

Aspects of avian thermal physiology and frugivory of indigenous and invasive fruits in South Africa

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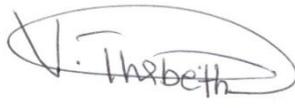
2014



Preface

The data described in this thesis were collected in Pietermaritzburg, Republic of South Africa from February 2013 to October 2014. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Colleen T. Downs.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Science and Engineering, University of KwaZulu-Natal, Pietermaritzburg campus, 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.



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November 2014

I certify that the above statement is correct and as the candidate's supervisor I have approved this thesis for submission.



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Professor Colleen T. Downs

Supervisor

November 2014

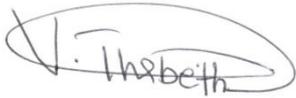
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Declaration 2 - Publications

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

Publication 1

Vuyisile Thabethe· Amy-Leigh Wilson· Lorinda A. Hart· Colleen T. Downs

Effect of invasive and indigenous avian species on seed germination of fleshy-fruited invasive alien plants in South Africa

Author contributions:

VT conceived paper with CTD, ALW, and LAH. VT collected and analysed data, and wrote the paper. CTD, ALW and LAH contributed valuable comments to the manuscript.

Publication 2

Vuyisile Thabethe· Amy-Leigh Wilson· Lorinda A. Hart· Colleen T. Downs

Invasive rose-ringed parakeets (*Psittacula krameri*) as seed predators of indigenous fig trees in South Africa: effects of their feeding behaviour on seed survival and germination.

Author contributions:

VT conceived paper with CTD, ALW, and LAH. VT collected and analysed data, and wrote the paper. CTD, ALW and LAH contributed valuable comments to the manuscript.

Publication 3

Vuyisile Thabethe· Amy-Leigh Wilson· Lorinda A. Hart· Colleen T. Downs

Digestive efficiency of indigenous and invasive avian species fed fruit of invasive alien plants in South Africa

Author contributions:

VT conceived paper with CTD, ALW, and LAH. VT collected and analysed data, and wrote the paper. CTD, ALW and LAH contributed valuable comments to the manuscript.

Publication 4

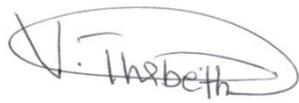
Vuyisile Thabethe· Lindy J. Thompson· Lorinda A. Hart· Mark Brown· Colleen T. Downs

Seasonal effects on the thermoregulation of invasive rose-ringed parakeets (*Psittacula krameri*)

Author contributions:

VT conceived paper with CTD, LJT, LAH and MB. VT collected and analysed data, and wrote the paper. CTD, LJT, LAH and MB contributed valuable comments to the manuscript.

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A handwritten signature in black ink, enclosed in a hand-drawn oval. The signature appears to read 'V. Thabethe'.

Vuyisile Thabethe

November 2014

Abstract

Indigenous and invasive plants have long been recognised as an important food source for avian frugivores worldwide. It has been suggested that seed germination success can vary amongst avian and plant species and that ingestion by avian frugivores can enhance, reduce or have no effect on seed germination. Few studies have looked at the role of both invasive and indigenous avian species on the germination success of invasive and indigenous plants in South Africa. Therefore the first aim of this study 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 invasive alien plant species (*Solanum mauritianum*, *Cinnamomum camphora*, *Psidium guajava*, and *Morus alba*). The second aim was to determine the effect of invasive rose-ringed parakeets on seed viability and germination of indigenous *Ficus* species (i.e. *F. lutea*, *F. burkei*, *F. sur* and *F. natalensis*).

Previous studies have shown that many avian frugivores prefer invasive alien fruits suggesting that they may be able to efficiently assimilate energy from these fruits. However few studies have focused on the consumption and digestive efficiency of invasive fleshy fruits by indigenous and invasive birds simultaneously in one study. Consequently this study also investigated the digestive efficiency of invasive and indigenous avian frugivores feeding on invasive fleshy fruits.

Finally, this study assessed the seasonal effects on the thermoregulation of invasive rose-ringed parakeets. As invasive bird species are spreading in South Africa, understanding the physiological responses that equip them to tolerate a wide range of climatic conditions would be useful for modelling potential distributions and effectively managing them.

