

# Ingestion by an invasive parakeet species reduces germination success of invasive alien plants relative to ingestion by indigenous turaco species in South Africa

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**Abstract** Avian frugivores play a key role in seed dispersal of many plant species, including invasive alien plants. We assessed the effect of gut passage on the germination of selected invasive alien plant species in South Africa. Fruits of four fleshy-fruited invasive alien plant species: *Solanum mauritianum*, *Cinnamomum camphora*, *Psidium guajava*, and *Morus alba*, were fed to two species of indigenous turacos, Knysna (*Tauraco corythaix*) and purple-crested (*Gallirex porphyreolophus*) turacos, and to invasive rose-ringed parakeets (*Psittacula krameri*). Seed retention time was determined as this can influence both seed dispersal and germination success. Germination success of ingested seeds was compared with that of manually de-pulped seeds, as well as to seeds in whole fruit. The germination success of seeds of all the invasive plant species increased significantly after ingestion by both turaco species compared with seeds from whole fruits. Germination success of manually de-pulped seeds did not differ significantly from that of turaco ingested seeds. In contrast, seed passage through the digestive tract of rose-ringed parakeets significantly reduced germination success and viability of ingested invasive plant species. Our results

suggest that Knysna and purple-crested turacos are legitimate seed dispersers of fleshy-fruited invasive plants, while rose-ringed parakeets are mainly seed predators. Although seed predation by rose-ringed parakeets negatively affects the reproductive success of these plants, it is unlikely that this will suppress the spread of these invasive alien plants in South Africa as they are already well established. Furthermore, they can facilitate dispersal by seed regurgitation and dropping uneaten fruits away from the parent plant. Similar trends could be expected for indigenous seeds that rose-ringed parakeets feed on and therefore these birds remain a negative influence within invaded ecosystems.

**Keywords** Avian frugivore · Pulp removal · Seed predation · Seed germination · Seed retention time

## Introduction

Avian frugivores play a key role in seed dispersal of many plant species worldwide (Cain et al. 2000; Renne et al. 2000; Vivian-Smith and Gosper 2010; Jordaan et al. 2011a; Mokotjomela et al. 2013b, 2015). The process of seed dispersal by avian frugivores usually involves the consumption of pulp and regurgitation or excretion of intact seeds (D'Avila et al. 2010; Fedriani et al. 2011; Czarnecka et al. 2012). This process is mutually beneficial as plants benefit from

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seed dispersal away from the parent plant to locations with fewer pathogens (Wenny 2001; Aslan 2011; Fricke et al. 2013) while frugivores benefit from important food resources and energy rewards (Jordaan et al. 2011b; Mokotjomela et al. 2013a). Avian frugivores consume both native and invasive fruit and therefore can facilitate the rapid spread of fruiting invasive species (Davis 2011; Mokotjomela et al. 2013b).

Ingestion by frugivores may increase, decrease, or have no effect on seed germination success of different plant species (Samuels and Levey 2005; Jordaan et al. 2012; Spotswood et al. 2012; Wilson and Downs 2012; Lessa et al. 2013). Many studies show that germination is more successful after seeds pass through the digestive tract of frugivores (Traveset 1998; Yagihashi et al. 1999; Traveset et al. 2001; Paulsen and Hogstedt 2002; LaFleur et al. 2009; D'Avila et al. 2010; Reid and Armesto 2011; Jordaan et al. 2011a). Seed ingestion by dispersers helps seeds escape predation, competition, and fungal attack under the parent tree, thereby increasing the chance of survival (Chimera and Drake 2010; Fedriani et al. 2011; Jordaan et al. 2011a). The chemical or mechanical modification of the seed coat structure due to ingestion has also been suggested to enhance germination (Wilson and Downs 2012).

Some studies have also found that seeds ingested by frugivores may lose viability and thus reduce germination or have no effect on germination success at all (LaRosa et al. 1985; Wilson and Downs 2012). This may be due to excessive abrasion of seeds or the toxicity and hydrophobic nature of excreta (Vivian-Smith and Gosper 2010; Reid and Armesto 2011). The germination response of ingested seeds can be influenced by several factors (Charalambidou et al. 2003). These include seed retention time, seed coat structure and seed sizes (Greenberg et al. 2001; Guix 2007). Seed retention time in frugivores' guts is the most important factor for some species in determining their germination success (Traveset 1998; Cain et al. 2000). Small seeds tend to have longer retention times and are less likely to be damaged during gut passage compared with large seeds (Charalambidou et al. 2003). However, in some species shorter transit times are observed and these fruits are preferred by avian frugivores (Wilson and Downs 2011).

