MARULA (*Sclerocarya birrea* subsp. *caffra*)
Dispersal by Mammals: Are Squirrels Seed Predators or Seed Dispersers?

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MARULA (SCLEROCARYA BIRREA SUBSP. CAFFRA) DISPERsal BY MAMMALS: ARE SQUIRRELS SEED PREDATORS OR SEED DISPERsERS?

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ABSTRACT

The marula (Sclerocarya birrea subsp. caffra) is a well known dioecious tree found across much of central and southern Africa. Dispersal mechanisms for marulas are still unclear, although it is known that endozoochory, especially by elephants, plays an important role by increasing the percentage germination of the seeds. The tree squirrel (Paraxerus cepapi subsp. cepapi) has been observed removing marulas from elephant dung, and there are a few observations of them scatterhoarding seeds. The goals of this study were: 1) to determine if tree squirrels scatterhoard marula seeds, 2) to examine natural predation rates of stones under adult trees, and 3) to investigate whether the possible dispersal relationship is visible in density and demographic signals across the landscape. To accomplish this, we performed cafeteria experiments and surveyed marula populations and seed predation inside and outside large herbivore exclusion plots at N'waxitshumbe, Shingwedzi, Skukuza and Pretoriuskop in the Kruger National Park, South Africa. Our findings confirmed that squirrels do scatterhoard and disperse marulas. They were observed burying 46% of marula stones (n = 50). The average burial depth was 0.53 cm (±0.31; n = 15) and mean dispersal distance 4.57 m (±6.81; n = 33). Predation rates of marulas under adult trees were lower than expected: between 30 and 56% of stones lying on the surface were not predated at all). Patterns of marula demography and distribution across the landscape varied greatly between sites, which is likely to be related to different fire regimes, herbivore densities and climates. It was, however, evident that scatter-hoarding could be an important dispersal mechanism for the marula, and could be the second phase of a diplochorous seed-dispersal relationship with elephants.
1. INTRODUCTION

The Marula (Sclerocarya birrea subsp. caffra) is a species found across Africa, and is known to be a keystone species for biodiversity (Hofmeyr 2003; Jacobs and Biggs 2002; Shackleton 2002). In the Kruger National Park this species has the widest distribution of any tree, and although it is rarely dominant, it is one of the most important tree species in a given landscape (Trollope and van Wyk 1974; von Teichman 1982; Coates Palgrave 2002; Schmidt et al. 2002). Marulas are a favoured food source for elephants (Loxodonta africana), which eat the fruit, leaves and bark, and are known to knock trees over (Whyte et al. 2003). In recent years the elephant population has grown significantly in the Kruger National Park (Whyte et al. 2003), and mature marulas are being damaged on a large scale (Eckhardt et al. 2000; Jacobs and Biggs 2002, Whyte et al. 2003), even disappearing from some landscapes. Because this species is so ecologically important, as much as possible must be known about its ecology to enable effective conservation. Seed dispersal, especially long distance dispersal, has been described as one of the lesser understood aspects of ecology (Janzen 1983; Nathan 2006), and is the initial determinant of plant success in a given landscape (Nathan and Muller-Landau 2000).

Surprisingly little is known about marula seed dispersal mechanisms. Past hypotheses concerning the dependence of plant species’ on a single dispersal mechanism have often been shown to be unrealistic (Chapman et al. 1992); in most cases there are multiple species and processes which interact to determine the pattern of seed dispersal across the landscape (Howe 1984; Herrera 1986). Vander Wall et al. (2005) state that although much present research is focused on primary dispersal, secondary dispersal may have an unrecognised but integral part to play in establishment; removal of seeds should also not be assumed to show predation (Vander Wall et al. 2005).

