

FLESHY-FRUITED INVASIVE ALIEN PLANTS AND FRUGIVORES IN SOUTH AFRICA

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Preface

The experimental work described in this dissertation was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg from January 2008 to June 2011, under the supervision of Professor Colleen T. Downs and co-supervision of Professor Steven D. Johnson.

This dissertation, submitted for the degree of Doctor of Philosophy in the Faculty of Science and Agriculture, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.



Lorinda A. Jordaan
September 2011

I certify that the above statement is correct



Professor Colleen T. Downs
Supervisor
September 2011

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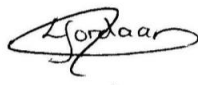
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Declaration 2 – Publications

Detail of contribution to publications that form part and/or include research presented in this thesis.

Publication 1

LA Jordaan, SD Johnson, and CT Downs. Digestion of fruit of invasive alien plants by three southern African avian frugivores.

Author contributions:

LJ and CTD conceived paper. LAJ collected and analyzed data, and wrote the paper. CTD and SDJ contributed valuable comments to the manuscript.

Publication 2

LA Jordaan, SD Johnson, and CT Downs. The role of avian frugivores in germination of seeds of fleshy-fruited invasive alien plants.

Author contributions:

LJ and CTD conceived paper. LAJ collected and analyzed data, and wrote the paper. CTD and SDJ contributed valuable comments to the manuscript.

Publication 3

LA Jordaan, SD Johnson, and CT Downs. Wahlberg's Epauletted Fruit Bat (*Epomophorus wahlbergi*) as a potential dispersal agent for fleshy-fruited invasive alien plants: effects of handling behaviour on seed germination.

Author contributions:

LJ and CTD conceived paper. LAJ collected and analyzed data, and wrote the paper. CTD and SDJ contributed valuable comments to the manuscript.

Publication 4

LA Jordaan and CT Downs. Forbidden fruit: nutritional and morphological traits of invasive and exotic fleshy-fruits in South Africa.

Author contributions:

LJ and CTD conceived paper. LAJ collected and analyzed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

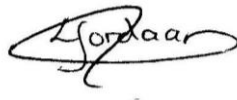
Publication 5

LA Jordaan and CT Downs. Comparison of germination rates and fruit traits of indigenous *Solanum giganteum* and invasive *S. mauritianum* in South Africa.

Author contributions:

LJ and CTD conceived paper. LAJ collected and analyzed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

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Lorinda A. Jordaan

September 2011

Abstract

South Africa is one of the world's most biologically invaded countries and has spent billions of rands on efforts to eradicate alien invasive plants. Chemical and mechanical control methods have varied in success and the need for integrated management strategies has been realised. This requires a better understanding of all aspects of the invasion process. Some of the most invasive plant species rely on vertebrate dispersers which facilitate long-distance seed dispersal. Frugivory is based on a mutualism in which the frugivores gain a resource and the plants benefit from seed dispersal away from the parent plant. Seed germination itself may either be enhanced, reduced or not affected at all after gut passage. The first aim of this study was to determine if generalist avian frugivores and a fruit bat species (*Epomophorus wahlbergi*) enhance or decrease seed germination of invasive alien plants in South Africa, by either pulp removal or seed coat abrasion, or if they serve as dispersers only. The second aim was to determine if avian frugivores are able to meet their energetic demands by feeding on a specific alien fruit diet. Finally, we also quantified the nutritional content and morphological characteristics of fleshy fruits of various invasive alien and exotic plant species. Avian frugivores: Red-winged Starlings (*Onychognathus morio*), Speckled Mousebirds (*Colius striatus*), and Dark-capped Bulbuls (*Pycnonotus tricolor*), varied in their effects on the germination success of seeds of four invasive alien species, namely: *Lantana camara*, *Solanum mauritianum*, *Cinnamomum camphora*, and *Psidium guajava*. However, this was not associated with differences in seed retention times. Similar germination success was observed for avian ingested and de-pulped seeds. This was also observed for fruit bat spat and de-pulped seeds of *Psidium guajava*, *Melia azedarach*, *Eriobotrya japonica*, and *Morus alba*. Therefore seed coat abrasion was not important for the germination of these fleshy-fruited invasive alien plants. Pulp removal resulted in significantly earlier seed germination as well as

higher seed germination percentages than in the case of whole fruit controls for some of these invasive species. Gut passage is thus important for long-distance dispersal, and in some cases, for enhanced germination of seeds. The invasive *Solanum mauritianum* and indigenous congener *S. giganteum* showed similar germination responses, with both ingested and de-pulped seeds germinating profusely. However, *S. giganteum* benefited from pulp removal as seeds from whole fruits had less germination. Avian frugivores varied significantly in most energetic parameters calculated when given diets of invasive alien fruit. Speckled Mousebirds and Dark-capped Bulbuls were able to maintain body mass and efficiently process fruits of all four alien invasive plants, while Red-winged Starlings were only able to do so on lipid-rich *C. camphora* and sugar-rich *S. mauritianum*. Furthermore, frugivores also adjusted their feeding behavior by eating more nutritionally poor fruit and less energetically rewarding fruit. Fruit bats consumed more fruit per gram body mass than avian frugivores did. They therefore process proportionately more seeds than avian dispersers and thus their role in invasive seed dispersal, which has previously been underestimated particularly in South Africa, is highlighted. Fruits of invasive plant species were similar in morphology, but greater in nutritional content, than fruits of indigenous species. These fruits also contained small, light seeds with approximately only 30% having more than 10 seeds per fruit. The ability of frugivores to efficiently process these fruits and the greater nutritional rewards offered by these provide new insights into why these invasive fruits are preferred by frugivores. In addition, invasive alien plants may have a competitive edge over indigenous species because of their larger reproductive outputs and not necessarily because of greater germination success.

Keywords: Frugivore • Invasive plant • Energy assimilation • Germination • Fruit morphology • Nutrient content • Seed dispersal

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"If you have faith as small as a mustard seed... nothing will be impossible."

- Matthew 17:20

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Chapter 1

Introduction

When introduced plants become naturalized and successfully spread outside of their native range they are considered invasive (Richardson *et al.* 2000a). This may result from many factors including decreased regulation from their natural enemies (Keane and Crawley 2002, Wolfe 2002), the ability to successfully disperse in the new habitat (Richardson *et al.* 2000a), the capacity to self fertilize (van Kleunen and Johnson 2007a), frequent and high seed set (Iponga *et al.* 2009), and rapid and profuse germination of seedlings (van Kleunen and Johnson 2007b).

There is a significant correlation between invasive alien species richness and indigenous species richness (Richardson *et al.* 2005). Thus areas rich in biodiversity will experience continuous invasions (Richardson *et al.* 2005), thereby posing a particular threat to both rare species and biodiversity in protected, remote, and mountainous areas (Latimer *et al.* 2004). This makes it particularly difficult to monitor invading weed population sizes and dispersal/invasion rates. For example, in South Africa only 6% of the land area is protected leaving most of the country vulnerable to development and invasion by alien plants (Turpie *et al.* 2008). Of the many introduced species, 117 have been identified as major invaders and 84 have been classified as emerging invaders (Nel *et al.* 2004). Invasive alien plants have been controlled with some success by government groups (e.g. Working for Water), but still occupy an estimated 10 million hectares of the country and continue to spread at exponential rates (Turpie *et al.* 2008). Initial clearing costs may be as high as R7000 per hectare, and continuous management must be implemented where there are seed banks or nearby sources of seeds on parent trees (Turpie *et al.* 2008). If left unmanaged, it is predicted that such increases will lead to a major decline in ecosystem services (Turpie *et al.* 2008, van Wilgen *et al.* 2008).

The numerous negative impacts of invasive alien species can include removing resources such as water (Le Maitre *et al.* 2002), shifting soil composition by adding resources, changing fire systems by altering biomass, reducing the recruitment of native species (Higgins and Richardson 1996, Richardson *et al.* 2000b), altering biogeochemical cycles (quantity and quality of nutrients), varying the landscape physically, changing light, sediment and water levels, modifying resources in trophic levels of food webs (Vitousek 1990), and resulting in great economic losses (van Wilgen *et al.* 2001). For example, it was estimated that the removal of the 180 invasive plant species in South Africa's priority fynbos ecosystem would cost \$1.2 billion (van Wilgen *et al.* 2001). In 2005 alone the South African government spent \$66 million in eradication efforts, and from the initiation of the Working for Water programme in 1995 to 2006, \$450 million was spent on efforts to control these plants (Woodworth 2006). Unfortunately, despite these attempts, they occupy more land today than ever before (Woodworth 2006).

Some of the most invasive plant species are trees or shrubs that are bird dispersed and produce numerous seeds (Cronk and Fuller 1995). The successful spread and establishment of fleshy-fruited alien plants is significantly enhanced (if not reliant on) the rapid formation of loose mutualisms with resident dispersers (Richardson *et al.* 2000a). However, the relationship between these plants and native frugivores remains poorly understood, particularly in terms of the direct benefits to the frugivore and the potential influence they may have on germination success. The loss of native fruiting species provides a gap for new (often invasive) species to enter an ecosystem (Lafleur *et al.* 2007) and replace indigenous species as a food source for resident frugivores (Buckley *et al.* 2006, Gosper and Vivian-Smith 2006). These increase the spread and density of alien plants, which may in turn displace native species (Loyn and French 1991). Invasive alien plants may become keystone food sources (Mokotjomela *et al.* 2009, Gleditsch and Carlo 2011) and be preferred to indigenous fruit (Fraser 1990, Lafleur *et al.* 2007).

Birds are considered the most important group of seed dispersers because of their abundance and ability to cover relatively long distances through flight (Ridley 1930), and in so doing facilitate long-distance seed dispersal (Higgins and Richardson 1999). Bird-dispersed fruits appear to have similar traits around the world (French 1991), highlighting that there is little specialization in plant-frugivore relationships. This may also explain why native bird species are attracted to invasive fruits (Loyn and French 1991). Bird-dispersed fruit are typically visually attractive (changing colour to signal ripeness), have soft fruit pulp, remain attached to the parent tree, and have mechanisms to protect seeds from being digested (Van der Pijl 1982). Keystone avian food sources tend to have typical invasive plant characteristics, such as a high reproductive output and the ability to attract a variety of dispersers (Mokotjomela *et al.* 2009). It is estimated that at least twice as many plant families are bird-dispersed than are bat or primate dispersed (Fleming and Kress 2011). This is likely due to their relative abundance, species diversity, and range of sizes (Fleming and Kress 2011).

Recently the paucity of invasion studies from Africa and Asia was highlighted, thereby limiting a global understanding of invasive traits and processes (Pysek *et al.* 2008). In terms of studies that consider the impact of frugivores on germination rates of the seeds of fleshy-fruited species, most are done in North America, on various islands and in Australia, 28%, 24% and 17% respectively (Table 1). In the past most of these studies considered the effects of birds in particular (Table 1) and only recently has this been done in South Africa (Jordaan *et al.* 2011a, Chapter 2). The role of fruit bats remains poorly defined (Howe 1986). Despite being highlighted as the most abundant frugivore feeding on an invasive tree species in South Africa (Voigt *et al.* 2011), they remain unrecognized as important dispersers of South African invasive alien plants (AGIS 2007, Henderson 2007). Like birds, fruit bats are endotherms with high energetic demands for flight (Sánchez 2006) and therefore consume relatively large amounts of food. It is not unusual for fruit bats to consume more than their body mass in fruit each night (Morrison 1980, Thomas 1984, Izhaki *et al.* 1995) and as Old World fruit bats

(family Pteropodidae) are generally larger than New World bats (family Phyllostomidae), they process proportionally more fruit per individual (Izhaki *et al.* 1995), thereby dispersing more seeds than both New World fruit bats and smaller avian frugivores.

Fruit size affects avian frugivore feeding behaviour as their gape width limits the size of fruit and seeds they can swallow (Wheelwright 1985, Debussche and Isenmann 1989, Green 1993, Stansbury and Vivian-Smith 2003). This is not the case for many fruit bats, which are able to bite and chew fruit to extract the fruit juice (Morrison 1980, Thomas 1984, Bonaccorso and Gush 1987, Monadjem *et al.* 2010). Fruits are usually carried to feeding sites whole or piece meal (Fenton *et al.* 1985, Corlett 2005) and while larger seeds and fruit pulp are spat out, small seeds may accidentally be swallowed (Shilton *et al.* 1999, Tang *et al.* 2007). While there is an obvious overlap in the roles of birds and bats as dispersers, birds remain essential in their role as dispersers for obligatory zoochorous seeds, too large for bats to ingest (Whittaker and Jones 1994).

Fruit bats have been shown to utilize invasive plant species as both feeding and roost sites within an urban environment (Corlett 2005), and may potentially fill a gap created by the loss of large avian dispersers and other mammalian frugivores that are absent in such environments. Globally, Pteropodidae are essential in maintaining forest ecosystems (Fleming and Heithaus 1981, Whittaker and Jones 1994), with nearly 300 plant species reliant on them for pollination and seed dispersal (Fujita and Tuttle 1991, Shilton *et al.* 1999). They play a particularly important role as dispersers to isolated habitats (Cox *et al.* 1991), covering great distances (Webb and Tidemann 1996, Richter and Cumming 2006), and crossing open areas to isolated patches that many bird species will not do (Muscarella and Fleming 2007).

The aim of this study was to determine what effect generalist avian frugivores and fruit bats have on invasive alien seed germination, and to investigate both the nutritional and morphological features of these fruits. Finally, whether or not avian frugivores are able to subsist on a pure diet of fruits of invasive species was also considered.

Factors influencing frugivore fruit selection

Frugivory is a mutually beneficial process (Jordano 1987, Schupp 1993, Kinnaird 1998), and while the plants benefit from dispersal away from the parent plant (Ridley 1930, Jordano 1987, Schupp 1993, Kinnaird 1998) and possibly enhanced germination success (Barnea *et al.* 1991, Traveset 1998), the energetic rewards to the frugivore are less known. While the nutritional benefits to the frugivore are an important component in driving the plant-frugivore relationship (Izhaki 1992), the process of fruit selection is a multi-faceted processes. Fruit traits such as nutrient concentration and type (Denslow *et al.* 1987, Levey 1987, Avery *et al.* 1995, Avery *et al.* 1999), colour (Wheelwright and Janson 1985, Avery *et al.* 1995), size (Paszkowski 1982, Flörchinger *et al.* 2010, Sobral *et al.* 2010), seed load (Murray *et al.* 1993, Stanley and Lill 2002a, Wilson and Downs 2011a), caloric content (Sorensen 1984, Johnson *et al.* 1985, Wilson and Downs 2011b), and secondary compounds (Sorensen 1983, Cipollini and Levey 1997a, Levey and Cipollini 1998, Schaefer *et al.* 2003, Sánchez *et al.* 2004) have all been shown to play a part in frugivore feeding behaviour. Furthermore, the abundance, crop size (Snow 1971, Murray 1987), variations in fruit over time (Debussche *et al.* 1987, Lepczyk *et al.* 2000, Pereira *et al.* 2010), accessibility (Denslow and Moermond 1982, Willson 1994), and the physiological needs and characteristics of the frugivore (Lepczyk *et al.* 2000) will further drive the fruit selection process.

Despite the overwhelming number of factors driving fruit selection, there appears to be a global similarity in both the cues used for fruit selection, as well as the characteristics of fleshy fruits (French 1991, Jordano 1995). It has been suggested that phylogenetic effects influence fruit traits more strongly than plant-disperser interactions (Jordano 1995) and evolutionary chronologies indicate that vertebrate frugivores lagged behind the evolution of the major fruiting families they fed on (Fleming and Kress 2011). However, patterns in fruit

traits associated with disperser groups indicate that frugivore selective pressures have, to some degree, driven the evolution of fruit traits (Lomáscolo *et al.* 2010).

Positive correlations exist between the number of frugivore species and invasive alien plants within an area (Gosper and Vivian-Smith 2009), as well as fruit display size and removal rates (Bach and Kelly 2004). Fruits of many invasive plant species have similar morphological characteristics to indigenous fruits and fruit year round (Henderson 2001, Corlett 2005). Consequently they present a reliable, familiar food supply. Indeed it has been shown that frugivores are able to recognise the quality of a food patch (Sánchez 2006) and would likely utilize fruits of invasive species, as in some cases these have been shown to have higher nutritional value than those native species (Kueffer *et al.* 2009). Fruits dispersed exclusively by birds or mammals have similar nutritional content (generally low in proteins and lipids, but high in carbohydrates), but vary in morphology (Jordano 1995). Mammal dispersed fruits tend to have larger, but not necessarily more seeds (Jordano 1995). A recent Australian survey on fruits of invasive plants indicated that these also had relatively low lipid and protein content (Gosper and Vivian-Smith 2010). However, compared to indigenous species, fruits of invasive species had high sugar content, smaller seeds, and longer fruiting periods (Gosper and Vivian-Smith 2010).

The role of frugivores in the germination success of invasive alien plants

Vertebrate seed dispersal is one of the many factors that lead to the successful invasion of exotic plants (Rejmánek 1996). The role of avian dispersal of seeds of invasive plants has been highlighted in many areas including North America (Greenberg *et al.* 2001, Renne *et al.* 2002, Drummond 2005, Bartuszevige and Gorchov 2006, McCay *et al.* 2009), Europe (Paireon *et al.* 2006, Deckers *et al.* 2008), various islands (Nogales *et al.* 2005, Buddenhagen and Jewell 2006, Linnebjerg *et al.* 2009), Australia (Bass 1990, Stansbury and Vivian-Smith

2003, Vivian-Smith *et al.* 2006a, Westcott *et al.* 2008), and Asia (Sharma *et al.* 2005, Corlett 2006). However, it remains poorly studied in Africa, and a study of such nature would contribute to a better global understanding (Pysek *et al.* 2008).

Studies that focus on the influence of frugivores on the germination success of seeds of fleshy-fruited species in particular require further investigation. Literature covering this topic are summarised in Table 1. Unfortunately, much of the information is largely anecdotal and published in obscure sources, thereby limiting the reader audience. Nevertheless, of the literature considered in Table 1, there is a clear geographical bias in where studies are conducted, thereby limiting a global perspective. Most of these studies only consider the effects of avian frugivores on germination and not mammals, which may vary in roles as dispersers. Also, many of these do not consider intact fruit seed germination which must be included in the experimental design in order to determine the effect of gut passage or pulp removal on seed germination success (Samuels and Levey 2005).

Frugivores may shorten the onset of seed germination, through pulp removal, which decreases the risk of seed predation, competition or pathogen attack (Howe 1986). Seed germination may also either be enhanced (Barnea *et al.* 1991), inhibited (Murray *et al.* 1994, Charalambidou *et al.* 2003) or not affected at all after passing through the digestive tracts of frugivores (Barnea *et al.* 1990, 1991). Generally germination is enhanced twice as often as inhibited and evidence suggests that increased germination may be characteristic of plants that occupy unpredictable environments, where this will be advantageous (see review Traveset 1998). In some cases, germination success can be linked to seed retention time (Sorensen 1984, Murray *et al.* 1994), which is usually rapid in avian frugivores (Karasov 1990). This quick digestive passage enables frugivores to rapidly process bulky fruit and also plays an important role in energy assimilation (Karasov and Levey 1990, Levey and Karasov 1994). Fruits of certain species (e.g. *Solanum* fruit (Cipollini and Levey 1997b)) contain secondary chemical compounds that may cause diarrhea or constipation, suggesting that some plants

may have some control on seed dispersal patterns (Murray *et al.* 1994, Cipollini and Levey 1997a, Wahaj *et al.* 1998).

Seed retention time (SRT) is important as this translates into the distance that a seed is carried away from a parent plant (Ridley 1930) and by combining such information with frugivore behavior (e.g. how long it remains in a fruiting tree) the potential seed shadow size can be determined (Stansbury and Vivian-Smith 2003). Longer SRT's of small seeds are costly for frugivores as these increase the handling cost of food, displace gut volume, (Sorensen 1984), and increase the energetic demands of flight (Fukui 2003). Therefore, larger seeded plants may be preferred by frugivores, and benefit from greater seed removal rates, while smaller seeded plants benefit from a greater dispersal distances (Fukui 2003). Germination success of tree seeds are typically more affected by frugivore ingestion than are those of shrubs or herbaceous plants (Traveset 1998).

As fruit bats rarely ingest large seeds (Whittaker and Jones 1994, Monadjem *et al.* 2010), these will not experience any seed coat abrasion in the digestive tract which may influence germination success (Evenari 1949, Agami and Waisel 1988, Barnea *et al.* 1990, 1991). Thus spat seeds may only have enhanced germination due to pulp removal (Evenari 1949, Barnea *et al.* 1991). Interestingly of the invasive species considered, more than 70% do not require seed coat abrasion for enhanced germination, with pulp removed and ingested seeds experiencing similar germination success (Table 1). This trend has also been observed where no frugivores are considered, and only manually de-pulped seeds are compared to seeds in intact fruit (Chimera and Drake 2010). However such studies would not identify any digestive effects on the seeds by local dispersers. Unfortunately, nearly half of germination studies do not consider whole fruit controls (Table 1), but when these are considered, 80% of these have less germination than ingested or de-pulped seeds (Table 1). An added benefit of pulp removal is the earlier onset of germination (Greenberg *et al.* 2001, Lafleur *et al.* 2009, Linnebjerg *et al.* 2009, Jordaan *et al.* 2011a, Chapter 2). Rapid germination decreases the risk

of being outcompeted by other seedlings (Ross and Harper 1972, Abul-Fatih and Bazzaz 1979) or mortality due to pathogens, microbes or predation (Howe 1986, Heer *et al.* 2010).

Table 1. Review of literature, summarizing of the effects of frugivore processing on the germination success of fleshy-fruited invasive alien species, where ‘+’ indicates a positive effect, ‘-’ indicates a negative effect, and ‘0’ indicates no difference.

Plant species	Disperser considered	Place of study	Effect of ingestion compared to:		Reference
			De-pulped seeds	Seeds in intact fruit	
<i>Amaranthus dubius</i>	bird	Galapagos Islands	0		(Buddenhagen and Jewell 2006)
<i>Passiflora edulis</i>	bird	Galapagos Islands	0		
<i>Rubus niveus</i>	bird	Galapagos Islands	0		
<i>Psidium guajava</i>	bird	Galapagos Islands	0		(Waibel 2009)
<i>Cestrum auriculatum</i>	bird	Galapagos Islands	- \ 0		
<i>Lantana camara</i>	bird	Galapagos Islands	0		
<i>Wikstroemia indica</i>	tortoise	Mascarene Islands	0	-	(Linnebjerg <i>et al.</i> 2009)
<i>Syzygium cumini</i>	tortoise	Mascarene Islands		-	
<i>Lantana camara</i>	tortoise	Mascarene Islands		0	
<i>Veitchia merrillii</i>	tortoise	Mascarene Islands		0	(Medeiros 2004)
<i>Mimusops coriacea</i>	tortoise	Mascarene Islands		+	
<i>Ligustrum robustum</i>	bird	Mauritius	0	+	
<i>Clidemia hirta</i>	bird	Mauritius	0	+	(Tassin <i>et al.</i> 2007)
<i>Clidemia hirta</i>	bird, rat	Hawaii	0		
<i>Hedychium gardnerianum</i>	bird	Hawaii	0		
<i>Psidium cattleianum</i>	bird	Hawaii	+		(Bourgeois <i>et al.</i> 2005)
<i>Schinus terebinthifolius</i>	bird	Reunion Island	0		
<i>Carpobrotus edulis</i>	rat	French Mediterranean Island	+		
<i>Carpobrotus edulis</i>	rabbit, mouse, shrew, cat, hedgehog	French Mediterranean Island	0		(Padron <i>et al.</i> 2011)
<i>Opuntia maxima</i>	lizard, stone marten	Canary Islands	+		
<i>Opuntia stricta</i>	lizard, stone marten	Canary Islands	+		
<i>Opuntia dillenii</i>	lizard, stone marten	Canary Islands	+		(Greenberg <i>et al.</i> 2001)
<i>Opuntia maxima</i>	bird, boar, tortoise, weasel, fox	Canary Islands	-		
<i>Opuntia stricta</i>	bird, boar, tortoise, weasel, fox	Canary Islands	-		
<i>Opuntia dillenii</i>	bird, boar, tortoise, weasel, fox	Canary Islands	-		(Bartuszevige and Gorchov 2006)
<i>Celastrus orbiculatus</i>	bird	North America	0	+	
<i>Lonicera maackii</i>	bird	North America	- \ 0		
<i>Elaeagnus umbellata</i>	bird	North America	0	+	(Lafleur <i>et al.</i> 2009)
<i>Celastrus orbiculatus</i>	bird	North America	0	+	(Renne <i>et al.</i> 2001)
<i>Rosa multiflora</i>	bird	North America	0	+	
<i>Sapium sebiferum</i>	bird	North America	0	+	
<i>Carpobrotus edulis</i>	deer, rabbit, jackrabbit	North America		+	(D'Antonio 1990)
<i>Duchesnea indica</i>	turtle	North America	0		(Braun and Brooks Jr. 1987)
<i>Morus alba</i>	turtle	North America	-		(Krefting and Roe 1949)
<i>Rubus phoenicolasius</i>	turtle	North America	0		
<i>Morus alba</i>	bird	North America	+		
<i>Rosa multiflora</i>	bird	North America	+ / -		(Krefting and Roe 1949)
<i>Lonicera tatarica</i>	bird	North America	+ / 0		

<i>Carpobrotus edulis</i>	deer, jackrabbit	North America		+	(Vila and D'Antonio 1998)
<i>Psidium guajava</i>	bird	South Africa	0	+	(Jordaan <i>et al.</i> 2011a)
<i>Cinnamomum camphora</i>	bird	South Africa	0	+	
<i>Lantana camara</i>	bird	South Africa	0	+	
<i>Solanum mauritianum</i>	bird	South Africa	0	+	
<i>Morus alba</i>	fruit bat	South Africa	+ / 0	+	(Jordaan <i>et al.</i> 2011b)
<i>Eriobotrya japonica</i>	fruit bat	South Africa	0	0	
<i>Psidium guajava</i>	fruit bat	South Africa	0	+	
<i>Melia azedarach</i>	fruit bat	South Africa	0	+	
<i>Melia azedarach</i>	fruit bat	South Africa	0	+	(Voigt <i>et al.</i> 2011)
<i>Annona glabra</i>	bird	Australia	0	0	(Westcott <i>et al.</i> 2008)
<i>Asparagus africanus</i>	bird	Australia	-	de-pulped > WF	(Vivian-Smith and Gosper 2010)
<i>Ochna serrulata</i>	bird	Australia	0	0	(Gosper <i>et al.</i> 2006)
<i>Ziziphus mauritiana</i>	wallabies, feral pigs, cattle	Australia		+	(Grice 1996)
<i>Schinus terebinthifolius</i>	bird	Australia	0	+	(Panetta and McKee 1997)
<i>Sambucus nigra</i>	possum	New Zealand	0		(Dungan <i>et al.</i> 2002)
<i>Morus nigra</i>	bird	Israel	+		(Barnea <i>et al.</i> 1991)
<i>Morus nigra</i>	fruit bat	Israel	0		(Izhaki <i>et al.</i> 1995)
<i>Eriobotrya japonica</i>	fruit bat	Israel	+		
<i>Schinus terebinthifolius</i>	bird	Brazil		+	(D'Avila <i>et al.</i> 2010)
<i>Ficus microcarpa</i>	bird	Brazil	+		(Guerrero and de Figueiredo 1997)

Choice of alien plant species and frugivores for germination experiments

Germination experiments following avian ingestion

We identified four fleshy-fruited alien plant species that occur along the eastern portion of South Africa and have become highly invasive in KwaZulu-Natal. These were *Lantana camara*, *Solanum mauritianum*, *Cinnamomum camphora*, and *Psidium guajava* (Fig. 1).

