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# Comparison of germination rates and fruit traits of indigenous *Solanum giganteum* and invasive *Solanum mauritianum* in South Africa

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## Abstract

There is a global threat of invasive alien plants to biodiversity and ecosystem services. Of these, fleshy-fruited species are credited as some of the worst invaders and this is largely due to their mutualisms with local dispersers. Comparative studies between invasive and indigenous species can shed new insights into the traits which promote invasive plants success over their indigenous counterparts. This study compared the germination success of indigenous *Solanum giganteum* and invasive *Solanum mauritianum*, following ingestion by Red-winged Starlings (*Onychognathus morio*, Sturnidae) and Speckled Mousebirds (*Colius striatus*, Coliidae) and compared these with de-pulped seed and whole fruit controls. Nutritive and morphological fruit traits were also considered. Seed retention times were only obtained for Red-winged Starlings on both diets, and these did not differ. For both plant species, ingested and de-pulped seeds had similar germination success and mean daily germination, irrespective of frugivore type. However, pulp removal was important for *S. giganteum*. The type of avian frugivore affected the onset of germination, with the comparatively larger Red-winged Starlings promoting earlier germination of both *S. mauritianum* and *S. giganteum* seeds when compared to their controls, except for de-pulped *S. mauritianum*. These germinated at the same time as ingested *S. mauritianum*, but significantly earlier than de-pulped *S. giganteum*. Speckled Mousebirds consumed more *S. mauritianum* than *S. giganteum*, while Red-winged Starlings showed the opposite. While *S. mauritianum* had larger yellow fruits, their seeds were smaller, lighter and more numerous than those in the red fruits of *S. giganteum*. Furthermore, *S. mauritianum* fruits contained considerably more sugar content than *S. giganteum* fruits. In summary, offering greater nutritional rewards and generating greater reproductive outputs than indigenous species, can explain why fleshy-fruited exotics become highly invasive.

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*Keywords:* Fleshy-fruit; Fruit morphology; Nutrient content; Invasive alien plant

## 1. Introduction

The negative impacts of invasive alien plants are well documented (Richardson and Van Wilgen, 2004; Van Wilgen et al., 2001, 2008). Of these species the most severe and successful invaders are those which produce fleshy fruits and are dispersed by avian frugivores (Buckley et al., 2006; Cronk and Fuller, 1995; Renne et al., 2002; Richardson et al., 2000). Avian frugivory is the most prevalent form of vertebrate dispersal in all angiosperm groups (Fleming and Kress, 2011) and it is this ability to form rapid mutualisms with native dispersers that

can give invasive alien plants a competitive edge (Richardson et al., 2000). Indeed, invasive success increases with frugivore diversity (Gosper and Vivian-Smith, 2009).

Numerous bird species show a diet shift relative to food availability (Levey and Martinez del Rio, 2001). Differences in phenology between native and invasive species indicate that longer fruiting seasons, especially when native fruits are patchy and scarce (Gosper, 2004; Gosper and Vivian-Smith, 2010), result in greater removal rates of invasive species (Greenberg and Walter, 2010). Display size also attracts frugivores, and the nearer a neighboring fruiting plant the greater the removal rate (Bach and Kelly, 2004). This is particularly alarming in terms of invasive alien plants which proliferate in disturbed and urbanized areas where native fruiting species are often lacking (Corlett, 2005; Davis, 2011; Gleditsch and Carlo, 2011).

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Fruit choice by frugivores is primarily influenced by the spatial and temporal changes in fruit morphology and availability, as well as the physiological requirements and traits of the frugivore (Lepczyk et al., 2000). Recent studies of the morphological and nutritional traits of invasive alien fruits indicate that fruits are generally small, multi-seeded, and offer higher nutritional rewards than indigenous fruits (Gosper and Vivian-Smith, 2010; Jordaan and Downs, in press). These traits are consistent with preference trends of frugivores (Green, 1993; Stansbury and Vivian-Smith, 2003) and can explain why these can outcompete indigenous plant species for dispersal agents (Bass, 1990; Lafleur et al., 2007).