Elephants are known to be a primary disperser of marula fruit (Lewis 1987), and warthogs, primates, and many species of antelope have been recorded eating them (Trollope and van Wyk 1974; Shackleton 2002). It has been shown that the passage of seeds through an elephant’s gut results in a significantly higher percentage of germination, both inside and outside dung piles (Lewis 1987), and seedlings have been observed growing out of other types of animal dung too (von Teichman 1982). Elephant dung may contain many seeds, so seedlings which germinate in a dung pile may experience high levels of intra and inter-
The use of elephant dung as a foraging medium by numerous species has been observed, and the consequent burial, scattering and predation of seeds aggregated in dung piles could actually promote the survival and fitness of marula seedlings (Dudley 2000). Scatter-hoarding – the removal and burial of seeds – is a common dispersal mechanism involving rodents (Vander Wall and Longland 2004). Squirrels, including many southern African species, are known to scatter-hoard (Skinner and Chimimba 2005; Briggs et al. 2009). The bush squirrel (Paraxerus cepapi cepapi) is one of the most widely distributed and common small mammals in the park (Pienaar 1964). This species relies on Marula seeds as an important source of nutrition (Trollope and van Wyk 1974) and has been observed removing marulas and other seeds from elephant dung (Pienaar 1968; Viljoen 1977a, b), and occasionally burying other hard seeds (Viljoen 1977a; Viljoen 1983; Skinner and Chimimba 2005). The above factors, combined with the widespread distribution of both species, suggest that it is likely that squirrels play a role in marula dispersal in the Kruger National Park, and possibly elsewhere.

This study aims to investigate the relationship between tree squirrels and marulas, and to determine whether they act merely as seed predators or also play a role in seed dispersal by moving and scatterhoarding the stones. If this is the case, I aim to critically assess the relative importance of this as a dispersal mechanism, in the presence and absence of elephants by investigating marula abundance, demography, and patterns of distribution across the landscape. From these findings it may be possible to infer the architects of these patterns, and to understand the importance of dispersal to marula establishment.

I hypothesise that although elephants are key dispersers of marulas, squirrels do disperse and scatterhoard marulas, and are especially important in environments where elephants are excluded. They may also act as a secondary diserper by removing and burying marula stones from elephant dung. If this is the case, I expect that marula stones left out will experience some predation, but that many will be buried by squirrels. I propose that, if this process occurs, there will be evidence in the landscape in the form of seed dispersal within large mammal herbivore-excluded plots and marula stones buried under seedlings.
2. METHODS

2.1 Species and Study Site Characteristics

Marula (*Sclerocarya birrea* subsp. *caffra*)

The marula is a medium-sized dioecious tree which grows up to 17m in height and is found from the KwaZulu-Natal south coast of South Africa to Ethiopia and Sudan in the north, and in parts of west Africa. (von Teichman 1982; Coates Palgrave 2002). The genus name *Sclerocarya* is derived from the Greek words for 'hard nut' (von Teichman 1982). Marulas are ecologically important because of the large amounts of fruit they produce (between February and June) which are valued by people and animals (Coates Palgrave 2002; Shackleton et al. 2002). Marula fruits are classified as drupes, and appear to be well-adapted to being passed through large herbivores unscathed. The stone consists of a hard, lignified endocarp containing 1 to 4 seeds each in a single locule. Locules are tightly sealed off by a lid, the operculum, and the stone is covered by the mesocarp: a fibrous fruit, and the exocarp, a tough peel (von Teichman et al. 1985). The operculum is always smaller than the seed, so seeds cannot be removed intact (von Teichman et al. 1985). Trees start producing fruit at approximately 7 years of age (von Teichman 1982).

Tree Squirrel (*Paraxerus cepapi* subsp. *cepapi*)

The tree squirrel is found in savanna woodlands in the southern parts of Africa, from northern South Africa to southern Tanzania and westwards to Angola (Skinner and Chimimba 2005). It is a small, diurnal rodent which resides in holes in tree trunks. Tree squirrels are territorial and have an average territory size of 4292m² (Viljoen 1977a). They feed predominantly on vegetable matter including seeds, which are a rich source of protein (Viljoen 1977b; Skinner and Chimimba 2005). They have occasionally been observed scatterhoarding hard seeds, and burial sites, in soft sand or under leaf litter, are carefully chosen (Viljoen 1977a).
Study Site

The Kruger National Park has an area of 18,998 km² and is situated in the northeastern Lowveld of South Africa (Smuts 1975). The climate is subtropical, with summer rainfall which alternates between wet and dry cycles with a periodicity of about 10 years (Jacobs and Biggs 2002). The park is divided roughly in half by its underlying substrate: granite in the west and basalt in the east (Venter et al. 2003).