The consumption of fruits by birds may not necessarily result in successful dispersal (Mandon-

Dalger et al. 2004; Westerman et al. 2006; Combs et al. 2011). This is because some frugivorous birds are seed predators (Jordano 1983). Seed predators usually crush the seeds during feeding and then excrete them damaged (Jordano 1983). However, some seed predators may contribute to the dispersal of invasive plants (Vila and Gimeno 2003). This occurs when predators do not consume the fruit immediately but carry them away to feeding roosts for later consumption where seeds are regurgitated or dropped (Carrion-Tacuri et al. 2012). This brings the regurgitated seeds into contact with the soil and forms seed banks that can successfully germinate, especially when the parental plants are removed (Witkowski and Garner 2008). It has been found that some seed predators such as parrots and Darwin's finches act as dispersers of native and invasive alien plants in Hawaii across both short and long distances (Jordano 1983; Carrion-Tacuri et al. 2012). However, few studies have been conducted that examine the possible role that seed predators play in the successful invasion or invasion suppression of invasive plants globally (Carrion-Tacuri et al. 2012).

South Africa is one of the countries that have been extensively invaded by fleshy-fruited invasive plants (Henderson 2001; van Wilgen et al. 2001; Nel et al. 2004; Richardson and van Wilgen 2004). Many studies have shown that these plants are consumed and dispersed by both invasive and indigenous birds (Jordaan et al. 2011a; Westcott and Fletcher 2011; Wilson and Downs 2012; Mokotjomela et al. 2013c). However, the role of invasive birds as seed dispersers or predators has received little attention, especially in terms of their effect on the dispersal and germination success of invasive plants in South Africa. Understanding the ecological principles underlying the invasive process such as how they are dispersed, as well as what influences their rapid growth, is crucial for the development of effective and viable management strategies to reduce the rate of spread of these species and for any control measures to be successful. To date, few studies have looked at the interaction between invasive bird species, indigenous bird species and invasive alien plant species, particularly in South Africa (Jordaan et al. 2011a). Therefore, our aim was to determine the effects of invasive rose-ringed parakeets (*Psittacula krameri*) and indigenous Knysna (*Tauraco corythaix*) and purple-crested (*Gallirex porphyreolophus*) turacos on seed germination of four

invasive alien plant species in South Africa. To investigate this, we compared the germination success (percentage and rate) of ingested seeds (those that have passed through the digestive tract or were regurgitated), manually de-pulped seeds and seeds within whole fruits. We predicted that fruit processing by these avian species would increase the germination success of invasive alien seeds. Results from this study may play a significant role in the implementation of effective management strategies of invasive plants in South Africa and worldwide.

## Methods

### Maintenance of study animals

Ten captive-bred rose-ringed parakeets, eight captive-bred Knysna turacos and two captive-bred purple-crested turacos were housed in outside aviaries ( $1 \times 2.12 \times 2.66$  m) at the University of KwaZulu-Natal (UKZN), Pietermaritzburg animal house before the experiments were conducted. Birds were fed a mixed fruit maintenance diet daily which consisted of pears, apples, bananas and oranges. All fruits were either grated or chopped and AviPlus Softbill/Mynah pellets and crumble (Avi-products, Durban, South Africa) were added to supplement the maintenance diets. Rose-ringed parakeets were also fed sunflower seeds daily. Water was provided ad libitum.

### Study species

Purple-crested and Knysna turacos are medium-sized (c. 300 and 310 g respectively) frugivorous bird species indigenous to South Africa (Sinclair and Ryan 2003). The rose-ringed parakeet (c. 120 g) is the most introduced parrot species in the world and has established feral populations in many countries, including South Africa (Butler 2003; Sinclair and Ryan 2003; Brooke 1997; Hart and Downs 2014). Rose-ringed parakeets are native to southern Asia and sub-Saharan Africa (Brooke 1997; Butler 2003). These frugivorous bird species were selected as Turacos and rose-ringed parakeets eat fruits of both invasive and indigenous plants and co-occur in KwaZulu-Natal, South Africa. Little is known about their effect on the dispersal and germination success of invasive plants in South Africa.

### Plant species

We used fruits of four invasive alien plant species, namely bugweed (*Solanum mauritianum*), camphor (*Cinnamomum camphora*), guava (*Psidium guajava*), and mulberry (*Morus alba*) in this study. These fruit species had been observed to be eaten by birds or were reported as a food source to frugivorous birds in the wild. All ripened fruits were collected from naturalized plants near UKZN and fruits were used within 48 h of collection.