Seed ingestion by Knysna and purple-crested turacos resulted in significantly higher germination success than those from whole fruits for all invasive alien plant species in this

study. Germination success of manually pulp-removed seeds did not differ from that of turacos ingested seeds, suggesting that seed coat abrasion was not important for germination of these invasive alien plants. Seed passage through the digestive tract of rose-ringed parakeets resulted in significantly reduced germination success and viability of all ingested plant species, suggesting that seed ingestion by this species is disadvantageous to these plant species.

These results suggest that Knysna and purple-crested turacos are legitimate seed dispersers of the four fleshy-fruited invasive plants, while rose-ringed parakeets are mainly seed predators. Results obtained from this study also suggest that rose-ringed parakeets are mainly seed predators of *Ficus* fruit, as none of the ingested seeds managed to germinate. In addition, all three avian species investigated managed to meet their energetic demands by feeding on invasive alien fruit only, suggesting that these plant species may sustain avian frugivores especially during periods of food scarcity.

Furthermore, the results obtained also suggest that rose-ringed parakeets show seasonal thermoregulatory responses representing energy conservation, as expected. This suggests that rose-ringed parakeets are physiologically equipped to cope with a range of environmental conditions and this partly explains their global success as an invasive species.

Keywords: Avian species, Digestive efficiency, Fleshy-fruited plants, Germination success, Seed dispersal, Thermoregulation

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CHAPTER 1: Introduction

Many plant species produce fleshy fruits (i.e. fruits consisting of nutritional fruit pulp surrounding the seeds), which are an important food resource for frugivorous animals worldwide (Herrera, 1995; Jordano, 2000; Gosper et al., 2005). This fruit pulp provides frugivores with a key source of nutrition and energy (Wilson and Downs, 2011b). In return, frugivores may play a vital role in long-distance seed dispersal of these fleshy-fruited plants (Cain et al., 2000; D'Avila et al., 2010; Czarnecka et al., 2012). Mutualistic relationships between plants and frugivorous animals play an essential role in maintaining the structure and diversity of many ecosystems ranging from the preservation to restoration of some important indigenous plants (Jordano, 2000; Shanahan et al., 2001; Kirika et al., 2008; Fedriani et al., 2011). It has been suggested that up to 90% of indigenous fleshy-fruited plant species are dispersed by frugivorous animals (Jordano, 2000; Bascompte and Jordano, 2007; Lomáscolo et al., 2010; Parr et al., 2011; Wilson and Downs, 2012). Therefore, it is of importance to understand the interaction between indigenous plants and frugivorous animals for effective management and restoration of these species (Bleher et al., 2003; David et al., 2015). Although the dispersal of indigenous plants is important and desirable, the dispersal of non-native plant species by frugivorous animals is undesirable (Cain et al., 2000; Buckley et al., 2006; Combs et al., 2011). Understanding the process of seed dispersal of invasive plant species is important as these plants have a variety of negative impacts on ecosystem processes (Tucker and Richardson, 1995).

The numerous negative impacts of invasive plant species include the major threats to biodiversity, water security, ecological functioning of natural systems and ecosystem functioning worldwide (Henderson, 2001; Combs et al., 2011). Invasive plant species are the second most important threat to biodiversity after habitat destruction (Iponga et al., 2009; Jordaan et al., 2011a). They cause dramatic environmental changes that lead to significant

declines in indigenous populations and diversity (Daehler, 2003; Davies and Sheley, 2007; Lafleur et al., 2007; Jordaan et al., 2012). South Africa is one of the countries that has been extremely affected by invasive alien plants (Richardson and van Wilgen, 2004; Iponga et al., 2009). Henderson (2001) reported that the problems associated with plant invasions in South Africa are escalating rapidly and will lead to a serious decline in ecosystem services if left unmanaged. Therefore, research and knowledge on the ecology and biology of invasive plants is required to assist in the development of better and more effective control strategies (Henderson, 2001; Nel, et al. 2004; Richardson and van Wilgen, 2004).