Field work was done in four main areas of the park with different vegetation types: the N’waxitshumbe enclosure and Shingwedzi are situated on Mopane Basalt Shrublands, where marula populations are generally low except in the Roan enclosure, and annual average rainfall is 507 mm (Jacobs and Biggs 2002; Mucina and Rutherford 2006). The enclosure has an area of 309 ha and has been in place for 33 years (Jacobs and Biggs 2002). Both Skukuza and Pretoriuskop are on granite. Skukuza’s vegetation is classified as Granite Lowveld, with an annual rainfall of 633 mm and Pretoriuskop’s Sour Bushveld receives an average of 677 mm of rainfall (Mucina and Rutherford 2006). The marula is one of the most important tall tree taxa in each of these landscapes (Mucina and Rutherford 2006), but its distribution is usually limited to the crests and midslopes and it is more common towards the south (Coetzee et al. 1979; Jacobs and Biggs 2002).
2.2 Sampling procedure

Seed predation experiments were performed in Shingwedzi (at the rest camp) and in Skukuza (on the golf course and in the surrounding natural vegetation). The two human-impacted landscapes were partially chosen because of a visible squirrel population, and because the more open landscapes made observation of the squirrels more viable.

To determine whether squirrels scatterhoard marula stones, preliminary work was done in Shingwedzi, where 5cm lengths of fluorescent string were glued onto 50 marula stones according to the methods used by Midgley and Anderson (2002). They were then dusted with fluorescent powder to facilitate recovery at night using an ultraviolet torch. They were left out in the afternoon before dusk, and replaced in the morning after sunrise in groups of 10 (during the period of activity for *P. cepapi cepapi*). The number of stones was intended to be large enough to evoke a caching response, similar to how fruit under a tree or in a dung pile would. Squirrels were observed, and followed to determine the fate of the stones.

A more comprehensive study to determine the fate of marula seeds in the presence of tree squirrels was done in Skukuza, where 20 nuts each were left under 10 female *S. birrea* trees in the natural vegetation and 10 nuts each were left under 10 female trees on the golf course. Nuts were put out and then checked every evening and morning for four days (to confirm that removal was by a diurnal animal). An ultraviolet torch was used to follow the trail of fluorescent powder and the strings were used to help find buried nuts. The number of nuts buried, moved, missing, and undisturbed was recorded. For buried nuts, the depth of burial was recorded; as were the distance that nuts were moved, and distance from the nearest other nut.

In Pretoriuskop, vegetation and predation surveys were done both inside and outside the exclosure in order to determine the relative importance of squirrels in the presence and absence of elephants, but in the vicinity of N’waxitshumbe, elephants had almost completely removed woody cover outside the enclosure, so surveys were only conducted inside. There was no herbivore exclosure in Skukuza. In N’waxitshumbe and Skukuza, transects were walked, and all mature female marulas (those that had evidence of old fruit beneath them) were measured. The area underneath the canopy was surveyed for seedlings, which were initially defined as individuals with a basal diameter of <1cm. This category was then expanded to include ‘juveniles’, which we defined as individuals with a diameter of <10cm,
due to the complete lack of small seedlings in the N’waxitshumbe enclosure. If a young seedling was found, we attempted to dig up the nut to determine whether it was buried, and if so, the depth of burial. To determine the natural predation rates of seeds still under the parent plant, nuts were removed from a 1m² area beneath the canopy and broken open with a hammer to measure the number of viable seeds left untouched. At all sites, GPS co-ordinates were taken, and later used to measure the distance between seedlings and nearest adults.

2.3 Data analysis

For the cafeteria experiments, the percentages of marula stones with a certain fate, and averages of dispersal characteristics, such as distance and burial depth, were calculated. The percentage locule predation per stone was calculated for stones collected during the vegetation surveys.