Bugweed is a shrub that usually grows up to 4 m in height and produces numerous round yellow berries 1–1.5 cm in diameter (Olckers 1999; Jordaan et al. 2011a). Each fruit contains c. 200 seeds that are 0.15–0.20 cm long (Jordaan et al. 2011a). Bugweed is native to Northern Argentina, Southern Brazil, Paraguay and Uruguay but has become a widespread invasive weed in many countries including South Africa (Olckers 1999; Jordaan et al. 2011a). The great invasive success of bugweed is facilitated by secondary distribution of the plant via seed dispersal by frugivorous animals (Olckers 1999; Henderson 2001).

Camphor is an evergreen tree growing up to 40 m high (Panetta 2001). This tree produces large quantities of dark blue to black fleshy fruits approximately 1–1.5 cm in diameter (Panetta 2001). Each fruit contains a single seed that is 0.75 cm in diameter (Jordaan et al. 2011a). Over 100,000 fruits can be produced on a mature tree (Panetta 2001). Ripe fruits are ingested by a number of bird species, and seeds may be either regurgitated or excreted after consumption (Li 2004). This species is native to Japan, China and eastern Asia but has become widely naturalised in many countries around the world (Panetta 2001).

Guava is a fast growing evergreen tree or shrub adapted to a wide range of environmental conditions (Henderson 2001). Guava trees produce yellow, rounded fruits 3–10 cm in diameter (Henderson 2001). Each fruit contains numerous seeds (c. 100–500) that are 0.3–0.5 cm in diameter (Jordaan et al. 2011a). This species is native to Central America (Berens et al. 2008).

Mulberry is a deciduous tree growing up to 15 m in height with juicy elongated purple-black fruits (Henderson 2001). The fruits are 2–3 cm long and each fruit contains up to c. 30 seeds (Henderson 2001). The mulberry is native to eastern United States and has

been widely introduced globally for its sweet and edible fruits (Henderson 2001).

#### Feeding trials

We moved birds to a constant environment room with a 12L:12D photoperiod at  $25 \pm 1^\circ\text{C}$  two weeks before trials were conducted and housed them individually in cages ( $42.7 \times 43 \times 59.3$  cm). Clean plastic trays, the same size as the cage's base, were placed in each cage to facilitate removal of faeces.

For two days prior to each experimental day, we incorporated the specific experimental fruit species into the maintenance diet. On the experimental day, we fed birds a diet of only each specific invasive alien fruit species, either whole or cut up. Each trial was run for 12 h (from 06h00–18h00). Fruits were weighed to 0.01 g before and after each trial to determine the amount of fruit eaten. Birds were also weighed to 0.5 g 30 min prior to, and again at the end, of each trial. Control fruits were placed in the experimental room and were also weighed prior to, and at the end, of each trial to control for evaporative water loss. Excreta were collected from the plastic trays at the end of each trial. A minimum of 3 days was left between each trial depending on fruit availability. The maintenance diet was fed between each trial to enable birds to regain any body mass lost during experiments.

#### Seed retention time

We determined seed retention time by recording the time when birds first started feeding, to the time when first undigested seeds appeared in excreta. For regurgitated seeds, the seed retention time was measured as the time when birds first fed to the time when undamaged seeds appeared in the regurgitated food. Seed retention time was measured on the experimental day only. In each retention time trial, a single specific fruit species for the particular trial was presented either whole or cut up to all birds individually. Previous studies have reported that the maximum gut retention time for turacos is ca. 12–35 min (Wilson and Downs 2012) while that of parakeets is ca. 30–50 min (Koutsos et al. 2001). As retention time may vary with fruit type, we measured seed retention time in order to determine the potential effect on germination success and potential seed dispersal distance.

#### Germination trials

We removed seeds from each individual bird's excreta or regurgitation and planted these in separate trays ( $265 \times 180 \times 75$  mm) containing potting soil with no additives within 24 h after the feeding experiment. Seeds were covered with a soil layer c. 0.5 cm deep. Manually de-pulped seeds and seeds within whole fruit of each species were planted concurrently in the same manner as ingested seeds. All trays were then placed in the shade house and watered daily. Seeds were considered germinated when seedlings first emerged through the soil surface. The number of germinated seeds was recorded daily for 100 days. The date of seedling emergence was recorded and once counted, seedlings were removed from the tray.