The benefits of frugivory to plants are essentially twofold. First, seeds are carried away from parent plants (Jordano, 1987; Kinnaird, 1998; Schupp, 1993), under which resource competition (Abul-Fatih and Bazzaz, 1979; Day et al., 2003; Ross and Harper, 1972) and predation risk increase (Howe, 1986). Secondly, germination can be enhanced by chemical and mechanical processes in the digestive tract (Barnea et al., 1991; McKey, 1975), which result in seed coat abrasion (Agami and Waisel, 1988; Barnea et al., 1990, 1991; Evenari, 1949) and/or pulp removal (Barnea et al., 1991; Evenari, 1949). These in turn reduce seed predator detection (Moles and Drake, 1999; Nystrand and Granstrom, 1997) and infection by pathogens (Howe, 1986; Moore, 2001; Witmer and Cheke, 1991).

The seed retention time (SRT) of a frugivore is important as this determines the time that seeds are exposed to digestive processes (Murray et al., 1994; Sorensen, 1984), and also determines the potential dispersal distance of ingested seeds (Ridley, 1930). Such information combined with movement patterns and seed deposition sites of frugivores (Bartuszevige and Gorchov, 2006) can facilitate modeling of potential long distance invasion patterns (Bartuszevige and Gorchov, 2006; Buckley et al., 2006; Cain et al., 2000; Higgins and Richardson, 1999). The germination of a variety of plants can be affected in similar or dissimilar ways by avian frugivores (Barnea et al., 1991). Therefore to gain a better understanding of potential plant-frugivore trends it is essential that comparative studies of such nature be done (Barnea et al., 1990; Traveset, 1998), particularly between invasive alien and co-occurring indigenous species.

*Solanum mauritianum* has a high reproductive output and is an important resource for avian frugivores in South Africa (Mokotjomela et al., 2009), which in turn are important long distance dispersal agents for this species (Olckers, 1999; Witkowski and Garner, 2008). Indeed, when compared to native plant species, a wider variety of birds has been shown to visit *S. mauritianum* (Mokotjomela et al., 2009). It is classified as a category 1 ‘transformer’ weed in South Africa as it outcompetes indigenous flora (Henderson, 2001). Consequently many efforts to eradicate this plant have been undertaken (Olckers, 1998, 1999; Pickers and Zimmermann, 1991).

The primary objectives of this study were to investigate the germination success of a co-occurring indigenous and highly invasive *Solanum* L. species (*Solanum giganteum* Jacq. and *S. mauritianum* Scop. respectively) following avian ingestion,

and to compare the nutritive and morphological traits between these. We also determined if seed retention time would differ for seeds of *S. giganteum* and *S. mauritianum* for a particular avian frugivore, and if any differences would be reflected in seed germination success. We predicted that invasive alien seeds would germinate more rapidly and in greater quantities and that they would offer greater nutritional rewards to frugivores than their indigenous counterparts. Finally, seed retention time would not influence the germination success of invasive alien seeds.

## 2. Materials and methods

*S. giganteum* and *S. mauritianum* share the same broad distributions in southern Africa, with *S. mauritianum* being more abundant (Boon, 2010). Their plant morphologies are superficially similar, both forming shrubs or small trees of c. 4 m (Boon, 2010). The main difference is that *S. mauritianum* is covered in velvety hairs, while *S. giganteum* has spines on the stem (Boon, 2010; Fig. 1). These plants are more easily discerned from each other when they are fruiting (Fig. 1). *S. giganteum* produces shiny, firm, red berries from February to July (Boon, 2010), while *S. mauritianum* produces larger, softer, yellow berries year-round (Henderson, 2001; Fig. 1). Differences in their fruit morphologies (Fig. 1) and nutritional value are highlighted in Table 1.