Robertson *et al.* (2003) prioritised alien invasive plant species using 17 different criteria to assess which species posed the biggest problem on a national scale in South Africa. *Lantana camara* had the highest prioritization score, *S. mauritianum* ranked 11th, *C. camphora* ranked 19th, and *P. guajava* ranked 38th (Robertson *et al.* 2003). Birds are recognised as primary dispersers of *S. mauritianum* (Olckers 1999, Witkowski and Garner 2008), *C. camphora* (Firth 1981, Li 2004), *P. guajava* (Samson 1986), and *L. camara* (Vivian-Smith *et al.* 2006b).

The three generalist frugivores used were Red-winged Starlings (*Onychognathus morio*), Speckled Mousebirds (*Colius striatus*), and Dark-capped Bulbuls (*Pycnonotus tricolor*) (Fig. 2), as these have been observed to feed on these fruit. These frugivores are distributed along the eastern coastline of South Africa (Hockey *et al.* 2005). Red-winged Starlings and Speckled Mousebirds extend further south than Dark-capped Bulbuls' do, with Speckled Mousebirds also occurring more inland (Hockey *et al.* 2005). These frugivore distributions overlap with those of the invasive alien plant species used in this study (Henderson 2001).



Fig. 1. Invasive alien fruits fed to avian frugivores: 1. *Solanum mauritianum*, 2. *Psidium guajava*, 3. *Cinnamomum camphora*, and 4. *Lantana camara*.

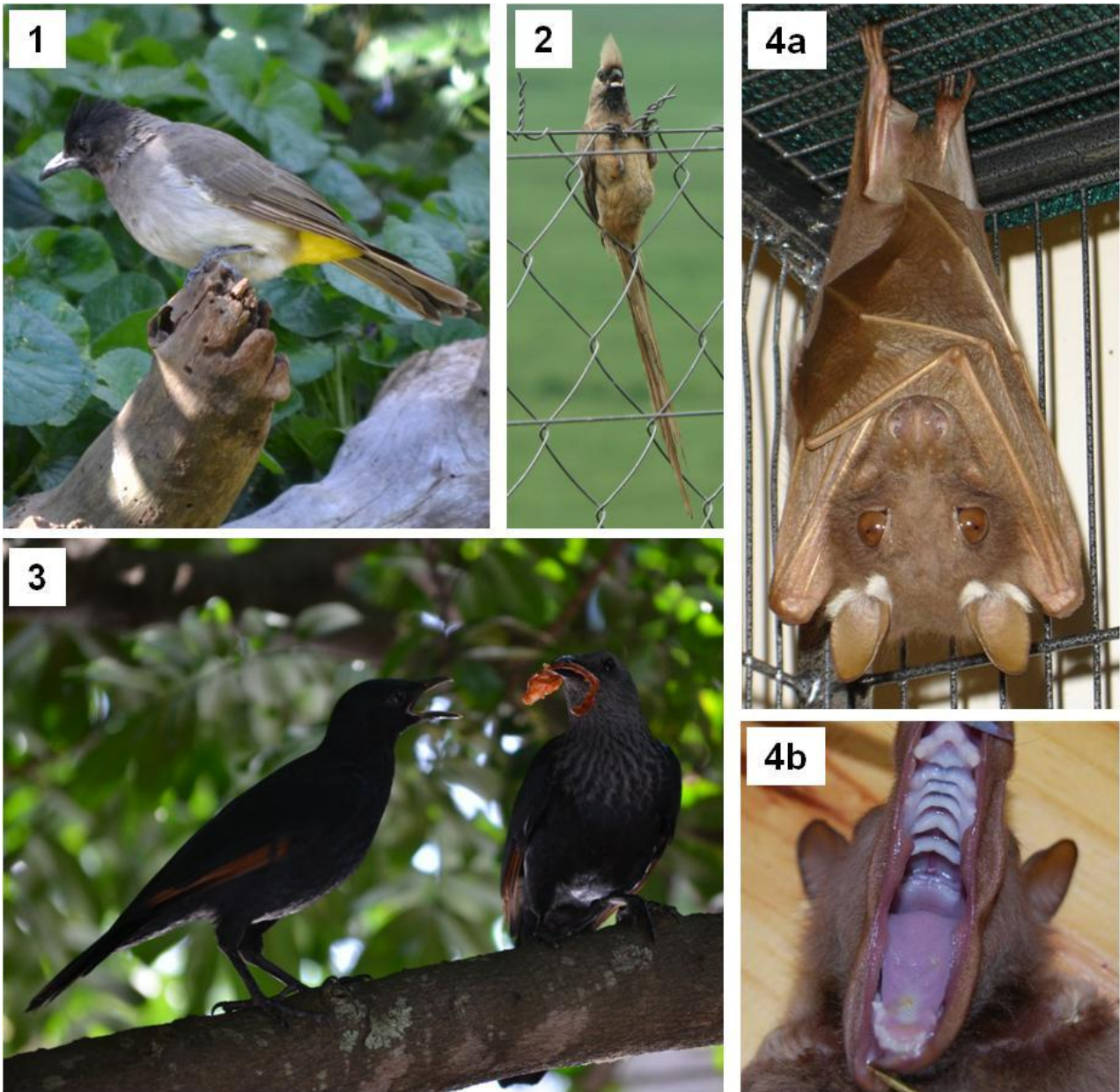


Fig. 2. Frugivore species used in this study: 1. Dark-capped Bulbul (*Pycnonotus tricolor*), 2. Speckled Mousebird (*Colius striatus*), 3. Red-winged Starling (*Onychognathus morio*), and 4b. Wahlberg's Epauletted Fruit Bat (*Epomophorus wahlbergi*). 4a. shows the ridged palette of *E. wahlbergi*.

A final aspect of the germination experiments following avian ingestion was to determine the effect of Red-winged Starlings and Speckled Mousebirds on the germination of invasive *S. mauritianum* and the indigenous congener *S. giganteum* (Fig. 3). Morphological and nutritive fruit traits were also compared.

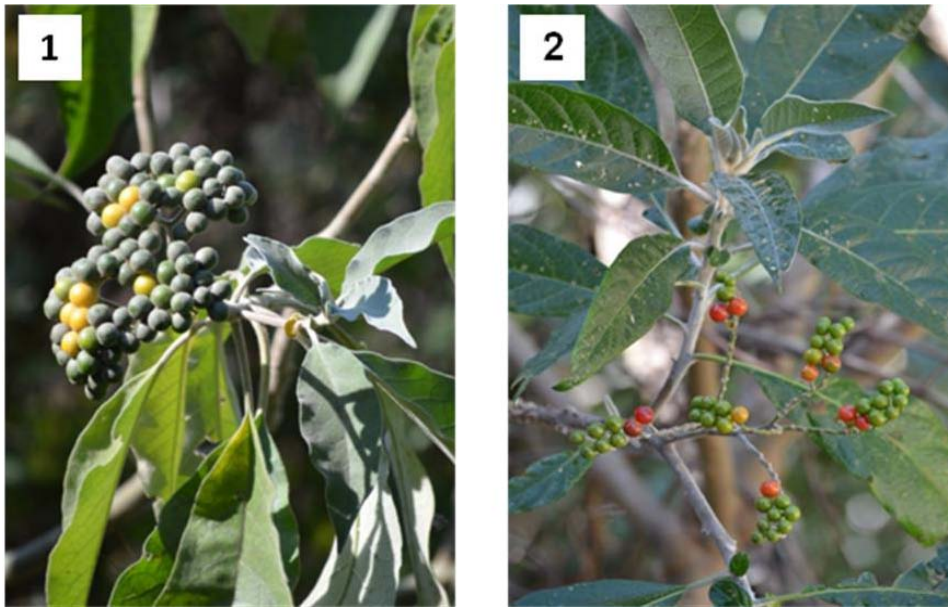


Fig. 3. Invasive *S. mauritianum* (1) and the indigenous congener *S. giganteum* (2).

Germination experiments following bat processing

Four invasive alien tree species were used for the germination experiments following bat processing. These included *Psidium guajava*, *Melia azedarach*, *Morus alba* and *Eriobotrya japonica* (Fig. 4). All these species are highly invasive in KwaZulu-Natal (Henderson 2001). Excluding *M. azedarach*, these fruits are cultivated for human consumption (Henderson 2001) and perhaps because of this their invasive status is understated and unrecognised by many. *Epomophorus wahlbergi* (Pteropodidae) is a large (100g), relatively common, Old World fruit bat (Monadjem *et al.* 2010) that has been observed to feed on these fruits (Corlett 2005, Voigt *et al.* 2011, Jordaan pers. obs.). It has a broad distribution along the east coast of southern Africa and occurs in forest and forest-edge habitats, but may also be found in peri-urban areas

with many trees (Monadjem *et al.* 2010). This overlaps with that of the invasive alien species used in this study (Henderson 2001).

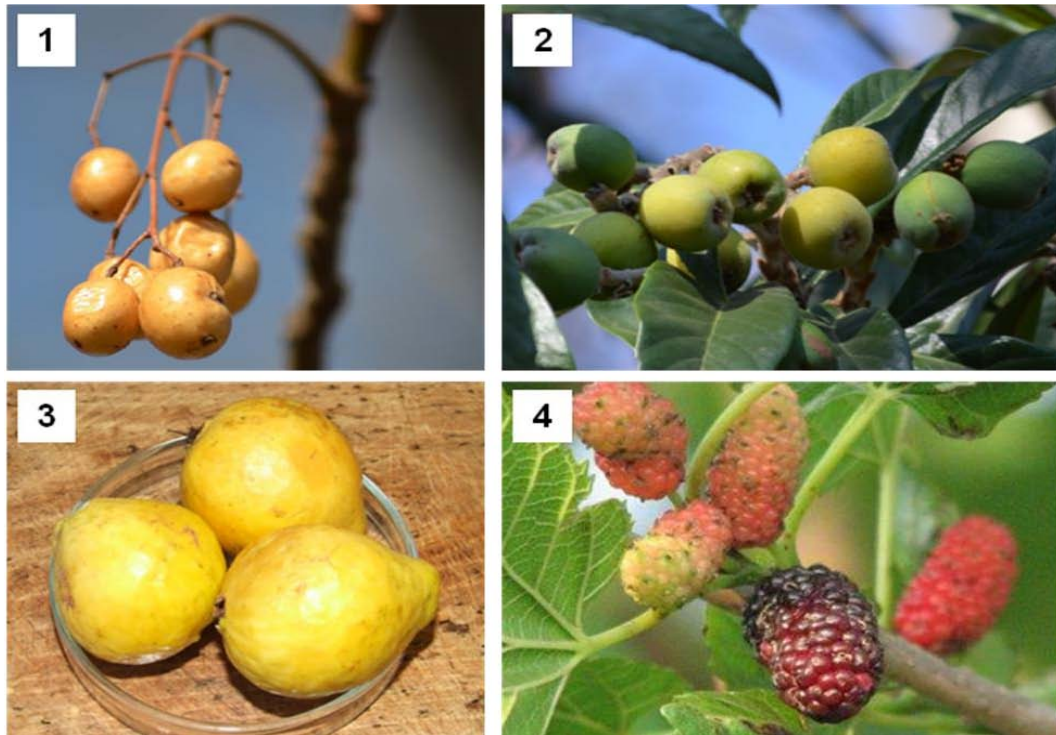


Fig. 4. Invasive alien fruits fed to *E. wahlbergi*: 1. *Melia azedarach*, 2. *Eriobotrya japonica*, 3. *Psidium guajava*, and 4. *Morus alba*.

Motivation for this study

This study was motivated by the severity of ecosystem invasion by these alien plant species in South Africa and the apparent lack of knowledge regarding their dispersal by native frugivores. Previous studies have found that various fruits have higher germination rates following frugivore digestion (see reviews Traveset 1998, Traveset *et al.* 2007). However, invasive alien plant seeds should not require specialized treatment in the digestive tracts of frugivores as these could then be disperser limited. Therefore, it was predicted that germination percentages of seeds of alien invasive plants would be similar for frugivore processed seeds and de-pulped seeds, and also that these seeds would germinate sooner than

whole fruit control seeds. Furthermore the duration that seeds remained in the digestive tract of avian frugivores was considered, and it was hypothesized that this would not influence germination success as chemical effects in the digestive tract were predicted to have no effect on seed germination rates. It was also expected that avian frugivores would meet their daily energetic demands when feeding on the various invasive alien fruit. Finally, it was anticipated that fruits of invasive alien plants would consist of similar or better nutritional and morphological traits than indigenous fruits to explain frugivore selection of these.

This study presents valuable insights into why frugivores may prefer fruits of invasive plant species and highlights their role in the recruitment process of several highly invasive species. Investigating these factors will allow further analysis of the potential and associated trends in the multi-faceted study of invasion ecology. Finally, such studies play a pivotal role in the implementation of effective management strategies of existing invasive alien plant populations and in the screening process of potential invasive plant threats.

Arrangement of thesis

The thesis is arranged as chapters prepared for publication in relevant peer-reviewed journals, and thus some repetition in the chapters was unavoidable. The respective hypotheses are presented in each chapter.

There are five experimental chapters:

Chapter 2. Digestion of fruit of invasive alien plants by three southern African avian frugivores.

Chapter 3. The role of avian frugivores in germination of seeds of fleshy-fruited invasive alien plants.

Chapter 4. Wahlberg's Epauletted Fruit Bat (*Epomophorus wahlbergi*) as a potential dispersal agent for fleshy-fruited invasive alien plants: effects of handling behaviour on seed germination.

Chapter 5. Forbidden fruit: nutritional and morphological traits of invasive and exotic fleshy-fruits in South Africa.

Chapter 6. Comparison of germination rates and fruit traits of indigenous *Solanum giganteum* and invasive *S. mauritianum* in South Africa.

Finally, the thesis has a concluding chapter that summarises the various components of this broad study, highlighting the importance of frugivory in the invasion success of fleshy fruited plants.

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Chapter 2

Short communication

Digestion of fruit of invasive alien plants by three southern African avian frugivores

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Many highly invasive plants are fleshy-fruited and owe their invasiveness largely to mutualisms formed with local dispersers. The energetic benefits gained by frugivores from ingestion of fruits of invasive alien plants remain poorly documented. We assess whether avian frugivores process fruits of invasive alien plants effectively to meet their daily energetic requirements. Four fleshy-fruited plant species that are invasive in southern Africa were considered – *Solanum mauritianum*, *Cinnamomum camphora*, *Lantana camara* and *Psidium guajava*. Their fruits were fed to three common generalist frugivores – Red-winged Starling *Onychognathus morio*, Speckled Mousebird *Colius striatus* and Dark-capped Bulbul *Pycnonotus tricolor* – to determine the efficiency of digestion. Energetic parameters calculated for all fruit diets varied significantly between frugivore species. Speckled Mousebirds and Dark-capped Bulbuls maintained body mass and efficiently processed all four fruit types, whereas Red-winged Starlings only did so on *C. camphora* and *S. mauritianum* diets. These results explain why these fruits are attractive to local avian frugivores. Furthermore, these avian frugivores processed large quantities of invasive fruits, thereby serving as potentially efficient dispersers.

Keywords: bird-dispersed fruit, energy assimilation, fruit processing, nutritional content, non-native.

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Many invasive plants are bird-dispersed (Cronk & Fuller 1995), enhancing their naturalization and spread by forming mutualisms with resident dispersers (Richardson *et al.* 2000). The loss of indigenous fruiting species allows invasive alien species to penetrate ecosystems (Lafleur *et al.* 2007) and replace them as a food supply (Buckley *et al.* 2006, Gosper & Vivian-Smith 2006). Invasive species are sometimes preferred by frugivores and may therefore compete with native plant species for dispersal agents (Bass 1990, Lafleur *et al.* 2007). Although invasive plants are a world-wide threat to biodiversity (Richardson & van Wilgen 2004), to our knowledge no studies have quantified the direct energetic benefits of their fruits to frugivores.

Three generalist, native frugivorous species were used in this study to determine if they were able to efficiently process fruits from four species of invasive alien plants. The chosen plant species are all highly invasive in South Africa and of conservation concern (Henderson 2001). They have overlapping ranges with the avian frugivores used in this study (Henderson 2001, Hockey *et al.* 2005), which have been observed to feed on these fruits in the wild (L. Jordaan, pers. obs.).

Energy assimilation has been quantified for artificial fruit diets (Witmer 1998, Wellmann & Downs 2009, Wilson & Downs 2011), nectar diets (Brown & Downs 2003, Brown *et al.* 2010) and indigenous fruit diets (Witmer & Van Soest 1998), but not for invasive alien fruits. Both native and invasive frugivores have shown a preference for these fruits (Lafleur *et al.* 2007), suggesting that they may be able to efficiently process and assimilate energy from them. This study assessed whether generalist avian frugivores are able to process invasive alien fruits efficiently and maintain their body mass on these diets.

METHODS

Red-winged Starlings *Onychognathus morio* ($n = 9$), Speckled Mousebirds *Colius striatus* ($n = 10$) and Dark-capped Bulbuls *Pycnonotus tricolor* ($n = 7$) were caught using mist-nets between July 2007 and February 2008 in the Pietermaritzburg area. Birds were ringed and housed in single-species groups in outside aviaries at the University of KwaZulu-Natal (UKZN) animal house. They were fed a mixed fruit maintenance diet for at least one month, after which feeding trials commenced based on the availability of fruit. Maintenance diets were supplemented with AviPlus Softbill/Mynah pellets and crumble (Avi-products, Durban, South Africa), and Starling and Bulbul diets were further supplemented with *Tenebrio molitor* larvae every third day. Water was provided *ad libitum*.

Each individual was placed in a cage in a constant environment room set at 25 °C, on a 12 : 12-h dark/light cycle and acclimatized for 3 days. Birds were

weighed twice daily (at 06:00 h, before the trial, and 18:00 h, afterwards) on sample days. Each individual was fed a specific fruit diet on two occasions. Body mass data were collected on both occasions and excreta, for the calculation of energetic parameters, were only collected on the second day.

Solanum mauritianum Scopoli (bugweed), *Cinnamomum camphora* L. J. Presl. (camphor), *Lantana camara* L. *sensu lato* (lantana) and *Psidium guajava* L. (yellow guava) fruit were collected from naturalized plants near UKZN and offered to the birds within 48 h. Sample fruit was incorporated into the maintenance diet prior to sampling days. Birds were fed only fruit of one alien plant species on a sample day. Fruits were presented whole *ad libitum* and weighed before and after each trial to calculate the total amount of fruit eaten per day.

To control for evaporative water loss from uneaten fruit, control fruit were placed in the room and weighed at the start and end of the trial. At the end of each sample day, excreta were collected, weighed, oven-dried at 60 °C to constant mass and re-weighed. Fruit samples were also oven-dried to constant mass. A bomb calorimeter was used to determine the gross energy (GE) of the excreta and fruit samples. Daily food intake (DFI) was

determined for each sample day by correcting the amount of fruit eaten for evaporative water loss and converting it to a dry weight based on water content of the fruits. By multiplying this value by the energy content of the fruit eaten, the gross energy intake (GEI) was determined. Excreta energy loss (EE) was calculated as the amount of dried excreta multiplied by its energy value. Daily apparent energy assimilation (DEA) was determined as $GEI - EE$. Apparent energy assimilation (AEA) was calculated as DEA/GEI and converted to a percentage. Finally, DFI, DEA, GEI and EE were all divided by the average body mass of each bird on the sample day.

The effect of different fruit diets on DFI and body mass (BM) of each bird species was analysed using repeated-measures analysis of variance (RMANOVA) and *post-hoc* Tukey tests. Energy assimilation parameters were tested using analysis of variance (ANOVA). All analyses were conducted using STATISTICA (Statsoft, Version 7, Tulsa, OK, USA).

RESULTS

All frugivore species maintained BM on the *S. mauritianum* and *C. camphora* diets (Fig. 1). When fed

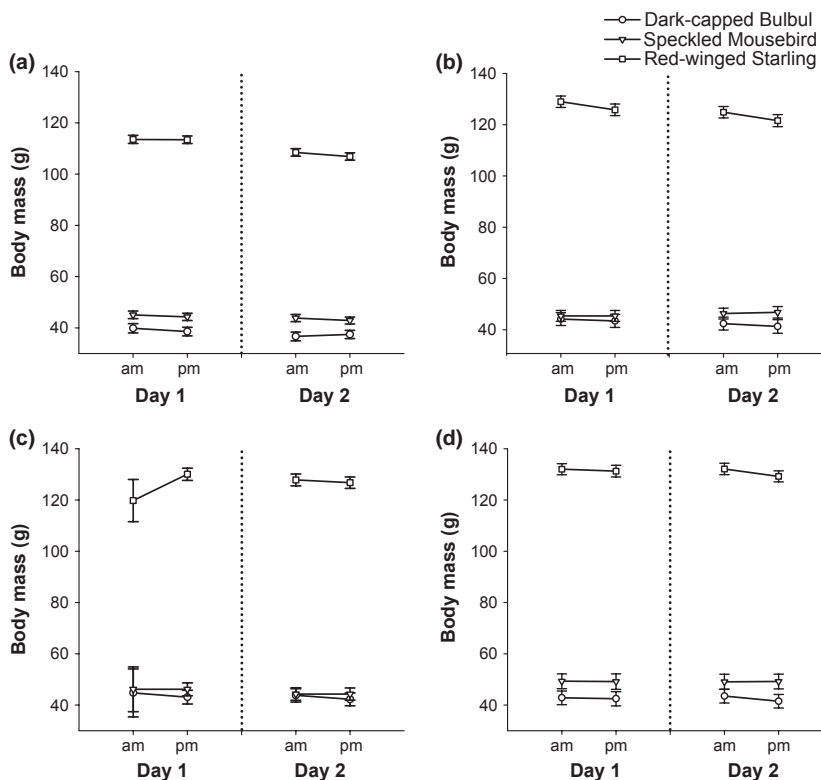


Figure 1. Dark-capped Bulbul, Speckled Mousebird and Red-winged Starling body masses (mean \pm se) before and after the respective diets of fruits of alien plants on two different sampling days. (a) *Solanum mauritianum*, (b) *Psidium guajava*, (c) *Cinnamomum camphora* and (d) *Lantana camara*.