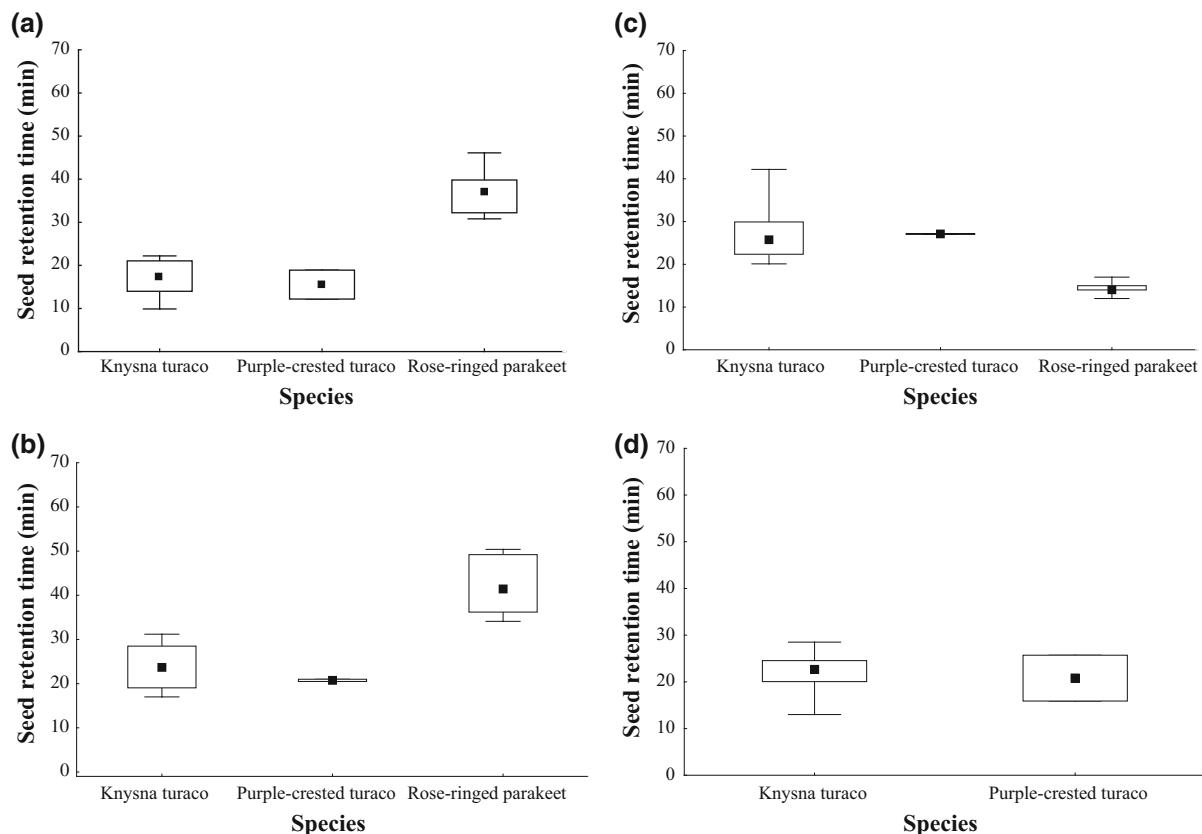
#### Data analysis

The cumulative percentage germination was determined for each tree species. Mean cumulative germination percentage was calculated for ingested, pulp manually removed and whole fruits seeds for each fruit species. Germination periods for each plant species were compared using Kruskal–Wallis ANOVA tests. Seed retention time for each individual bird and for a specific fruit was also analyzed using Kruskal–Wallis ANOVA tests. Kruskal–Wallis ANOVA tests were also used to compare germination success of ingested seeds to manually de-pulped seeds and whole-fruit controls. Further investigations with post hoc Tukey tests were performed where significant differences were evident. All statistical analyses were conducted using STATISTICA (Statsoft, Tulsa, version 7, USA).

## Results

#### Seed retention time

Seed retention time did not vary significantly between Knysna and purple-crested turacos but varied significantly between rose-ringed parakeets and both species of turacos for most invasive plant species (Fig. 1). Knysna and purple-crested turacos had shorter retention times (10–22 and 12–19 min respectively) when fed *M. alba* seeds than rose-ringed parakeets (31–46 min,