Using mist nets nine Red-winged Starlings (*Onychognathus morio* Linnaeus, Sturnidae) and ten Speckled Mousebirds (*Colius striatus* Gmelin, Coliidae) were caught between July 2007 and February 2008 near the University of KwaZulu-Natal (UKZN) 29°44'57"S 30°48'50"E and 29°29'32"S 30°18'7"E respectively. These avian frugivores have been observed to feed on the fruits used in this study (pers. obs.), are relatively abundant and have overlapping distributions with the plant species used in this study (Hockey et al., 2005). Birds were housed in outside aviaries in species groups at the UKZN Animal House and were fed on a maintenance diet of mixed commercial fruit and AviPlus Softbill/Mynah pellets and crumble (Avi-products, Durban, South Africa), for approximately one month prior to sampling. Red-winged Starling maintenance diets were supplemented with *Tenebrio molitor* larvae every third day and water was provided *ad libitum*.

For feeding trials birds were placed in individual cages in a constant environment room set at 25 °C, on a 12:12 dark:light cycle. They were acclimated for three days during which time sample fruit were incorporated into maintenance diets. Fruits of *S. mauritianum* and *S. giganteum* were collected from plants near UKZN and only ripe, intact fruits were offered within 48 h of picking. Only one fruit species was offered during each trial. Fruits were weighed before and after trials to determine the amount of fruit consumed by each individual over an eight hour period. This was corrected for evaporative water loss by placing control fruit in the same room and determining the percentage water lost per gram of fruit. For Red-winged Starlings (n=9), seed retention time (SRT) was recorded once on each fruit diet and was measured from the time of fruit ingestion to the time seeds first appeared in excreta. SRT was not measured



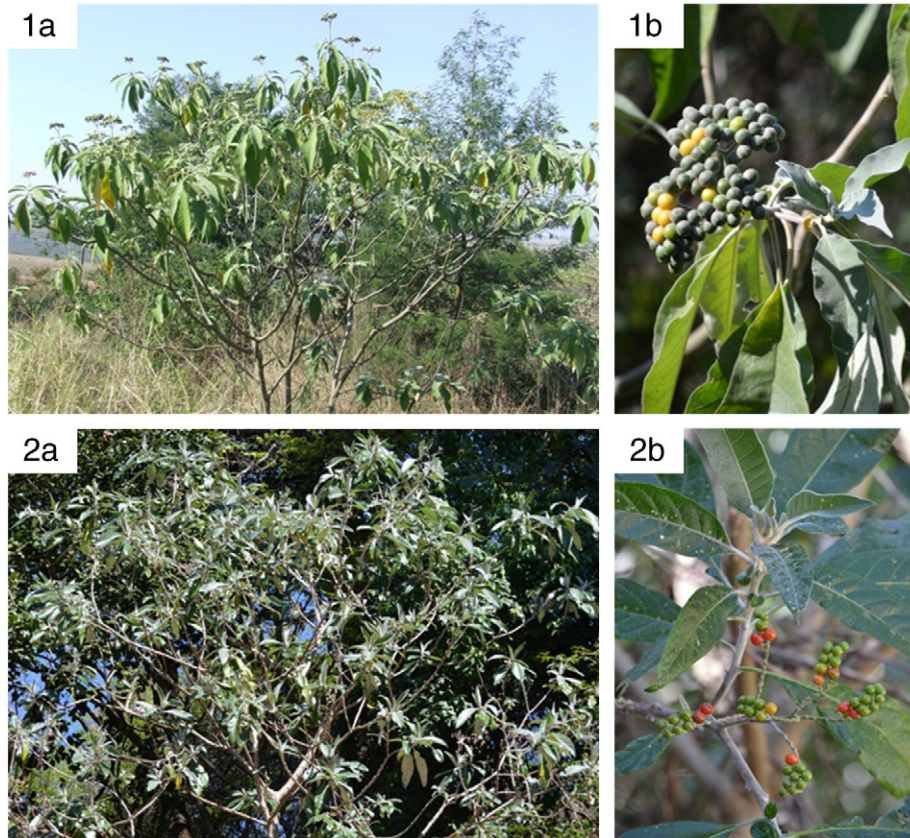


Fig. 1. Gross plant morphology and fruit cluster of *S. mauritianum* (1a and 1b respectively) and *S. giganteum* (2a and 2b respectively).