Most of the worst globally invasive alien plant species rely on frugivorous animals for seed dispersal (Jordaan et al. 2011a; Mokotjomela et al., 2013c). Birds are particularly efficient dispersers of invasive fruit, probably due to their mobility and ability to move between similar habitats. Both invasive and indigenous bird species have been seen utilizing invasive plants as both feeding and nesting/roosting sites (Richardson, 2000b; Lawrie, 2002). The success of invasive plants has been widely attributed to their capacity to form successful mutualisms with seed dispersers (Richardson et al., 2000a; Richardson and Rejmánek, 2011). However, the relationship between invasive plants and avian frugivores remains poorly understood, particularly in terms of the direct benefits to the frugivores and the potential influence they may have on germination success of these plants (Sallabanks, 1993; Vivian-Smith and Gosper, 2010; Gosper et al., 2005).

Despite numerous negative effects, it has been suggested that invasive plants may also have positive impacts, such as by providing habitat or food resources for indigenous animals (Gosper and Vivian-Smith, 2006). Fruits of invasive plants often offer greater nutritional rewards than indigenous fruits (Jordaan et al., 2011b; Jordaan and Down, 2012). Indeed, several studies have shown that indigenous bird species often prefer and select fruits of invasive plants over those of indigenous plants (Vila and D'Antonio, 1998; Drummond,

2005; Buckley et al., 2006; Mokotjomela et al., 2013a), suggesting that avian frugivores may be able to efficiently process and assimilate energy from these fruit species (Jordaan et al., 2011b).

Invasive fruiting plants may also act as a food source for invasive birds in many regions, especially in urban areas (Bonier et al., 2007; Aslan, 2011). This may facilitate the establishment, persistence and spread of these bird species (Lodge, 1993). Invasive birds and plants may thus facilitate the spread and establishment of each other (Mandon-Dalger et al., 2004). For instance avian frugivores gain various resources which may sustain their population and the plants benefit from seed dispersal away from the parent plant (Manchester and Bullock 2000; Mandon-Dalger et al., 2004). The easy accessibility of fleshy fruits of invasive plants, particularly during dry seasons, may aid invasive avian frugivores to survive harsh environmental conditions (Mandon-Dalger et al., 2004).

Furthermore, it has been suggested that invasive birds are able to tolerate wide varieties of environmental conditions as a result of their abilities to undergo physiological changes which enables them to maintain a constant internal environment in changing climates (Weathers and Caccamise, 1978; Bonier et al., 2007; Thabethe et al., 2013). Species with a wide range of physiological tolerance often withstand extreme environmental conditions (Dawson, 2003; McKechnie, 2008; Shwartz et al., 2009; Thabethe et al., 2013). Therefore, understanding the physiological responses that equip invasive birds to tolerate a wide range of climatic conditions would be useful for future management of the invaders, particularly in terms of predicting future invasion pathways (Shwartz et al., 2009; Thabethe et al., 2013).

The aim of this study was to determine what effect the ingestion of seeds by invasive alien and indigenous bird species has on the germination success of invasive alien plants in South Africa. The second aim of this study was to determine the digestive efficiency of

invasive and indigenous avian frugivores feeding on invasive fleshy fruits and whether these birds are able to maintain their body mass and meet their energy demands on a pure diet of invasive fruit. The third aim was to determine the impacts of invasive rose-ringed parakeets on seed germination success of indigenous tree species in South Africa in South Africa. In addition, germination success of whole seeds following ingestion and regurgitation was quantified. Finally, the fourth aim was to determine the effect of seasonal changes on the thermoregulation of invasive rose-ringed parakeets.

Invasive fruit traits favouring selection

Fruits are a major food resource for many frugivorous birds worldwide (Aslan, 2011; Davis, 2011). Several studies have shown that birds usually prefer and select certain fruits over others, and this may influence the distribution and abundance of plants (Drummond, 2005; Lafleur et al., 2007; Wilson and Downs, 2011b). The selection of fleshy fruits by birds is presumably dependent on the behaviour, morphology, and nutritional requirements of birds (Jordaan et al., 2012; Jordaan and Downs, 2012). Fruit traits such as colour, lipid content, carotenoids, proteins, fruit ripeness and fruit size, number and size of seeds, fruiting display, secondary metabolites and mass of pulp relative to fruit mass are also important factors influencing avian fruit selection (Mokotjomela et al., 2013a; Gleditsch and Carlo, 2011; Wilson and Downs, 2011a; Wilson and Downs, 2011a). Fruit preference may also be influenced by digestive ability, energy rewards, fruit accessibility and availability (Wilson and Downs, 2011b; Mokotjomela et al., 2013a).