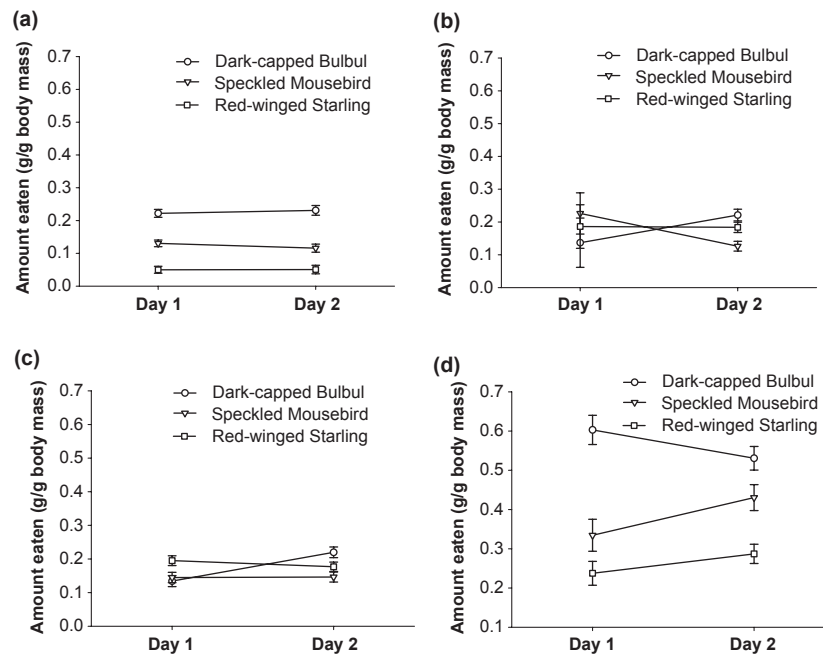


Figure 2. Food intake (mean \pm se) of Dark-capped Bulbul, Speckled Mousebird and Red-winged Starling fed the respective diets of fruits of alien plants on two different sampling days. (a) *Solanum mauritianum*, (b) *Psidium guajava*, (c) *Cinnamomum camphora* and (d) *Lantana camara*.

L. camara and *P. guajava*, only Speckled Mousebirds and Dark-capped Bulbuls maintained body mass (Fig. 1). On the *P. guajava* diet, Red-winged Starling body mass decreased significantly (*post-hoc* Tukey, $P < 0.050$) on both sample days (Fig. 1). On the *L. camara* diet, Red-winged Starling body mass was maintained on the first sample day, but decreased significantly (*post-hoc* Tukey, $P < 0.050$) on the second sample day (Fig. 1).

There was no significant difference in DFI per gram body mass (per g BM) between sample days among bird species fed *S. mauritianum* (RMANOVA, $F_{2,23} = 2.2$; $P = 0.13$) and *P. guajava* (RMANOVA, $F_{2,23} = 1.5$; $P = 0.24$) (Fig. 2). However, DFI did vary significantly between days for all three frugivore species when fed *C. camphora* (RMANOVA, $F_{2,21} = 7.3$; $P < 0.05$) and *L. camara* (RMANOVA, $F_{2,18} = 9.9$; $P < 0.05$ Fig. 2). Dark-capped Bulbuls consumed significantly more *C. camphora* fruit on the second sample day than on the first (*post-hoc* Tukey, $P = 0.01$), whereas Speckled Mousebirds showed this trend when fed *L. camara* (*post-hoc* Tukey, $P = 0.04$, Fig. 2).

GEI and EE (per g BM) were significantly different among bird species for all fruit diets (Table 1). A similar trend was observed for DEA and AE, except for *C. camphora* and *L. camara* diets, respectively (Table 1). All frugivores had the highest AE on the *P. guajava* diet, which follows from high GEI and DEA, and relatively low EE (Table 1). Conversely, moderate GEI and relatively high EE on the *L. camara* fruit diet resulted in the

lowest AE for all frugivore species (Table 1). While GEI was lowest for all frugivores on the *S. mauritianum* diet, AE was second highest for this plant species. Despite Dark-capped Bulbuls having the highest GEI on *S. mauritianum*, *C. camphora* and *L. camara* diets, Speckled Mousebirds had the highest AE for all plant species except *S. mauritianum* (Table 1).

DISCUSSION

Most energetic parameters calculated for each fruit diet varied significantly between frugivore species, indicating that each species may have different feeding and digestive strategies. Efficient resource utilization and energy assimilation is determined by the digestive strategy employed (Place & Stiles 1992, Afik & Karasov 1995), which is in turn influenced by the nutritional content of fruit (Witmer 1996). Birds are able to discriminate between the nutritional content of different fruit (Schaefer *et al.* 2003). Results from this and other studies suggest that birds may adjust their feeding behaviour to obtain their daily energetic requirements by consuming proportionately less lipid-rich fruits, such as *C. camphora* (Bosque & Deparra 1992, Place & Stiles 1992). In contrast, more nutritionally poor *L. camara* (Gosper & Vivian-Smith 2010) was consumed.

Fruits of many invasive plants have higher energetic values than native species (Kueffer *et al.* 2009). *Psidium*

Table 1. Significance of difference between the energetic parameters (mean \pm se) per gram body mass of generalist frugivore species fed on various invasive alien fruit diets (ANOVA).

Plant species	Bird species	n	GEI, kJ/g BM			EE, kJ/g BM			DEA, kJ/g BM			AE, %		
			mean \pm se	F ₂	P	mean \pm se	F ₂	P	mean \pm se	F ₂	P	mean \pm se	F ₂	P
<i>Solanum mauritianum</i>	Dark-capped Bulbul	7	4.78 \pm 0.31	42.3	< 0.05	1.05 \pm 0.09	24.2	< 0.05	3.73 \pm 0.26	36.3	< 0.05	77.39 \pm 2.87	3.0	0.07
	Speckled Mousebird	10	2.40 \pm 0.26			0.72 \pm 0.08			1.68 \pm 0.22			70.3 \pm 2.40		
<i>Cinnamomum camphora</i>	Red-winged Starling	9	1.05 \pm 0.27			0.23 \pm 0.08			3.52 \pm 0.30			78.1 \pm 2.50		
	Dark-capped Bulbul	7	5.87 \pm 0.42	8.3	< 0.05	2.08 \pm 0.11	61.1	< 0.05	3.79 \pm 0.34	1.1	0.35	63.6 \pm 1.70	56.8	< 0.05
<i>Psidium guajava</i>	Speckled Mousebird	8	3.55 \pm 0.39			0.43 \pm 0.10			3.12 \pm 0.31			87.9 \pm 1.60		
	Red-winged Starling	9	4.72 \pm 0.37			1.21 \pm 0.10			3.52 \pm 0.30			74.69 \pm 1.47		
<i>Lantana camara</i>	Dark-capped Bulbul	7	11.22 \pm 0.76	65.9	< 0.05	1.51 \pm 0.12	28.8	< 0.05	9.70 \pm 0.74	56.8	< 0.05	86.0 \pm 1.00	2.3	0.12
	Speckled Mousebird	10	18.40 \pm 0.64			2.19 \pm 0.10			16.22 \pm 0.62			88.0 \pm 0.80		
<i>Lantana camara</i>	Red-winged Starling	9	8.05 \pm 0.67			1.13 \pm 0.10			6.92 \pm 0.65			85.8 \pm 0.80		
	Dark-capped Bulbul	6	9.82 \pm 0.54	21.3	< 0.05	3.86 \pm 0.28	7.5	< 0.05	5.95 \pm 0.28	41.9	< 0.05	60.8 \pm 1.20	23.0	< 0.05
<i>Lantana camara</i>	Speckled Mousebird	6	7.87 \pm 0.54			2.79 \pm 0.28			5.08 \pm 0.28			64.5 \pm 1.20		
	Red-winged Starling	9	5.31 \pm 0.44			2.47 \pm 0.23			2.84 \pm 0.23			54.1 \pm 0.10		

N, number of individuals from each bird species. AAE, apparent assimilation efficiency; BM, body mass; DEA, daily energy assimilated; EE, excreta energy loss; GEI, gross energy intake.

guava, *L. camara* and especially *S. mauritianum* fruit have proportionally higher sugar and lower lipid content, whereas *C. camphora* fruit are relatively high in lipids and low in sugar (Chan & Kwok 1975, Gosper & Vivian-Smith 2010). Although Speckled Mousebirds and Dark-capped Bulbuls met their daily energetic demands on all four fruit types, larger Red-winged Starlings were only able to do this on lipid-rich *C. camphora* and sugar-rich *S. mauritianum* fruit diets (Gosper & Vivian-Smith 2010).

The ability of native frugivores to gain their daily energy requirements from fruits of invasive alien species provides new insights into the dynamic interaction between these species. Further studies should determine feeding behaviour, as well as visitation and feeding rates of frugivores on invasive plants in the field, in order to understand frugivore behaviour in terms of seed dispersal and fruit preference. The role of avian dispersers in terms of the amount of fruit eaten, and therefore seeds processed, should not be underestimated in the process of invasion.

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The role of avian frugivores in germination of seeds of fleshy-fruited invasive alien plants

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Abstract Many highly invasive plant species have fleshy fruits which are eaten by native frugivorous animals. These frugivores play an important role in long-distance seed dispersal, and may also affect germination success. The aim of this study was to determine whether generalist frugivores enhance or decrease seed germination of invasive alien species through pulp removal or seed coat abrasion, besides serving as dispersal agents. Fruits of four fleshy-fruited invasive alien plant species, namely *Solanum mauritianum*, *Cinnamomum camphora*, *Lantana camara* and *Psidium guajava*, were fed to three generalist avian frugivorous species, which have been observed feeding on these fruits in the wild. Seed retention time was recorded as this affects dispersal distance and the duration that seeds are exposed to the effects of the gut. Seeds removed from excreta, seeds from manually de-pulped fruit, and whole fruit were planted in soil trays housed in a greenhouse. Daily germination counts were done. Seed retention

times differed significantly between bird species for all fruits, except those of *C. camphora*. However, all frugivores had a similar effect on the germination success of seeds of *S. mauritianum*, *L. camara* and *P. guajava*, showing that gut retention time was not important. Germination of seeds from manually de-pulped fruits did not differ from that of ingested seeds of all plant species, suggesting that seed coat abrasion was also not important. Pulp removal resulted in significantly higher germination rates, both in the two species with larger, multi-seeded fruit (*S. mauritianum* and *P. guajava*), and in the two species having single-seeded fruit with waxy exocarps (*C. camphora* and *L. camara*). Pulp removal also resulted in significantly earlier germination of *L. camara* and *P. guajava* seeds. Therefore, frugivores not only accelerate dispersal, but also greatly enhance seed germination of all fleshy-fruited invasive alien species in this study.

Keywords Avian frugivory · Emergence time · Pulp removal · Seed abrasion · Seed dispersal · Seed retention

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Introduction

Invasive alien plants are non-native, naturalized species that have successfully spread outside of their native range (Richardson et al. 2000a). Worldwide, natural ecosystems are being invaded by introduced

species which can disrupt their functioning and result in economic losses (van Wilgen et al. 2001, 2008; Richardson and van Wilgen 2004). After direct habitat destruction, biological invasions are recognized as the second-largest threat to biodiversity (Richardson and van Wilgen 2004). Invasive plant species that have the greatest impact on natural habitats are often trees or shrubs that are shade tolerant, grow rapidly, reproduce early, produce numerous seeds, and have fleshy fruits associated with bird-dispersal (Cronk and Fuller 1995). Recent studies highlight the importance of fruit traits associated with avian frugivore preferences, such as morphology (Gosper and Vivian-Smith 2009) and nutritional composition (Gosper and Vivian-Smith 2010).

Small, single-seeded fruit or those with fewer seeds (Gosper and Vivian-Smith 2009), as well as soft, many-seeded fruits tend to be visited more often by frugivores (Green 1993). Fruit size is also one of the most important factors determining fruit choice (Debussche and Isenmann 1989; Green 1993; Stansbury and Vivian-Smith 2003). In Australian surveys it was found that plant species with smaller fruits (<15 mm diameter) were visited by more avian frugivorous species than those with larger fruits (Green 1993; Stansbury and Vivian-Smith 2003), as the latter rely on frugivores with larger gape widths (Wheelwright 1985).

The successful spread and establishment of fleshy-fruited alien plants is greatly enhanced by the rapid formation of loose mutualisms with resident dispersers (particularly birds and mammals) (Richardson et al. 2000b). It has been shown that plant invasiveness increases when avian frugivore communities are more diverse (Gosper and Vivian-Smith 2009). Of further concern is the possibility that alien vegetation may compete with indigenous plant species for the attention of dispersal agents (Bass 1990; Lafleur et al. 2007). In some cases frugivores may prefer (Fraser 1990; Lafleur et al. 2007) or disproportionately consume fruits of invasive plants (Chimera and Drake 2010).

The process of seed dispersal by frugivorous animals usually involves the consumption of fruit pulp and the regurgitation or defecation of intact, viable seeds (Ridley 1930). This relationship is mutually beneficial as dispersers receive a resource (i.e. fruit pulp) and the plant's seeds are dispersed away from the parent plant (Jordano 1987; Schupp

1993; Kinnaird 1998). Seedlings are unlikely to survive under parent plants due to resource competition (Day et al. 2003), and furthermore the risk of seed predation increases under the parent plant (Howe 1986). Thus, frugivores are expected to play an important role in the process of invasion of exotic fleshy-fruited species.

Once ingested, seeds may undergo both chemical and mechanical treatment in the digestive tract, influencing their germination success (McKey 1975; Barnea et al. 1991). Seed coat abrasion (Evenari 1949; Agami and Waisel 1988; Barnea et al. 1990, 1991) and pulp removal (Evenari 1949; Barnea et al. 1991) are the predominant ways in which germination rates may be affected by frugivores. Benefits following pulp removal may include evading seed predators dependent on olfactory or visual cues (Nystrand and Granstrom 1997; Moles and Drake 1999), as well as reduced bacterial and fungal attack (Witmer and Cheke 1991; Moore 2001). In addition to processing behaviour and digestive physiology of different frugivorous species (Jordano 2000), seed retention time may influence the degree of seed coat abrasion (Sorensen 1984; Murray et al. 1994) and potential dispersal distance (Ridley 1930).

Long distance seed dispersal is an important factor to consider in predicting plant movement patterns and range expansion processes (Higgins and Richardson 1999; Cain et al. 2000). The effect that frugivores' digestive tracts may have on seeds, the reliability and speed of fruit removal (McKey 1975), the movement patterns of frugivores, seed retention time, as well as the site of seed deposition (Bartuszevige and Gorchov 2006), may all determine the pattern of seed dispersal. Birds have been shown to play an important role in dispersal of seeds of fleshy-fruited invasive alien weeds (Richardson et al. 2000b; Day et al. 2003; Gosper et al. 2005; Bartuszevige and Gorchov 2006; Voigt et al. 2011). Plants with generalized avian dispersal systems are more likely to be invasive (Renne et al. 2002), and indeed many of the most detrimental invasive plant species are dispersed by avian frugivores (Buckley et al. 2006). However, the consistency with which particular frugivores affect the germination of various plant taxa requires further investigation (Barnea et al. 1990; Traveset 1998). Different bird species may affect the same plant species in different ways (Barnea et al. 1991). Conversely, the same bird

species may have varying effects on different plant species (Barnea et al. 1990).

Buckley et al. (2006) highlight the shortage of practical information regarding how invasive plant population dynamics and spread are affected by frugivores and vice versa. By integrating knowledge on how different generalist frugivores influence the germination of seeds of invasive plant species, we can better understand the role that frugivores play in facilitating or hindering the invasion process. If important dispersers are identified, knowledge of these species can translate into more effective modelling of seed dispersal directions and distances (Bartuszevige and Gorchov 2006; Buckley et al. 2006). By using case studies such as this, more useful generalizations based on plant and frugivore traits can be made and incorporated into management strategies (Buckley et al. 2006).

This study considered seed retention time, seed germination percentages and the time taken for germination to occur. The latter was considered because seeds which fail to germinate rapidly may succumb to pathogens or predation (Howe 1986) or be out-competed by earlier established seedlings (Ross and Harper 1972; Abul-Fatih and Bazzaz 1979). The aims of this study were to (1) determine what effect three generalist frugivores have on the germination of seeds of four invasive alien species, and (2) to establish the physical effects of pulp removal or seed coat abrasion. Due to loose mutualisms between invasive alien plants and resident frugivores (Richardson et al. 2000b), further highlighted by the positive relationship between frugivore diversity and plant invasiveness (Gosper and Vivian-Smith 2009), we hypothesised that germination rates would not be affected by different generalist frugivores. Furthermore, specialized gut treatment should not be necessary for high germination rates as invasive alien plants would then be disperser limited.

Methods

Plant species

In this study four invasive alien plant species namely: *Solanum mauritianum* Scopoli (Solanaceae), *Cinnamomum camphora* (L.) J. Presl. (Lauraceae), *Lantana camara* L. *sensu lato* (Verbenaceae), and *Psidium*

guajava L. (Myrtaceae) were considered. In South Africa, *S. mauritianum*, *C. camphora*, and *L. camara* are declared category 1 weeds (according to the regulations under the Conservation of Agricultural Resources Act), which means they are prohibited everywhere and must be controlled (Henderson 2001). *Psidium guajava* is a category 2 weed, and is allowed only in demarcated areas outside of which it must also be controlled (Henderson 2001). All four plant species are well established and of great concern, particularly in KwaZulu-Natal (Henderson 2001).

Solanum mauritianum produces clusters of yellow fruit, c. 10 mm in diameter (Henderson 2001), each containing up to 193 seeds (Witkowski and Garner 2008). Smaller plants (1.5–1.8 m) produce 40–70 berries per inflorescence, and larger plants (3.3 m) can produce 100,000–200,000 seeds annually, with 79% seed viability (Witkowski and Garner 2008). Birds often prefer *S. mauritianum* fruit over those of native species (Olckers and Zimmermann 1991; Olckers 1999) and disperse them over great distances (Oatley 1984; Olckers 1999; Witkowski and Garner 2008).

Psidium guajava produces soft, yellow fruit with pink flesh, 25–100 mm in diameter (Henderson 2001). Each fruit contains up to 570 seeds (Adsule and Kadam 1995) that are 3–5 mm in diameter (Cull and Lindsay 1995). It is an adaptable and hardy plant, growing successfully under many different environmental conditions (Cull and Lindsay 1995), and is grown commercially in both tropical and subtropical regions (Mittra and Bose 1985; Ray 2002). In many cases it has spread as a weed, mainly through bird dispersal (Samson 1986). In a Kenyan study, 40 frugivorous bird species were observed in *P. guajava* trees of which Speckled Mousebirds and Common Bulbuls were the most abundant (Berens et al. 2008). Visitation rates to *P. guajava* trees matched those of indigenous fruiting species (Berens et al. 2008).

Cinnamomum camphora produces blue-black berries, c. 9 mm in diameter (Stansbury and Vivian-Smith 2003), each containing a single seed, 7.5 mm in diameter (Panetta 2001), inside a tough, waxy exocarp. Mature trees can produce over 100,000 fruit per season (Firth 1981). Avian frugivores may regurgitate (Li 2004) or excrete seeds shortly after consumption (Firth 1981).

Lantana camara fruit consist of up to 20 purple-black drupes (Parsons and Cuthbertson 2001), each

c. 5–7 mm in diameter (Swarbrick et al. 1995; Sharma et al. 2005). These drupes have a thin, waxy exocarp and pulpy mesocarp surrounding a single, oval seed, 2–4 mm long (Parsons and Cuthbertson 2001), containing 1–2 embryos (Sharma et al. 2005). In South Africa *L. camara* fruits year round (Graaff 1987), setting an average of 856 seeds/plant/year (Spies 1983–1984). Birds are the main dispersers (Vivian-Smith et al. 2006), facilitating long-distance dispersal and the invasion of new areas (Cronk and Fuller 1995). Seed germination rates are low (4–45%), but are counterbalanced by low seedling mortality (Sahu and Panda 1998).

Capture and maintenance of birds

This study was conducted at the University of KwaZulu-Natal (UKZN), Pietermaritzburg. Nine Red-winged Starlings (*Onychognathus morio*, Sturnidae), ten Speckled Mousebirds (*Colius striatus*, Coliidae), and seven Dark-capped Bulbuls (*Pycnonotus tricolor*, Pycnonotidae) were captured at various locations near UKZN between July 2007 and February 2008. These generalist native frugivorous species were observed feeding on the invasive alien species fruit used in this study (L. Jordaan, unpublished observations). They were fed a mixed fruit maintenance diet, supplemented with AviPlus Softbill/Mynah pellets and crumble (Avi-products, Durban, South Africa). Three mealworm larvae (*Tenebrio molitor*) were fed to each individual Dark-capped Bulbul and Red-winged Starling every third day as these species naturally supplement their diets with insects (Hockey et al. 2005). Water was provided ad libitum. Prior to sampling days, invasive alien fruit were incorporated into the birds' maintenance diet. Birds were weighed daily on maintenance days and twice daily (before and after trials) on sample days.

Feeding trials

Trials were conducted when fruit was available. *Solanum mauritianum* trials were run during March, *C. camphora* and *P. guajava* were fed to the birds during April (a minimum of 3 days was left between fruit species), and *L. camara* was offered in June. During feeding trials, birds were housed individually in cages and acclimated for a minimum of 3 days in a constant environment room set at 25°C, on a 12:12

dark light cycle. On sample days birds were fed a specific invasive alien fruit within 48 h of picking from wild growing plants near UKZN. Fruit were presented whole and weighed before and after each trial to calculate the amount of fruit eaten. Fishing line was used to join *S. mauritianum* fruit together to imitate fruit bundles and facilitate feeding as birds were unable to gulp loose whole fruit. Each fruit species was offered to an individual bird once for a 12 h period. To control for evaporative water loss from uneaten fruit, control fruit were placed in the room and weighed prior to and at the end of feeding trials. Excreta were collected at the end of the trial. Birds were observed at the start of each trial to record seed retention times. Seed retention time was measured as the time from fruit and seed ingestion to the first appearance of seeds in the excreta. In the case of *P. guajava*, birds were allowed to feed on whole fruit until the seeds were exposed. This was considered the time of ingestion. Five Speckled Mousebirds did not eat *L. camara* fruit and two did not feed on *C. camphora* fruit.

Germination trials

Seeds were extracted from the respective individual birds' excreta, for each diet, the morning after trial termination and planted in separate trays (265 × 180 × 75 mm) containing soil (Table 1). The soil used for propagation is the standard used for most plant species at the University Botanical Gardens, and contained no additives. While plant species may vary in terms of soil type for optimal growth and germination, we used the same soil type for all plant species to allow for comparison of germination rates and survivorship. Seeds were covered with a soil layer approximately 0.5 cm deep. Trays were housed in a greenhouse and watered daily. De-pulped seeds and whole fruit controls of each invasive species were planted in the same way as ingested seeds (Table 1). After daily germination counts, seedlings were removed. Seeds were considered germinated when seedlings first broke the soil surface and were visible. Trays were observed for 9 months, after which they were terminated if there was no germination in any trays for a 2-week period. No germination occurred after 8 months for *P. guajava* and 7 months for *L. camara*. For analysis of cumulative germination the duration of trials was kept constant, at 213 days, for all

Table 1 Number of seeds planted in soil trays for each frugivore species on a pure diet of fruit of each invasive alien plant species

Plant species	Bird species	Number of seeds per tray	Number of trays	Number of seeds from de-pulped fruits in controls	Number of whole fruits in controls
<i>Solanum mauritianum</i>	Dark-capped Bulbul	100	7	200	10
	Speckled Mousebird	200	10	200	10
	Red-winged Starling	200	6	200	10
		70	1		
		100	1		
<i>Psidium guajava</i>	Dark-capped Bulbul	40	7	40	3
	Speckled Mousebird	40	10	40	3
	Red-winged Starling	40	9	40	3
<i>Cinnamomum camphora</i>	Dark-capped Bulbul	8	4	8	8
		4	3		
	Speckled Mousebird	15 ^a	7	15	15
		10 ^a	1		
	Red-winged Starling	30 ^b	9	30	30
<i>Lantana camara</i>	Dark-capped Bulbul	40	6	40	40
	Speckled Mousebird	30	5	30	30
	Red-winged Starling	50	9	50	50

Number of seeds varied per plant species because of seed type and amount ingested per bird species

^a Speckled Mousebirds did not ingest *C. camphora* seeds but removed the pulp from around the seed

^b Red-winged Starlings regurgitated *C. camphora* seeds

plant species except, *C. camphora*, which was terminated after 96 days due to rodent predation.

Analyses

The average number of seeds per fruit of *S. mauritianum* and *P. guajava* was used to calculate germination percentages for whole-fruit controls. The mean cumulative germination percentage was calculated for each individual and control tray, and arcsin transformed. The effect of different frugivorous species on each plant species' cumulative germination percentage was tested using one-way analysis of variance (ANOVA) and further investigated with *post-hoc* Tukey tests where significant differences were evident. This was also done to compare germination success of seeds ingested by specific frugivorous species to seeds from de-pulped fruits and whole-fruit controls. The number of days from the time of sowing until first seedling emergence was analyzed using Kruskal–Wallis tests as the data could not be normalized. Seed retention times for each bird species were compared for a specific plant species

using Kruskal–Wallis tests. All analyses were conducted using STATISTICA (Statsoft, Tulsa, version 7, USA).