Seedling to adult distances were calculated using the GPS points and the Garmin MapSource programme (Garmin 2007) and used to create a spatial distribution of the seedling populations in the landscape, and to calculate average seedling to adult distances for each site. An analysis of variance (ANOVA) test was performed using Statistica 7 (StatSoft Inc. 2004). Demographic data was used to construct a size-class distribution based on basal diameter (for individuals <1.3m tall) and diameter at breast height for taller individuals. Seedling to adult ratios were calculated for all sites for new seedlings, juveniles and all seedlings.

3. Results

Squirrels were observed dispersing and predating marula stones. Preliminary results from Shingwedzi showed that 46% of the 50 marula stones left out were buried (Figure 4a). By the time we realised the squirrels were active, 34% were missing and many of these are likely to have been buried. We observed 8% of the stones being eaten. In one instance, two squirrels took a nut each, moving a few metres away to a safe location, and took between 5 and 10 minutes to eat both locules of the stones. This action was repeated once or twice until the squirrels were satiated. They then proceeded to disperse the rest of the stones by grasping them in the mouth and running with them to a suitable area, where they dug a shallow hole
with their forefeet, placing the stone in it. They took time to cover them up, ensuring that they were completely hidden, to the extent that stones were almost impossible to recover even if the process had been watched from nearby. They favoured areas with soft sand or leaf litter near a marker such as a tuft of grass or tree stump. Dispersal distances ranged from 7 to 33m.

Of the 300 marula stones that were left out in the Skukuza cafeteria experiment, 15 were buried (5%) and 87 were missing (29%), many of which may have been buried (Figure 4b). The average burial depth was relatively shallow at 0.53cm (±0.31), and the dispersal distance of the 33 stones that were moved or buried was 4.57m (±6.81). The mean distance of a dispersed stone to the nearest other stone was 1.30m (±3.26). Of all the available seeds in the marula stones that were recovered, 51.52% (±50.75) were predated. For stones that had seeds predated, every locule was predated. With regards to differences in squirrel behaviour between the golf course and natural vegetation: a higher percentage of nuts were buried on the golf course (14%) than in the natural vegetation (0.5%), and more nuts were moved (10%) and missing (36%) on the golf course compared to the natural vegetation (4% and 25.5% respectively).
There was also evidence of burial in recruitment patterns in the landscape. Of the 10 small seedlings (<1cm diameter) that were found in Skukuza, closer inspection revealed that 5 had a stone that was still present and buried in the soil. The average burial depth of these stones is 0.9cm (±0.55). Predation rates of marula stones recovered under adults during vegetation surveys show that there were a few unpredated and many partially predated stones (Figure 5). Of all the trees surveyed in N’waxitshumbe and Skukuza, only 3 had fruited this year, so most of the predation levels recorded were over time periods of greater than a year. Of nuts with at least one locule left unpredated, 29.6% of them were partially predated, with a tiny hole being made in the operculum but the seed remaining untouched.
Figure 6. Seedling-adult distances a) inside N’waxitshumbe Roan enclosure (n = 24), b) in the natural vegetation around Skukuza (n = 12), and c) inside (n = 38) and outside (n = 64) the herbivore enclosure near Pretoriuskop. This represents the spatial distribution of the seedling populations in the landscape, with the percentage of the seedling population present within a certain distance from the nearest adult indicated.

Figure 7. Average seedling to nearest adult distances. (F3, 134) = 2.79; p = 0.4)
The spatial pattern of seedling distribution (in relation to the nearest adult) varied across the sites (Figure 6). At N'waxitshumbe, the highest percentage of immature marulas were found between 10 and 15m from the nearest adult, and there was little recruitment under the canopy (within 5m from an adult). In Skukuza, the highest percentage of seedlings was found within 5m from the nearest adult, with all other seedlings found more than 20m away, and one seedling found 238m from the nearest adult. At Pretoriuskop, the patterns were reversed. Inside the exclosure, there were more seedlings within 5m from the nearest adult, while outside there was a similar percentage distributed at all distances. There was no difference in seedling-adult dispersal distances between the four sites (Figure 7). Skukuza had a very high standard deviation because of the seedling that was found 238m from the nearest adult. Average distances were, however, between 15 and 30m, which is within the dispersal range of squirrels observed at Shingwedzi.

