-western Cameroon. Cochrane (2003) and Chapman et al. (1992) concluded that *B. wilsoniana* seed dispersal by African forest elephants greatly increases probability of survival, and without forest elephants, long-term persistence of *B. wilsoniana* is unlikely, given that its seed size excludes other effective dispersers.

These studies suggest a potential mutualism between *B. wilsoniana* and forest elephants. While such narrow mutualisms are rare in nature, some have developed over time. Other plant-animal mutualism examples that have co-evolved include the dodo (*Raphus cucullatus*) and *Calvaria major* and the Indian rhinoceros (*Rhinoceros unicornus*) and *Trewia nudiflora* (Babweteera et al. 2007). In the case of the dodo, which is now extinct, *C. major* populations have been dramatically reduced on the island of Mauritius, where the dodo was endemic. Seeds of *C. major* may have required passage through the dodo gut for enhanced germination (Temple 1977). Given these examples, similar relationships may exist between other large-bodied herbivorous land mammals, such as African savannah elephants and some species of trees.

The effectiveness of dispersers for particular tree species can also depend on characteristics of the tree itself. Certain tree species exhibit traits that indicate that they can only be dispersed effectively by large land animals; this idea is referred to as the megafaunal fruit hypothesis or the megafaunal species syndrome (Janzen and

Martin 1982, Zaya and Howe 2009, Campos-Arceiz and Blake 2011). Trees with the megafaunal syndrome exhibit one or more of the following traits: long indehiscent seedpods with numerous extremely hard seeds, large fruits with large seeds that have a thick seed coat, and/or high concentrations of secondary compounds in the fruits or seeds (Alexandre 1978, Feer 1995, Guimaraes et al. 2008).

During the Pleistocene, animal biomass in North and South America was much greater than it is today. The land was dominated by megafauna such as mammoths, gomphotheres (extinct Proboscideans) and giant ground sloths, which may have acted as seed dispersal agents for tree species with these megafaunal syndrome characteristics. Due to the presumed anthropogenic extinction of North and South American megafauna, these tree species lost their potential dispersers and their geographic distributions may have been greatly reduced, such as the Kentucky coffee tree (*Gymnocladus dioica*) (Zaya and Howe 2009), or the species may have gone extinct due to the loss of their dispersers (Janzen and Martin 1982). In addition, other tree species with extant relatives of their prehistoric dispersers may now also be facing extinction. If effectiveness of seed dispersers is not addressed, plant species and their animal dispersal agents may be lost forever.

The goal of this thesis was to assess the effectiveness of African savannah elephants as seed dispersers. I focused on three tree species, *Acacia tortilis* (umbrella thorn Acacia), *Tamarindus indica* (tamarind), and *Balanites aegyptiaca* (desert date). I chose these three species because they exhibit characteristics

outlined by the megafaunal species syndrome and may only be effectively dispersed by African savannah elephants. Savannah elephants consume seeds from numerous tree species in their habitats, ranging from 33-200 species, depending on location (Campos-Arceiz and Blake 2011), but in most cases post-dispersal seed fate has not been experimentally addressed. Likewise, published experimental data regarding dung as a protective barrier for seeds are also rare. Several studies have been conducted on the seed dispersal capabilities of African forest elephants across much of Central Africa, perhaps because their contribution to seed dispersal is higher than African savannah elephants, given their habitat (Campos-Arceiz and Blake 2011). African savannah elephants, however, may be equally important in their role as seed dispersers, yet studies are sorely lacking. This study therefore examined seed protection from beetle larvae infestation through African savannah elephant dispersal and deposition in dung for the three potential megafaunal syndrome tree species.

## Chapter I

### **Seed Protection Through Dispersal by African Savannah Elephants (*Loxodonta africana africana*) in Northern Tanzania.**

#### **Abstract**

Seed dispersal by animals is important for increasing individual fitness within many tree species. The Janzen-Connell hypothesis, states that trees are under selective pressures to have their seeds dispersed away from the parent plant and into an environment more suitable for growth. Seeds typically do not survive underneath the parent plant for a myriad of reasons, including density-dependent factors such as light and nutrient limitations, as well as excessive predation, especially by bruchid beetle larvae. Large-seeded tree species in particular are affected by these factors because their seeds cannot be dispersed by abiotic factors, such as wind. Trees with large seeds that can only be effectively dispersed by large-bodied animals are referred to as megafaunal syndrome species. Studies focused on forest elephant contribution to tree recruitment and effective seed dispersal are more common than studies on African savannah elephants. African savannah elephants have been suggested as critical seed dispersers, although experimental data are few.

I examined the effectiveness of savannah elephant dung as a protective barrier for three tree species, *Acacia tortilis*, *Tamarindus indica*, and *Balanites*

*aegyptiaca*, which are potential representatives of the megafaunal syndrome. Seeds were collected from dung and underneath adult trees in Tarangire National Park, Tanzania. Experimental treatments were established to measure the effect of dung in protecting passed seeds, the effect of exclosures in limiting disturbance to small organisms such as insects, and the removal of seeds by larger seed predators such as rodents. Sites were established during each field season underneath conspecifics, where seed predation was likely highest. I also experimentally addressed the Janzen-Connell model. I predicted that seeds in dung and seeds away from the parent tree would experience less beetle infestation than fresh seeds not in dung.