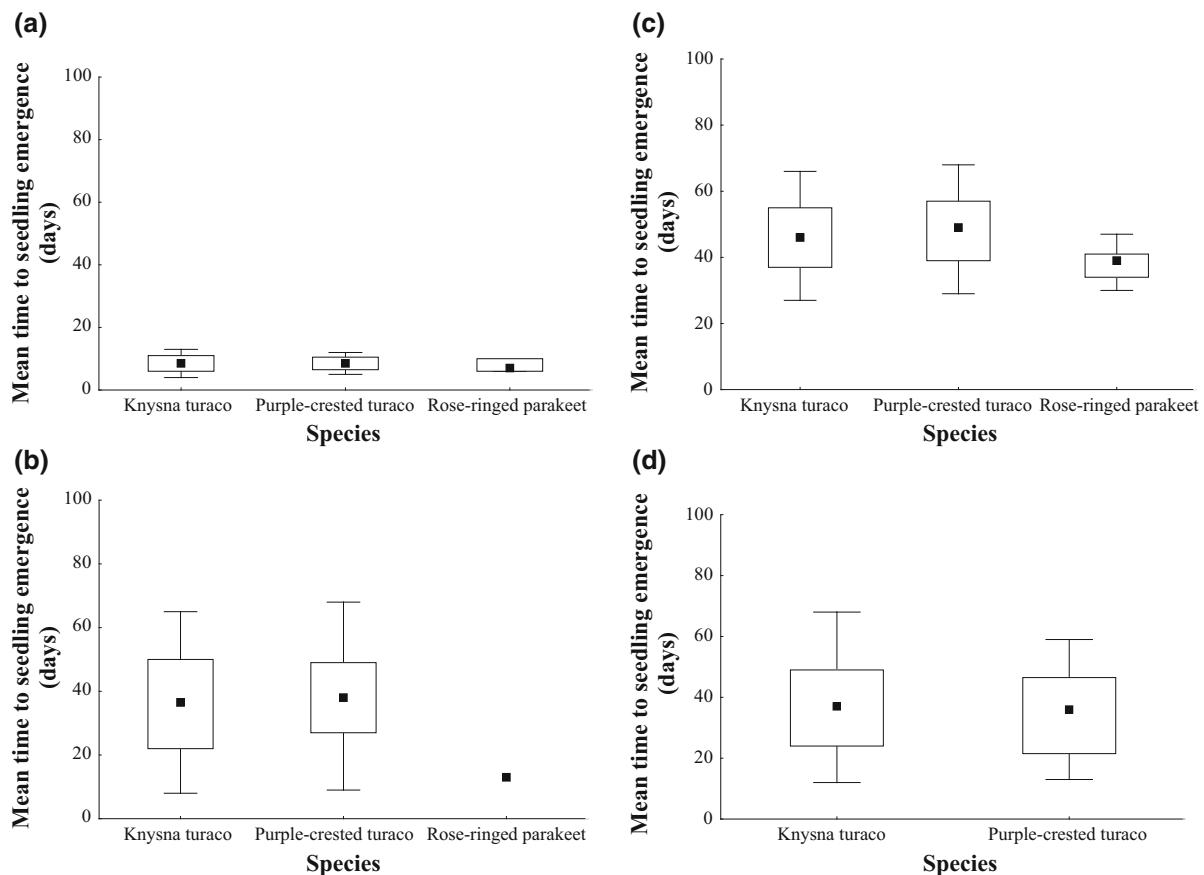


**Fig. 1** Seed retention time for three avian species feeding on fruits of **a** *M. alba*, **b** *P. guajava*, **c** *C. camphora*, and **d** *S. mauritianum*, where boxes are 25 and 75 % quartiles, the solid black squares within the boxes the medians, bars show 10 and 90 % values

Kruskal-Wallis ANOVA  $H_2 = 14.36$ ,  $n = 20$ ,  $P = 0.001$ , Fig. 1a). Similarly, both turaco species had significantly shorter seed retention times (17–31 min and 20–21 min respectively) than rose-ringed parakeets (34–50 min) when fed *P. guajava* fruit (Kruskal-Wallis ANOVA  $H_2 = 14.36$ ,  $n = 20$ ,  $P = 0.001$  (Fig. 1b). Retention times for *C. camphora* seeds did not vary significantly between purple-crested turacos and rose-ringed parakeets (post hoc Tukey,  $P = 0.14$ , Fig. 1c) but varied significantly between Knysna turacos and rose-ringed parakeets (post hoc Tukey,  $P = 0.009$ , Fig. 1c) (Kruskal-Wallis ANOVA  $H_2 = 9.39$ ,  $n = 15$ ,  $P = 0.009$ , Fig. 1c). Seed retention time did not differ significantly between Knysna and purple-crested turacos when fed *S. mauritianum* fruits (Kruskal-Wallis ANOVA  $H_1 = 0.068$ ,  $n = 10$ ,  $P = 0.79$ , Fig. 1d). Rose-ringed parakeets regurgitated *C. camphora* seed; excreted few *M. alba* and *P. guajava* seeds but did not ingest *S. mauritianum* seeds at all.

#### Mean time to seedling emergence

The mean time for emergence of seedlings did not vary between avian species for all invasive plant species (Fig. 2). However, seedling emergence from ingested seeds varied significantly among the invasive plant species (Kruskal-Wallis ANOVA  $H_3 = 70.57$ ,  $n = 174$ ,  $P = 0.00$ , Fig. 2). *M. alba* seeds germinated significantly sooner than all species while *C. camphora* seedlings emerged significantly later than those of other invasive plant species (Fig. 2a, c). All *M. alba* ingested by avian species germinated after ca. 5 days (Fig. 2a), which was not significantly earlier than manually de-pulped seeds but significantly sooner than whole fruit seeds (Kruskal-Wallis ANOVA  $H_4 = 22.84$ ,  $n = 38$ ,  $P = 0.00$ , Fig. 3a). Ingested *S. mauritianum* seeds started germinating after ca. 13 days (Fig. 2d); this was not significantly earlier than manually de-pulped seeds (Fig. 3d) but significantly sooner than whole fruit seeds,