![N'waxitshumbe](image1)

![Skukuza](image2)

![Pretoriuskop](image3)

Figure 8. Size class distribution for *Sclerocarya birrea* subsp. *caffra* a) inside N’waxitshumbe Roan enclosure (n = 93), b) in the natural vegetation around Skukuza (n = 33), and c) inside and outside the herbivore exclosure near Pretoriuskop (n = 126 and n = 66 respectively). A diameter of <1cm represents new seedlings of approximately 1 or 2 years of age, while the size class between 1 and 10cm represents ‘juveniles’.
Table I. Seedling to adult ratios for the study sites. New seedling (<1 cm diameter) and juvenile (between 1 and 10 cm diameter) data was combined for the seedling:adult category.

<table>
<thead>
<tr>
<th>Site</th>
<th>New Seedling:Adult</th>
<th>Juvenile:Adult</th>
<th>Seedling:Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>N'waxitshumbe</td>
<td>0.00</td>
<td>0.33</td>
<td>0.33</td>
</tr>
<tr>
<td>Skukuza</td>
<td>0.48</td>
<td>0.10</td>
<td>0.57</td>
</tr>
<tr>
<td>Pretoriuskop (Inside)</td>
<td>0.75</td>
<td>1.55</td>
<td>2.30</td>
</tr>
<tr>
<td>Pretoriuskop (Outside)</td>
<td>0.65</td>
<td>1.09</td>
<td>1.74</td>
</tr>
</tbody>
</table>

The demographic data for the marula populations at each of the four sites revealed some interesting patterns (Figure 8). At N’waxitshumbe, 54% of the seedling and juvenile population were resprouts, and there were no new seedlings. The majority of recruitment was in the middle size classes. This contrasted greatly from patterns seen in other areas; inside the exclosure at Pretoriuskop, only 11% of the seedling and juvenile population were resprouts, while 23% were new seedlings. The distribution of the population inside and outside the exclosure at Pretoriuskop was very similar, with the highest classes being in the juvenile and new seedling classes respectively. Seedling to adult ratios differed from expected results at Pretoriuskop, because they were higher inside the exclosure where only squirrels were present (Table I).
4. DISCUSSION

The most important finding from this study is that squirrels have been shown to act as both marula seed predators and dispersers. This was confirmed by 1) direct and indirect observation, and dispersal patterns in the landscape: 2) evidence of seedlings growing out of buried marula stones in Skukuza and Pretoriuskop, and 3) the mean distances between seedlings and adults in the enclosures being within the range of distances that squirrels were observed to disperse stones in Shingwedzi.

While this study suggests that squirrels can act as primary dispersers, I believe that they are likely to be more important for marula recruitment as secondary dispersers, as part of a diplochorous dispersal syndrome where elephants are the primary disperser. There is support for Vander Wall and Longland’s (2004) argument: that the combination of endozoochory and scatter-hoarding by rodents is a common two-phase dispersal syndrome which is currently under-recognised. The characteristics of diplochory they identified fit remarkably well with the marula and its dispersers: phase one dispersal generally results in the removal of seeds from the parent plant, decreasing density-dependant mortality and often allowing colonisation of new areas. Yumoto et al. (1985) confirm that elephants are important for this step, along with Dudley (2000), who reports that elephants have a potential dispersal distance of 20 to 30 kilometers. Colonisation ability is likely to become increasingly important for marula survival as elephants damage marulas and remove them from certain areas, as we observed near N’waxitshumbe (Eckhardt et al. 2000; Jacobs and Biggs 2002, Whyte et al. 2003).

Another benefit of phase one dispersal by elephants would be the loosening of the operculum (von Teichman et al. 1983; Lewis 1987; Funston 1993). Phase two dispersal moves seeds to suitable microsites: from the high competition and predation likely to be experienced in a dung pile (van der Pijl 1982; Lewis 1987; Dudley 2000) to the safety of the soil, which would be especially beneficial to marulas because moisture stress is a major inhibitor of marula survival (M. Hofmeyr pers. comm.). Buried seeds are more likely to escape predation because they are only vulnerable to predators who find food using smell (apart from the individual who cached them) (Vander Wall 1993).

