Examining marula (*Sclerocarya birrea* subsp. *caffra*) seed dispersal in the Kruger National Park

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Abstract

The marula tree (*Sclerocarya birrea* subsp. *caffra*), is a keystone species within savanna ecosystems that exhibits a patchy recruitment pattern and a skewed age-class distribution. However, this patchy distribution is unexpected and unexplained since marula trees produce a large quantity of fruit each year. The fruiting body of the marula tree is widely eaten by the animals of the savanna ecosystem, indicating that animals play a key role in seed dispersal. In this study, we examined seed dispersal of marula trees to determine if this life stage has an impact on the recruitment pattern observed in the Kruger National Park, South Africa. To do this, we attempted to identify dispersal agents based on distance marula seeds traveled from the parent tree's base, and the size and motivation of dispersers via a monitored seed cache with variable, size-based access. We found that most seeds are dispersed far distances, indicating that large animals are the main dispersers. However, we also found that mainly small animals with varying motivations most likely took seeds from our caches, thus demonstrating that they play a role in marula seed dispersal, as well. From this study we predict that large animals, such as elephants, are the primary dispersers of marula seeds, while rodents may be secondary dispersers. By identifying seed dispersal agents, we gain a better understanding of the cause of the observed patchy distribution and recruitment patterns of the marula tree. As such, conservation efforts may be properly directed toward maintaining marula trees and their necessary dispersers.

Introduction

The marula tree (*Sclerocarya birrea* subsp. *caffra*) is a functional keystone species in eastern South Africa that occurs within semi-arid savanna ecosystems (Jacobs and Biggs 2002). They are deciduous and grow to a height of 15m under favorable conditions (Howe and Smallwood 1982). Marula trees are the most widely distributed tree species in Kruger National Park (Schmidt *et al.* 2002, Shackleton *et al.* 2002). Frequently a dominant tree species, the marula plays a critical role in plant and animal ecology and community (Helm 2009). Marula trees provide a significant source of shade for other species (Schmidt *et al.* 2002). The marula tree also provides food in the form of fruit each summer that is consumed by herbivores such as elephants, baboons, kudu, vervets, warthogs, and rhinoceros (Helm 2009). The fruiting season is from January to March, and on average, female marula trees produce approximately 3,500 fruits each year (Schmidt *et al.* 2002, Shackleton *et al.* 2002).

Because marula trees are a dominant species and their fruits are so popular among all sizes of savanna herbivores, we would expect to see seeds dispersed evenly across the landscape. However, marula trees are patchily distributed in most savannas in South Africa, including in the Kruger National Park (Lewis 1987). The age-class distribution of marula trees is greatly skewed toward adults and young seedlings due to a combination of fire and elephant herbivory pressures on the intermediate saplings (Gadd 2002, Jacob and Biggs 2002). The population structure is unstable due to little regeneration and recruitment (Jacobs and Biggs 2002). Elephants threaten adult trees as they both uproot and strip them of bark (Hemborg and Bond 2006). As marula trees are ecologically important but also currently demonstrate an unstable population structure, we were interested in investigating seed dispersal as a means of understanding their patchy recruitment pattern.

Previous studies have confirmed that animals are key dispersers of marula seeds (Lewis 1987, Jacobs and Biggs 2002, Hemborg and Bond 2006,). Large mammals, such as elephants, have been noted to be exceptionally important in marula seed dispersal as intact seeds are often present in dung piles (Gonthier 2007). In a study by Lewis (1987), scarified marula seeds were found to have a much higher germination rate than uneaten or undigested seeds. Because large animals have greater travel range, they are likely to disperse seeds further away from the parent tree, avoiding intraspecific competition (Janzen 1970).

Although the marula tree produces fruit appealing to larger mammals, cache hoarders, such as squirrels, also utilize the seeds for later consumption. This scatter-hoarding technique may be key in dispersal, as quantities of each cache can be prodigious (Vander Wall 2001). Seeds are buried, which protects them from further predation. Stored nuts that are unrecovered by rodents can germinate once the environment warms during the next growing season (Vander Wall 2001). Animals often cache nuts in habitats that favor establishment such as early successional and old-field micro-habitats (Vander Wall 2005). Because of this dispersal method, competition from the parent tree and other mature trees is likewise avoided.

Due to the weight of marula seeds, without animal dispersers it is assumed that seeds would simply drop from the parent tree, accumulating at the base as seed rain. As such, a greater abundance of seeds would be found directly beneath the parent tree and few seeds would be found far from the parent tree (Nathan 2000). Alternatively, the Janzen-Connell hypothesis suggests that while seeds may be in highest density directly under the parent tree, few seedlings are found there because there is high-density-dependent mortality due to the pressures of pathogens, predation, and herbivory that can occur directly under the parent tree (Janzen 1970).