Results

Seed retention time

Bird species varied significantly in their retention of seeds of *S. mauritianum*, *P. guajava*, and *L. camara* (Table 2). Retention times for seeds consumed by Dark-capped Bulbuls (4–10 min) were significantly shorter than for Speckled Mousebirds ($P = 0.038$) and Red-winged Starlings ($P < 0.050$, Fig. 1). Red-winged Starlings regurgitated *C. camphora* seeds [as is done by most native frugivores of this species (Li 2004)], Dark-capped Bulbuls mostly excreted them, while Speckled Mousebirds did not ingest them at all. *Cinnamomum camphora* had the largest seeds used during experiments and seeds were generally retained longer (retention time of 23–55 min for Dark-capped Bulbuls and 10–42 min for Red-winged Starlings)

than any of the smaller seeded plant species. However, retention times for *C. camphora* seeds did not vary significantly between Dark-capped Bulbuls and Red-winged Starlings (Table 2; Fig. 1). Regurgitated seeds were very clean with no pulp fragments, while defecated and de-pulped seeds still had some pulp attached to the seed (L. Jordaan, unpublished observations).

Dark-capped Bulbuls had significantly shorter seed retention times (6–10 min) when fed *P. guajava* fruits than Speckled Mousebirds (12–28 min, $P = 0.047$) and Red-winged Starlings (19–69 min, $P < 0.050$). Red-winged Starlings also retained *L. camara* seeds significantly longer (18–31 min) than Dark-capped Bulbuls (6–32 min, $P = 0.040$).

Table 2 Significance of difference between three avian frugivore species (Dark-capped Bulbul, Speckled Mousebird and Red-winged Starling) in seed retention time (Kruskal–Wallis),

mean time to first seedling emergence (Kruskal–Wallis), and germination percentage (ANOVA) of ingested seeds of four invasive alien plant species

Plant species	Mean seed diameter (mm) n = 10	Seed retention time			Germination percentage			Mean time to first seedling emergence					
		H ₂	n	P	F ₂	n	P	H ₂	n	P			
<i>Solanum mauritianum</i>	1.5	19.455	26	< 0.050	S	2.892	25	0.077	NS	8.879	25	0.012	S
<i>Psidium guajava</i>	2.8	20.267	26	< 0.050	S	0.128	26	0.881	NS	0.272	26	0.873	NS
<i>Cinnamomum camphora</i>	6.5	2.470	12	0.116	NS	13.17	24	< 0.050	S	12.880	24	0.002	S
<i>Lantana camara</i>	2.7	7.236	20	0.027	S	1.428	20	0.267	NS	2.629	20	0.269	NS

NS not significant, S significant at $P \leq 0.05$

Fig. 1 Seed retention time for three avian frugivores feeding on fruits of **a** *S. mauritianum*, **b** *P. guajava*, **c** *C. camphora* and **d** *L. camara*, where boxes are 25 and 75% quartiles, the lines within the boxes indicate the medians, and bars show 10 and 90% values

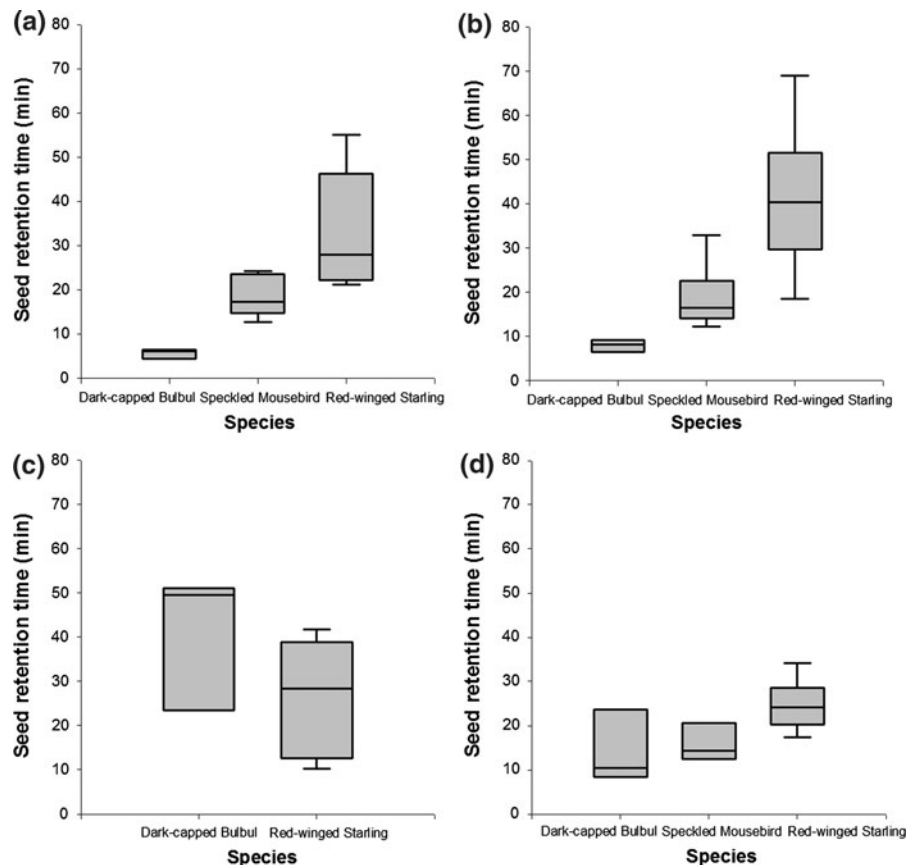
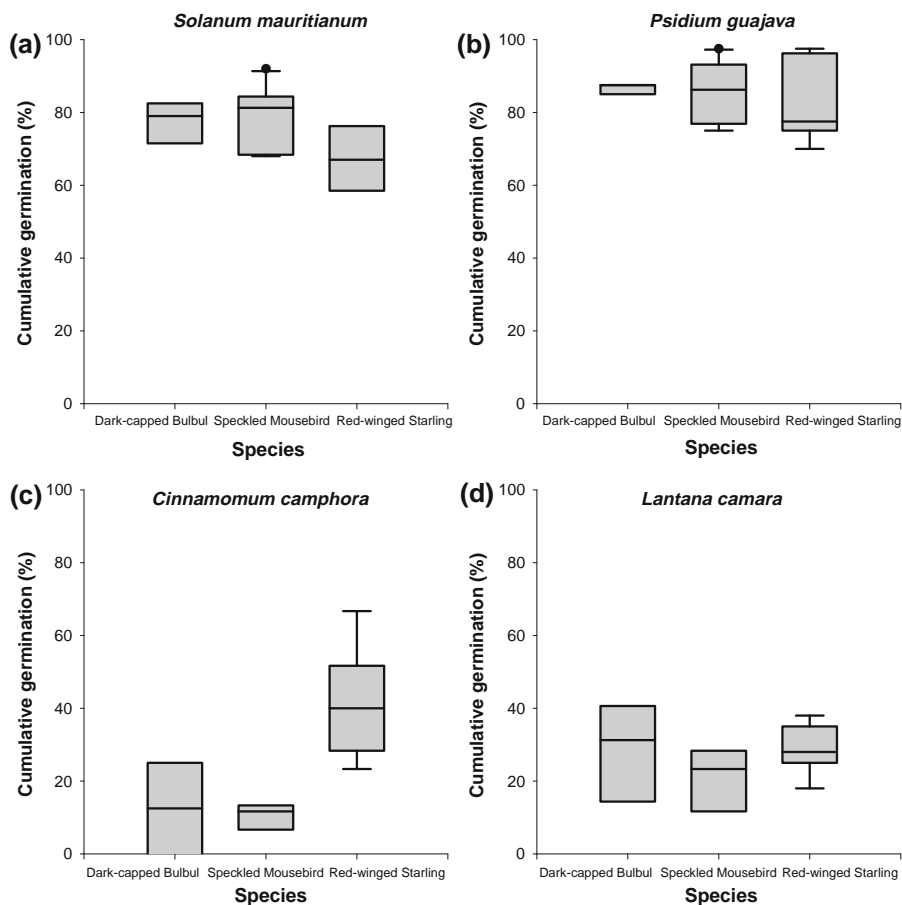


Fig. 2 Cumulative germination percentage of seeds ingested by three avian frugivores (or de-pulped without ingestion by Speckled Mousebirds in the case of *C. camphora*) for **a** *S. mauritianum* after 213 days, **b** *P. guajava* after 213 days, **c** *C. camphora* after 96 days and **d** *L. camara* after 213 days, where boxes are 25 and 75% quartiles, the lines within the boxes indicate the medians, bars show 10 and 90% values, and dots highlight outliers



Germination percentage

Frugivores varied significantly in their effect on germination percentage only in the case of the large-seeded species *C. camphora* (Table 2). Seeds ingested by Red-winged Starlings were more likely to germinate than those ingested both by Speckled Mousebirds (*post-hoc* Tukey, $P < 0.050$) and Dark-capped Bulbuls (*post-hoc* Tukey, $P < 0.050$). *Solanum mauritianum* and *P. guajava* had high cumulative germination percentages for all frugivores, while *C. camphora* and *L. camara* germinations were relatively low (Fig. 2). Germination percentages of seeds from de-pulped fruits were similar to, and sometimes higher than, ingested seeds for all fruit species (Fig. 3). However, none of these differences were significant (Table 3).

All germination percentages were significantly higher than they were for whole fruit controls for the larger, multi-seeded fruit species, *S. mauritianum* and *P. guajava*, (Table 3). However, it must be noted that

despite relatively low proportions of whole fruit seeds germinating, once fruit decomposed an average of 644 ± 144.4 (mean \pm S.E.) *S. mauritianum* seeds and 75 ± 36.1 *P. guajava* seeds germinated per tray. Seeds ingested by Red-winged Starlings and Speckled Mousebirds had significantly higher germination percentages than did seeds from whole fruits of *C. camphora* (Table 3). *Lantana camara* seeds ingested by Red-winged Starlings also germinated significantly sooner than did seeds from whole fruit (Table 3).

Mean time to first seedling emergence

Shortly after planting, *S. mauritianum* and *P. guajava* seeds had an initial phase of high germination after which very little germination occurred (Fig. 3). *Lantana camara* and *C. camphora* seeds had germination events occurring throughout the trial period (Fig. 3). First seedling emergence of *S. mauritianum* and *C. camphora* varied significantly between

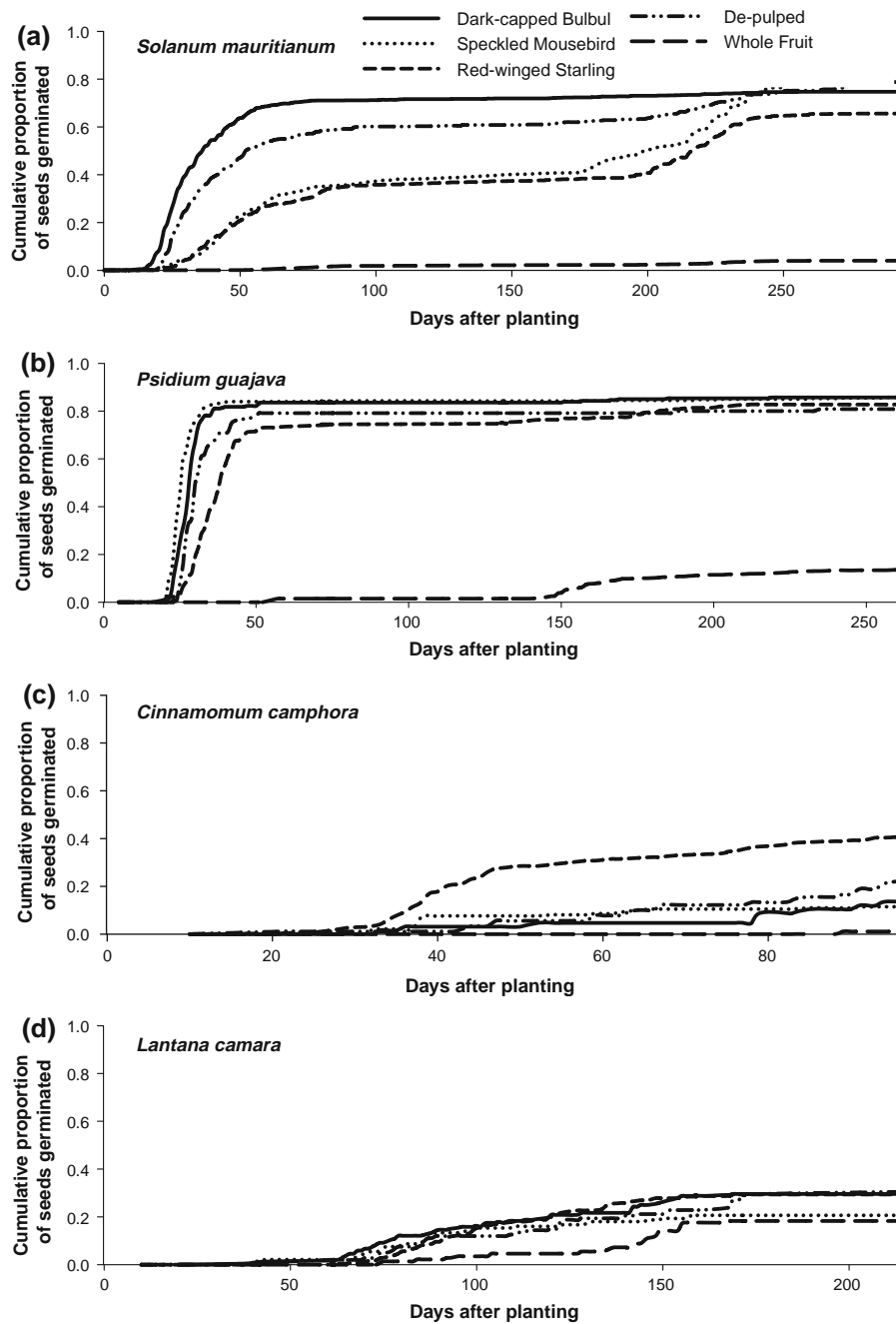


Fig. 3 Mean cumulative germination for the duration of the study of seeds ingested by three avian frugivores (or de-pulped without ingestion by Speckled Mousebird in the case of *C. camphora*) for **a** *S. mauritianum*, **b** *P. guajava*, **c** *C. camphora*, **d** *L. camara*

frugivorous species, but not for *L. camara* and *P. guajava* (Table 2).

Solanum mauritianum seeds ingested by Dark-capped Bulbuls emerged sooner than those ingested by Red-winged Starlings (Fig. 4). Ingested *S. mauritianum*

seeds started emerging after approximately 10 days (Fig. 4), but this was not significantly earlier than de-pulped or whole fruit controls (Table 4). *Cinnamomum camphora* seeds ingested by Red-winged Starlings began germinating after approximately 20 days

Table 3 Significance of difference between percentage germination of ingested seeds and that of seeds from manually de-pulped fruits and whole fruits, for three avian frugivore species fed fruits of four invasive alien plant species

Plant species	Bird Species	n	Germination percentage of seeds from					
			Manually de-pulped fruit compared to ingested seeds			Whole fruit compared to ingested seeds		
			F ₁	P		F ₁	P	
<i>Solanum mauritianum</i>	Dark-capped Bulbul	10	0.284	0.608	NS	14.9	< 0.050	S
	Speckled Mousebird	13	0.004	0.949	NS	27.43	< 0.050	S
	Red-winged Starling	11	2.273	0.166	NS	6.04	0.036	S
<i>Psidium guajava</i>	Dark-capped Bulbul	10	1.901	0.205	NS	157.9	< 0.050	S
	Speckled Mousebird	13	1.008	0.337	NS	66.17	< 0.050	S
	Red-winged Starling	12	0.237	0.637	NS	37.81	< 0.050	S
<i>Cinnamomum camphora</i>	Dark-capped Bulbul	10	0.274	0.615	NS	2.082	0.187	NS
	Speckled Mousebird	11	1.365	0.273	NS	7.312	0.024	S
	Red-winged Starling	12	4.035	0.072	NS	18.28	0.002	S
<i>Lantana camara</i>	Dark-capped Bulbul	9	0.005	0.945	NS	1.615	0.244	NS
	Speckled Mousebird	8	1.985	0.208	NS	0.195	0.675	NS
	Red-winged Starling	12	0.053	0.822	NS	6.976	0.025	S

n number trays used for each plant species

NS not significant, S significant at $P \leq 0.05$

(Fig. 3), which was significantly earlier than seeds ingested by Dark-capped Bulbuls ($P = 0.005$, Fig. 4). Ingested *C. camphora* seeds did not germinate significantly earlier than seed from de-pulped fruit or whole-fruit controls (Fig. 3; Table 4).

Lantana camara seedlings emerged later than those of the other invasive alien species (Fig. 4). Dark-capped Bulbul- and Red-winged Starling-ingested seeds emerged significantly earlier than whole-fruit seeds (Fig. 3; Table 4). *Psidium guajava* seeds ingested by Speckled Mousebirds germinated earlier than seeds from de-pulped fruit (Table 4), while seeds ingested by Dark-capped Bulbuls and Red-winged Starlings emerged at approximately the same time (Fig. 3). All *P. guajava* seeds ingested by frugivores germinated after about 20 days (Fig. 4), which was significantly sooner than whole-fruit seeds (Table 4), which only started emerging after approximately 117 days.

Discussion

As was found in past studies (Barnea et al. 1991; Panetta and McKee 1997; Meyer and Witmer 1998; Voigt et al. 2011), the mechanical removal of fruit

pulp had a similar effect to that of frugivore gut passage for all species used in this study. Consistent with previous research, pulp removal increased seed germination percentages for *L. camara* (Day et al. 2003) and *C. camphora* (Panetta 2001), which have tough, waxy exocarps and do not decompose easily. Larger fruited species (i.e. *P. guajava* and *S. mauritianum*) also benefited from earlier germination due to pulp removal, as fruits of these species took longer to decompose. Pulp removal by birds increases germination (Panetta 2001) as the pericarp may contain inhibitory substances (Firth 1981). Furthermore, pulp may be used by some seed predators to detect fruits (Moles and Drake 1999) and may also result in higher pathogen infection rates (Witmer and Cheke 1991; Moore 2001). Ingestion is essential for species in which seeds lose viability before the pulp has decomposed (Panetta and McKee 1997; Yagihashi et al. 1998) and the seeds of some such fruits only germinate once this happens (Yagihashi et al. 1998, 1999).

The rate of pulp decomposition and removal has been shown to influence the rate of germination (Yagihashi et al. 1999). This was evident for *P. guajava* and *L. camara*, as seeds from whole fruit germinated significantly later than other seeds. Pulp

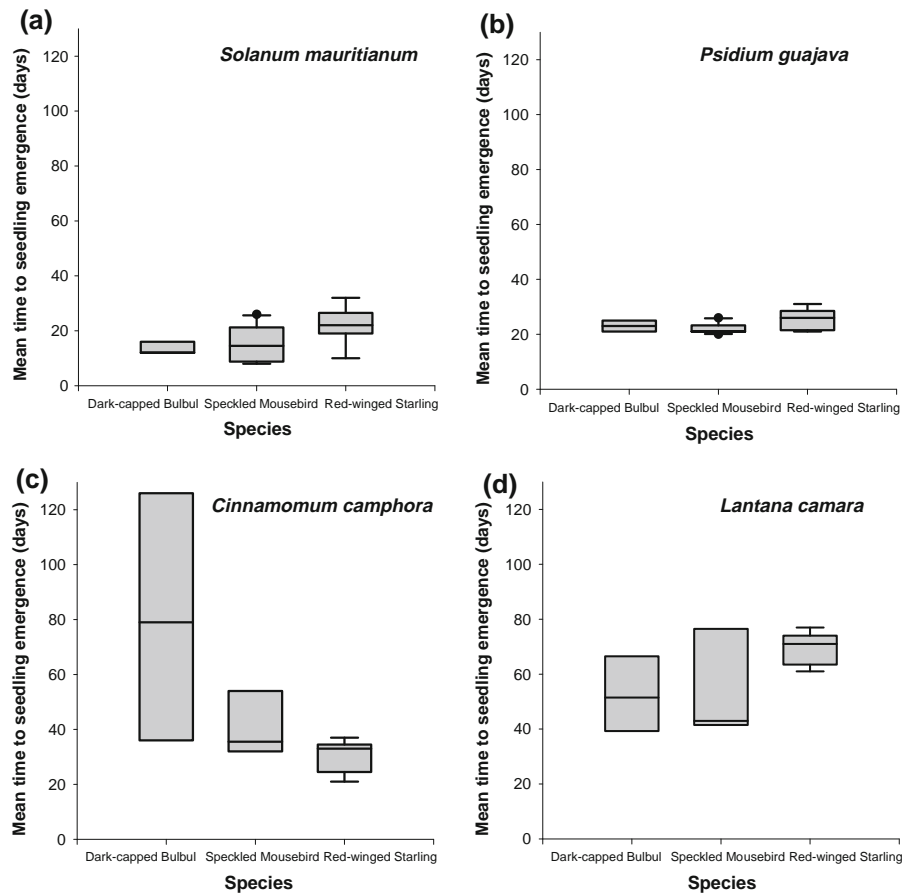


Fig. 4 Mean time to first seedling emergence of seeds ingested by three avian frugivores (or de-pulped without ingestion by Speckled Mousebird in the case of *C. camphora*) for **a** *S. mauritianum*, **b** *P. guajava*, **c** *C. camphora* and

d *L. camara*, where boxes are 25 and 75% quartiles, the lines within the boxes indicate the medians, bars show 10 and 90% values, and dots highlight outliers

decomposition may delay germination by up to a year. Low whole fruit germination of *C. camphora* is consistent with results of an earlier study (Panetta 2001), and may be attributed to seed dormancy. Mature *C. camphora* seeds may remain dormant for 4–20 weeks (Firth 1981), but are short-lived, with only 1% viable after 12 months (Panetta 2001). The combination of low seed viability and production of numerous animal-dispersed seeds is characteristic of large, invasive, ornamental species in mesic areas (Panetta and McKee 1997). Such species may rely on re-colonization of cleared areas, rather than seed banks (Panetta 2001).

There is contradictory evidence about the effect of long versus short seed retention times on seed germination. Some studies show increased seed germination

success associated with longer seed retention times (Barnea et al. 1991), while others show a decrease (Murray et al. 1994; Charalambidou et al. 2003) or no effect (Barnea et al. 1990, 1991). In such cases frugivores are primarily seed dispersers. Seed coat abrasion did not play a role in germination success of seeds of *S. mauritianum*, *P. guajava*, or *L. camara*. Despite seed retention times varying between frugivores, germination percentages for each plant species were similar for ingested seeds and seeds of de-pulped fruits.

While seed retention time did not vary significantly among various bird species on the *C. camphora* diet, considerably more regurgitated Red-winged Starling seeds germinated than those ingested by other frugivores. However, ingested Red-winged

Table 4 Significance of difference between time to first seedling emergence of ingested seeds and that of seeds from manually de-pulped fruit and whole fruit, for three avian frugivore species fed fruit of four invasive alien plant species

Plant species	Bird species	n	Time to first seedling emergence of seeds from					
			Manually de-pulped fruit compared to ingested seeds			Whole fruit compared to ingested seeds		
			H ₁	P		H ₁	P	
<i>Solanum mauritianum</i>	Dark-capped Bulbul	10	2.642	0.104	NS	2.004	0.157	NS
	Speckled Mousebird	13	0.59	0.443	NS	2.881	0.09	NS
	Red-winged Starling	12	1.239	0.266	NS	1.038	0.308	NS
<i>Cinnamomum camphora</i>	Dark-capped Bulbul	10	0.117	0.732	NS	2.208	0.137	NS
	Speckled Mousebird	11	0.17	0.68	NS	0.682	0.409	NS
	Red-winged Starling	12	0.861	0.354	NS	0.697	0.404	NS
<i>Psidium guajava</i>	Dark-capped Bulbul	10	1.929	0.165	NS	5.762	0.016	S
	Speckled Mousebird	13	4.01	0.045	S	6.802	0.009	S
	Red-winged Starling	12	0.035	0.852	NS	6.342	0.012	S
<i>Lantana camara</i>	Dark-capped Bulbul	9	0.42	0.517	NS	4.857	0.028	S
	Speckled Mousebird	8	0.202	0.653	NS	2.721	0.1	NS
	Red-winged Starling	12	0.7	0.403	NS	4.618	0.032	S

n number germination trays used

NS not significant, S significant at $P \leq 0.05$

Starling seeds and de-pulped seeds had similar germination rates. Furthermore, these results only reflect 96 days of data and more germination occurred after that time. Thus frugivores may also have had a similar effect on germination (albeit it more delayed for Dark-capped Bulbuls and Speckled Mousebirds). The low germination of *L. camara* seeds is similar to trends in other studies (Spies 1983–1984; Graaff 1987; Sahu and Panda 1998) and may be attributed to dormancy, low viability (Graaff 1987), or possibly meiotic instability (Spies 1983–1984). Germination deficits may be offset by low seedling mortality (Sahu and Panda 1998), and/or prolific sexual and vegetative reproduction (Graaff 1987; Swarbrick et al. 1995).