for Speckled Mousebirds as they struggled to manipulate *S. giganteum* fruit, thus accurate measurements of ingestion were not possible. Ten fruits from each species were used to determine morphological traits (Table 1). Fruits from both species were also de-pulped and freeze dried to constant mass. Dried pulp was then milled, sieved through a 750  $\mu\text{m}$  mesh, and sent to the University of Pretoria for nutritional analysis. Gross energy was determined using a MC 1000 Modular Bomb Calorimeter and fruit sugar content was analyzed according to Liu et al. (1999) using a HPLC (Agilent 1100 series) with

Table 1

Comparison of morphological and nutritive fruit traits (mean $\pm$ SE) of *S. giganteum* and *S. mauritianum* (n=10) (Jordaan and Downs, in press), where nutritive data is presented on a dry matter basis. Protein content calculated using the conversion factor of 5.64 as recommended by Levey et al. (2000).

Fruit trait	<i>S. giganteum</i>	<i>S. mauritianum</i>
Ripe fruit color	Red	Yellow
Fruit diameter (mm)	7.17 $\pm$ 0.19	13.70 $\pm$ 0.37
Number of seeds/fruit	16 $\pm$ 1.63	181.5 $\pm$ 4.87
Seed mass (g)	0.0032 $\pm$ 0.0002	0.0019 $\pm$ 0.0002
Seed diameter (mm)	2.48 $\pm$ 0.07	1.54 $\pm$ 0.04
Pulp water content (%)	71.47 $\pm$ 0.28	68.93 $\pm$ 0.38
Nitrogen content (g/100 g)	1.8	1.5
Protein content (g/100 g)	10.2	8.2
Lipid content (g/100 g)	1.2	0.7
Gross energy (g/100 g)	20.9	19.3
Fructose (mg/g)	113.1	175.5
Glucose (mg/g)	94.9	259.0
Sucrose (mg/g)	0.0	81.0

RID detection. Nitrogen content was established by using the Dumas combustion method (AOAC, 2000b) and lipid content was measured by ether extraction (AOAC, 2000a).

Following feeding trials, seeds were collected from each individual's excreta and planted c. 5 mm deep in separate soil trays. The soil used was composted garden soil, with no added chemicals. Fifty *S. giganteum* seeds were collected from each Speckled Mousebird (n=4) and Red-winged Starling (n=8) and 200 *S. mauritianum* seeds were collected from each Speckled Mousebird (n=10) and Red-winged Starling (n=9). One tray containing the same number of manually de-pulped seeds for each plant species, as well as one tray each containing ten whole fruits of each species, was planted as controls for each bird species diet trial. Trays were randomly placed on a bench in a greenhouse and watered as required. The amount of germination was recorded daily for each tray and seedlings were removed once counted to avoid duplication. Trays were observed until no germination occurred for a period longer than three weeks. For whole fruit controls the amount of germination was calculated using the average number of seeds per fruit (Table 1). For germination comparisons the number of seeds that germinated after 238 days was considered. Red-winged Starling and Speckled Mousebird *S. mauritianum* germination data and Red-winged Starling SRT data were used from Jordaan et al. (2011a) and nutritive and morphological fruit data for *S. mauritianum* were from Jordaan and Downs (in press).

Germination percentage data were arcsine transformed and the effect of different treatments (avian ingestion, de-pulped

Table 2  
Significance of difference between plant species, tray treatments (frugivore ingested, de-pulped and whole fruit seeds) and the interaction of these for amounts of germination including and excluding whole fruit controls and for the time to first seedling emergence for Speckled Mousebird and Red-winged Starling trial groups (Factorial ANOVA). Where 'n' indicates the total number of germination trays used.