For Experiment 1 in January 2013, all treatments experienced similar removal. Ants and termites likely removed passed seeds in dung. Fresh seeds experienced increased levels of beetle larvae emergence compared with seeds that had passed through the elephant digestive system. Results from a two-way ANOVA and Tukey's HSD indicated that there was no treatment effect for Experiment 1. For Experiments 2 and 3 in October 2013, seeds in dung experienced less beetle infestation than fresh seeds. Results from a two-way ANOVA and Tukey's HSD indicated that treatment effect was significant. Passed seeds at distances greater than five meters experienced less beetle infestation than fresh seeds underneath conspecific trees. This study was the first to experimentally address post-dispersal seed fate for megafaunal syndrome species by savannah elephants in northern Tanzania.

## **Introduction**

Seed dispersal by animals is important for maintaining persistent populations of many tree species, particularly across the tropics. The process of seed dispersal is best described by the Janzen-Connell hypothesis, which states that trees are under selective pressures to have their seeds dispersed away from the parent plant and into an environment more suitable for growth (Janzen 1970, Connell 1971). Seeds typically do not survive underneath the parent plant for a myriad of reasons. One reason is that seed crops underneath the canopy of the parent plant are negatively affected by density-dependent factors (nutrient and light requirements). Another reason is that, underneath parent trees, seeds are at high densities and are easily detected by seed predators (insects and vertebrates) and pathogens (particularly fungi). It is not uncommon for a seed predator or pathogen to decimate almost an entire crop of seeds under an individual tree (Cochrane 2003, Babweteera et al. 2007).

While some animals may be seed predators, they may also be seed dispersers. Elephants are generalist browsers with a wide dietary breadth and consume numerous species of seeds (Campos-Arceiz and Blake 2011). Elephants have been suggested as superb dispersal agents for large-seeded tropical tree species given their dietary breadth, paired with their large gape and body size and vast home ranges (Campos-Arceiz and Blake 2011); thus, elephants potentially

increase tree diversity across landscapes. In consuming seeds, elephants may also prevent seed predators from destroying seeds.

Bruchid beetles are common seed predators in tropical ecosystems. Bruchids will oviposit their eggs on the seedpods and seeds that are still on the tree or that have fallen to the ground. Elephants will consume entire branches with seedpods, ingesting potentially thousands of seeds during one feeding bout. It is highly likely that many of those seeds have not been infested or that elephant gut treatment may kill the beetle eggs or larvae on the seeds (Coe and Coe 1987, Miller 1993, 1995, Mucunguzi 1995, Or and Ward 2003). Assuming that the seeds have not been crushed during mastication in the elephant's mouth, seeds will typically survive gut treatment, given that elephants are monogastric hindgut fermenters (Campos-Arceiz and Blake 2011), and their digestive system is relatively inefficient. After a bout of feeding, time to defecation is approximately 48 hours (Cochrane 2003), and the elephant will likely have moved a great distance, during that time (>200 meters, Blake et al. 2009), away from the parent plant. An elephant will likely drop dung containing seeds in an environment that is suitable for seedling growth. By consuming seeds, largely pre-infestation, elephants may contribute substantially to successful tree recruitment in tropical ecosystems.

While numerous studies have been conducted on African forest elephants (*Loxodonta africana cyclotis*), experimental studies on savannah elephant seed dispersal are rare (Campos-Arceiz and Blake 2011). Studies measuring the numbers

of seeds in savannah elephant dung piles suggested that their dispersal capabilities are comparable to those of forest elephants (Dudley 1999, 2000), although these studies were observational. Of extreme importance is post-dispersal seed fate, which has not been well studied (Babweteera et al. 2007, Campos-Arceiz and Blake 2011). Seeds in dung would likely experience either secondary dispersal or predation. Ungulates, pigs, and baboons have all been observed sifting through elephant dung piles (likely in search of seeds) (Dudley 1999, Cochrane 2003, Babweteera et al. 2007). Rodents also search out elephant dung as foraging sites for seeds. Any of these animals could serve as a seed predator or secondary dispersal agent.

Dispersal is especially important for large-seeded tree species. Some of these species have been identified as potential representatives of the megafaunal fruit hypothesis or the megafaunal species syndrome (Janzen and Martin 1982, Guimares et al. 2008). These tree species exhibit traits such as long indehiscent pods of extremely hard seeds, large-seeded fruits, and fruits or pods containing high concentrations of secondary compounds. One or more of these traits employed by a given tree species might indicate that only large-bodied animals could effectively transport and pass viable seeds. Over evolutionary time, these species likely co-evolved with prehistoric megafauna, which are now extinct. While these mutualistic relationships may have been common during the Pleistocene (Janzen and Martin 1982), narrow plant-animal mutualisms today in nature are rare (Babweteera et al.

2007). The anachronistic quality of certain tree species might indicate that their once-common dispersal agents have been lost. Only remaining relatives, such as elephants, of such dispersers could fill niches left by prehistoric megafauna, and their numbers, too, are dwindling.

Through consumption and defecation, savannah elephants may effectively disperse megafaunal syndrome seeds and provide protection from seed predators. For this study, I selected three species that exhibit traits indicative of the megafaunal syndrome: the iconic *Acacia tortilis* (umbrella thorn acacia), *Tamarindus indica* (tamarind), and *Balanites aegyptiaca* (desert date). This study focused on elephant dung as a protective environment for consumed seeds compared to seeds that were not consumed and therefore potentially more susceptible to seed predators. This study also addressed the Janzen-Connell hypothesis by comparing passed and fresh seeds, both in dung and alone, underneath the tree canopy and away from a conspecific adult. I predicted that passed seeds in dung would experience less beetle larvae infestation than seeds that had not passed through the elephant digestive system, and distance from an adult tree was important for seed survival (supporting the Janzen-Connell hypothesis).