There are many factors to consider simultaneously during the reproductive and establishment phases of both invasive and native species to identify which of these may influence the invasive potential of a plant (Ferrerias and Galetto 2010). The successful invasion of *S. mauritianum* for example has been accredited to a combination of high fruit set and great dispersal distance from the parent plant by frugivorous birds, which preferentially feed on these fruits (Olckers 1999). While rapid and profuse germination is a trait

of some invasive species in this study (*S. mauritianum* and *P. guajava*) and others (Van Kleunen and Johnson 2007), this is not the case for *C. camphora* and *L. camara*.

When seed coat abrasion is not essential for germination, as is the case for all species of this study, plants maintain the ability to invade an area in the absence of a suitable disperser. The severity of such invasions has been highlighted for *S. mauritianum* and the problems associated with its control. Once parent plants are cleared, persistent seed banks germinate (Witkowski and Garner 2008), and as highlighted by the results of this study, this will happen regardless of frugivore ingestion. Furthermore, *S. mauritianum* is self-compatible and is not pollinator limited (Rambuda and Johnson 2004). The successful germination of a single plant dispersed into a new area may mark the start of a new invasive front. This highlights the importance of targeting such satellite populations resulting from avian dispersal (Buchanan 1989), especially before they reach sexual maturity. In undisturbed habitats only competition from indigenous plants may limit further spread of bird-dispersed invasive species (Loyn and French 1991).

Laboratory-based studies provide valuable insight into the potential effects that different frugivores may have on alien plant germination. Coupled with behavioural aspects and field based observations [such as the correlation between the number of available dispersers and a plant's invasiveness (Stansbury and Vivian-Smith 2003)], such information will aid in employing more effective control strategies. For example, measures could be taken to manipulate perches and edges (known sites of weed seed dispersal) to serve as seed sinks (Buckley et al. 2006). By incorporating information of frugivory, better risk screening processes and prioritization can be developed for potentially invasive plants as well as highlight areas for monitoring and controlling established invasions (Buckley et al. 2006; Gosper and Vivian-Smith 2009).

For the plant species in this study, it is evident that frugivores are not only important in their role as seed dispersers, but that they also greatly enhance the speed and overall proportion of seed germination through pulp removal. Results support the hypothesis that fleshy-fruited invasive alien species rely on loose mutualisms with frugivorous dispersers, in which pulp removal is sufficient for high germination success and specialized gut treatment is not required. This study highlights the importance of generalist frugivores in their role as seed dispersers and germination enhancers of invasive alien plants, especially in terms of establishing new satellite populations.

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Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) as a potential dispersal agent for fleshy-fruited invasive alien plants: effects of handling behaviour on seed germination

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Abstract The spread of invasive alien plants into natural habitats is of growing global concern. Several studies have investigated the role that avian frugivores play in the dispersal of these seeds and their effects on germination success. Fruit bats have however received little attention as important dispersal agents of invasive alien plants, despite their recognized role as long distance dispersal agents of various native flora. We investigated whether Wahlberg's epauletted fruit bats, *Epomophorus wahlbergi*, would positively influence the germination of seeds of invasive alien plants. These fruit bats were fed fruits of four invasive alien plant species—*Psidium guajava*, *Melia azedarach*, *Eriobotrya japonica*, and *Morus alba*. *Epomophorus wahlbergi* were able to process more fruit per gram body mass than birds have been observed to do. Spat and de-pulped control seeds had similar germination success and germinated at approximately the same time for most species. While seeds retained in whole fruit had significantly less germination success than

spat seeds for all species, except *M. azedarach*, they mostly germinated at approximately the same time. *Epomophorus wahlbergi* can swallow small seeds (< 2 mm), while seeds larger than this are generally spat out. Large fruit are usually carried away to feeding roosts where seeds are dropped, thereby dispersing seeds and fruits which are too large for some bird species to ingest. *Epomophorus wahlbergi* should not be underestimated as dispersers of these invasive alien plants as they consume proportionally large amounts (0.62 ± 0.09 to 0.99 ± 0.11 g.g⁻¹ body mass) of fruit, except for *M. azedarach*, and positively affect their seed germination rates.

Keywords Bat dispersal · Emergence time · Frugivory · Germination success · Invasive traits · Spats

Introduction

Animals have long been recognized as important dispersers of seeds (Ridley 1930; Van der Pijl 1982). This is true for the successful spread and persistence of many invasive alien plants which is largely attributed to mutualisms formed with local frugivores (Richardson et al. 2000). Indeed, where frugivore communities are more diverse, plant invasiveness increases (Gosper and Vivian-Smith 2009). Most studies have

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investigated the relationship between local avian frugivores and invasive alien plants (Bartuszevige and Gorchoy 2006; Buckley et al. 2006; Gosper and Vivian-Smith 2006; Jordaan et al. 2011), while the role of fruit bats has received less attention (Izhaki et al. 1995; Corlett 2005; Voigt et al. 2011), particularly in terms of their effect on the germination success of these plants (Izhaki et al. 1995). In South Africa fruit bats are seldom recognized as dispersers of invasive alien plants (AGIS 2007; Henderson 2007), despite having been observed to feed on them (Skinner and Chimimba 2005; Voigt et al. 2011; pers. obs.).

Invasive alien plants can out-compete indigenous species by attracting dispersal agents (Bass 1990; Lafleur et al. 2007) with fruits which have been shown to be preferred over those of indigenous species (Fraser 1990; Lafleur et al. 2007). Many invasive alien species form dense homogenous stands (Henderson 2001), which present a large, easily accessible food source to frugivores. Consequently these plants may benefit from greater fruit removal rates as this increases with decreasing distance to a neighbouring fruiting plant (Bach and Kelly 2004). Furthermore, numerous invasive alien fruit share characteristics with indigenous species (Gosper and Vivian-Smith 2010), fruit year round (Henderson 2001; Corlett 2005), and in some cases present fruits with greater nutritive value (Kueffer et al. 2009; Gosper and Vivian-Smith 2010). Fruit bats are endotherms with high energetic demands for flight and so must feed optimally (Sánchez 2006). It has been shown that some fruit bat species select fruit based on their sugar content (Nelson et al. 2005) and are able to recognise the quality of a food patch, feeding longer in areas rich in food (Sánchez 2006). Thus, dense stands of invasive alien fruit provide a reliable and familiar resource to fruit bats. Vertebrate dispersal has been recognised as a key component in the successful invasion of a plant species in semi-natural habitats (Lloret et al. 2005). Where natural fruiting species are declining (particularly in urban areas), these exotic species are greatly utilized and provide valuable food sources and roosting sites to both birds and fruit bats (Corlett 2005).

The effect of fruit size on avian frugivore feeding behaviour has received much attention (Debussche and Isenmann 1989; Green 1993; Stansbury and Vivian-Smith 2003), as bird gape size limits the size of fruit and seeds which can be consumed (Wheelwright 1985). For example, birds with small gape sizes

are limited to small fruit or large, soft fruits (Corlett 2005). However, this is not true for fruit bats. *Epomophorus wahlbergi* often pick fruit and fly to a feeding roost where they chew and squeeze the fruit between their tongues and palette ridges to extract the juice (Monadjem et al. 2010). Mouthfuls of seeds, exocarp and pulp fibre are then spat out (termed spats). Small seeds may be swallowed during this process (Shilton et al. 1999; Tang et al. 2007). Fruit which are too large to be carried away will often be eaten in the parent tree (Fenton et al. 1985; Corlett 2005), however large mouthfuls may still be taken and processed at a feeding roost. Birds and bats overlap in their roles as seed dispersers, but differ in that birds play a greater role in dispersing obligatory zoochorous seeds, too large for bats to ingest, while bats disperse partially-zoochorous larger seeds (Whittaker and Jones 1994).

In urban Hong Kong fruit bats are the only dispersers of large pale fruits, carrying large seeds (18 mm diameter) up to 40 m away from parent plants (Corlett 2005). Smaller seeds are ingested (Shilton et al. 1999; Tang et al. 2007; Tsoar et al. 2011) and dispersed further (Corlett 2005). Many fruit bats rarely ingest large seeds (Whittaker and Jones 1994; Monadjem et al. 2010) and thus germination success cannot be enhanced by the chemical effects of the digestive tract which abrade the seed coat (Evenari 1949; Agami and Waisel 1988; Barnea et al. 1990, 1991). Such seeds will only benefit from pulp removal, which may free seeds from inhibitory compounds in the pulp (Evenari 1949; Barnea et al. 1991). An added benefit of pulp removal is the earlier onset of germination (Izhaki et al. 1995; see review Traveset 1998; Jordaan et al. 2011). Seeds which germinate soon after dispersal are less likely to be outcompeted by other seedlings (Ross and Harper 1972; Abul-Fatih and Bazzaz 1979) or be lost to pathogens or predation (Howe 1986).

Old World fruit bats (Megachiroptera, Pteropodidae) have been recognised as key components in maintaining forest ecosystems (Fleming and Heithaus 1981; Whittaker and Jones 1994), with nearly 300 plant species reliant on them for pollination and seed dispersal (Fujita and Tuttle 1991; Shilton et al. 1999). Bats disperse seeds to isolated habitats (Cox et al. 1991) as they can travel great distances (Webb and Tidemann 1996; Richter and Cumming 2006) through fast and direct flight patterns (Tsoar et al. 2011), crossing open expanses to fragmented landscapes

which many bird species will not do (Muscarella and Fleming 2007). Furthermore, fruit bats tend to forage far from roost trees and spend long periods resting in non-fruiting trees, thereby establishing new satellite seed deposition sites (Tsoar et al. 2011).

The negative impacts of invasive alien plants to natural ecosystems and the economy are well documented (van Wilgen et al. 2001, 2008; Richardson and van Wilgen 2004). To develop effective control strategies and risk screening processes, management must consider the multifaceted nature of plant invasions. The importance of frugivores as dispersers of invasive alien plants forms part of this. A recent study highlighted the importance of avian frugivores as dispersers of invasive alien plants, and showed that frugivore ingestion was not a pre-requisite for germination success (Jordaan et al. 2011). Therefore, it is important that we gain a better understanding of the role that fruit bats play in the dispersal of invasive alien plants so as to develop more comprehensive, integrated control strategies. To do this we investigated the effect of Wahlberg's epauletted fruit bats, *Epomophorus wahlbergi* (Pteropodidae), on the germination success of seeds from four fleshy-fruited invasive alien plant species in South Africa. Based on previous results by Jordaan et al. (2011), that pulp removal and not seed coat abrasion played a greater role in the germination success of invasive alien plants, we hypothesised that germination rates would be similar for spat and de-pulped seeds, but not whole fruit seeds. In addition de-pulped and spat seeds would further benefit from an earlier onset of germination, when compared with whole fruit seeds. We predicted that fruit processing by *E. wahlbergi* would facilitate rapid and profuse germination of invasive alien seeds, especially those with large fruits and seeds which birds are unable to ingest.

Methods

Study animal

Epomophorus wahlbergi (Sundevall, 1846) is a relatively large (100 g) and common Old World fruit bat (Monadjem et al. 2010), which typically roosts in dense, leafy trees (Fenton et al. 1985). It has a broad distribution along the east coast of southern Africa and occurs in forest and forest-edge habitats, but may also

be found in peri-urban areas with many trees (Monadjem et al. 2010). They feed on a wide variety of fruit (Monadjem et al. 2010) and cover several kilometres in search of these (Fenton et al. 1985).

This study was conducted at the Animal House of the University of KwaZulu-Natal (UKZN), South Africa. Bats were captured using mist-nets near UKZN (29°38'956"S; 30°25'199"E) from September to October 2009, under permit OP 3879/2011 from Ezemvelo KZN Wildlife. They were sexed and housed in male and female groups in outside flight cages (400 × 220 × 260 cm). They were fed a maintenance diet each evening of fresh diced, commercial mixed fruit and a 20% sugar solution. Water was provided ad libitum.

Plant Species

Fruits of *Psidium guajava* L. (Myrtaceae) and *Melia azedarach* L. (Meliaceae) were picked in May, while those of *Eriobotrya japonica* (Thunb.) Lindl. (Rosaceae), and *Morus alba* L. (Moraceae) were picked during September. All fruits were sourced from locations near UKZN, Pietermaritzburg. *Solanum mauritianum* Scopoli (Solanaceae) and *Cinnamomum camphora* (L.) J. Presl. (Lauraceae) fruits were also offered to the fruit bats; however these were not eaten by any of the individuals in the laboratory.

Psidium guajava trees produce large (up to 100 mm in diameter), soft, yellow fruit with pink pulp (Henderson 2001). While each fruit may contain up to 570 seeds (Adsule and Kadam 1995), fruit from this study had $c. 184 \pm 26.64$ seeds (mean \pm SE, $n = 10$ fruit). *Psidium guava* escaped from commercially grown orchards though dispersal by native frugivorous birds and mammals (Samson 1986; Corlett 2005; Henderson 2007; Gosper and Vivian-Smith 2010). *Melia azedarach* fruits are also yellow when ripe and are $c. 12$ mm in diameter, becoming wrinkled as they ripen (Henderson 2001). While they are considered poisonous (Henderson 2001), both birds and bats feed on them (Corlett 2005). Each fruit contains a ridged stone which generally holds 5 seeds (Florido and de Mesa 2002). *Eriobotrya japonica* has yellow-orange fruit which are 35–50 mm in diameter (Henderson 2001). On average, fruits from this study were 21.93 ± 0.57 mm in diameter containing two large seeds, each 10.26 ± 0.45 mm in diameter ($n = 10$ fruit). These fruits were originally grown for human consumption

(Henderson 2001). While both birds and bats feed on these fruits (Gosper and Vivian-Smith 2010), these large seeds will most likely fall under the parent tree as a result of avian feeding. *Morus alba* fruit are purple-black syncarps which are approximately 20 mm long (Henderson 2001) and each fruit from this study had 28.70 ± 4.82 seeds ($n = 10$ fruit). These trees are cultivated worldwide for their foliage and edible fruits (Vijayan et al. 1997).

Feeding trials

Three adult male (mean body mass 134.63 ± 3.76 g) and three young, non-reproductive female (mean body mass 93.67 ± 9.47 g) fruit bats were used for each diet trial. Bats were housed individually in cages ($75 \times 51 \times 80$ cm), in a constant environment room set at 25°C , on a 12:12 dark light cycle. They were acclimated for a minimum of 1 week prior to sampling and at least 3 days were left between consecutive feeding trials. During these times bats were fed the maintenance diet. Trial fruit were incorporated into maintenance diets the day prior to sampling. Fruits of each species were offered to an individual once, within 48 h of picking, for 12 h (18:00–06:00). Fruit were weighed before trials and presented whole in suspended feeding trays. Upon trial termination, dropped fruit were collected and the total amount of uneaten fruit was weighed. To account for evaporative water loss, control fruit were placed in the same room and weighed before and after trials.

Germination trials

As *E. wahlbergi* rarely swallowed fruit solids, seeds collected following bat-processing were referred to as 'spat seeds'. Only some small seeds of *M. alba* were swallowed, and so for this species both spat and fecal seeds were collected. Seeds were extracted from each individual's spats, planted in separate soil trays approximately 0.5 cm deep, and placed in a greenhouse. The soil consisted of decomposed garden refuse with no additives. Manually de-pulped seeds and whole fruit of each species were planted in separate trays as controls. Trays were watered daily following germination counts, after which counted seedlings were removed. Trays were observed until there was no germination for a minimum of eight consecutive weeks.

For *P. guajava* 40 seeds were collected from each bat ($n = 5$) and two trays of 40 de-pulped seeds and two trays containing two whole fruit each were planted. For *E. japonica* 27 seeds were collected from each bat ($n = 5$), two trays with 27 de-pulped seeds and two trays of 4 whole fruit each were planted. A total of 30 fecal and 30 spat *M. Alba* seeds were collected from each bat ($n = 6$) and four trays with 30 de-pulped seeds and four trays containing 5 whole fruit each were planted as controls. Finally, 24 ($n = 3$), 6 ($n = 1$) and 10 ($n = 1$) spat stones were collected and planted for *M. azedarach*. Two trays with 24 de-pulped stones and two trays of 24 whole fruit each were planted as controls.

Analyses

Daily food intake (DFI) per gram body mass (g^{-1}mb) was corrected for evaporative water loss and compared between the various fruit diets. These data were analyzed using a one-way analysis of variance (ANOVA). Where significant differences were evident, *post-hoc* Tukey tests were used for further investigation. The mean cumulative germination percentage was calculated for bat processed, de-pulped and whole fruit seeds for each fruit species. For multi-seeded whole fruit controls the average number of seeds per fruit ($n = 10$) was used to calculate the average cumulative germination. The effect of plant species, type of seed handling, as well as the interaction of these two variables on the proportion of seeds that germinated was analyzed using Generalized Linear Models (GZLM) (McCullagh and Nelder 1989) that incorporated a binomial error structure. Significance was assessed using likelihood ratio tests. Significance of posteriori pairwise comparisons of germination among spat, de-pulped and whole fruit treatments for each fruit species was assessed using the Dunn-Šidák procedure (Kutner et al. 2005). This was also done to compare fecal *M. alba* germination rates to those of spat, de-pulped, and whole fruit seeds. Cumulative germination of *M. azedarach* seeds was analyzed for 110 days only due to rodent predation on the trays at this time. Finally, the duration from planting until first germination for each fruit species was compared between spat seeds and de-pulped and whole fruit controls, with a Mann-Whitney U Test. ANOVA and Mann-Whitney U Tests were conducted using STATISTICA 7 (Statsoft, Tulsa, USA) and

Generalized Linear Models were run using PASW Statistics 18 (SPSS, Chicago, USA).

Results

Daily food intake (DFI)

Fruit bats ate significantly different amounts of fruit of the four species ($F_{3,16} = 8.35$; $P < 0.050$) (Fig. 1). In particular, they consumed a more *E. japonica* (*post-hoc* Tukey, $P < 0.050$) and *P. guajava* (*post-hoc* Tukey, $P = 0.036$) relative to their body mass than they did of fruits of *M. azedarach* (Fig. 1). Bats almost processed their body mass in *E. japonica* fruit ($0.995 \pm 0.111 \text{ g.g}^{-1}\text{mb}$, mean \pm SE), resulting in an average of 40 seeds dispersed per bat in one night. Similar amounts of *M. alba* and *P. guajava* fruits were eaten (Fig. 1). While *M. azedarach* fruits were least consumed ($0.261 \pm 0.099 \text{ g.g}^{-1}\text{mb}$), each bat was able to process an average of 20 fruit, resulting in an average of 100 seeds dispersed per bat in a night.

Germination of seeds of invasive alien plants

Spat seeds started germinating at approximately the same time as de-pulped and whole fruit controls for *P. guajava* and *E. japonica* (Fig. 2). Despite having

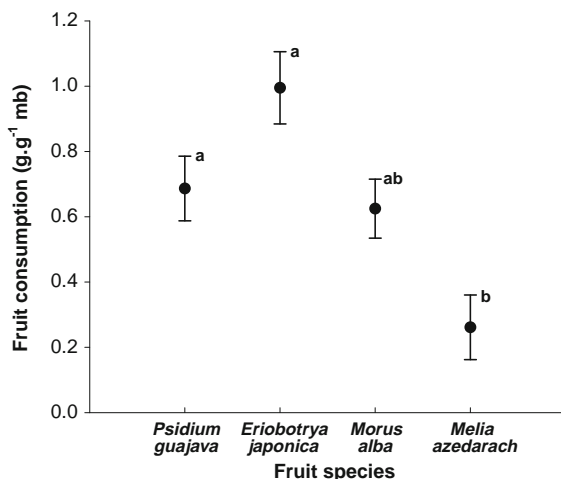


Fig. 1 Mean mass of fruit (\pm SE) per unit body mass consumed by *E. wahlbergi* bats for *P. guava* ($n = 5$), *E. japonica* ($n = 4$), *M. alba* ($n = 6$), and *M. azedarach* ($n = 5$), where n = number of *E. wahlbergi* individuals, and superscript letters indicate significance of difference for $P \leq 0.05$

the largest seeds, *E. japonica* germinated after 27.75 ± 0.75 (mean \pm SE) days, while the relatively smaller seeds of *P. guajava* only started germinating after 69.00 ± 22.90 days (Fig. 2). Bat processing resulted in significantly earlier germination for both fecal (Mann–Whitney U, $P = 0.010$) and spat (Mann–Whitney U, $P = 0.010$) *M. alba* seeds when compared to whole fruit seeds. De-pulped *M. alba* seeds germinated significantly sooner than fecal seeds (Mann–Whitney U, $P = 0.019$), but not spat seeds. The onset of *M. alba* germination was rapid and approximately the same for both spat (9.33 ± 1.09) and fecal (11.50 ± 0.81) seeds (Fig. 2). Spat *M. azedarach* stones had the most delayed germination (73.00 ± 1.00) of all the invasive species sampled, with all seeds germinating at approximately the same time (Fig. 2). The hard stone needs to first break open before germination can begin. For all invasive alien species in this study the initial onset of seed germination was followed by a rapid increase in germination rates, after which very little germination occurred (Fig. 2).

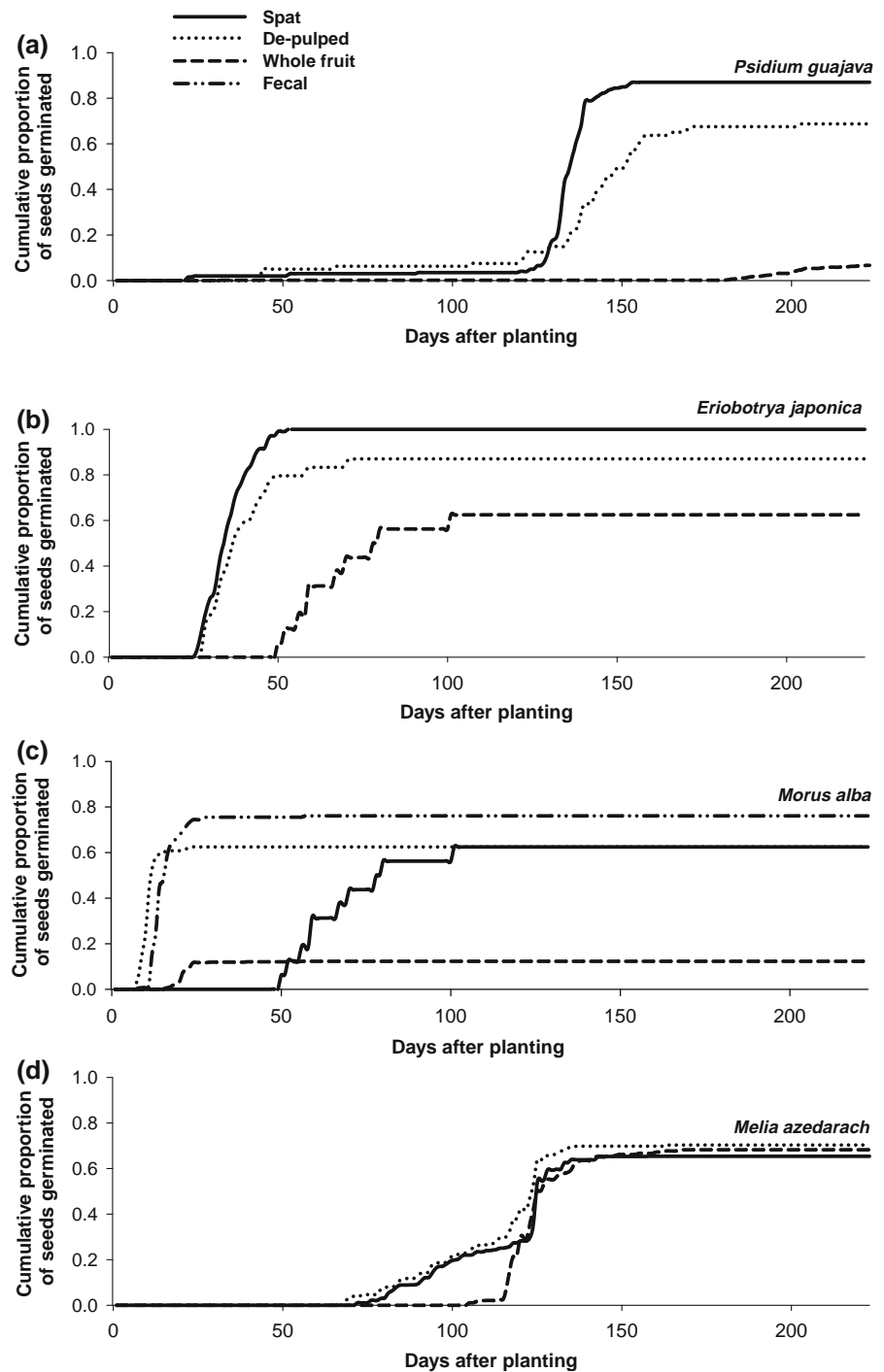
The type of plant species ($\chi^2 = 303.4$, $df = 3$, $P < 0.05$), type of handling ($\chi^2 = 130.4$, $df = 2$, $P < 0.05$), and the interaction of these two variables ($\chi^2 = 32.40$, $df = 6$, $P < 0.05$) all had significant effects on the germination amounts of the plant species in this study. The amount of germination of de-pulped seeds did not differ significantly from that of bat spat seeds (Table 1). Significantly more spat seeds germinated than whole fruit control seeds for all the tested species, except *E. japonica* (Table 1). Germination amounts were relatively high for all spat seeds which were observed for the full duration of the study (Table 1).