Data analyzed	Factor	n	df	F	P
Amount of germination including whole fruit controls	Tray treatment	39	3	3.416	0.030 *
	Plant sp.	39	1	9.018	0.005 *
	Tray treatment * plant sp.	39	3	3.365	0.031 *
Amount of germination excluding whole fruit controls	Tray treatment	35	2	0.441	0.648
	Plant sp.	35	1	1.668	0.207
	Tray treatment * plant sp.	35	2	1.886	0.170
Speckled Mousebird germination rate	Tray treatment	18	2	3.150	0.080
	Plant sp.	18	1	14.810	0.002 *
	Tray treatment * plant sp.	18	2	0.620	0.553
Red-winged Starling germination rate	Tray treatment	21	2	16.810	<0.05 *
	Plant sp.	21	1	25.000	<0.05 *
	Tray treatment * plant sp.	21	2	3.880	0.042 *

\* Significant at  $P \leq 0.05$ .

seeds and whole fruit) on the germination rate of both *S. mauritanium* and *S. giganteum* was investigated using a Factorial ANOVA. Where significant differences were found, *post-hoc* Tukey tests were done. The time to first seedling emergence was also considered. These data were log transformed and analyzed using a factorial ANOVA and, following significant differences, further analyzed using *post-hoc* Tukey tests. Mean daily germination (MDG) and peak value (PV) were calculated for each treatment according to Czabator (1962). MDG provides a measure of germination vigor relative to the full duration of the sampling period (Czabator, 1962). PV expresses the vigor of germination and essentially represents the highest mean daily germination of the seed batch (Djavanshir and Pourbeik, 1976). The amount of fruit eaten by Red-winged Starlings was square-root transformed to normalize data and the amount eaten by each species for a specific fruit diet was compared using independent sample t-tests. Seed retention time for both fruit diets was only available for Red-winged Starlings and this was also analyzed using independent sample t-tests.

### 3. Results

Visually *S. giganteum* fruits differed from *S. mauritanium* fruits as they had firm, small, red berries as opposed to the larger, yellow, soft fruits of *S. mauritanium* (Table 1; Fig. 1). *Solanum* fruits also differed in their seed loads as *S. giganteum* had fewer, but larger, seeds per fruit than *S. mauritanium* (Table 1). They also had more gross energy per gram of pulp, which is consistent with greater lipid content than *S. mauritanium* (Table 1). However, *S. mauritanium* fruits contained much higher sugar levels for all sugar types than *S. giganteum* fruits did (Table 1).

Germination percentages varied significantly between tray treatments, plant species, and the interaction of these factors (Table 2). Significant differences were only attributed to factors compared to *S. mauritanium* whole fruit controls. Both Red-winged Starling ingested *S. giganteum* ( $P < 0.05$ ) and *S. mauritanium* ( $P = 0.04$ ) and Speckled Mousebird ingested *S.*

*giganteum* ( $P = 0.04$ ) and *S. mauritanium* ( $P < 0.05$ ) had significantly higher germination than *S. mauritanium* whole fruit controls (Fig. 2). When whole fruit controls were excluded from analysis no significant differences in germination percentages were evident regardless of tray treatment and/or plant species (Table 2). MDG was similar for frugivore ingested and de-pulped seeds and was lowest for whole fruit controls (Table 3). A similar trend was observed for PVs, with the highest daily germination event occurring in de-pulped *S. mauritanium* trays (Table 3).