## **Methods**

**Study area.** This study was conducted in Tarangire National Park, Tanzania (3.8333° S, 36.0000° E). The park is 2850 km<sup>2</sup> and is 118 km southwest of Arusha, in

north-central Tanzania. Tarangire National Park contains numerous habitat types present within a single park, ranging from dry savannah to hilly areas dotted with many microphyllaceous tree species and the distinctive *Adansonia digitata* (baobab). Tarangire National Park experiences heavy rains in April and May (650 mm/year on average) before entering a long dry season from June through September. A short rainy season also typically occurs from November through December, followed by a short dry season in January and February.

**Sampling procedures.** *Experiment 1* – *Acacia tortilis* seeds were collected in October 2012 from elephant dung and from beneath adult trees. Passed seeds (from dung) and fresh seeds (from trees) were stored separately from each other in large, clear plastic bags and sequestered from potential pests. In early January, passed seeds and fresh seeds were separated into groups of 100. Exclosures (small wire mesh cages) (galvanized 19 gauge, 1.27 cm mesh) were constructed to only admit organisms such as insects. I established 14 sites with three treatments each: 100 passed seeds placed in fresh dung in an exclosure (henceforth, Dung), 100 fresh seeds not in dung in an exclosure (Exclosure), and 100 fresh seeds placed nearby and not in an exclosure (Open)(Table 1). The three treatment piles were placed one meter from each other, at the periphery of the conspecific canopy. The dung treatment was established to measure the effect of dung compared to the exclosure treatment, and the open treatment was established to measure unrestricted removal rate by seed predators, such as rodents. Sites were checked initially for the

first three consecutive days and then on days 11, 18, and 25. During each check, the number of intact, potentially-viable remaining seeds were recorded. The intact, potentially-viable remaining seeds that were not used in the field experiments were counted and examined for beetle emergence holes (indicating previous infestation).

*Experiments 2 and 3* – I collected fresh and passed seeds of *Tamarindus indica* and *Balanites aegyptiaca* on 12 October 2013 along 285 km of road in the park. These seeds were separated into groups of 20 (*T. indica*) and 10 (*B. aegyptiaca*), keeping the passed and fresh seeds separate. I established 19 sites for *T. indica* experiments, and six sites for *B. aegyptiaca* experiments. For *T. indica*, each site had the same three treatments used in Experiment 1: 20 passed seeds in dung in an enclosure (Dung), 20 fresh seeds in an enclosure not in dung (Exclosure), and 20 fresh seeds not in an enclosure not in dung (Open)(Table 1). Sites were checked initially for the first three consecutive days and then every other day through day 16. For the *B. aegyptiaca* experiments, I established six sites with four treatments: passed seeds in dung, passed seeds not in dung, fresh seeds in dung, and fresh seeds not in dung. All treatments had exclosures. At three sites, the four treatments were placed under the canopy of the tree (referred to as 'NEAR'), and the same four treatments were placed five meters from the tree (referred to as 'AWAY'). At the remaining three sites, the setup was exactly the same, except that the AWAY treatments were 15 meters from the tree. The sites were monitored the same days

as the *T. indica* experiments. The *B. aegyptiaca* sites were closed after 7 days due to disturbance of the enclosures.

**Data analysis.** To determine beetle emergence rates of seeds in Experiment 1 and beetle larvae infestation rates of seeds in Experiment 2, I used simple linear regression analysis and measured beetle emergence and seed infestation as a function of time. The slopes of the regressions represented daily removal rates. Chi-square analysis was used to compare beetle emergence rates between passed and fresh seeds not used in Experiment 1 in the field. I performed a two-way analysis of variance (ANOVA) for both the Experiments 1 and 2 to compare differences among the means. The full-model ANOVA compared factors of time in days, differences between the treatments and their interaction. I also performed a Tukey's HSD test on Experiment 1 and 2 datasets to test for differences between pairs of treatments from the ANOVA. For the experiment on *B. aegyptiaca*, I used loglinear analysis, which employed maximum likelihood, to examine the importance of distance and treatment. All data analysis was conducted with the statistical program 'R', with the exception of the loglinear analysis, for which the SAS (SAS Institute Inc. 1990) statistical program was used.

## Results

*Experiment 1* – For seeds not used in the field experiments, a total of 836 of 3,671 unpassed seeds (23%) showed signs of beetle larvae emergence, while only

82 of 2,775 (3%) passed seeds showed similar signs ( $\chi^2 = 508.22$ ,  $P < 0.0001$ ).

Linear regression analysis for the field experiments showed that daily removal rates for the Dung, Exclosure, and Open treatments were 2.88, 3.18, and 3.27 seeds/day, respectively (Figure 1). ANOVA indicated that time was significant (F value = 26.062,  $P < 0.0001$ ), while treatment was not significant (F value = 0.790,  $P = 0.456$ ). The interaction of treatment and time was also not significant (F value = 0.268,  $P = 0.987$ ). In addition, Tukey's HSD test also indicated that there were no differences between 'dung and exclosure' ( $P_{adj} = 0.49$ ), 'dung and open' ( $P_{adj} = 1.00$ ) or 'open and exclosure' ( $P_{adj} = 0.55$ ). There was thus no difference among the three treatments, and seeds in all treatments showed similar levels of removal over time.