**Fig. 2** Mean time to first seedling emergence of seeds ingested by three avian species (or regurgitation by rose-ringed parakeet in the case of *C. camphora*) for **a** *M. alba*, **b** *P. guajava*, **c**

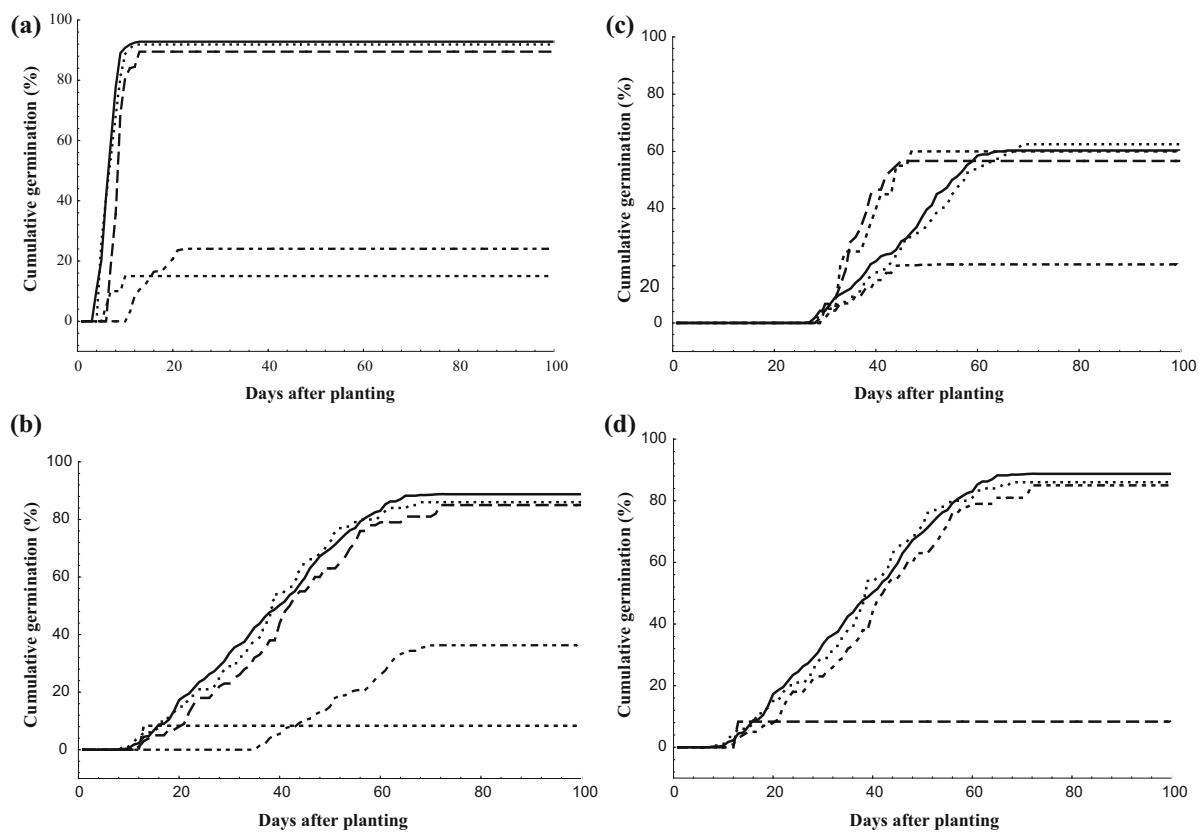
*C. camphora*, and **d** *S. mauritianum*, where boxes are 25 and 75 % quartiles, the solid black squares within the boxes the medians, bars show 10 and 90 % values

which only started emerging after 45 days (Kruskal–Wallis ANOVA  $H_3 = 17.75$ ,  $n = 144$ ,  $P = 0.001$ , Fig. 3d). Similarly, ingested *P. guajava* seeds began germinating after ca. 9 days (Fig. 2b) which was similar to manually de-pulped seeds (Fig. 3b) but significantly earlier than whole fruit seeds (Kruskal–Wallis ANOVA  $H_4 = 30.98$ ,  $n = 168$ ,  $P = 0.00$ , Fig. 3b). Seeds contained in whole fruit of *P. guajava* and *S. mauritianum* showed significantly lower germination rates than ingested and manually de-pulped seeds (Fig. 3b, d), while seeds contained in whole fruit of *C. camphora* emerged at approximately the same time with ingested and manually de-pulped seeds (Fig. 3a, c).