The second analysis of *M. alba*, which included fecal seeds, also indicated that the type of handling significantly influenced the amount of germination ($\chi^2 = 398.267$, $df = 3$, $P < 0.05$). Whole fruit seeds germinated significantly less than spat, fecal and de-pulped seeds ($P < 0.05$). While fecal seeds germinated more than both spat and de-pulped seeds, this was only significant for de-pulped seeds ($P = 0.037$).

Discussion

The fruit bats in this study generally consumed up to twice as much invasive alien fruit (per gram body

Fig. 2 Mean cumulative germination for the duration of the study of seeds spat out by *E. wahlbergi*, ingested by *E. wahlbergi* (only applies to *M. alba*), de-pulped and contained in whole fruit for **a** *P. guajava*, **b** *E. japonica*, **c** *M. alba*, and **d** *M. azedarach*



mass) than co-occurring native avian frugivores do (Jordaan et al. 2011). It is not unusual for fruit bat species to consume more than their body mass in fruit (Morrison 1980; Thomas 1984; Izhaki et al. 1995), particularly during reproduction (Korine et al. 2004).

Rousettus aegyptiacus have been observed to consume up to 150% of their body mass when feeding on *E. japonica* fruits (Izhaki et al. 1995), and in this study *E. wahlbergi* consumed these fruits in the largest quantities (up to 110% of their body mass). Old World

Table 1 Proportion of germination for spat, de-pulped, and whole fruit seeds (mean \pm SE), where superscript letters 'a' and 'b' indicate significance of difference for $P \leq 0.05$

Plant species	Type of handling		
	Spat	De-pulped	Whole fruit
<i>Psidium guajava</i>	0.86 \pm 0.03 ^a	0.69 \pm 0.05 ^a	0.07 \pm 0.01 ^b
<i>Eriobotrya japonica</i>	0.96 \pm 0.02 ^a	0.87 \pm 0.05 ^a	0.63 \pm 0.12 ^a
<i>Melia azedarach</i>	0.30 \pm 0.02 ^a	0.21 \pm 0.03 ^a	0.02 \pm 0.01 ^b
<i>Morus alba</i>	0.68 \pm 0.04 ^a	0.63 \pm 0.04 ^a	0.12 \pm 0.01 ^b

fruit bat species are generally larger than New World bat species (family Phyllostomidae) and can therefore play a greater role in seed dispersal, as they process proportionally more fruit per individual (Izhaki et al. 1995). Consequently *E. wahlbergi* individuals have the potential to disperse comparatively more seeds than local bird species. For example, consuming 150 g of mulberry fruit, a fruit bat may disperse > 5000 seeds in a night (Izhaki et al. 1995). While larger seeds are carried to nearby feeding roosts and spat out, they can still be dispersed relatively far from the parent tree. Izhaki et al. (1995) reported that the stones of *M. azedarach* were carried up to 400 m away from the parent tree. Smaller seeds are often ingested and may remain in the gut until the following night, and are therefore generally transported further than larger seeds (Shilton et al. 1999).

Our results further concur with those of Jordaan et al. (2011) in that de-pulped and frugivore processed seeds had similar germination amounts, while whole fruit seeds tended to have less. Similar trends were observed by Heer et al. (2010) who found that fruit bats positively influenced fig seed dispersal by pulp removal, while whole fruits failed to germinate due to fungal infection, and Voigt et al. (2011) who recorded a positive effect of bat handling on the germination of seeds of *M. azedarach*. *Melia azedarach* seeds from this study, which were not eaten by rodents (including whole fruit), germinated profusely. It is therefore predicted that germination rates would have been high for this species, as observed by Voigt et al. (2011). Unlike the other species in this study, *M. azedarach* fruit have less pulp as they become dry and wrinkled as they ripen. Thus we expect that the initial trend (that whole fruit and spat seeds had similar germination amounts, Fig. 2) would persist. Delayed germination for this species is likely determined by the opening of the stone, rather than pulp decomposition rates. *Eriobotrya japonica* seeds spat by *R. aegyptiacus* had similar germination success to de-pulped seeds (c.

80%) (Izhaki et al. 1995), and while *E. japonica* seeds spat by *E. wahlbergi* in this study also had similar germination amounts to de-pulped seeds, spat seeds had comparatively higher germination success (c. 96%).

Of further interest is the comparison of ingested and fecal *M. alba* seed germination. While spat seeds had slightly less germination than fecal seeds, this difference was not significant and both had high germination rates. Similar germination rates of fecal, spat, and de-pulped seeds have been previously reported (Tang et al. 2007), however in some cases ingestion by fruit bats has been shown to increase germination success (Izhaki et al. 1995). The rapid and profuse germination of invasive alien plants has been previously reported (van Kleunen and Johnson 2007; Jordaan et al. 2011) and it has been suggested that such species may rely on continuous and regular dispersal events, rather than seed banks (Panetta 2001). Indeed the invasive alien plants used in this study followed this trend and it would be interesting to note if this is a common trait for most vertebrate dispersed invasive alien plant species.

Despite *E. wahlbergi* having been observed to feed on invasive alien fruits of this study (pers. obs.), they have only formally been reported to feed on *P. guajava* (Skinner and Chimimba 2005), and more recently *M. azedarach* (Voigt et al. 2011). Their role as dispersers of these fruits in South Africa is therefore underestimated. In urban China fruit bats utilize invasive alien plants as sources of nectar and fruit (among these are *M. azedarach* and *P. guajava*) and in the process function as pollinators and dispersers of these (Corlett 2005). In the Mediterranean, of 14 plant species identified in *R. aegyptiacus*' diet, 12 were introduced (Korine et al. 1999). These bats are recognised as efficient dispersers of invasive alien fruits which include *Morus nigra* (black mulberry), *E. japonica* and *M. azedarach* (Izhaki et al. 1995). The role of *R. aegyptiacus*, as dispersers of invasive alien

plants is further exacerbated as these bats occur within urban and peri-urban environments, where a large variety of invasive alien plants occur, thereby increasing encounters with these (Tsoar et al. 2011). Indeed exotic fruits have been recognised as an important food source for urban frugivores where indigenous fruits are often less abundant (Corlett 2005). Based on such trends, and the morphological similarities, overlapping distribution, and relatedness between *R. aegyptiacus* and *E. wahlbergi* (Monadjem et al. 2010), it is likely that *E. wahlbergi* fulfils a similar role as a disperser of invasive alien plants in South Africa. In particular, this can be expected in many South African urban environments where availability of indigenous fruits is seasonal or low compared with invasive alien fruits (Downs unpublished data).

Three of the four alien invasive plants fed to *E. wahlbergi* bats in this study are grown for human consumption in South Africa (Henderson 2001). Indeed the use of cultivated fruits by fruit bats is well documented (Korine et al. 1999; Skinner and Chimimba 2005; Monadjem et al. 2010). The refusal of *E. wahlbergi* individuals to feed on some invasive alien species offered to them indicates that they have strong preferences for the fruits on which they feed. Such preferences and how fruit bats discriminate and locate food, for example through olfaction (Elangovan et al. 2006; Raghuram et al. 2009), in a nocturnal environment should be further investigated and used as screening tools to identify potential bat-dispersed invasive alien fruits. To fully appreciate the role of fruit bats in seed dispersal and seedling recruitment, observations of their feeding behaviour must be combined with their movement patterns within and between various habitats. For example, fruit bats may carry small *P. guajava* fruit away from parent trees, while larger ones are fed on in the tree (Corlett 2005).

There is a need for more comprehensive screening tools for identifying potential plant invaders and more directed management policies for current threats (Rejmanek and Richardson 1996). Vertebrate dispersers have tentatively been acknowledged as enhancing the spread of invasive plants (Rejmanek and Richardson 1996), especially into undisturbed habitats (Bass 1990). The results from this study, together with observations that *E. wahlbergi* commonly feed on fruits of invasive alien species (Skinner and Chimimba 2005; Voigt et al. 2011; pers. obs.), clearly highlight the important role that fruit bats play in the invasion

process. Furthermore, the prolific germination of invasive alien seeds without ingestion has been a previously understated characteristic and such traits should be incorporated into the screening protocol and management strategies of both potential and current invasive species.

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Chapter 5

Forbidden Fruit: Nutritional and Morphological Traits of Invasive and Exotic Fleshy-fruits in South Africa

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Running header: Traits of invasive alien fruit

ABSTRACT

While fleshy-fruited invasive alien plants are recognised as some of the worst invaders on a global scale, until recently little consideration has been given to the frugivores which feed on these fruits and more specifically the fruit traits which may influence this. We investigated a series of morphological and nutritive fruit traits for c. 30 species of fleshy-fruited invasive alien and exotic species in South Africa. Invasive alien fruit traits were compared with comparable traits of a similar sample size of indigenous fleshy fruits, which occur in the same area. Data was also available to allow for the comparison of traits for the same invasive alien species in Australia. Invasive alien fleshy fruits were similar in morphology, but greater in some nutritive aspects when compared to indigenous fruits. Furthermore, they were very similar in all aspects to their counterparts in Australia, which indicates that these fruits present a desirable food source elsewhere and that local frugivore selective pressures have not changed these fruits. Most seeds of invasive fleshy fruits were small and had low seed mass, which may explain some of their invasive success, as benefits associated with small seededness may promote invasive potential. Nutritionally, most invasive alien fleshy-fruits were hexose dominant, containing low lipid and nitrogen content. While frugivore preference trends remain to be formally investigated, this study provides insights into fruit traits which may tentatively outline why invasive fruits are universally fed on and thus successfully spread.

Key words: frugivore preference; fruit morphology; indigenous fruit; invasive fruit; nutritional content; seed morphology

INVASIVE ALIEN PLANTS ARE OF GLOBAL CONCERN, BOTH FROM AN ECOLOGICAL (van Wilgen *et al.* 2008) and economic (van Wilgen *et al.* 2001) perspective. Competitor avoidance and exploitation of empty niches and dispersers are important for successful invasion (Lloret *et al.* 2005). Traits associated with some of the worst invaders include: shade tolerance, rapid growth, tree and shrub growth forms, early reproduction, production of numerous seeds, and fleshy bird-dispersed fruits (Cronk & Fuller 1995). More recently, the role of fruit traits associated with frugivore preferences, such as morphology (Gosper & Vivian-Smith 2009), and nutritional composition (Gosper & Vivian-Smith 2010) have been recognised.

Plants generally attract many disperser species through a combination of various fruit traits and adaptations to disperser groups (Howe 1986). These ‘dispersal syndromes’ (Ridley 1930) are based on a concept of mutual benefits which drive the co-evolution of fruit and frugivore traits (Jordano 1995). However, fleshy-fruited species were present long before their current vertebrate dispersers (Fleming & Kress 2011) and phylogenetic effects have now been recognised to more strongly influence fruit traits than plant-disperser interactions (Jordano 1995). Endozoochory is a loosely co-evolved interaction (Meisenburg & Fox 2002), which explains the rapid formation of mutualistic relationships between local frugivores and initially novel invasive fruits (Richardson *et al.* 2000). Vertebrate dispersal and frugivore diversity have been associated with many invasive plants’ success (Rejmánek 1996, Gosper & Vivian-Smith 2009) and it is therefore necessary that we investigate fruit traits which may influence frugivore selection.

Factors influencing the process of fruit selection may include the physiological needs and characteristics of frugivores, and the spatial and temporal variations in fruit morphology (Lepczyk *et al.* 2000). Concentration and type of nutrients (Levey 1987, Avery *et al.* 1999), seed load (Stanley & Lill 2002b, Wilson & Downs 2011a), caloric content (Sorensen 1984, Wilson & Downs 2011b), fruit colour (Avery *et al.* 1995, Schaefer *et al.* 2007), fruit size (Flörchinger *et al.* 2010, Sobral *et al.* 2010), secondary compounds (Levey & Cipollini 1998, Schaefer *et al.* 2003), abundance and / or fruit crop size (Murray 1987, Blendinger *et al.* 2008), temporal variation / seasonality of fruit types (Lepczyk *et al.* 2000, Pereira *et al.* 2010), and fruit accessibility (Denslow & Moermond 1982, Willson 1994) have all been shown to influence frugivore fruit selection.

Despite the multi-faceted nature of this process, there appears to be a worldwide similarity in both the cues frugivores utilize for fruit selection, as well as the characteristics of fleshy fruits (French 1991, Jordano 1995). Of all the frugivore groups, bat-dispersed fruits

differ most from those dispersed by other vertebrates (Fleming & Kress 2011). Globally, Angiosperm fruits are generally low in protein and lipid content, but high in carbohydrates (Jordano 1995). Furthermore, fruits dispersed exclusively by birds or mammals have similar nutritional content, but differ morphologically, where mammal-dispersed fruits are larger, but do not necessarily have more seeds (Jordano 1995). Frugivory has evolved independently in vertebrate groups on several occasions, with avian frugivory being most common in all Angiosperm groups (Fleming & Kress 2011).

Most fruit are ‘nutritionally bulky’, consisting of a large fraction of indigestible seeds with dilute sugars and amino acids in their pulp (Karasov & Levey 1990). Combined with rapid food transit rates and limited gut capacity, this can limit energy assimilation efficiency of fruits (Sorensen 1984, Karasov & Levey 1990, Levey & Karasov 1994). Rapid food transit rates of frugivores could possibly increase the net energy intake and compensate for these effects (Karasov & Levey 1990). In contrast, frugivores which feed on lipid-rich fruits have longer retention times and process proportionately less fruit (Bosque & Deparra 1992, Place & Stiles 1992). The nutritional benefits to the frugivore thus influence the digestive strategies employed, which in turn determine efficient resource utilization (Place & Stiles 1992, Afik & Karasov 1995).

Long- and short- distance seed dispersal play a vital role in the population dynamics and spread of invasive species (Pergl *et al.* 2011). Seed shadows are determined by the seed retention times (SRT) of frugivores (Ridley 1930), which may also affect germination rates (Sorensen 1984, Murray *et al.* 1994). While seed size has been suggested to influence SRT, both small (Wilson & Downs 2011a) and large (Stanley & Lill 2002b) seeds have been shown to have shorter retention times than seeds of opposite sizes, and vary in preference by avian frugivores. Seed size may also influence the competitive ability (Crawley *et al.* 1997), survival potential (Katz & Shafroth 2003), and the time it takes to germinate (Norden *et al.*

2009). The longer a seed takes to germinate, the more likely the risk of pathogen infection or predation (Howe 1986). Finally, the number and mass of seeds per fruit can also have important implications in fruit choice as this limits gut capacity available for digestible fruit pulp (Sorensen 1984) and increases energetic demands. Despite the implications that seed size may have on frugivore fruit preferences, few studies have investigated seed morphologies of invasive alien plant assemblages.

These numerous morphological and nutritional traits may all influence frugivore selection and so, to successfully attract frugivores, an invasive plant should present a resource of equal or greater value than neighbouring indigenous fruits. Thus, we hypothesized that invasive alien fruits in South Africa will have similar morphologies, thereby offering a recognisable food source, but have greater or similar nutritive value than native fruits. Furthermore, we also hypothesized that invasive alien fruit traits for a given species are similar between different regions as invasive alien fruits would be dispersed by generalist frugivores with similar preferences. Smaller seeds tend to germinate faster (Norden *et al.* 2009), thereby giving them a competitive edge. Furthermore, frugivores have shown preference for smaller seeds as they take up less gut capacity (Sorensen 1984) and have shorter retention times (Wilson & Downs 2011a). Thus, we predicted that invasive fruits would tend to have numerous, small seeds which weigh very little.

METHODS

Ripe invasive and exotic fruits were collected for a period of one year, when they were available, from several locations in Pietermaritzburg and Durban, KwaZulu-Natal, South Africa. Fruit selection was based on location and availability of fruits in order to represent the fleshy-fruited invasive plants of the area. The South African Conservation of Agricultural Resources Act (CARA) has assigned categories to alien plant species in terms of the severity

of their invasiveness. In summary, Category 1 indicates plants which are declared weeds, are prohibited in South Africa, and must be eradicated where possible (Henderson 2003). Category 2 plants are declared invaders allowed in demarcated areas, but outside of which they must be eradicated (Henderson 2003) (often associated with agriculturally important species). Category 3 also contains declared invaders which may not be planted and existing plants must be prevented from spreading. Finally, there are exotic species which require further investigation before they can formally be added to CARA and these are listed as 'proposed' (Henderson 2003). A list of fruit species collected and their associated categories is provided in Table 1. Ten fruits from several individuals for each species were used to calculate average morphological traits including: fruit diameter (mm), seed diameter (mm), wet seed mass (g), and the average number of seeds per fruit (Supplementary Table 1). For species with multi-seeded endocarps, the number of seeds within an endocarp was used. For fruits consisting of multiple drupes (e.g. *L. camara*), fruit diameter was measured as a single drupe, as would be consumed by an avian frugivore. The colour of ripe fruit as perceived by humans was also recorded.

Fruit were de-pulped and frozen (c. -18°C). Fruit pulp was freeze-dried to constant mass and water content (%) for each species was subsequently calculated. Dried pulp was milled and sieved through a 750μ mesh. Samples were then sent to a laboratory at the University of Pretoria for nutritional analysis. Sugar type and concentration ($n = 43$), lipid and nitrogen content, as well as gross energy ($n = 40$) values were obtained on a dry and wet matter basis for invasive and exotic fruits (Supplementary Table 2). Fruit sugars were determined according to (Liu *et al.* 1999) and analysed using a HPLC (Agilent 1100 series) with RID detection. Gross energy was calculated using a MC 1000 Modular Bomb Calorimeter. Fruit lipid content (crude fat) was determined by ether extraction (AOAC 2000b)

and nitrogen content was established by using the Dumas combustion method (AOAC 2000a).

Indigenous fruit data was used from Wilson and Downs (2011c) for comparison with declared and proposed invasive alien fruit collected in this study. Indigenous fruits were collected during the same time period and in the same area as invasive fruits. Indigenous fruit selection was also based on availability during the fruit collection period (Wilson pers. comm.). For indigenous fruit size data presented with ranges, the median was used for comparison and only fruit diameter was considered. For multiple values of one species, an average of a parameter was calculated. Therefore no species was represented twice in any comparison analyses. Indigenous fruit protein content was converted to nitrogen content using a 6.25 conversion factor. Glucose and fruit diameter were compared between fruit types using independent sample t-tests and where data distributions could not be normalized Mann-Whitney U tests were run on STATISTICA (Statsoft, Version 7, Tulsa, USA). Nitrogen and sucrose content variances could not be homogenized and were analyzed by means of a t-test for unequal variances (Welch's test) (Ruxton 2006) using PASW Statistics 18 (SPSS, Chicago, USA).

Data available for the same invasive species for the same parameters were used from Gosper and Vivian-Smith (supplementary data, 2010) and compared with data from this study to determine if the fruit traits of the same invasive alien species differ between regions. This was done using chi-square tests on Megastat for Microsoft Excel 2007 (McGraw-Hill Higher Education, Version 9.4, New York, USA). For PCA analysis, fruits were broadly divided into three categories: declared invasive, proposed invasive, and exotic species. This was analyzed using STATISTICA (Statsoft, Version 7, Tulsa, USA). PCA's based on correlations of the seven nutritive and four morphological traits were performed on 32 species (due to missing values) of exotic and declared and proposed invasive species of this study. For all analyses

nutritive traits were based on wet matter content, except for comparisons with indigenous fruit data from (Wilson & Downs 2011c), due to missing water content values.

RESULTS

Most invasive and proposed invasive fruits collected in this study were shades of yellow, red or purple-black (c. 20% each) (Fig. 1; Supplementary Table 1). Most seeds were 10 mm or less in diameter, with less than 10% larger than 24 mm (Fig. 1; Supplementary Table 1). Single seeded fruits were most common (c. 33%) with most (40%) multi-seeded species having 2 – 10 seeds per fruit (Fig. 1; Supplementary Table 1). Invasive alien seeds were predominantly small and had low seed mass (Fig. 1; Supplementary Table 1). Most fruits consisted of relatively little nitrogen, but this was present at varying levels in many fruits (0.08 – 0.91%; Fig. 1). Invasive fruits were mostly low in lipid content, with > 89% of fruits containing < 3% (Fig. 1; Supplementary Table 2). However, there were a few exceptions, particularly from the Lauraceae family, which had considerably higher lipid levels (Fig. 1; Supplementary Table 2). Most fruits consisted of high water content and offered little gross energy (Fig. 1; Supplementary Table 2). Fruits were mostly hexose dominant with a range of glucose and fructose sugar content (Fig. 1; Supplementary Table 2). Sucrose was mostly present in low levels or not detectable in many fruits (Fig. 1; Supplementary Table 2), with only 9% of fruits being sucrose dominant.

Fructose, glucose and sucrose were significantly higher in invasive fruits than in indigenous fruits (Table 2). Indigenous fruit contained significantly more lipids than invasive fruits (Table 2), while nitrogen content, and water content were similar between these groups (Table 2). Invasive alien fruits were smaller in fruit diameter, but this was also not significant (Table 2). While there are differences between invasive and indigenous fruit parameters, no significant differences were observed for both morphological and nutritive traits for the same

invasive species from South Africa and Australia (Table 3). Both morphological and nutritive parameters were very similar for these fruits (Table 3).

For the PCA analysis where nutritional content of fruit were analysed per wet weight of pulp, then water content and gross energy were highly correlated ($r = -0.96$), as was seed mass and seed diameter ($r = 0.91$). Thus water content and seed mass were excluded from this PCA analysis. Factor 1 explained 29.42% of the variance and factor 2 accounted for 24.07% (Fig. 2a). Nitrogen content (+0.80) was highly correlated with factor 1, while fructose (+0.93) and glucose amounts (+0.94) were strongly correlated with factor 2 (Fig. 2a). Gross energy (+0.69), the number of seeds per fruit (+0.66), lipid content (+0.59), fruit diameter (+0.58), and seed diameter (+0.53) were moderately correlated with factor 1 (Fig. 2a). Sucrose content was more strongly correlated with factor 2 (+0.42) (Fig. 2a). In contrast, when PCA analysis was repeated based on nutritional content of fruit expressed per dry weight of pulp, then lipids and gross energy were highly correlated ($r = 0.84$). As before seed mass and seed diameter ($r = 0.91$) were also highly correlated. Therefore gross energy and seed mass were excluded from analysis. Factor 1 explained 25.12% of the variance and factor 2 accounted for 23.01% (Fig. 2b). Water, lipid, protein, fructose, sucrose and glucose content, as well as seed diameter were similarly correlated to factor 1 and 2 as in the previous PCA analyses. However, seed number (-0.74) was more strongly correlated to factor two when considering exotic species. Additionally, fruit diameter correlated equally with both factors (0.44 and 0.49) (Fig. 2b). There was no obvious clustering in the ordination plot where fruit nutritional content was considered per dry weight of pulp, with declared invasives, proposed invasive and exotic species relating similarly to both factors (Fig. 2b). However, when fruit nutritional content was considered per wet weight of pulp, proposed and declared invasive alien plants were more associated, with exotic species forming a more distinct cluster (Fig. 2a).

DISCUSSION

Traditionally nutritive values of foods are expressed per dry weight, as water content within a particular food item may vary considerably, thereby allowing valid comparisons between foods (MacDonald *et al.* 1998). However, animals do not perceive foods on a dry matter basis and consequently data were presented as dry matter and as wet matter basis respectively. In particular the comparison of the ordination plots generated using these two methods highlighted the variation that may occur when considering the nutritional content of food on a dry versus wet weight comparison. The latter highlighted that fruits with high water content had lower gross energy per gram, which can influence frugivore fruit choice (Izhaki 1992).

Sugar concentration and type appear to be of particular importance in frugivore fruit choice. Numerous fruit eating species have shown a preference for monosaccharide glucose and fructose over sucrose (Martinez del Rio *et al.* 1995), which many bird species are unable to digest (Malcarney *et al.* 1994). Yet, some species have shown a preference for sucrose (Wellmann & Downs 2009). Generally, fruits consumed by passerines have been observed to be hexose dominant, while fruit consumed by chiropterans are sucrose rich (Baker *et al.* 1998). In South Africa, indigenous fruits are predominantly hexose rich, with only 16% sucrose dominant (Wilson & Downs 2011c). Invasive fruits from this study are also hexose dominant and only 9% were sucrose dominant. High levels of hexose sugars and very little sucrose have previously been found in invasive fruit elsewhere (Gosper 2004, Gosper & Vivian-Smith 2010), which follows the preference trends of many avian frugivores (Martinez del Rio *et al.* 1995). This is not surprising as avian frugivory is more common (Fleming & Kress 2011) and birds are relatively more abundant, particularly in urban and disturbed areas where invasive plants are commonly found.

Recently an Australian study of more than 30 fleshy-fruited, vertebrate-dispersed invasive alien fruits showed that these had relatively low lipid and protein content (Gosper &

Vivian-Smith 2010). However, when compared to indigenous species, they had higher sugar content, more variable nitrogen amounts, smaller seeds, and longer fruiting seasons (Gosper & Vivian-Smith 2010). Similarly, South African invasive fruits were also alike in size and contained higher sugar content than indigenous fruits. However, these indigenous fruits did contain more lipids than invasive fruits. There appears to be a dichotomy in fruit types. Fruits may offer either sugars or lipids as an energetic reward to attract frugivores (Lepczyk *et al.* 2000). Some bird species prefer fruits with higher lipid content as they are more energetically dense than carbohydrate dominant fruits (Place & Stiles 1992). However, these fruits take longer to digest and as gut capacity is limiting, frugivores are unlikely to meet their energetic demands on an exclusive diet of lipid rich fruits (Place & Stiles 1992, Lepczyk *et al.* 2000).