For Speckled Mousebird germination rates, only the plant species had a significant effect on the time to germination (Table 2). Thus, Speckled Mousebird ingested, de-pulped, and whole fruit *S. mauritanium* seeds all germinated at approximately the same time ( $P = 1.00$  and  $P = 0.20$  respectively), as did *S. giganteum* treatments ( $P = 0.93$  and  $P = 0.92$ ). However, Speckled Mousebird ingested *S. mauritanium* seeds germinated significantly earlier than ingested *S. giganteum* ( $P < 0.05$ ), de-pulped *S. giganteum* ( $P = 0.02$ ), and whole fruit *S. giganteum* ( $P = 0.02$ ). For Red-winged Starling trays germination rates were significantly influenced by tray treatments, plant species, and the interaction of these (Table 2). Red-winged Starling ingested *S. giganteum* seeds germinated significantly sooner than de-pulped ( $P = 0.01$ ) and whole fruit ( $P = 0.01$ ) *S. giganteum* controls. However, Red-winged Starling ingested *S. mauritanium* seeds did not germinate sooner than de-pulped *S. mauritanium* ( $P = 1.00$ ), but did germinate earlier than the whole fruit control ( $P = 0.02$ ). De-pulped *S. giganteum* ( $P < 0.05$ ) and whole fruit controls ( $P < 0.05$ ) germinated later than Red-winged Starling ingested *S. mauritanium*. While Red-winged Starling ingested *S. mauritanium* and *S. giganteum* seeds germinated at approximately the same time, de-pulped *S. mauritanium* seeds germinated sooner than de-pulped *S. giganteum* seeds ( $P = 0.02$ ).

After an initial germination event at day 20, most *S. mauritanium* germination occurred after 150 days. Similarly, *S. giganteum* seeds initially germinated after c. 20 days, but this was nearly half of the total germination for this species, which also showed a second peak after 200 days (Fig. 2).