If elephants are dispersing seeds far from the parent tree, rodents are dispersing seeds an intermediate distance from the parent tree, and some seeds are dropping from the tree and collecting beneath the tree, then seedlings should be spread evenly across the savanna landscape. However, this is not seen. In South Africa, it has been observed that seedlings of marulas are seldom found directly under adults (Gallaher *et al.* 2010). The purpose of this study was to determine the cause of the observed patchy distribution of marula seedlings. We did this by looking at the distance marula seeds are dispersed, the size of the dispersal agents, and whether the dispersal agents were primarily interested in the fruit flesh or the seed inside the fruit. This would shed light on the role of animals in the dispersal of marula seeds. We predicted that if animals do not remove seeds from beneath the tree canopy, there would be larger seed banks under adult trees. If seeds are removed by large animals, we expected that seeds with flesh would be scarified and dispersed far distances from the parent tree. If seeds are removed and cached by small animals, we expected seeds without flesh to be dispersed intermediate distances from the parent tree.

Methods

Study site and design

This study was conducted in the lowveld near Skukuza in the Kruger National Park from September 9 – 12, 2014. As such, it was the dry season during which marula trees do not fruit. A total of 21 sites, defined as the chosen parent tree, were used for this study.

The dispersal distance of seeds was examined by digging for seeds in soil at 12 sites with elevations ranging from 230m to 340m. Approximate GPS locations are S25.047°, E031.589° (four trees) and S25.98°, E031.78° (eight trees).

Size and food preference of dispersal agents were examined by putting out caches of marula seeds (previously frozen from fruiting season) at nine sites at an elevation of approximately 240m. Three sites were located within the Nkuhlu full exclosure, which is inaccessible to animals larger than rodents (S24.99°, E031.775°). Three sites were fully accessible to all sizes of animals (S24.986°, E031.775°), and three sites were located within a partial exclosure, which excluded animals larger than approximately two meters tall (S24.981°, E031.777°). The aim of our investigation was not directly related to understanding seed predation when large animals were excluded from access; rather, exclosures were used due to our limited supply of fruit and our consequent fear that a single elephant or baboon may eat all of the fruit, thus not modeling the true range of dispersal agents. For the same reason we constructed exclosures that would only allow access for rodents regardless of whether the fruits were inside a larger exclosure.

Examining dispersal distance

We examined the distance seeds were dispersed by digging holes of approximately 50x50x15 cm at distances of two, 10, and 30 meters away from 12 different female marula trees. Every tree was at least 100m from another marula tree and was deemed female if kernels were found near the base of the tree (as per methods established by Shackleton *et al.* 2002). We sifted the dirt from each of these 36 holes, looking for seeds. We compared the mean densities of seeds in the soil at the three distances away from the tree using a Kruskal-Wallis test (data were not normal).

Examining size of dispersers

Twenty marula seeds were left at each of nine trees (six marula, two *Philenoptera violacea*, one *Balanites maughamii*) in order to examine the dispersal of seeds by animals. Ten seeds with flesh and ten seeds without flesh were left at each site for approximately two days. Seeds both with and without flesh were left out to identify the food preference of the dispersal agents. Larger animals, like elephants, might be expected to eat the seed with flesh while impalas might only eat the flesh and leave the seed behind; tree squirrels are typically seed hoarders (Lewis 1987). In our results, we defined “taken” as the whole seed, with or without flesh, to be missing from the site. To identify seed dispersers, Bushnell camera traps were set up at each site, pointing at the seed caches.

Seeds without flesh had holes drilled into them; we glued small magnets into these holes. This allowed us to search for the seeds with a magnetometer and determine how far from the source seeds are typically dispersed. We looked at a circular area of radius five meters around the marula tree.

We controlled for access variability by constructing rodent-accessible cages that would provide only small rodents access to the seeds placed within. One rodent-accessible cage was placed at each of the nine trees; of the ten seeds with flesh and ten seeds without flesh at each site, five seeds with flesh and five seeds without flesh were placed within the cage. The rodent-accessible cages allowed us to determine what size animal was responsible for the seeds missing from the sites.

A chi square contingency test was conducted to ensure that the use of three different exclosures did not have an impact on the frequencies of disappearance. To analyze the motivations of dispersal agents, we conducted a chi-square test to compare the frequencies of disappearance of seeds with and without flesh. Similarly, a chi-square test was performed to compare the frequencies of disappearance of seeds within and outside of rodent-accessible cages. This was done to analyze the size of dispersal agents.