Nutritional aspects that have not been considered in this study, but which have been shown to influence fruit selection is micronutrients and secondary metabolites. While secondary metabolites can prevent fungal infections of the fruit (Cipollini & Levey 1997b), increased levels of these metabolites may deter frugivores (Cipollini & Levey 1997a, Saxton *et al.* 2011). Secondary metabolites have also been shown to affect retention time, thereby manipulating seed shadows (Wahaj *et al.* 1998). For example, it has been suggested that calcium rich invasive fruits may provide a valuable resource to fruit bats during lactation (Panetta & Sparkes 2001). Micronutrients have been investigated in invasive fruits elsewhere (Gosper & Vivian-Smith 2010), but a comprehensive perspective remains to be achieved.

Morphologically, invasive fruits have been shown to resemble native species (Gosper & Vivian-Smith 2009). Indeed, fruit size was similar between South African indigenous and invasive species. Unfortunately, seed data were not available for comparison, but elsewhere it has been shown that invasive species have proportionally smaller seeds than indigenous species (Gosper & Vivian-Smith 2010). Small fruit containing one or few seeds (Gosper & Vivian-Smith 2009), and soft multi-seeded fruits are preferred by frugivores (Green 1993).

For avian frugivores fruit size is certainly an important factor determining fruit selection (Green 1993, Stansbury & Vivian-Smith 2003), as they are limited by gape width (Wheelwright 1985). Generally fruits < 15 mm in diameter are preferred by avian frugivores (Green 1993, Stansbury & Vivian-Smith 2003). Birds may consume larger fruits piece-meal (mashers) or swallow smaller fruits whole (gulpers) (Levey 1987). Large fruits with larger seeds may therefore rely on mammal species for dispersal as they are able to carry them away to feeding sites (Monadjem *et al.* 2010). Most invasive fruits from this and other studies are small (Stansbury & Vivian-Smith 2003, Gosper & Vivian-Smith 2010), and are therefore not disperser limited.

Few studies have considered the spectral hues from a frugivore's point of view; for example birds can see UV (Burns *et al.* 2009). Thus perceptions from colour studies may be skewed by human interpretation. Fruit colour not only attracts frugivores, but is also used as an honest indication of nutritional rewards (Schaefer *et al.* 2007). Indigenous fruits in KwaZulu-Natal are predominantly red or black (Wilson & Downs 2011c) and it is generally believed that birds show a preference for these colours (Ridley 1930, Bach & Kelly 2004). However, in some cases frugivores have shown no colour preference at all (Traveset *et al.* 2001). Invasive species from this study had fruits from a range of colours, but were predominantly hues of red and black, consistent with indigenous fruit colour trends (Wilson & Downs 2011c). Unlike indigenous fruits, none were brown or green. As there is no geographical variation in fruit colour, it is suggested that the spectral contrast between leaf and fruit colour may be of greater importance (Burns *et al.* 2009). In a nocturnal environment colour is less important and olfaction plays a greater role in attracting dispersers (Raghuram *et al.* 2009). Studies of such nature remain sparse, especially in terms of invasive species, and require further investigation.

Most seeds from fruits in this study were small and had low seed mass, but surprisingly few species (c. 30%) had more than 10 seeds per fruit. This is consistent with results from Gosper and Vivian-Smith (2009, 2010). It contradicts the theory that good invaders should produce numerous small seeds due to trade-offs between seed size and number (Harper 1977). However, producing proportionately larger seeds when dispersers are not limiting may be more advantageous (Rejmanek & Richardson 1996), as they outcompete smaller seeds (Crawley *et al.* 1997) and are more robust to environmental pressures (Katz & Shafroth 2003). However, such benefits may be overcome as small seeds have been shown to germinate faster than larger seeds (Norden *et al.* 2009), and may thus be an important trait of invasive species. Invasive species seeds generally have a low seed mass (Rejmánek 1996), which has been shown to be similar to that of native species when growth form is accounted for (Mason *et al.* 2008). However, invasive total seed production is greater (Mason *et al.* 2008) and this is most likely due to longer fruiting seasons, and consequently greater fruit outputs which have been linked with invasiveness (Rejmánek 1996, Gosper & Vivian-Smith 2009).

In conclusion we support the hypothesis that invasive alien fleshy fruits resemble a recognisable food source to native frugivores, due to their similar fruit morphology when compared to indigenous fruiting species. Furthermore, coupled with large fruit displays (Henderson 2001), their invasive success may further be promoted by their small, light seeds packaged in a sugar-rich fruit pulp. This study highlights traits which may explain invasive success due to their ability to attract frugivores. Interestingly, these traits are almost identical when compared between countries and thus such data may be transferrable between regions. Traits such as these may be incorporated into screening protocols for potential invader species, and could be implemented in management strategies for current problem plants. The

next step would be to investigate frugivore preferences and feeding behaviours to fully appreciate the dynamic interaction between invasive alien plants and their dispersers.

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TABLE 1. *Proposed and declared invasive alien and exotic plant species from which fruits were collected in KwaZulu-Natal, South Africa. Invasive categories are assigned according to CARA legislation, Act 43 of 1983, amended in 2001 (Henderson 2001,2003).*

Plant Species	Family	Invasive category
<i>Ardisia crenata</i>	Myrsinaceae	1
<i>Capsicum frutescens</i>	Solanaceae	naturalized
<i>Celtis australis</i>	Ulmaceae	proposed 3
<i>Cestrum laevigatum</i>	Solanaceae	1
<i>Cinnamomum camphora</i>	Lauraceae	1
<i>Coffea arabica</i>	Rubiaceae	proposed 2
<i>Cotoneaster pannosus</i>	Rosaceae	3
<i>Crataegus pubescens</i>	Rosaceae	proposed 2
<i>Cyphomandra betacea</i>	Solanaceae	proposed 2
<i>Duranta erecta</i>	Verbenaceae	proposed 3
<i>Eriobotrya japonica</i>	Rosaceae	3
<i>Ficus benjamina</i>	Moraceae	exotic
<i>Ficus benjamina</i> var. <i>comosa</i> Kurz	Moraceae	exotic
<i>Ficus macrophylla</i>	Moraceae	exotic
<i>Ilex aquifolium</i>	Aquifoliaceae	exotic
<i>Lantana camara</i>	Verbenaceae	1
<i>Ligustrum japonicum</i>	Oleaceae	3
<i>Litsea glutinosa</i>	Lauraceae	1
<i>Melia azedarach</i>	Meliaceae	3
<i>Morus alba</i>	Moraceae	3
<i>Passiflora suberosa</i>	Passifloraceae	1
<i>Pereskia aculeata</i>	Cactaceae	1
<i>Phytolacca dioica</i>	Phytolaccaceae	3
<i>Psidium cattleianum</i>	Myrtaceae	3
<i>Psidium guajava</i>	Myrtaceae	2
<i>Pyracantha angustifolia</i>	Rosaceae	3
<i>Pyracantha crenulata</i>	Rosaceae	3
<i>Rivina humilis</i>	Phytolaccaceae	1
<i>Schefflera actinophylla</i>	Araliaceae	proposed 1
<i>Schefflera arboricola</i>	Araliaceae	proposed 3
<i>Schinus terebinthifolius</i>	Anacardiaceae	1
<i>Solanum lycopersicum</i>	Solanaceae	exotic
<i>Solanum mauritianum</i>	Solanaceae	1
<i>Solanum pseudocapsicum</i>	Solanaceae	proposed 3
<i>Solanum rantonnetii</i>	Solanaceae	exotic
<i>Solanum seaforthianum</i>	Solanaceae	1
<i>Symphoricarpos albus</i>	Caprifoliaceae	exotic
<i>Syzygium paniculatum</i>	Myrtaceae	proposed 3
<i>Syzygium smithii</i>	Myrtaceae	exotic

TABLE 2. Fruit traits of declared and proposed invasive alien species compared with co-occurring indigenous fruits from Wilson and Downs (2011c), where nutritive values are represented as per dry weight of fruit pulp. All 'Z' values are derived from Mann-Whitney U tests, except where '*' indicates independent samples t-test statistic and '#' indicates t-test for unequal variances (Welch's test).

Trait	Invasive (mean ± SE)	Indigenous (mean ± SE)	Z	P	Invasive (n)	Indigenous (n)
Fruit diameter (mm)	12.25 ± 1.65	16.84 ± 1.79	1.853*	0.068	28	38
Water content %	71.40 ± 3.35	68.07 ± 2.26	1.05	0.294	30	30
Nitrogen %	1.35 ± 0.14	1.31 ± 0.09	0.246 [#]	0.807	27	30
Lipids %	4.72 ± 1.85	9.31 ± 2.21	-3.436	0.001	27	30
Fructose (mg/g)	116.63 ± 13.26	24.69 ± 3.20	5.55	< 0.001	30	32
Glucose (mg/g)	128.00 ± 13.44	23.99 ± 3.29	6.389*	< 0.001	30	32
Sucrose (mg/g)	57.02 ± 22.57	8.60 ± 2.61	2.132 [#]	0.041	30	27

TABLE 3. Comparison of fruit traits for identical invasive alien plant species from South Africa and Australia (Gosper & Vivian-Smith 2010, supplementary material), where nutritive values are represented as per wet weight of fruit pulp.

Trait	Chi-square	df	P	South Africa (mean \pm SE)	Australia (mean \pm SE)
Fruit diameter (mm)	1.333	10	0.999	12.17 \pm 3.12	13.31 \pm 3.78
Seed number per fruit	1.608	10	0.999	56.51 \pm 34.99	49.70 \pm 30.21
Seed diameter (mm)	0.890	11	1.000	4.17 \pm 0.90	4.44 \pm 0.94
Total seed wet weight (g)	4.778	11	0.941	0.17 \pm 0.10	0.91 \pm 0.58
% water in pulp	7.028	11	0.797	69.75 \pm 5.85	76.24 \pm 5.71
Lipid (g/100g)	0.218	4	0.994	1.36 \pm 1.00	1.00 \pm 0.80
Nitrogen (g/100g)	0.013	4	1.000	0.39 \pm 0.03	0.28 \pm 0.03
Fructose (g/100g)	0.770	6	0.993	3.15 \pm 0.65	2.70 \pm 0.70
Glucose (g/100g)	1.523	6	0.958	2.82 \pm 0.94	2.87 \pm 1.16
Sucrose (g/100g)	0.473	5	0.993	0.59 \pm 0.36	0.11 \pm 0.11

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FIGURE 1. Categorical representation of morphological and nutritional traits per wet weight of fruit pulp (Supplementary Table 1 and 2 respectively) measured for proposed and declared invasive alien plants listed in Table 1. Each trait consists of 12 equally sized categories, where the maximum value on the x-axis represents the maximum value measured for fruits in this study.

FIGURE 2. Ordination plots of declared invasive ($n = 17$), proposed invasive ($n = 8$), and exotic species ($n = 7$), where a. is based on fruit nutritive traits per wet weight of pulp where factor 1 accounts for 29.4% of the variance and factor 2 for 24.1%, and b. expresses fruit nutritive values per dry weight of pulp, with factor 1 accounting for 26.02% of the variance and factor 2 accounting for 20.93%.

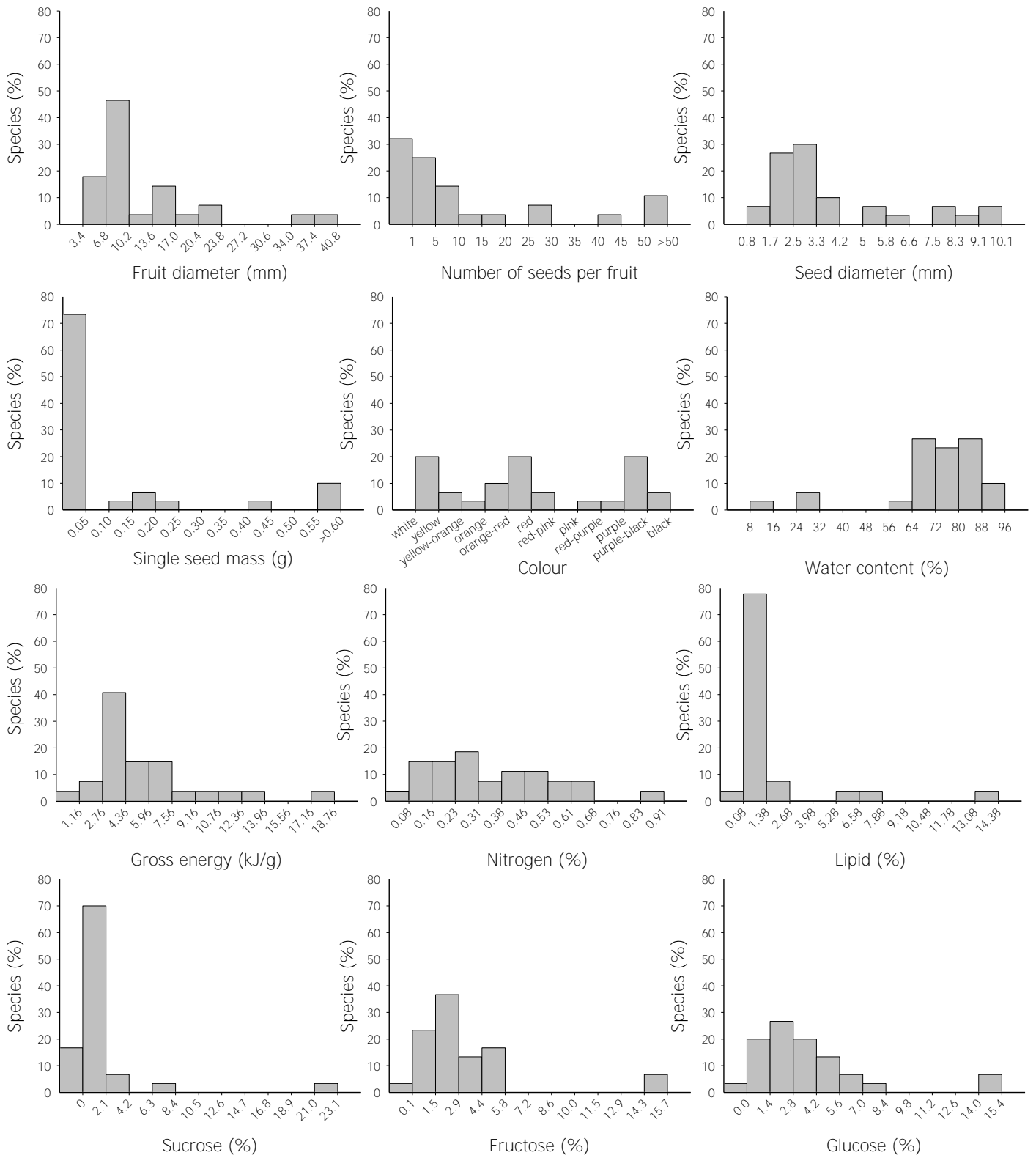


FIGURE 1.

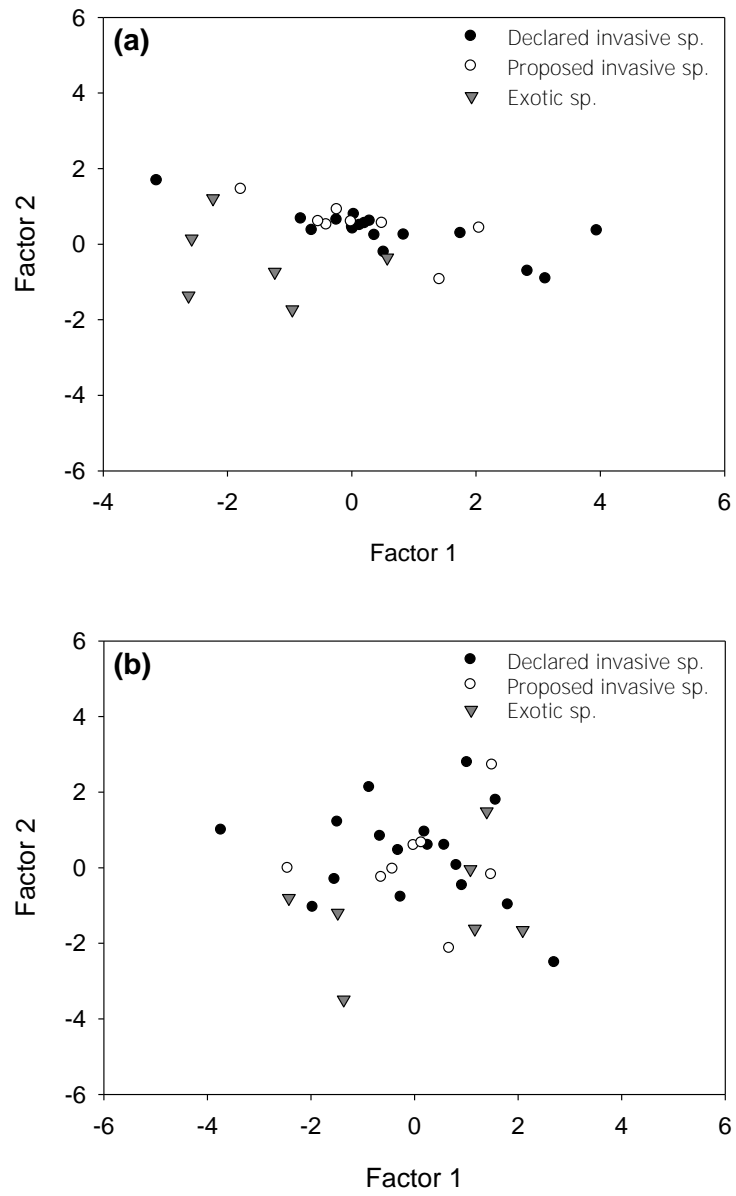


FIGURE 2.

SUPPLEMENTARY TABLE 1. Morphological fruit traits of invasive and exotic plants in KwaZulu-Natal, South Africa

Plant Species	ripe fruit colour	fruit diameter (mm) (n = 10)		seeds / fruit (n= 10)		wet seed mass (g) (n= 10)		seed diameter (mm) (n = 10)	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
<i>Ardisia crenata</i>	pink/red	8.40	0.11	1	0.00	0.1032	0.0032	5.40	0.09
<i>Capsicum frutescens</i>	red	5.76	0.21	18	0.83	0.0049	0.0004	2.77	0.08
<i>Celtis australis</i>	black	9.36	0.11	1	0.00	0.2102	0.0111	6.06	0.09
<i>Cestrum laevigatum</i>	purple/black	5.63	0.16	7	1.02	0.0103	0.0006	2.36	0.10
<i>Cinnamomum camphora</i>	purple/black	8.62	0.27	1	0.00	0.1731	0.0105	6.53	0.23
<i>Coffea arabica</i>	orange/red			2.00	0.00	1.0916	0.0953	10.26	0.31
<i>Cotoneaster pannosus</i>	red	6.94	0.13	2	0.00	0.0122	0.0009	2.98	0.08
<i>Crataegus pubescens</i>	orange	22.59	0.30	4	0.28	0.2125	0.0191	5.28	0.27
<i>Cyphomandra betacea</i>	red/orange	36.56	0.82	141	18.16	0.0096	0.0004	3.35	0.16
<i>Duranta erecta</i>	yellow/orange	7.84	0.39	4	0.00	0.0184	0.0011	3.46	0.10
<i>Eriobotrya japonica</i>	yellow	21.93	0.57	2	0.18	0.7204	0.0864	10.26	0.45
<i>Ficus benjamina</i>	red	9.033	0.1815	>200		< 0.001		0.58	0.07
<i>Ficus benjamina</i> var. <i>comosa</i> Kurz	yellow	16.29	0.30	>200		< 0.002		0.67	0.05
<i>Ficus macrophylla</i>	red	12.30	0.42	>200		< 0.003		0.90	0.05
<i>Ilex aquifolium</i>	red	7.95	0.26	4	0.16	0.0398	0.0018	4.15	0.55
<i>Lantana camara</i>	purple/black	4.74	0.10	2	0.00	0.0230	0.0010	2.71	0.12
<i>Ligustrum japonicum</i>	purple	5.26	0.20	1	0.00	0.0444	0.0014	3.58	0.09
<i>Litsea glutinosa</i>	black	9.82	0.17	1	0.00	0.2502	0.0083	7.70	0.13
<i>Melia azedarach</i>	yellow	11.91	0.18	5	0.00	0.6542	0.0264	8.99	0.18
<i>Morus alba</i>	purple-black	9.14	0.25	29	4.82	0.0018	0.0002	1.78	0.05
<i>Passiflora suberosa</i>	purple/black	9.77	0.34	20	1.24	0.0063	0.0003	2.31	0.07
<i>Pereskia aculeata</i>	yellow	9.37	0.25	2	0.20	0.0046	0.0009	3.67	0.09
<i>Phytolacca dioica</i>	yellow	12.19	0.18	10	0.45	0.0131	0.0007	3.07	0.09
<i>Psidium cattleianum</i>	purple/red	19.84	0.48	7	0.65	0.0337	0.0013	3.26	0.23

<i>Psidium guajava</i>	yellow	45.24	1.23	276	26.64	0.0178	0.0007	2.42	0.11
<i>Pyracantha angustifolia</i>	yellow/orange	8.58	0.10	5	0.10	0.0074	0.0004	1.97	0.05
<i>Pyracantha crenulata</i>	red					0.0026	0.0002	1.21	0.04
<i>Rivina humilis</i>	red	5.00	0.17	1	0.00	0.0038	0.0002	2.12	0.03
<i>Schefflera actinophylla</i>	purple/black	7.09	0.29	14	0.68	0.0087	0.0008	3.21	0.11
<i>Schefflera arboricola</i>	red/orange	7.34	0.14	6	0.30	0.0069	0.0008	2.66	0.10
<i>Schinus terebinthifolius</i>	red	4.39	0.10	1	0.00	0.0151	0.0008	2.87	0.10
<i>Solanum lycopersicum</i>	red	26.61	0.42	121	4.43	0.0037	0.0002	2.26	0.08
<i>Solanum mauritianum</i>	yellow	13.70	0.37	182	4.87	0.0019	0.0002	1.54	0.04
<i>Solanum pseudocapsicum</i>	red	14.01	0.38	43	2.23	0.0062	0.0004	2.81	0.10
<i>Solanum rantonnetii</i>	yellow	16.94	0.60	40	6.09	0.0055	0.0004	2.41	0.08
<i>Solanum seaforthianum</i>	red	8.94	0.35	29	1.88	0.0026	0.0002	2.35	0.07
<i>Symphoricarpos albus</i>	white	7.87	0.37	5	0.48	0.0102	0.0005	2.13	0.11
<i>Syzygium paniculatum</i>	pink/red	14.41	0.37	1	0.00	0.4501	0.0306	7.99	0.35
<i>Syzygium smithii</i>	white/pink					0.2322	0.0189	8.46	0.17

SUPPLEMENTARY TABLE 2. Nutritive fruits traits per dry weight of fruit pulp of invasive and exotic plants in KwaZulu Natal, South Africa

Plant Species	Water Content (%)	N (g/100g)	Lipids (g/100g)	Gross Energy (kJ/g)	Fructose (mg/g)	Glucose (mg/g)	Sucrose (mg/g)
<i>Ardisia crenata</i>	86.20	0.57	1.99	15.74	87.08	156.01	39.65
<i>Capsicum frutescens</i>	69.20	3.10	7.44	22.07	31.13	12.86	32.90
<i>Celtis australis</i>	29.67	0.58	0.34	16.27	221.94	218.26	6.01
<i>Cestrum laevigatum</i>	75.21				140.29	115.92	7.35
<i>Cinnamomum camphora</i>	69.32	0.98	17.37	25.88	67.09	74.87	1.56
<i>Coffea arabica</i>	60.84	1.63	1.29	17.94	54.68	108.16	23.10
<i>Cotoneaster pannosus</i>	78.95	1.19	1.73	17.75	18.92	248.54	6.06
<i>Crataegus pubescens</i>	68.10	0.37	1.41	17.61	61.42	88.29	206.16
<i>Cyphomandra betacea</i>	81.74	1.60	0.87	17.52	91.79	84.75	93.03
<i>Duranta erecta</i>	80.70	2.19	1.14	18.94	148.87	61.95	13.67
<i>Eriobotrya japonica</i>	75.76	0.65	0.84	16.93	228.19	171.80	70.05
<i>Ficus benjamina</i>	78.06	2.12	2.33	17.92	7.50	8.45	4.96
<i>Ficus benjamina</i> var. <i>comosa</i> Kurz	82.11	3.14	3.84	17.22	6.52	7.02	2.30
<i>Ficus macrophylla</i>	76.90	1.04	3.16	17.63	135.72	152.63	2.25
<i>Ilex aquifolium</i>	58.04	0.91	0.86	17.90	246.82	198.08	30.76
<i>Lantana camara</i>	74.31	1.28	0.28	18.49	218.47	131.83	2.03
<i>Ligustrum japonicum</i>	70.85	1.02	5.23	23.20	3.09	164.50	7.03
<i>Litsea glutinosa</i>	67.21	1.86	43.23	28.99	48.73	0.00	0.00
<i>Melia azedarach</i>	29.14	1.28	1.40	17.64	204.38	206.40	22.84
<i>Morus alba</i>	81.31	2.45	2.85	17.96	235.33	210.95	0.00
<i>Passiflora suberosa</i>	83.00	2.67	5.64	19.67	156.15	155.27	3.67
<i>Pereskia aculeata</i>	88.44	2.89	1.87	14.44	36.87	17.35	139.75
<i>Phytolacca dioica</i>	64.85	1.43	1.01	16.86	43.57	41.01	642.42

<i>Psidium cattleianum</i>	79.74	0.69	1.09	16.58	172.16	124.43	181.94
<i>Psidium guajava</i>	81.75		0.99	17.90	210.56	130.27	32.34
<i>Pyracantha angustifolia</i>	69.27	0.67	1.27	18.88	15.59	139.02	1.43
<i>Pyracantha crenulata</i>	77.15	0.68	1.76	17.85	82.57	259.82	2.25
<i>Rivina humilis</i>	90.19				124.21	56.08	0.00
<i>Schefflera actinophylla</i>	72.25	2.09	26.81	24.45	68.74	50.79	0.00
<i>Schefflera arboricola</i>	81.47	1.47	1.91	17.08	100.02	101.57	1.40
<i>Schinus terebinthifolius</i>	10.40	0.67	1.78	20.71	60.05	65.55	0.00
<i>Solanum lycopersicum</i>	92.05	1.73	1.51	17.69	242.32	204.88	0.00
<i>Solanum mauritianum</i>	68.93	1.46	0.67	19.27	175.51	259.03	80.99
<i>Solanum pseudocapsicum</i>	82.75	1.49	1.46	18.86	214.05	234.95	83.35
<i>Solanum rantonnetii</i>	74.95	2.44	11.60	19.43	49.65	80.71	158.50
<i>Solanum seaforthianum</i>	69.76				71.80	52.87	40.31
<i>Symphoricarpos albus</i>	90.16	1.50	1.16	18.66	227.33	192.56	4.50
<i>Syzygium paniculatum</i>	92.78	1.19	1.23	15.99	136.80	109.66	2.36
<i>Syzygium smithii</i>	78.60	1.02	2.57	20.09	49.91	14.16	6.76

For sugar analysis '0' values are under the minimum detection limit, and therefore should be seen as below detection limit and not zero.