#### Germination success

Seeds ingested by Knysna and purple-crested turacos had higher germination percentages than those

ingested by rose-ringed parakeets for all invasive plant species, except those of *C. camphora* (Table 1; Fig. 3). There was no significant difference in germination percentage of ingested seeds between Knysna and purple-crested turacos for all plant species tested, and these seeds had similar germination percentages to those from manually de-pulped seeds (Table 1; Fig. 3). These germination percentages were significantly higher than for whole fruit seeds for all invasive plant species (Table 1). In contrast, seeds that passed through the digestive tract of rose-ringed parakeets (i.e. *M. alba* and *P. guajava*) had significantly lower germination percentages compared with turaco ingested and manually de-pulped seeds (Table 1; Fig. 3a, b). Furthermore, germination percentages of seeds passed through the digestive tract of this species was significantly lower than seeds from whole fruits (Table 1). Rose-ringed parakeets *C. camphora*



**Fig. 3** Cumulative proportion of seeds (%) germinated for Knysna turaco (—), purple-crested turaco (· · · · ·), rose-ringed parakeet (— — —), manually de-pulped (— — —), and whole

fruit (— — —) seeds from **a** *M. alba*, **b** *P. guajava*, **c** *C. camphora*, and **d** *S. mauritianum*

**Table 1** Difference between percentage germination of ingested seeds and that of pulp manually de-pulped seeds, whole fruits and ingested seeds, for all bird species fed fruits of four invasive alien plant species (NS not significant; S significant)

Plant species	Avian species	Germination percentage of seeds from					
		Pulp manually de-pulped fruit compared to ingested seeds			Whole fruit seeds compared to ingested seeds		
		F <sub>1</sub>	P		F <sub>1</sub>	P	
<i>M. alba</i>	Knysna turaco	2.650	0.105	NS	985.3	<0.050	S
	Purple-crested turaco	1.556	0.213	NS	930.0	<0.050	S
	Rose-ringed parakeet	879.8	<0.050	S	60.71	<0.050	S
<i>P. guajava</i>	Knysna turacos	1.103	0.295	NS	109.8	<0.050	S
	Purple-crested turaco	0.623	0.431	NS	105.4	<0.050	S
	Rose-ringed parakeet	176.4	<0.050	S	39.55	<0.050	S
<i>C. camphora</i>	Knysna turacos	0.649	0.421	NS	53.70	<0.050	S
	Purple-crested turaco	0.900	0.343	NS	48.41	<0.050	S
	Rose-ringed parakeet	0.108	0.743	NS	78.03	<0.050	S
<i>S. mauritianum</i>	Knysna turacos	2.049	0.154	NS	152.6	<0.050	S
	Purple-crested turaco	0.938	0.334	NS	143.3	<0.050	S

regurgitated seeds had higher germination percentage than seeds contained in whole fruit (Table 1; Fig. 3c), but this was not significantly different to manually de-pulped and turaco ingested seeds (Table 1).

## Discussion

Knysna and purple-crested turacos gut passage positively affected germination success of all plant species used in this study. In contrast, seed passage through the digestive tracts of rose-ringed parakeets reduced germination success and viability of these fleshy-fruited invasive plants. Effect of ingestion on germination success has often been attributed to several factors including the degree of seed coat abrasion, associated with morphological traits of the avian species' digestive tracts (Barnea et al. 1991; Traveset and Willson 1997; Yagihashi et al. 1999). Our results suggest that Knysna and purple-crested turacos are legitimate seed dispersal agents of fleshy-fruited invasive plants, while rose-ringed parakeets are mainly seed predators and rarely seed dispersers. This supports a potential case of 'invasive meltdown' as one invasive species is negatively influencing another. This is also perhaps one of the first studies highlighting the destructive behaviour of rose-ringed parakeets on fruiting plant species in South Africa. Should rose-ringed parakeets become more numerous, as is indicated by Hart and Downs (2014), they could potentially out-compete indigenous frugivores, which would have further negative effects for plant species, particularly in urban and peri-urban areas. Although ingested seeds are destroyed by parakeets, dropped and partially eaten invasive fruits must also be considered as these would readily germinate without ingestion (Jordaan et al. 2011a, 2012) and further contribute to the spread of these invasive plant species. Consistent with previous studies, manual pulp-removal increased germination success of seeds of all invasive plant species in this study, suggesting that dispersal is not the only benefit that these frugivores provide (Jordano 1983; Charalambidou et al. 2003; Chimera and Drake 2010; Jordaan et al. 2011a, 2012). The removal of pulp may prevent microbial attacks to seeds and thus enhance germination (Figueroa and Castro 2002). Pulp-removal is also essential for shorter germination times which would reduce the likelihood of seed predation (Fricke et al. 2013).