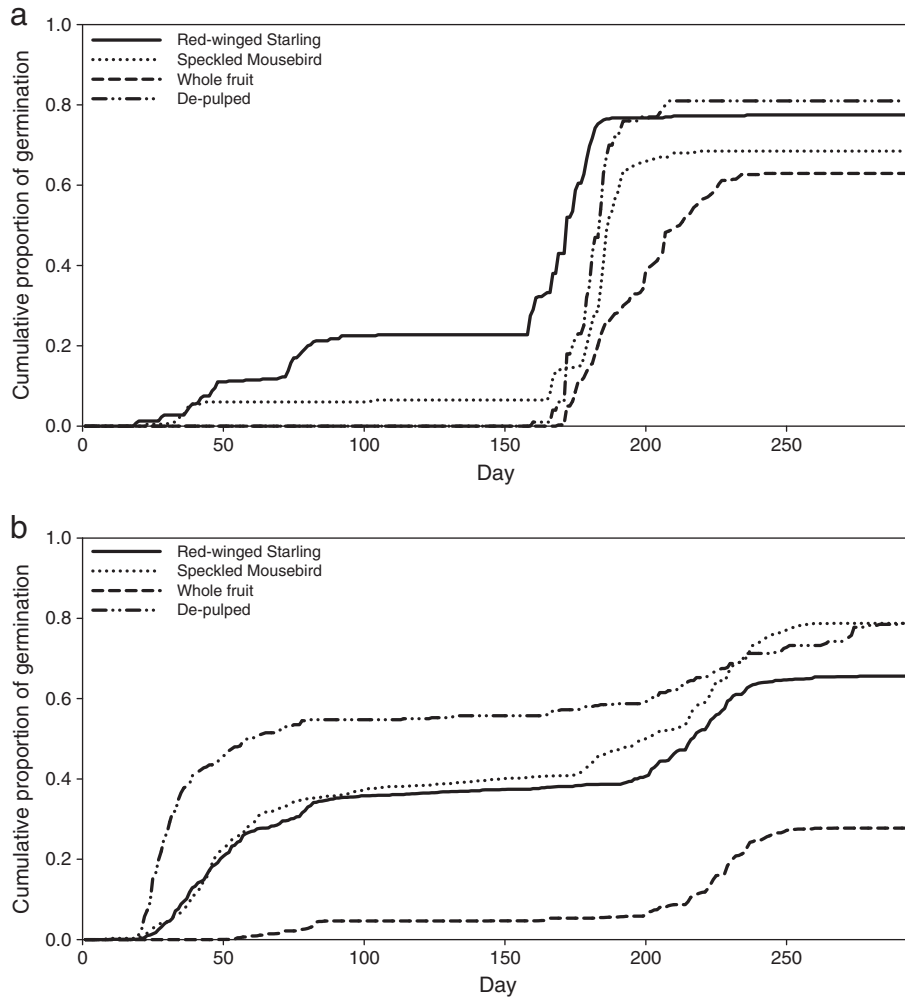


Fig. 2. Mean cumulative proportion of seeds germinated for (a) *S. mauritianum* (Red-winged Starling ingested (n=8), Speckled Mousebird ingested (n=10), de-pulped seed controls (n=3), and whole fruit controls (n=3)) and (b) *S. giganteum* (Red-winged Starling ingested (n=8), Speckled Mousebird ingested (n=4), de-pulped seed controls (n=2), and whole fruit controls (n=2)) for the duration of the study. Where 'n' indicates the number of trays used for each treatment. *S. mauritianum* data were used from Jordaan et al. (2011a).

While the initial germination rate of *S. mauritianum* appears to lag behind that of *S. giganteum*, the final germination amount is very high for all *S. mauritianum* treatments, as opposed to *S. giganteum* which has lower whole fruit germination (Fig. 2).

Table 3

Mean daily germination (MDG) and peak values calculated for *S. giganteum* (SG) and *S. mauritianum* (SM) for frugivore ingested, de-pulped and whole fruit seed controls.

Treatment	Mean daily germination (MDG)	Peak value (PV)
Red-winged Starling ingested SG	0.265	0.412
Speckled Mousebird ingested SG	0.235	0.332
De-pulped SG	0.277	0.396
Whole fruit SG	0.216	0.269
Red-winged Starling ingested SM	0.225	0.455
Speckled Mousebird ingested SM	0.270	0.494
De-pulped SM	0.270	1.049
Whole fruit SM	0.095	0.109

Speckled Mousebirds ( $t=2.54$ ; d.f. = 12;  $P=0.03$ ) and Red-winged Starlings ( $t=20.68$ ; d.f. = 15;  $P<0.05$ ) both varied significantly in the amount of each fruit species they ate. Speckled Mousebirds ate c.  $11.66\pm 0.71$  g (mean  $\pm$  SE) of *S. mauritianum* and c.  $8.02\pm 1.41$  g of *S. giganteum*. Conversely, Red-winged Starlings consumed less *S. mauritianum* ( $11.11\pm 0.69$  g) than *S. giganteum* ( $70.61\pm 3.89$  g). Red-winged Starling seed retention time did not differ between the two fruit diets ( $t=0.49$ ; d.f. = 11;  $P=0.63$ ). Seeds were retained for  $33.96\pm 4.36$  (n=9) min on the *S. mauritianum* diet and for  $30.44\pm 3.93$  (n=4) min on the *S. giganteum* fruit diet.

#### 4. Discussion

Frugivore species differed in the amounts of fruit they consumed on each fruit diet, but had similar effects on the total germination amounts of both plant species. While, they differed in their influence on the onset of germination these differences were not attributed to variations in seed retention time. Therefore seed coat abrasion is not important for both these species;



however pulp removal was important for *S. giganteum* as whole fruit seeds had considerably lower germination success. These trends were further reflected in the MDG and PV which were similar for frugivore ingested and de-pulped seeds and lowest for whole fruit controls. The primary role of frugivores as dispersers and not necessarily enhancing germination success of invasive alien plants in South Africa has been previously highlighted (Jordaan et al., 2011a,b). It has been suggested that the role of frugivores for the scarification of seed coats can be more important in more unpredictable, arid habitats where moisture permeability for germination is more important (Barnea et al., 1990).

Speckled Mousebirds did not affect *S. mauritianum* and *S. giganteum* germination rates, but Red-winged Starling ingested seeds for both species germinated earlier than their respective controls, except for de-pulped *S. mauritianum* which germinated at the same time as ingested *S. mauritianum* seeds. While *S. mauritianum* germination does appear to lag behind that of *S. giganteum*, this has no effect on the final germination amount and can be explained by the requirement of these seeds to endure a brief dry period at ambient temperatures to release embryo dormancy (Campbell and Van Staden, 1983). Rapid germination can be beneficial to plants as this reduces the risk of pathogen infection or predation (Howe, 1986) and also decreases the chance of being out-competed by earlier established seedlings (Abul-Fatih and Bazzaz, 1979; Ross and Harper, 1972).