*Experiments 2 and 3* - After the first five days of checking *T. indica* sites, 5 out of 200 (3%) Dung seeds had holes, 77 out of 200 (39%) Exclosure seeds had holes, and 120 out of 200 (60%) Open seeds had holes or were removed. Linear regression analysis indicated that infestation rates for the Dung and Exclosure treatments and removal rate for the Open treatment were 0.5371, 1.0050, 1.0801 seeds/day (respectively) (Figure 2). ANOVA indicated that time (F value = 27.049,  $P < 0.0001$ ) and treatment (F value = 87.932,  $P < 0.0001$ ) were significant. The interaction of treatment and time was also significant (F value = 2.307,  $P = 0.002$ ). Similarly, Tukey's HSD test revealed that there were statistically significant differences between all treatments over time. The differences between 'dung and exclosure' and 'dung and open' were particularly pronounced ( $P_{adj} = <0.00001$ , for both). The

difference between 'exclosure and open' was also significant ( $P_{\text{adj.}} = 0.03$ ). The results of the ANOVA and Tukey's HSD test therefore showed that there were distinct differences in infestation and removal rates among the three treatments over time.

Loglinear analysis indicated that distance and treatment were significant for intact, potentially viable seeds, ( $\chi^2 = 106.74$ ,  $P = <0.0001$ ), ( $\chi^2 = 18.69$ ,  $P = 0.0003$ ) indicating that distance from the conspecific tree does matter and that seeds farther away from the conspecific experienced less infestation than seeds immediately underneath the tree canopy. The interaction of treatment and distance was also significant ( $\chi^2 = 18.44$ ,  $P = 0.0052$ ). Overall, seeds at distances greater than or equal to five meters experienced less infestation by beetles than seeds immediately underneath the conspecific tree canopy. Treatment was also significant, demonstrating that dung also served as a protective barrier to *B. aegyptiaca* seeds, compared to fresh seeds not in dung.

## **Discussion**

Previous studies on forest elephants suggested that they are effective seed dispersers, especially in the case of large-seeded tree species (Chapman et al. 1992, Cochrane 2003, Babweteera et al. 2007). The potential for similar dispersal abilities has been suggested for African savannah elephants, but experimental data are rare. This study examined the effectiveness of African savannah elephants as seed

dispersers of three tree species that display traits reminiscent of only being effectively dispersed by large-bodied land animals (the megafaunal syndrome). To address the effectiveness of savannah elephants, I assessed the efficacy of dung as a protective barrier for dispersed seeds (Dung treatment) compared to fresh seeds preyed upon by either insects (Exclosure treatment) or larger-bodied seed predators, such as rodents or ungulates (Open treatment).

*Experiment 1* – Of the 3671 fresh and 2775 passed *Acacia tortilis* seeds that were not used in the field experiments, 23% of fresh seeds had beetle emergence holes compared to 3% of passed seeds that had similar holes. This difference indicates that consumption by elephants pre- or post-infestation has a positive effect on the probability of seeds to survive to the next stage in their life cycle. To determine if seeds were actually viable following savannah elephant gut passage, germination experiments could have been conducted but were beyond the scope of this project. Previous studies on forest elephants that included germination experiments found that seeds' passage through the elephant gut did indeed enhance germination and reduce time to germination (Cochrane 2003, Chapman et al. 2007).

For the field experiments, each of the three treatments (Dung, Exclosure, and Open) experienced similar emergence and/or removal over time (2.88, 3.18, and 3.27 seeds/day, respectively). Linear regression analysis indicated that seeds in Dung were not protected any better or subject to less removal than seeds in either of the other treatments (Exclosure or Open). This finding did not support my

prediction and is likely due to seasonal variation and natural history characteristics of this system. These field experiments were conducted in January when seeds of the study species are not present in the environment. *Acacia tortilis* has two fruiting events: one in May and another in September or October (Hegazy and Elhag 2006). Seedpods produced in May are false fruits and only consist of pods, with no seeds, while seedpods produced in September or October contain viable seeds. One hypothesis for this false fruiting that has been suggested is that over evolutionary time, it was advantageous to fruit twice, potentially to satiate seed predators. Still, it seems counter-intuitive to have evolved such an energetically-expensive trait. In the case of this study's field experiments, it could be expected that placing a resource in the environment that is sought by organisms ranging from insects to large vertebrates, at a time when such a resource is normally rare (if not completely absent), would result in use of this resource regardless of potential barriers (dung or exclosures). It is extremely common, regardless of season, to find beetles, ants, and termites occupying elephant dung piles (pers. obs.). Some of the removal of seeds in the field experiments encountered during Experiment 1 is likely attributable to insects other than beetles. Results from the ANOVA and Tukey's HSD support this suggestion. Treatment in the ANOVA was not significant (Table 3), and there were no significant differences among multiple comparisons of the treatments (Table 4).