Results

Examining dispersal distance

Only two holes contained seeds, both of which were 2m from the base of the tree. The mean for these holes was 0.02   0.07 seeds.m^{-3} (Figure 1). The number of seeds found did not differ based on distance from tree ($H_{(2)} = 0.649$, $p > 0.05$).

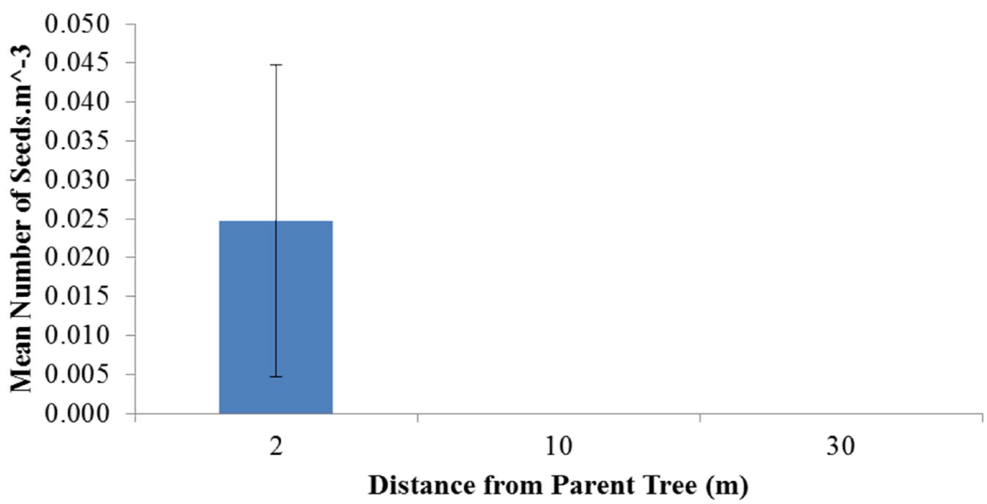

Figure 1. Mean number of marula seeds found per cubic meter of dirt sifted (standard error) as a function of distance from the parent tree (m). Soils were sifted to search for seeds below 12 parent trees in the Skukuza Region of the Kruger National Park, South Africa.

Examining size of dispersers

There was no difference in frequency of seeds taken from each tree site depending on exclosure type (full exclosure, partial exclosure, fully outside) ($\chi^2_{(2)} = 0.079$, $p > 0.05$). As such, we did not differentiate between exclosure type for the remainder of the study.

A total of 87 seeds without flesh and 126 seeds with flesh were placed beneath trees. Of the seeds without flesh, 33 were taken for a seed without flesh disappearance relative frequency of 0.379. A seed with flesh disappearance relative frequency of 0.222 was observed, as 28 marula seeds with flesh were taken. In addition to those that disappeared, 13 seeds with flesh were chewed on or partially eaten. There was no difference between the disappearance frequency of seeds with or without flesh ($\chi^2_{(1)}=1.724$, $p>0.05$) (Figure 2). None of the magnetized seeds were recovered by the magnetometer.

A total of 99 marula seeds were placed within cages; 114 placed outside and adjacent to the cages. Of these, 0.333 of the seeds within the cages were taken while 0.246 of the seeds outside of the cages were taken. There was no difference between the disappearance relative frequency of seeds inside versus outside of the cages ($\chi^2_{(1)} = 1.774$, $p > 0.05$) (Figure 2). Camera traps revealed a single francolin pecking at one of the caged setups in the full exclosure.