Nutrient discrimination abilities of avian frugivores (Schaefer et al., 2003) can play an important role in preferences for invasive fruits (Buckley et al., 2006; Lafleur et al., 2007). Recently it has been shown that invasive alien plants offer more nutritive fruit pulp than their indigenous counterparts (Gosper and Vivian-Smith, 2010; Jordaan and Downs, in press). The varying amounts of each fruit species consumed by the different frugivores in this study can be explained by their digestive strategies which determine the efficiency by which a particular fruit is processed, and thus energetic gains received (Afik and Karasov, 1995; Brown and Downs, 2003; Place and Stiles, 1992). Frugivores have been shown to vary in their digestive efficiencies of invasive fruits, but are able to meet their energetic demands on a diet of these fruits (Jordaan et al., 2011c).

Frugivores adjust their feeding strategies by consuming greater quantities of nutritionally poor fruits and smaller amounts of nutritionally rich fruits (Jordaan and Downs, in press). Indeed, in this study Red-winged Starlings consumed considerably more *S. giganteum* fruit, which offer comparably less nutritional rewards. Contrastingly, Speckled Mousebirds consumed more *S. mauritianum* fruits. This could be explained by the inability of Speckled Mousebirds to manipulate the firm round fruits of *S. giganteum* as opposed to the softer, larger *S. mauritianum* fruits, which were eaten piecemeal (Symes and Downs, 2001). Five Speckled Mousebirds did not consume any *S. giganteum*. Red-winged Starlings were observed palpat-ing *S. giganteum* fruits and appeared to dislike the taste of these. They were also observed rinsing these fruits in water (Jordaan, pers. obs.), although reasons for this are not known.

Such behaviors should therefore be considered when interpreting feeding data.

While some birds, including White-eye and Mousebird species, have shown a preference for sucrose-rich diets (Brown et al., 2010; Wellmann and Downs, 2009), several avian frugivores including Starling, Catbird and Robin species, have shown an intolerance to these (Avery et al., 1995; Darnell et al., 1994; Malcarney et al., 1994; Martinez del Rio et al., 1995). While the sucrose content was higher in *S. mauritianum* fruits than in *S. giganteum* fruits, hexose sugars were present in greater comparative quantities. Thus *S. mauritianum* fruits are not considered sucrose dominant and Red-winged Starlings are able to digest these fruits efficiently, with apparent assimilation efficiencies of up to 80% on pure *S. mauritianum* diets (Jordaan et al., 2011c).

*S. mauritianum* has several characteristics which can explain why it has become a successful invader. It fruits year round, producing 20–80 berries per inflorescence (Campbell and Van Staden, 1983; Henderson, 2001; Witkowski and Garner, 2008), which contain greater nutritional rewards than many indigenous fruits (Jordaan and Downs, in press). It is able to self-pollinate (Rambuda and Johnson, 2004), yielding fruits which contain upwards of 150 seeds, with up to 98% seed viability (Campbell and Van Staden, 1983). Seed banks are retained and readily germinate following parent plant removal (Witkowski and Garner, 2008). Finally, seeds germinate irrespective of frugivore ingestion (Jordaan et al., 2011a).

## 5. Conclusion

The germination capabilities are similar and unaffected by frugivore type, except for *S. giganteum* which requires pulp removal for greater germination success. We therefore suggest that the proportionately greater reproductive outputs in terms of fruits per area and number of seeds per fruit of *S. mauritianum*, and the greater nutritional rewards offered to a wider range of bird species can have facilitated its invasive progress. Such traits have been shown to result in greater fruit removal rates of invasive plants (Chimera and Drake, 2010). Thus plant traits associated with frugivore interactions should not be discounted when assessing the invasive potential of exotic species.

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