*Experiments 2 and 3*– Initial observations for the field experiments in October 2013 supported my prediction that seeds in Dung would experience less infestation than other treatments (Exclosure or Open). After three consecutive days of observations, only 3% of seeds in Dung had infestation holes, while 39% of seeds in Exclosure and 60% of seeds in Open exhibited holes. Seeds in Dung also experienced a rate of infestation of 0.54 seeds/day. Fresh seeds in Exclosure and Open experienced infestation and/or removal rates of 1.01 and 1.08 seeds/day (respectively). Simple linear regression analysis indicated that seeds in Dung were protected post-dispersal, compared to fresh seeds in the Exclosure and Open treatments, which experienced greater infestation or removal. Results from the ANOVA further supported my hypothesis. The factors of time and treatment and their interaction were all significant, (Table 5). This indicated that over time, seeds in Dung experienced less infestation than either Exclosure or Open, and that these two treatments were also different from one another. Tukey's HSD further supported these findings using multiple comparisons, showing strong differences between Dung vs. Exclosure and Dung vs. Open, as well as differences between Exclosure and Open (Table 6). The dung in an exclosure (Dung) provided a protective barrier to passed seeds and only permitted insects to access the seeds inside. I emphasize again that exclosures were placed underneath conspecific tree canopies to measure the effect of dung as a protective barrier, given that beetle infestation is highest in this location as suggested by the Janzen-Connell model. The

fresh seeds in the Exclosure treatment did not have the protective dung barrier and thus exhibited increased signs of infestation. Similarly, fresh seeds in the Open treatment were subject to infestation and removal by seed predators. These findings supported my prediction that dung served as a protective barrier for seeds, post-dispersal.

Loglinear analysis indicated that distance and treatment were significant for the *B. aegyptiaca* experiments (Table 7). Seeds at distances of five meters and 15 meters from the adult conspecific experienced less infestation than seeds immediately under the tree canopy. In some cases, regardless of treatment, seeds underneath the adult *B. aegyptiaca* experienced infestation (even seeds in dung). Still, fresh seeds not in dung underneath the tree canopy experienced more infestation than seeds that had passed through the elephant digestive system (in dung or not). It should be noted that fresh seeds placed in dung experienced less infestation compared to fresh seeds not in dung for sites 1, 3, and 5. These results support my second prediction that seeds at distances greater than or equal to five meters from an adult conspecific tree will experience less infestation than seeds underneath the conspecific tree canopy. The results also provide support for the Janzen-Connell model.

Differences between experiments 1 and 2 were pronounced and were likely due to seasonal variation and the differences in life history characteristics for each of the organisms in this system. For example, different stages of the beetle life cycle

contributed to differences in effects on seeds between the two seasons. Also, trees of the study species do not produce seeds in January, which may have affected the results. For all experiments, it should be noted that sites were similar in that each site consisted of an adult conspecific and the treatments established underneath the tree canopy. However, the sites varied in surrounding habitat, as some sites were near the river and others were up on hills. While the sites represent the different habitats found throughout the northern part of Tarangire National Park, differences among these sites may exist but have not been thoroughly examined.

The contribution of forest elephants in maintaining habitat through seed dispersal is better than that of their savannah relatives. This study examined post-dispersal seed fate of three tropical tree species that are potentially only effectively dispersed by savannah elephants in northern Tanzania. Similar to studies on *Balanites wilsoniana* and forest elephants, the survival of these species may not rest entirely on savannah elephants but may be greatly enhanced by consumption and dispersal of their seeds. It is extremely likely, given the current state of elephant populations in Tanzania that local extinction of elephant populations could lead to dramatic changes in tree populations across the landscape in the near future.

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## Conclusion

African forest elephants have been the subjects of several seed dispersal studies (Chapman et al. 1992, Cochrane 2003, Babweteera et al. 2007), yet their savannah relatives have been less studied. Similarly rare are experimental data regarding post-dispersal seed fate in relation to predation, in particular by beetle larvae infestation. This study was the first to experimentally examine fates of seeds that had passed through the elephant digestive system and were deposited in dung, in comparison to fresh seeds underneath a conspecific adult. This study also highlighted three species that are likely representatives of the megafaunal species syndrome and may only be effectively dispersed by large animals, such as elephants. Currently, this is the only study that has employed exclosures to measure beetle larvae infestation of *Acacia tortilis* and *Tamarindus indica* seeds and provide support for the Janzen-Connell hypothesis using seeds of *Balanites aegyptiaca*.

Forest elephants are highly-effective dispersers of many tree species, especially large-seeded tree species such as *Balanites wilsoniana*, that conform to the megafaunal syndrome (Chapman et al. 1992, Cochrane 2003, Babweteera et al. 2007). My study highlighted the importance of elephant dung as a protective barrier for seeds post-dispersal. This study also supported the Janzen-Connell model by indicating that seeds at distances greater than or equal to five meters from an adult conspecific experienced less beetle infestation than seeds immediately under the

tree canopy. The *B. aegyptiaca* experiments also supported the notion that dung provides a protective barrier for seeds, even when under the adult tree canopy.

In my study, I did not complete germination experiments. For a truer measure of disperser effectiveness, seed germination and seedling establishment should be measured in the field to gain a better understanding of survival post-dispersal. This would be beneficial, as several studies on forest elephants and other tree species have found that gut treatment enhances seed germination and reduces time to germination (Chapman et al. 1992, Cochrane 2003). Identifying similar relationships with savannah elephants and the tree species that they effectively disperse could help elucidate savannah elephants' role in providing ecosystem services, such as seed dispersal, that ultimately result in tree recruitment and maintain their habitat naturally.