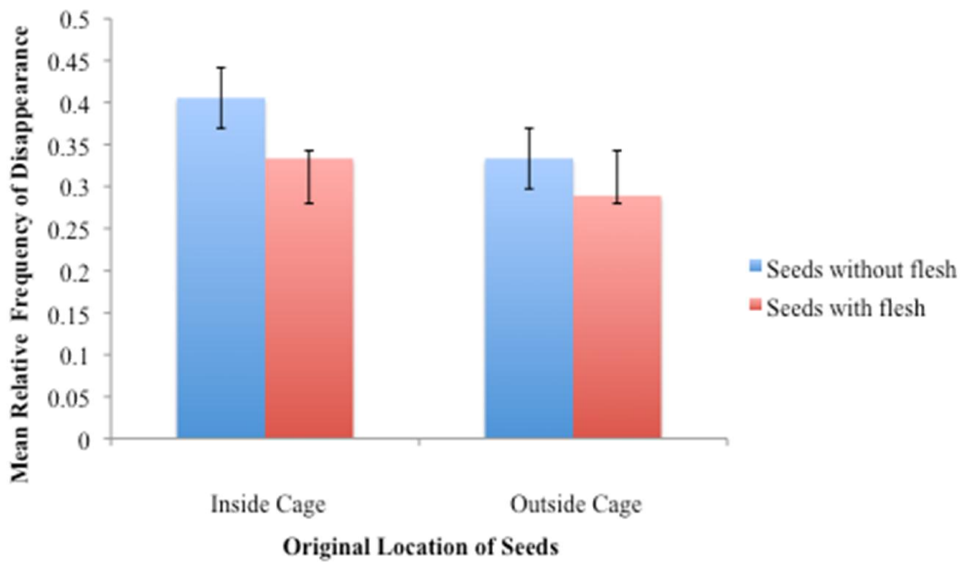

Figure 2. Mean relative frequency of disappearance of marula seeds with and without flesh found either within or outside of rodent-accessible cages (standard error). Marula seeds both with and without flesh were placed inside of and adjacent to rodent-accessible cages at the base of nine trees in the Kruger National Park, South Africa.

Discussion

Since zero seeds were found in most holes, we concluded that most seeds are being dispersed long distances by large animals. This is a surprising result considering the vast amount of fruit produced by a single tree each year. Even with animals acting as major dispersers of marula seeds, we expected a larger number of seeds left beneath the tree. Not finding these seeds indicates animals are dispersing almost all of the marula seeds each year from each tree.

Despite not finding any seeds at an intermediate distance from the trees, from the data collected in the seed cache experiment, we found that rodents do take marula seeds when they are available, as is supported by Vander Wall *et al*. (2005). We know rodents were taking marula seeds because at many sample locations only some of the seeds were taken. A larger animal would have taken all of the available food and could have potentially destroyed the cages. With knowledge of their feeding habits, we infer that impala most likely fed on the partially eaten seeds with flesh, only dispersing them a few centimeters (Apps 2012). Smaller animals that could access the rodent-accessible cages are most likely responsible for the dispersal of the remaining seeds; however, they could not be identified more specifically in this study, since camera trap results were inconclusive. We would have expected to find seeds dispersed by rodents at an intermediate distance, but the magnetometer proved ineffective and seeds could not be retrieved.

Conducting this study when the marula trees were not fruiting may have contributed to the discrepancy between the observed and expected relationship between number of seeds found beneath the trees and the dispersal agents involved in the seed caching experiment. If this study were conducted during the marula tree's fruiting season, more animals would have been actively seeking marula seeds, and we may have seen a larger impact by elephants on the seed caches. Additionally, if the seeds used in this study were fresh, they may have been more appealing to potential dispersers. In reality, rodents may not have this primary access and instead typically act as secondary dispersers (Midgley *et. al.* 2012). Squirrels are known to scatter-hoard seeds and might do so after another animal has already moved or digested the seed.

Synthesizing our results, we conclude that both large and small animals are responsible for the large-scale dispersal of nearly all marula seeds from beneath the parent tree. As Janzen-Connell hypothesized, there are no seedlings underneath parent trees (Janzen 1970). However, this is not due to competition with the parent tree, but rather, due to the complete removal of seeds from this area (Janzen 1970). Furthermore, unlike Janzen-Connell, we found that these seeds are dispersed an expansive distance by large animals, such as elephants, instead of a more intermediate distance. From these results, we can hypothesize that the observed patchy distribution pattern of marula seedlings is the result of two size classes of dispersal agents. The large dispersal agents, such as elephants, eat the marula seeds with flesh and travel a long distance while digesting them, excreting the scarified seeds kilometers away from the parent tree (Gonthier 2007). Small secondary dispersers take the scarified seeds from dung piles and proceed to disperse them at an intermediate distrance from this dung pile, creating a patchy distribution around the dung pile (Vander Wall *et al.* 2005). Under fertile soil conditions, we would expect successful recruitment of marula trees (Lewis 1987). Alternative explanations for the lack of seeds under the parent tree include rodents taking seeds further distances than we expected or predating the seeds (Vander Wall *et al*. 2005).

With the knowledge of a potential two-step dispersal process, we can recommend that future researchers investigate the extent of the role of secondary dispersal in the creation of patchy distribution of marula trees. Our study confirms that both large and small dispersers are essential to marula seed dispersal and tree recruitment but cannot substantiate our hypothesis of secondary dispersal. In considering conservation management strategies of marula trees, we must also consider the role of dispersal agents in their recruitment pattern.

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