Furthermore, it has been suggested that minor abrasion may facilitate germination success of ingested seeds, while excessive abrasion of seeds may reduce germination success (D'Avila et al. 2010). Barnea et al. (1991) reported that there are plant species that require seed coat abrasion for germination or that require only pulp removal for germination. Since manually de-pulped seeds germinated equally well as turaco-ingested seeds for all invasive plant species, positive effects of seed ingestion by these species are mainly through fruit pulp removal, probably because of the removal of germination inhibitors and release of osmotic pressure. This result indicates that seed coat abrasion may affect germination but was not essential for germination of all species in this study. Similar results were obtained by Jordaan et al. (2011a), where seed coat abrasion was not important for germination of invasive plant species.

Germination success of turaco-ingested and manually de-pulped seeds was significantly higher than that of whole fruit seeds, suggesting that pulp removal is essential for enhanced germination success. Similarly, seeds from whole fruits had lower germination success than seeds ingested by frugivorous birds or manually de-pulped seeds (Yagihashi et al. 1999). Pulp removal significantly increased seed germination rate of larger fruited species (i.e. *P. guajava* and *S. mauritianum*), as pulp of these species took longer to decompose. Likewise, Jordaan et al. (2011a) also found that *P. guajava* and *S. mauritianum* seeds contained in whole fruits took significantly longer to germinate than those ingested by birds or manually de-pulped. Consistent with other studies *M. alba* (Jordaan et al. 2012) and *C. camphora* (Panetta 2001) seeds greatly benefited from higher germination percentage due to pulp-removal. The seeds of many other invasive plant species have also been shown to benefit from ingestion by birds (Daehler 2003; Corlett 2005; Bartuszevige and Gorchov 2006; Chimera and Drake 2010; Aslan 2011; Combs et al. 2011; Carrion-Tacuri et al. 2012; Czarnecka et al. 2012).

It has been reported that seeds that pass rapidly through a digestive tract of avian species are more likely to germinate (Murray et al. 1994), while those that remain longer may suffer excessive abrasion and therefore reduced viability and germination success. However, there is contradictory evidence about the effect of seed retention times on germination success, with other studies finding the opposite. In this study,

seed retention time did not play a role in seed germination success of all studied invasive alien plants, but was only important in terms of potential dispersal distance. It was assumed as with most parrot species that rose-ringed parakeets further damage the seeds during digestion, thus reducing the viability and germination success. The higher germination success of seeds from whole fruit than seeds that passed through the digestive tracts of rose-ringed parakeets suggests that ingestion of seeds by this species is detrimental to fleshy-fruited plants. The negative effect of rose-ringed parakeets on ingested seeds is not new, Lambert (1989) and Janzen (1981) reported that this species inhibits germination strength of ingested seeds probably due to excessive damage to the seeds caused by its digestive acids. Lambert (1989) also suggested that rose-ringed parakeets have grit in their muscular gizzard and long small intestines that may assist destruction of ingested seeds. Furthermore, parakeets also grind most seeds before consumption thus decreasing or inhibiting germination strength.

While seed passage through the digestive tracts of rose-ringed parakeets reduced the germination success, regurgitation by this species positively affected the germination success of *C. camphora* seeds. Regurgitated *C. camphora* seeds germinated significantly earlier and had higher germination percentage than those from whole fruit, however the proportion to germinated seeds was significantly lower (suggesting that few whole seeds were regurgitated). Similar findings were obtained by Corlett (1998) who reported that seed predators such as the rock pigeon (*Columba livia*) and the Eurasian collared dove (*Streptopelia decaocto*) also regurgitate few whole seeds that germinated. However, David et al. (2015) insisted that although parakeets may regurgitate whole seeds they are not seed dispersers, as they usually regurgitate these seeds below parental plants and thus do not aid seed dispersal. Furthermore the proportion of regurgitated seeds is very low.

In conclusion, our results suggest that indigenous Knysna and purple-crested turacos are efficient seed dispersers, while rose-ringed parakeets are seed predators. It is evident that indigenous turacos facilitate the establishment of fleshy-fruited invasive plants in this study, not only through dispersal, but also through seed ingestion that greatly enhances seed germination success through pulp removal. Invasive rose-ringed parakeets destroyed many of the invasive

plants' seeds in this study, and therefore have a negative impact on the reproductive success of these plants. Similar trends could be expected for indigenous seeds that rose-ringed parakeets feed on and therefore these birds remain a negative influence within invaded ecosystems. Rose-ringed parakeets can also facilitate dispersal by dropping uneaten or partially eaten fruits and also by regurgitating larger seeds away from the parent plants.

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