Several studies have shown that invasive plants often have longer fruiting periods than indigenous species (Drummond, 2005; Gleditsch and Carlo, 2011). Fruits of invasive plants usually have higher sugar content, more variable nitrogen amounts and smaller seed loads when compared with indigenous species (Stanley and Lill, 2002; Gosper et al., 2005).

These fruits also have greater nutritional rewards and are easily accessible throughout the year compared with indigenous fruits, but have similar morphological characteristics to indigenous fruits (Mokotjomela et al., 2013a; Mokotjomela et al., 2013b; Spotswood et al., 2013). Consequently, they present a reliable food source and are thus preferred to indigenous fruits (Spotswood et al., 2012; Mokotjomela et al., 2013c). Both invasive and indigenous frugivorous birds have shown a preference for invasive alien fruits suggesting that they may be able to efficiently process and assimilate energy from them (Vila and D'Antonio, 1998; Mokotjomela et al., 2013c). These birds play a significant role in dispersing invasive plants worldwide through consumption (Gleditsch and Carlo, 2011; Jordaan et al., 2011a; Jordaan et al., 2011b; Mokotjomela et al., 2013a). The selection and dispersal of invasive plant species by birds has major negative implications for indigenous plants and animals (Vila and D'Antonio, 1998). To successfully manage and control invasive plants in South Africa, it is necessary to characterize invasive plants that are preferred by different bird species and facilitate the recovery of indigenous plants that have similar characteristics (Jordaan et al., 2011a; Jordaan and Downs, 2012; Mokotjomela et al., 2013a).

The role of avian frugivores on seed germination

Avian seed dispersal plays a crucial role in the colonization of new habitats, including the maintenance of indigenous plants and the spread of alien plants (Corlett, 2005, Gleditsch and Carlo, 2011). Fruit consumption by frugivores may have an important influence on the germination success of seeds (Charalambidou et al., 2003; Samuels and Levey, 2005). Seed germination may either be enhanced (Paulsen and Högstedt, 2002; Jordaan et al., 2011a; Fricke et al., 2013) reduced (LaRosa et al., 1985) or may be unaffected after passing through the gut passage (Wilson and Downs, 2012). Many studies have found that seeds ingested by frugivores often have increased germination success compared with that of non-ingested

seeds (Paulsen and Högstedt, 2002; Czarnecka et al. 2012; Jordaan et al. 2012). Traveset (1998) found that enhancement of germination occurs about twice as often as inhibition. Seed germination success may be enhanced due to removal of pulp, which reduces the risk of seed predation and microbial attacks (Traveset 1998; Chimera and Drake, 2010; Fricke et al., 2013). The chemical or mechanical modification of seed coat structure due to ingestion may also enhance germination success of seeds (D'Avila, 2010; Fricke et al., 2013). Moreover, the residues in defecated seeds may provide nutrients that promote germination and seedling establishment (Figueroa and Castro, 2002).

Seed germination may also be inhibited (Murray et al., 1994, Charalambidou et al., 2003) after passing through the digestive tracts of frugivores (Barnea et al., 1991) probably due to the toxicity and hydrophobic nature of excreta (Chimera and Drake, 2010). Some frugivorous species have no effect on the germination success of seeds and thus act solely as seed dispersers (Wilson and Downs, 2012). Only a few studies have found that seed ingestion by birds lower the germination rate and percentage (Nogales et al., 1995). Factors such as type of food ingested, seed size, seed coat structure and seed retention time may influence the germination success of ingested seeds (Charalambidou et al., 2003). Seed retention time is considered to be the most important factor as it may translate into a distance that a seed is transported away from a parent plant (Jordaan et al., 2011a; Wilson and Downs, 2012). Shorter seed retention times may increase or reduce the ability of seeds to germinate, while longer seed retention times may enhance the possibility that seeds are moved far away from the parent plant, thus promoting long distance dispersal (Charalambidou et al., 2003; Jordaan et al., 2011a). It has been found that small seeds are usually retained longer in the digestive tract and are more likely to be abraded and consequently increase germination success (Fedriani et al., 2011).