Chapter 6

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

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Running header: Comparison in invasive and indigenous *Solanum* species

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 *S. mauritianum*, following ingestion by Red-winged Starlings (*Onychognathus morio* Linnaeus, Sturnidae) and Speckled Mousebirds (*Colius striatus* Gmelin, 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.

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; 2008; van Wilgen et al., 2001). 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 neighbouring 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).

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, 2011). 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 a 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* species (*S. giganteum* and *S. mauritianum* 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

Solanum 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). *Solanum 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 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 μ 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 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 (2011).

Germination percentage data were arcsine transformed and the effect of different treatments (avian ingestion, de-pulped seeds and whole fruit) on the germination rate of both

S. mauritianum 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 values (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. mauritianum* fruits as they had firm, small, red berries as opposed to the larger, yellow, soft fruits of *S. mauritianum* (Table 1; Fig 1). *Solanum* fruits also differed in their seed loads as *S. giganteum* had fewer, but larger, seeds per fruit than *S. mauritianum* (Table 1). They also had more gross energy per gram of pulp, which is consistent with greater lipid content than *S. mauritianum* (Table 1). However, *S. mauritianum* 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. mauritianum* whole fruit controls. Both Red-winged Starling ingested

S. giganteum ($P < 0.05$) and *S. mauritianum* ($P = 0.04$) and Speckled Mousebird ingested *S. giganteum* ($P = 0.04$) and *S. mauritianum* ($P < 0.05$) had significantly higher germination than *S. mauritianum* 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 PV's, with the highest daily germination event occurring in de-pulped *S. mauritianum* 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. mauritianum* 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. mauritianum* 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. mauritianum* seeds did not germinate sooner than de-pulped *S. mauritianum* ($P = 1.00$), 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. mauritianum*. While Red-winged Starling ingested *S. mauritianum* and *S. giganteum* seeds germinated at approximately the same time, de-pulped *S. mauritianum* seeds germinated sooner than de-pulped *S. giganteum* seeds ($P = 0.02$).

After an initial germination event at day 20, most *S. mauritianum* 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). 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).

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 ± 0.71 g (mean \pm SE) of *S. mauritianum* and c. 8.02 ± 1.41 g of *S. giganteum*. Conversely, Red-winged Starlings consumed less *S. mauritianum* (11.11 ± 0.69 g) than *S. giganteum* (70.61 ± 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 ± 4.36 (n = 9) min on the *S. mauritianum* diet and for 30.44 ± 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 values 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; Jordaan et al., 2011b). 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, 2011). 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, 2011).

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 palpating *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 behaviours 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).

Solanum 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, 2011). 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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Table 1

Comparison of morphological and nutritive fruit traits (mean \pm SE) of *S. giganteum* and *S. mauritianum* (n = 10) (Jordaan and Downs, 2011), 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 colour	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/100g)	1.8	1.5
Protein content (g/100g)	10.2	8.2
Lipid content (g/100g)	1.2	0.7
Gross energy (g/100g)	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

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 $P \leq 0.05$

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 <i>SG</i>	0.265	0.412
Speckled Mousebird ingested <i>SG</i>	0.235	0.332
De-pulped <i>SG</i>	0.277	0.396
Whole fruit <i>SG</i>	0.216	0.269
Red-winged Starling ingested <i>SM</i>	0.225	0.455
Speckled Mousebird ingested <i>SM</i>	0.270	0.494
De-pulped <i>SM</i>	0.270	1.049
Whole fruit <i>SM</i>	0.095	0.109

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

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).



Fig. 1.

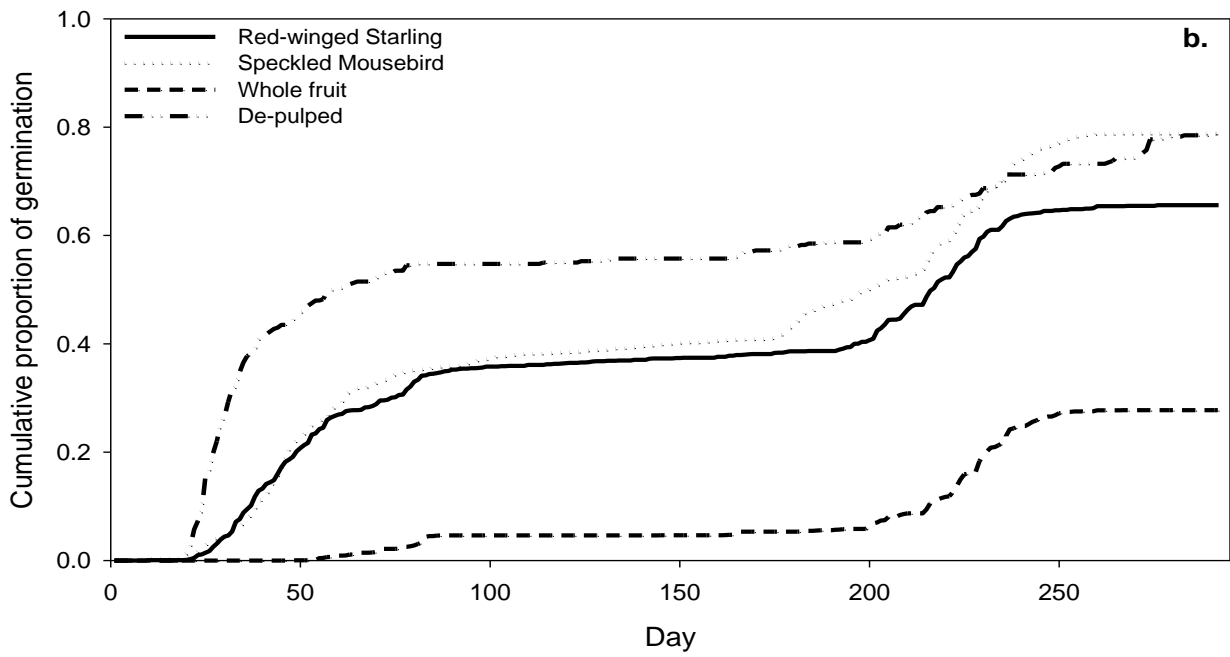
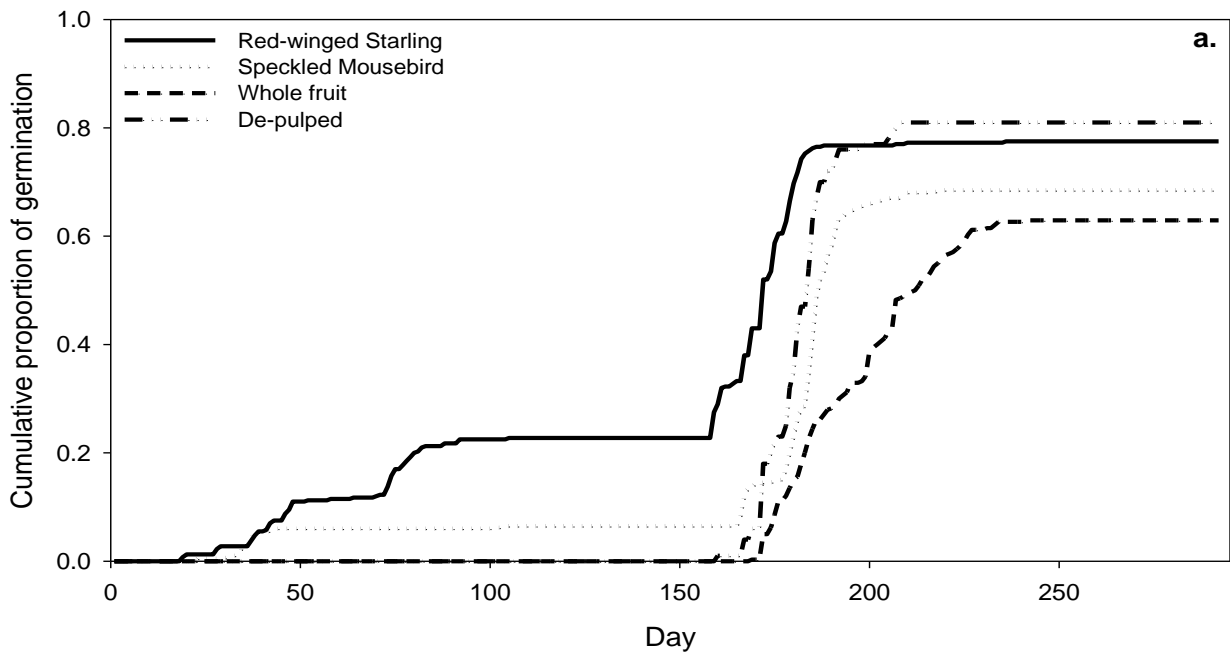


Fig. 2.

Chapter 7

Conclusion

South Africa is one of the countries that is most invaded by alien invasive plants (Milton and Dean 1998, Henderson 2001a). Alien invasive plants owe their success to their ability to overcome abiotic and biotic barriers, that may otherwise impede their spread (Richardson *et al.* 2000a). This is due to their dispersal abilities within a new habitat (Richardson *et al.* 2000b), their lack of natural enemies (Keane and Crawley 2002, Wolfe 2002), and their aggressive qualities which include outcompeting indigenous species for resources, efficient seed dispersal, and quick establishment (Sharma *et al.* 2005). Many invasive alien plants in South Africa are not pollinator limited as they are self-compatible or apomictic (Rambuda and Johnson 2004). Furthermore ‘showy’ floral displays of invasive alien plants have been shown to reduce pollinator visitation rates to indigenous congeners, resulting in the reduced seed set of these (Brown *et al.* 2002). A similar trend has been observed whereby plants with greater fruiting displays (as is often the case with invasive alien plants (Henderson 2001b)) experience increased fruit removal rates (Bach and Kelly 2004).

Frugivory is a mutually beneficial relationship as dispersers receive a food resource and plant seeds are dispersed away from the parent plant (Jordano 1987, Schupp 1993, Kinnaird 1998). Many destructive and aggressive invasive alien species have been linked with bird-dispersal (Buckley *et al.* 2006), with the role of other vertebrate dispersers rarely being considered. Knowledge of frugivores and their role in long-distance seed dispersal would facilitate predicting range expansion processes and plant movement patterns of invasive alien plants (Higgins and Richardson 1999, Cain *et al.* 2000). Frugivory information is valuable to all stages of invasive weed control, from assessing pre-entry risk to the eradication and management of existing problem plants (Buckley *et al.* 2006). Functional group approaches

which consider both plant and frugivore traits will allow for more practical generalizations, but such studies have remained scarce (Buckley et al. 2006). Such studies should also consider the importance of phylogenetic relatedness. Conventional methods of mechanical and / or chemical control have been largely unsuccessful, as has the release of biocontrol agents for some species (Olckers 1999, Ghisalberti 2000, Day *et al.* 2003). This has given rise to the idea and motivation for using integrated control methods (Olckers 1999, Ghisalberti 2000, Day *et al.* 2003), however to efficiently do so, better knowledge of invasive plants' dispersal mechanisms needs to be generated.

The main objective of this study was to consider invasive alien plants from both plant and frugivore perspectives. Consequently, this study was broadly divided into two sections: the effect that frugivores have on seed germination of invasive alien plants and the direct benefits to the frugivores when feeding on their fruits.

Frugivore effect on seed germination

Germination rates of seeds of invasive alien plants following processing by both avian frugivores and fruit bats were determined. In this study three generalist avian frugivore species were selected, namely: Red-winged Starlings (*Onychognathus morio*), Speckled Mousebirds (*Colius striatus*), and Dark-capped Bulbuls (*Pycnonotus tricolor*). These were fed four alien invasive plant species in separate trials and included: *Solanum mauritianum* Scopoli (bugweed), *Cinnamomum camphora* (camphor), *Lantana camara* (lantana), and *Psidium guajava* (yellow guava). Their effect on seed germination (Chapter 3) and digestion (Chapter 2) of these fruits was investigated. In a separate trial Wahlberg's Epauletted Fruit Bats (*Epomophorus wahlbergi*) were fed *P. guajava*, *Melia azedarach* L. (syringa), *Eriobotrya japonica* (Thunb.) Lindl. (loquat), and *Morus alba* L. (mulberry) (Chapter 4). Finally, Red-winged Starlings and Speckled Mousebirds were used in a comparative study to determine if

indigenous *Solanum giganteum* varied in its germination success from invasive *S. mauritianum* following frugivore ingestion (Chapter 6). Fruit morphology and nutritive traits were also compared (Chapter 5).

These frugivores were chosen as they have been observed feeding on the alien invasive fruit selected for this study (Jordaan pers. obs. Voigt *et al.* 2011), and are potentially efficient seed dispersers as they are common and wide ranging frugivores (Lafleur *et al.* 2007). Furthermore, these plants (Henderson 2001b, Boon 2010) and frugivores (Hockey *et al.* 2005, Monadjem *et al.* 2010) have overlapping distributions along the east coast of South Africa. In South Africa birds are noted as the primary dispersers of *S. mauritianum*, *C. camphora*, *P. guajava*, *L. camara*, *M. alba*, *M. Azedarach*, and *Eriobotrya japonica* (Henderson 2007). Mammals are also listed as dispersers of *P. guajava*, but as a group, fruit bats remain poorly recognised for their contribution as dispersers of these plants.

Seed retention time has been shown to influence germination (Traveset 1998). This is because of the duration that seeds are exposed to the effects of the digestive tract, which in turn determines the level of seed coat abrasion (Evenari 1949, Agami and Waisel 1988, Barnea *et al.* 1990, 1991). However, this was not the case with the invasive plants used in this study, as manually de-pulped seeds generally germinated at similar rates and amounts to frugivore processed seeds (Chapter 3; Chapter 4; Chapter 6). The similar effect of mechanical pulp removal and avian frugivore ingestion has been well documented (Barnea *et al.* 1991, Panetta and McKee 1997, Meyer and Witmer 1998). However, the influence of fruit bats, which mostly do not ingest seeds, on germination rates remains poorly documented.

Pulp removal was particularly beneficial for the removal of waxy exocarps of *L. camara* and *C. camphora* fruit, and also allowed for a more rapid onset of germination for the large-fruited *P. guajava* (Chapter 3). While seeds contained within whole fruit did germinate, these amounts were generally lower than frugivore processed and de-pulped seeds (Chapter 3;

Chapter 4; Chapter 6). This suggests that frugivores may facilitate enhanced germination success and earlier onset of germination through pulp removal, but serve primarily as dispersers of these plants as whole fruit seeds did still germinate. The invasive alien plants used in this study generally had rapid establishment and high germination percentages (Chapter 3; Chapter 4; Chapter 6), which would play an important role in the invasion process. When the indigenous congener *S. giganteum* was compared to *S. mauritanum*, they responded in a similar way, with both de-pulped and ingested seeds germinating equally (Chapter 6). However, *S. giganteum* seeds in whole fruit did have lower germination success than all those in other treatments and may therefore rely more on frugivores for pulp removal (Chapter 6).

Frugivore benefits

While frugivores are recognised for their role as dispersers of invasive alien plants (Richardson *et al.* 2000b, Renne *et al.* 2002, Buckley *et al.* 2006), the energetic gains obtained by them when feeding on invasive alien plants have only now been considered. Results from this study have shown that all three avian frugivore species were able to meet their energetic demands by feeding on invasive alien fruit only, with the exception of Red-winged Starlings on the *P. guajava* and *L. camara* diets (Chapter 2). Avian frugivores were also able to adjust their feeding behaviour by eating more nutritionally poor fruit and less energy rich fruits (Chapter 2). A similar trend was also observed on the indigenous *S. giganteum* diet (Chapter 6).

There was great variation in the energetic parameters calculated for different frugivores and fruit types (Chapter 2). Such variation in fruit-frugivore relationships is widely accepted (Sallabanks and Courtney 1993) and creates difficulties when making generalizations regarding such interactions. Variation in fruit morphology and nutritional value (Tsahar *et al.*

2003) affect birds feeding modes (Stiles 1993, Symes and Downs 2001). Such inconsistencies and variation in trends between different plant and frugivore species is not unusual (Sallabanks and Courtney 1993) and in future can be combated by using larger species sample sizes and grouping species with similar traits.

Frugivores have been shown to prefer fruit of invasive plant species over those of indigenous species (Fraser 1990, Lafleur *et al.* 2007). In South Africa, fruits of invasive alien plants are similar in morphology, but offer greater nutritional rewards than indigenous fruits (Chapter 5). This has also been observed elsewhere (Gosper and Vivian-Smith 2010). The nutrient trends observed in fruits of invasive species mirror the preferences of many frugivorous birds (Baker *et al.* 1998), which is not surprising as avian frugivory is more common (Fleming and Kress 2011) and birds are relatively more abundant (Lafleur *et al.* 2007). Invasive fruits in this study were hexose dominant with little lipid and protein content (Chapter 5), a trend observed in fruits of invasive plants in Australia (Gosper and Vivian-Smith 2010), fruits of indigenous plants in South Africa (Wilson and Downs 2011), and bird dispersed fruits on a global scale (Baker *et al.* 1998). Fruits of invasive plants also tended to have small, light seeds (Chapter 5). Such data could explain why frugivores readily feed on these novel fruits, often in large flocks (Berens *et al.* 2008), and provides new insights into the alien plant-frugivore relationship. Future studies should investigate the types of micronutrients, the importance of these to frugivores, and the potential impact they may have on fruit preference and feeding behaviour.

Frugivores have been shown to prefer small fruit containing one or few seeds (Gosper and Vivian-Smith 2009), and / or soft multi-seeded fruits (Green 1993). Fruit size is particularly important for avian frugivores (Green 1993, Stansbury and Vivian-Smith 2003), as their gape size limits the size of fruit that can be ingested whole (Wheelwright 1985). Bigger fruits may be consumed piece-meal (mashers) (Levey 1987, Symes and Downs 2001),

and thus large fruits with larger seeds would rely on mammal dispersal as they are able to carry these to feeding sites (Monadjem *et al.* 2010). Most fruits of invasive plants from this (Chapter 5) and other studies are not disperser limited as they are small (Stansbury and Vivian-Smith 2003, Gosper and Vivian-Smith 2010).

Many invasive alien species form dense, homogenous stands with persistent seed banks (Henderson 2001b, Lugo 2004). They also fruit year round (Henderson 2001b, Corlett 2005), producing proportionately greater fruiting outputs (Rejmánek 1996). In South Africa *L. camara* (Graaff 1987) and *S. mauritianum* (Henderson 2001b) are examples of invasive plant species that fruit throughout the year. Not surprisingly *S. mauritianum* is considered one of the five worst invasive plants in South Africa (Witkowski and Garner 2008), while *L. camara* is ranked as one of the worst invasive plants worldwide (Sharma *et al.* 2005). Large fruit displays contribute in attracting frugivores and increase fruit removal rates (Bach and Kelly 2004). Avian frugivores have been noted to shift their diets relative to fruit availability (Levey and Martinez del Rio 2001) and in light of this, large fruit displays would enhance the competitive ability of invasive plants in attracting dispersers. Fruit colour attracts frugivores and indicates the nutritional rewards of the fruit (Schaefer *et al.* 2007). However, nocturnal frugivores may rely more on olfaction to detect ripe fruits (Raghuram *et al.* 2009), but such studies remain sparse. Birds generally show a preference for red or black fruits (Ridley 1930, Bach and Kelly 2004) and while invasive fruits from this study varied in colour, most were shades of red and black (Chapter 5). This was also found for indigenous fruits in South Africa (Wilson and Downs 2011).

Seed load also influences frugivore fruit preference, with frugivores varying in their choice of seed size and number (Stanley and Lill 2002a, 2002b, Wilson and Downs 2010). It has been suggested that ‘good invaders’ should produce numerous small seeds (Harper 1977), yet most fruits from this study contained small, light seeds, with only c. 30% having more

than 10 seeds per fruit (Chapter 5). This was also found for invasives elsewhere (Gosper and Vivian-Smith 2009, 2010). Small seeds can germinate faster than larger seeds (Norden *et al.* 2009) and therefore give invasives a competitive edge. Although invasive seeds are generally smaller (Rejmánek 1996), their total seed production is greater (Mason *et al.* 2008) because of a combination of other invasive traits which include greater fruiting outputs and longer fruiting seasons (Rejmánek 1996).

Wahlberg's Epauletted Fruit Bats were able to process more fruit per gram body mass (Chapter 4) than the various frugivore bird species were observed to do (Chapter 3; Chapter 6). They would sometimes consume more than their body mass in fruit in one evening (Chapter 4), which is not unusual for fruit bats (Morrison 1980, Thomas 1984, Izhaki *et al.* 1995). Furthermore, their relatively large size compared with other indigenous bat species (Monadjem *et al.* 2010) means they can process proportionally more fruit per individual (Izhaki *et al.* 1995). *Epomophorus wahlbergi* can potentially disperse more than 5000 *M. alba* seeds in one evening (Izhaki *et al.* 1995). Fruit bats are able to carry larger seeds and fruits away from parent trees to roosting sites (Fenton *et al.* 1985, Corlett 2005, Monadjem *et al.* 2010). These two factors combined make fruit bats highly efficient and important dispersers of invasive alien seeds and their role in this should thus be formally acknowledged. The next step would be to investigate their feeding behaviour and movement patterns to determine their seed shadows and efficiency as dispersers.

Conclusion

While vertebrate dispersers have been broadly acknowledged for their role in facilitating and enhancing the spread of invasive plants (Rejmanek and Richardson 1996), especially into undisturbed habitats (Bass 1990), results from this study confirm it. The importance of resource benefits to the frugivore have been highlighted (Chapter 2; Chapter 5),

as these encourage frugivores to feed on these invasive fruits. The role of frugivores as dispersers of these plants has also been elucidated (Chapter 3; Chapter 4; Chapter 6).

Invasive alien plants offer morphologically similar, yet more rewarding fruit (Chapter 5), and this can explain why in many cases these are preferred by frugivores (Fraser 1990, Lafleur *et al.* 2007). Added to this large and prolonged fruit displays (Henderson 2001b) increase their reproductive output and facilitate the invasive process. Studies on frugivore fruit preferences and feeding behaviours would enable a comprehensive understanding of the dynamic interaction between invasive alien plants and their dispersers. The ability of invasive alien plants to germinate rapidly and prolifically without frugivore ingestion has been previously under-recognised, but may not necessarily differ from that of indigenous species trends. Their competitive edge over indigenous species could therefore be attributed to their proportionally larger reproductive outputs. Invasion biology would be benefitted by more comprehensive comparative studies to facilitate the identification of invasive traits. Combining these data with that of future field based observations we can begin to complete our understanding of the multifaceted invasion process and start to formulate more integrated control methods. Indeed this may be the only way to win the battle against invasive plants.

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