African elephants once ranged from the Mediterranean to the Cape of Good Hope, but are now only found in areas that compose about 22% of the African continent (Campos-Arceiz and Blake 2011). Elephants remaining in these places exist in highly-fragmented habitat. Their interactions with humans are increasing as human population continues to grow and encroach on suitable elephant habitat. The conservation of elephants is extremely complex, indeed. Elephants were not first studied until the 1960s and by that time had already experienced intense hunting pressure. Thus, truly evaluating the consequences of losing elephant populations is difficult given that baseline data do not exist and that currently, populations

continue to plummet largely due to illegal killing for the ivory trade. Without strict policies and enforcement of such policies on the ground, elephant numbers will continue to fall, even inside of protected areas such as national parks. Given the long generation times for not only the elephants but also the species of trees whose seeds the elephants disperse, studies need to be conducted over many years, a logistical hurdle that may be impossible given the current rate of loss of elephant individuals and forested habitat. It is extremely likely that without the international collaboration of major NGOs, governmental bodies, research scientists, and other stakeholders in protecting African elephants, the loss of elephant populations could drastically change the African landscape permanently, in perhaps as little as 50 years. Given that the tourism industry provides substantial financial support for many African nations, it is also very likely that the extinction of such an iconic animal such as the elephant will lead to negative ecological consequences as well as detrimental social and economic effects for the continent as a whole.

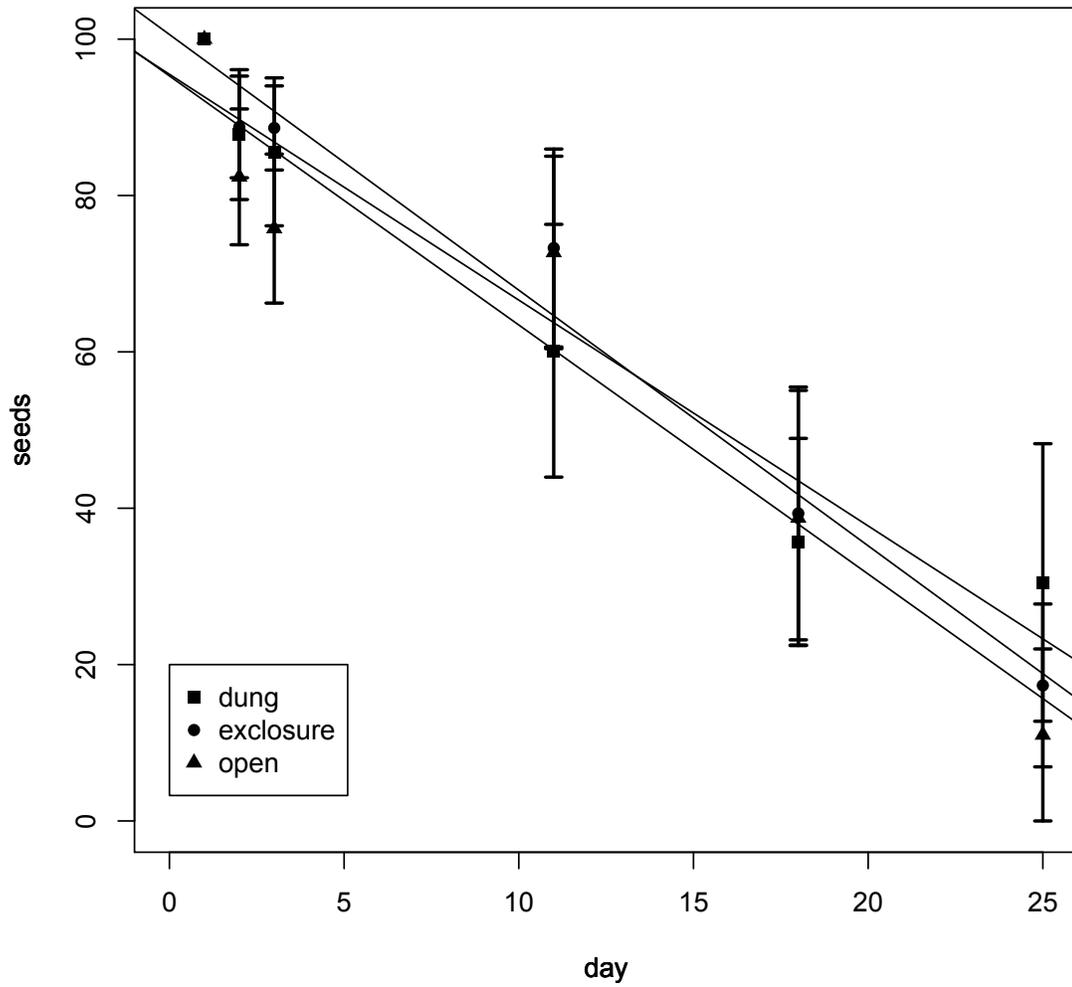


Figure 1. Intact, potentially-viable seeds of *Acacia tortilis* remaining over time in Experiment 1 in January 2013. Bars indicate standard errors.