However, the consumption of seeds by birds may not necessarily result in successful dispersal (Westerman et al., 2006; Combs et al., 2011). This is because some bird species, particularly parrots, are seed predators, killing the seed embryo (Jordano, 1983). These species have the capacity to digest both seeds and fruit pulp or crush seeds before ingestion (Debussche and Isenmann, 1994; Witkowski and Garner, 2008). Previous research provided some evidence demonstrating that seed predators cause significant declines in indigenous plant fitness (Crawley, 2000; Francisco et al., 2008; Vaz Ferreira et al., 2011). For example, Jordano (1983) documented that seed predators (especially parrots) consumed nearly 94% of *Ficus continifolia* seeds in Costa Rica. However, some seed predators may contribute to the dispersal of fleshy-fruited plants (Vila and Gimeno, 2003; Carrion-Tacuri et al., 2012). This occurs when frugivores do not consume the fruit immediately but carry them away to feeding roosts for later consumption where seeds are then 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 (Vila and Gimeno, 2003; Pairen et al., 2006). Generally, invasive plants are able to successfully germinate after parental plants are removed and this poses challenges for conservation and management of invasive plants (Vila and Gimeno, 2003).

The successful spread and establishment of fleshy-fruited invasive alien plants is thought to be significantly enhanced by frugivorous birds (Gleditsch and Carlo, 2011; Jordaan et al., 2011a; Jordaan et al., 2011b). The role of avian dispersal of seeds of invasive plants has been highlighted in many studies globally (Linnebjerg et al., 2009; Pairen et al., 2006; Vivian-Smith and Gosper, 2010). However, studies on the role of avian species on seed dispersal of invasive plants remain poorly investigated in Africa (Jordaan et al., 2011a; Mokotjomela et al., 2013a). In particular, studies on the influence of avian species on the germination of seeds of fleshy-fruited invasive plants require further investigation

(Sallabanks, 1993; LaFleur et al., 2009; Gosper et al., 2005; Vivian-Smith and Gosper, 2010) for implementation of effective management strategies of existing invasive alien plants.

Energy requirements and temperature regulation in invasive birds

Avian frugivores meet their energy demands by relying on high quality fruits (Wilson and Downs 2011b). Several studies have found that many avian frugivores prefer invasive fruits to those of native plants suggesting that they may be able to efficiently process and assimilate energy from them (Gosper et al. 2005; Buckley et al. 2006; Jordaan et al. 2011a). Fleshly-fruited invasive alien plants may thus facilitate the establishment and persistence of invasive bird species by providing reliable food resource during a period of food scarcity especially in winter.

While it is important to understand fruit digestion and germination of invasive plants, it is also vital that we consider how the energy requirements of invasive avian frugivores who feed on these plants differ seasonally. Invasive birds are able to adapt to a rapidly changing environment and therefore have selective advantages over indigenous birds (Bonier et al., 2007; Zheng et al., 2008; Nzama et al., 2010; Thabethe et al., 2013). Several studies suggest that invasive birds manage to tolerate wide varieties of environmental conditions as a result of their abilities to undergo physiological, morphological and behavioural mechanisms which aid them to maintain a constant internal environment in changing climates (Weathers, 1979; Swanson and Weinacht, 1997; Dawson, 2003; Smit et al., 2008; Zungu et al., 2013).

The ability to alter basal metabolic rate (defined as the minimum rate of energy expenditure by a post-absorptive, non-reproductive endotherm that is in its thermo-neutral zone in the inactive phase of the circadian cycle (Zungu et al., 2013; Zheng et al., 2008;

Thabethe et al., 2013) in response to environmental changes is considered as a key component of physiological responses that enable invasive bird species to survive harsh environmental conditions (McKechnie, 2008; Zheng et al., 2008; Nzama et al., 2010; Smit and McKechnie, 2010; Thabethe et al., 2013; Zungu et al., 2013). It is therefore fundamental to understand the effects that changing environmental conditions have on physiological responses of invasive birds. Understanding the physiological responses that equip invasive species to tolerate a wide range of climatic conditions would be useful for future management of these invaders, particularly in terms of predicting future invasion pathways (Thabethe et al., 2013).