Dispersal patterns were similar to those found in other studies where rodents removed seeds from dung: Wenny (1999), and Feer and Forget (2002) found dispersal distances of 5 – 15m and 1 – 3cm deep for agoutis and spiny rats (Vander Wall and Longland 2004). They found
that over a third of seeds buried by rodents were still buried by the time of germination, and if tree squirrels are similar in their seed recovery habits this could provide vast benefits for marulas.

Another method by which marulas could be afforded benefits from squirrel dispersal is if they employ a form of mast seeding, whereby large amounts of seeds are produced at long time intervals interspersed with periods of low production (Silvertown 1980; Fenner 1985). The fact that all but three of the mature trees surveyed only showed evidence of seeds produced in previous years adds credibility to this idea, because large fruit crops appeared to be episodic in the study areas. Vander Wall (2002) found that seed removal rates and dispersal distances by rodents increased during masting years, when it is likely that a higher proportion of seeds will be forgotten, possibly causing higher recruitment rates.

The comparison of the fate of marula stones on the golf course with fate in the surrounding natural vegetation (Figure 4b) was intended to identify the effect of close proximity to humans on squirrel behaviour. In landscapes outside national parks, elephants and other large mammal dispersers are not present, and examining whether *P. cepapi cepapi* would be able to disperse seeds in these environments could suggest the relative importance of this species for marula seed dispersal in the absence of other large dispersers. According to Moore and Swihart (2007), seed-dispersing animals which are able to tolerate fragmented environments are likely to increase in ecological importance in the future. The fact that more marula stones were disturbed on the golf course than in the natural vegetation could, however, be because they are more visible to squirrels in open environments.

There were many stones which were removed but not located in Skukuza, due to the squirrels removing many of the strings before moving the stones. Judging by burial rates of removed stones observed in Shingwedzi, it can be postulated that the majority of those that were missing were buried. If so, this supports the idea that squirrels play an important role as marula dispersers. Seed recovery methods were much more effective for finding seeds within approximately 10m of the parent tree (because of the fluorescent powder trail left behind), and safety and time constraints meant that there was limited scope for finding stones dispersed further than this. This means that dispersal distances and distances between dispersed seeds are also likely to be much higher than reflected by the results, entrenching the importance of squirrels as an important disperser.
We expected predation rates of marulas under adult trees to be high due to this species being such an important food source for squirrels and other animals (Shackleton et al. 2002). There were, however, still many stones which had not even one locule eaten (Figure 5). This suggests that squirrels do not decimate marula seed populations, even if they have been on the surface for over a year. Many of the seeds had small holes bitten in the operculum, but were not predated. The operculum is thought to be a barrier to oxygen (von Teichman et al. 1985), so we thought these partially predated seeds could be at a germination advantage. The operculum is still a physical barrier to growth, which suggests that squirrels alone are not likely to be able to drastically increase marula germination. Marula seeds may remain dormant for some time, and rain water may eventually dissolve the cement-like layer between the seed and operculum (von Teichman 1982). This could allow seeds that were buried by squirrels but have not passed through an elephant to germinate. Levels of germination success tested by Lewis (1987) were, however, much lower in seeds that had not passed through an elephant, which supports the hypothesis that the highest levels of recruitment could be obtained in landscapes with both elephant and squirrel dispersers.

As to whether these predation and dispersal patterns are reflected in the landscape, the fact that marula seedlings and juveniles were not located under adult canopies in N’waxitshumbe and Pretoriuskop exclosures suggests that dispersal is occurring in the absence of elephants and other large herbivores (Figure 6). It is likely to be by squirrels but this process was not actually observed, and needs to be confirmed. The higher percentage of seedlings under tree canopies in Skukuza is likely not to be the result of the germination of seeds that fell from the tree, as most of them were buried. It is likely that the Pretoriuskop data is more accurate because of the much larger sample sizes. N’waxitshumbe and Skukuza had sample sizes of 24 and 12 seedlings respectively, while Pretoriuskop had 38 seedlings inside and 64 outside.