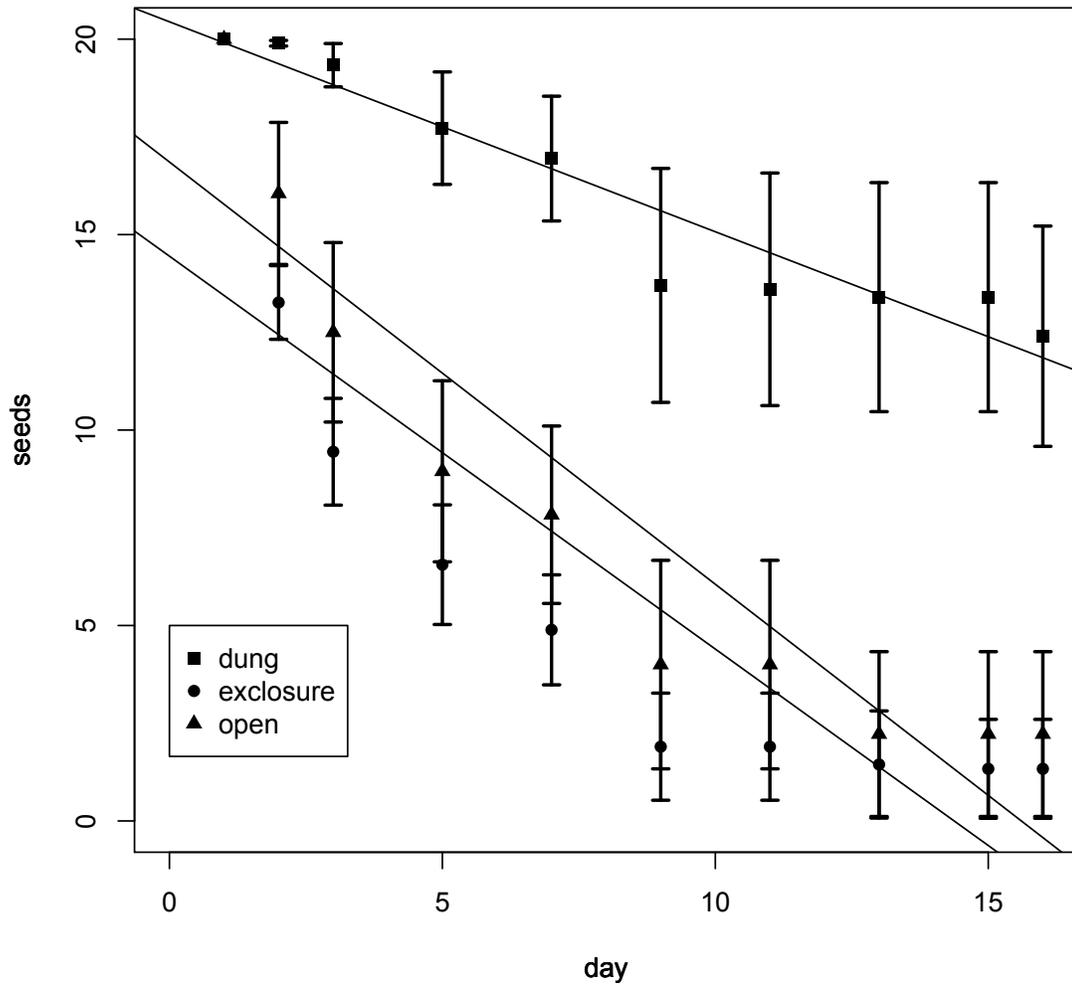


Figure 2. Intact, potentially-viable seeds of *Tamarindus indica* remaining over time in Experiment 2 in October 2013. Bars indicate standard errors.

Table 1. Experimental treatment groups and numbers of seeds per treatment for Experiment 1 and Experiment 2.

<b>Table 1</b>		
<b>Treatment</b>	<b>Experiment 1</b>	<b>Experiment 2</b>
	No. of <i>Acacia tortilis</i> seeds	No. of <i>Tamarindus indica</i> seeds
DUNG - Passed seeds in dung in an exclosure	100	20
EXCLOSURE - Fresh seeds not in dung in an exclosure	100	20
OPEN - Fresh seeds not in dung, not in an exclosure	100	20

Table 2. Experimental treatments and number of seeds per treatment for *Balanites aegyptiaca* experiments.

<b>Table 2</b>	<b>Sites 2, 5, 6</b>		<b>Sites 1, 3, 4</b>	
Treatment	NEAR	AWAY 5 meters	NEAR	AWAY 15 meters
	No. of <i>Balanites aegyptiaca</i>		No. of <i>Balanites aegyptiaca</i>	
Passed seeds in dung	10	10	10	10
Passed seeds not in dung	10	10	10	10
Fresh seeds in dung	10	10	10	10
Fresh seeds not in dung	10	10	10	10

Table 3. Analysis of variance results for *A. tortilis* experiments.

<b>Table 3: ANOVA for <i>A. tortilis</i> experiments</b>		
	F value	P value
Time	26.062	< 0.0001
Treatment	0.790	0.456
Treatment x Time	0.268	0.987

Table 4. Results of Tukey's HSD test for *A. tortilis* experiments.

<b>Table 4: Tukey's HSD for <i>A. tortilis</i> experiments</b>	
	Adjusted P ( $\alpha = 0.05$ )
Dung vs. Exclosure	0.49
Dung vs. Open	1.00
Exclosure vs. Open	0.55

Table 5. Analysis of variance results for *T. indica* experiments.

<b>Table 5: ANOVA for <i>T. indica</i> experiments</b>		
	F value	P value
Time	27.049	< 0.0001
Treatment	87.932	< 0.0001
Treatment x Time	2.307	0.002

Table 6. Results of Tukey's HSD test for *T. indica* experiments.

<b>Table 6: Tukey's HSD for <i>T. indica</i> experiments</b>	
	Adjusted P ( $\alpha = 0.05$ )
Dung vs. Exclosure	<0.00001
Dung vs. Open	<0.00001
Exclosure vs. Open	0.03

Table 7. Results of loglinear analysis of variance for *Balanites aegyptiaca* experiments.

<b>Table 7: Maximum Likelihood Analysis of Variance</b>		
	$\chi^2$ value	P value
Treatment	18.69	0.0003
Distance	106.74	<0.0001
Treatment x Distance	18.44	0.0052

## References

- Alexandre, D. Y. 1978. "Dispersal of seeds by elephants in Tai forest, Ivory-Coast." *Rev. Ecol. Terre Vie*, 32, 47-72.
- Babweteera, F., Savill, P., & Brown, N. 2007. "Balanites wilsoniana: Regeneration with an without elephants." *Biological Conservation*, 134, 40-47.
- Blake, S., Deem, S. L., Mossimbo, E., Maisels, F., Walsh, P. 2009. "Forest Elephants: Tree Planters of the Congo." *Biotropica*, 41(4), 459-486.
- Campos-Arceiz, A., & Blake, S. 2011. "Megagardners of the forest - the role of elephants in seed dispersal." *Acta Oecologica*, 37, 542-553.
- Chapman, L. J., Chapman, C. A., & Wrangham, R. W. 1992. "Balantities wilsoniana: Elephant Dependent Dispersal?" *Journal of Tropical Ecology*, 8(3), 275-283.
- Cochrane, E. P. 2003. "The Need to Be Eaten: Balanites wilsoniana with and without Elephant Seed-Dispersal." *Journal of Tropical Ecology*, 19(5), 579-589.
- Coe, M., & Coe, C. 1987. "Large herbivores, Acacia trees, and bruchid beetles." *South African Journal of Science*, 83, 624-635.
- Connell, J.H. 1971. "On the role of natural enemies in preventing competitive exclusion in some marine mammals and in rain forest trees." *Dynamics of Populations*, 298-312.
- Dudley, J. P. 1999. "Seed dispersal of Acacia erioloba in African bush elephants in Hwange National Park, Zimbabwe." *African Journal of Ecology*, 37, 375-385.
- Dudley, J. P. 2000. "Seed Dispersal by Elephants in Semiarid Woodland Habitats of Hwange National Park, Zimbabwe." *Biotropica*, 32(3), 556-561.
- Feer, F. 1995. "Morphology of fruits dispersed by African forest elephants." *African Journal of Ecology*, 33, 279-284.
- Gonthier, D. J. 2007. "Notes on seeds deposited in elephant dung at Tarangire National Park, Tanzania." *African Journal of Ecology*, 47, 252-256.

- Guimaraes, P. R., Galetti, M., Jordano, P. 2008. "Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate." *PLoS One*, 3(3), e1745. Doi: 10.1371/journal.pone.0001745
- Hall, J. B. 1992. "Ecology of a key African multipurpose tree species, *Balanites aegyptiaca* (Balanitaceae); the state-of-knowledge." *Forest Ecology and Management*, 50, 1-30.
- Harms, K. E., Wright, S. J., Calderon, O., Hernandez, A., Herre, E. A. 2000. "Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest." *Nature*, 404, 493-495.
- Hegazy, A. K., & Elhag, M. 2006. "Considerations of Demography and Life Table Analysis for Conservation of *Acacia tortilis* in South Sinai." *World Applied Sciences Journal*, 1(2), 97-106.
- Janzen, D. H. 1970. "Herbivores and the number of trees in tropical forests." *American Naturalist*, 104, 501-529.
- Janzen, D. H., & Martin, P. S. 1982, January 1. "Neotropical anachronisms: Fruits the Gomphotheres Ate." *Science*, 215, 19-27.
- Miller, M. F. 1993. "Is it advantageous for *Acacia* seeds to be eaten by ungulates?" *Oikos*, 66(2), 364-368.
- Miller, M. F. 1995. "Acacia seed survival, seed germination, and seedling growth following pod consumption by large herbivores and seed chewing by rodents." *African Journal of Ecology*, 33, 194-210.
- Mucunguzi, P. 1995. "Bruchids and survival of *Acacia* seeds." *African Journal of Ecology*, 33, 175-183.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. B., & Kent, J. 2000. "Biodiversity hotspots for conservation priorities." *Nature*, 403, 853-858.
- Nchanji, A. C., & Plumptre, A. J. 2003. "Seed germination and early seedling establishment of some elephant-dispersed species in Banyang-Mbo Wildlife Sanctuary, south-west Cameroon." *Journal of Tropical Ecology*, 19, 229-237.
- Or, K., & Ward, D. 2003. "Three-way interactions between *Acacia*, large mammalian herbivores, and bruchid beetles - a review." *African Journal of Ecology*, 41, 257-265.

Owen-Smith, N. 1988. "Megaherbivores. The Influence of Very Large Body Size on Ecology." Cambridge University Press.

Schupp, E.W. 1993. "Quantity, quality, and the effectiveness of seed dispersal by animals." *Vegetatio*, 108, 15-29.

Zaya, D. N., & Howe, H. F. 2009. "The anomalous Kentucky coffeetree: megafaunal fruit sinking into extinction?" *Oecologia*, 161, 221-226.