The lack of new seedlings in N’waxitshumbe (Figure 8; Table I) suggests that there had been little recent recruitment. At Pretoriuskop, there was recruitment occurring, which is likely to be because environmental conditions in the south of the park are more conducive to marula growth and establishment (Coetzee et al. 1979; Jacobs and Biggs 2002). Contrary to what was expected, seedling to adult ratios were higher inside the exclosure than outside. Because there are so many factors interacting, it is difficult to draw conclusions from this, but the very similar percentage of seedlings inside and outside that are a) new seedlings, and b) resprouts suggests that fire, rather than differences in dispersal, is the most important determinant of
recruitment success, assuming that fire regimes were constant for both. Skukuza had a high ratio of new seedlings to adults (0.48), but this did not translate into a high ratio of juveniles to adults (0.10). This suggests that while early recruitment is high, there are bottlenecks which prevent the survival of seedlings in the juvenile size class. This could be because of higher browsing pressure, as impala were seen to congregate near the golf course, presumably for safety from predators. Haig (1999) found that impala herbivory of marula seedlings caused high mortality. There was also much evidence of elephant and squirrel activity in this area, with marula seedlings growing out of a dung pile, and many buried stones. To unpick these patterns further, elephant, squirrel and herbivore data would be needed from all of the sites.

There are many factors that were uncovered in this study which need to be comprehensively studied to provide conclusive evidence for a seed dispersal relationship between marulas and squirrels. Squirrel distributions (including other species which scatterhoard) need to be compared with marula and elephant distributions to confirm that this relationship could occur over most of the marula’s range. Preliminary data suggests that other species of Paraxerus with similar habits and diets are present through much of Sub-saharan Africa, although there is an apparent lack of squirrel species in north-eastern Africa (Kingdon 1997). This suggests that the relationship that has been observed in Kruger could extend to other squirrel species and other parts of Africa.

To determine whether a germination advantage is obtained from seed burial, the optimal burial depth for both seeds and their disperser should be compared, as suggested by Vander Wall (1993). Removal rates of untreated marulas from under adult trees, should be compared with removal from elephant dung to determine whether squirrels prefer stones which have been passed through an elephant; following this, it should be determined whether the seed dispersal patterns set up by squirrels and elephants are translated into germination success in the landscape. The results of this study were limited by the fact that the study was done well after fruiting season, making results less ecologically significant because squirrels are under greater food stress (Viljoen 1977b). Identifying female trees was also difficult, and is necessary to determine more accurate dispersal distances; future studies should therefore be done in the fruiting season.

Conclusions
The tree squirrel (*Paraxerus cepapi*) was shown to predate, disperse and scatter-hoard marula stones, a process which, to my knowledge was previously undocumented. This is surprising, given the fact that the marula is one of Africa's most ecologically and economically important tree species. Although elephants are known to be a main disperser of marula (*Sclerocarya birrea*) seeds, squirrel dispersal is likely to confer significant benefits to the marula. Especially in the presence of elephants, squirrel removal and burial of seeds from dung piles is likely to move the seeds to a safe and predictable microclimate where germination success rates are improved beyond the increased germination rates recorded after passing through an elephant. In the absence of elephants, squirrels are likely to be dispersing marulas and increasing germination success. These findings have important implications for management of marulas: because the dispersal relationship between mammals and marulas appears to be so strong, it is important that all species are considered during management decisions. Species are declining at an ever accelerating rate and many complex dispersal systems are not yet understood (Vander Wall and Longland 2004). This means that we must attempt to understand these dispersal relationships to help us conserve the necessary elements for the survival of this keystone species. This is especially important with the predicted effects of habitat fragmentation and global climate change, as facilitation of germination and establishment will become increasingly important as ecosystems are affected (Dudley 2000; Moore and Swihart 2007). By understanding how an ecologically important species, such as the marula, interacts with other species, we are better-able to preserve it through well-informed management decisions.

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