Alien and indigenous plant and bird species used for experiments

We identified four highly invasive fleshly-fruited plant species that occur in KwaZulu-Natal, South Africa. These plants were bugweed (*Solanum mauritianum*), camphor (*Cinnamomum camphora*), guava (*Psidium guajava*) and mulberry (*Morus alba*) (Figure 1). Many avian frugivore species have been reported to feed on these plant species and the successful spread and establishment of these plants is thought to be significantly enhanced by indigenous and invasive frugivorous birds (Morales and Aizen 2006; Witkowski and Garner 2008; Jordaan et al. 2011a). In this study, indigenous turacos (namely purple-crested (*Gallirex porphyreolophus*) and Knysna turacos (*Tauraco corythaix*)) and invasive rose-ringed parakeets (*Psittacula krameri*) were used (Figure 2), as they have all been reported to feed on these plants in the wild. Ezemvelo KwaZulu-Natal Wildlife granted the permit and ethics approval for the experiments. These bird species were chosen as they co-occur in the same habitats in the greater Durban area in KwaZulu-Natal, and their distribution also overlaps with those of the invasive alien plants used in this study. Little is known about their effect on the dispersal and germination of invasive plants and their contribution to the invasion of

alien plants in South Africa. In this study, we also identified four indigenous *Ficus* trees namely *F. lutea*, *F. burkei*, *F. sur* and *F. natalensis* (Figure 3) that occur in KwaZulu-Natal and overlap with rose-ringed parakeets and turacos. *Ficus* species are known as keystone species for frugivorous animals worldwide.



Fig. 1. Invasive alien fruits fed to turacos and rose-ringed parakeets: 1. *Cinnamomum camphora*, 2. *Psidium guajava*, 3. *Morus alba* and 4. *Solanum mauritianum*.



Fig. 2. Avian species used in this study: 1. rose-ringed parakeets (*Psittacula krameri*), 2. purple-crested turacos (*Gallirex porphyreolophus*) and 3. Knysna turacos (*Tauraco corythaix*)



Fig. 3. Indigenous *Ficus* fruits fed to rose-ringed parakeets: 1. *F. natalensis*, 2. *F. burkei*, 3. *F. sur* and 4. *F. lutea*.

Motivation for the study

There are several factors that prompted this study; firstly the severe effects of invasive alien plant species in South Africa and the lack of knowledge regarding their biology and ecology. Most of the worst invasive plants produce fleshy fruits that are consumed and dispersed by both indigenous and invasive avian species (Samuels and Levey, 2005; D'Avila et al., 2010; Czarnecka et al., 2012). Previous studies have found that many fruits have higher germination rates after frugivore gut passage (Barnea et al., 1991; Yagihashi et al., 1999; Traveset et al., 2001; Paulsen and Högstedt, 2002). It was then predicted that the frugivore-processed seeds would germinate sooner and have a higher germination success than pulp-

removed seeds and whole fruit control seeds. It was also predicted that both indigenous and invasive frugivorous birds will meet their energy demands when feeding on the various fruits of invasive plants. Understanding how avian species influence the spread of invasive plants may provide important information for implementation of effective control strategies.

This study was also motivated by the rapid increase of invasive rose-ringed parakeets in South Africa and the lack of knowledge concerning their ecology, biology, physiology and effects on indigenous fruiting tree species. Rose-ringed parakeets are regarded as major crop pests and seed predators in their native range (Butler, 2003, 2005). Thus it was predicted that this species would negatively affect the dispersal, germination and recruitment of indigenous *Ficus* species and invasive plant species in South Africa. Lastly, it was predicted that rose-ringed parakeets would successfully conserve energy and alter their physiology to survive in wide variety of environmental conditions, facilitating their invasive spread to a range of habitats. Since invasive bird species appear to be increasing in South Africa, information on their physiological capabilities would be useful for future management of these invaders, particularly in terms of predicting future invasion pathways. Furthermore, information on the role of rose-ringed parakeets on indigenous plants' germination success and survival would be useful for future conservation and management purposes. This study provides important insights into how avian species influence the spread of invasive plants. Results obtained from this study will provide important information for biodiversity conservation at the regional and global scale, in terms of implementation of effective management strategies of these alien plants worldwide. Overall, these results will add to the limited information available on the interaction between fruiting plants and their dispersers in southern Africa and will improve our understanding of plant-frugivore interactions.

Thesis arrangement

This thesis consists of four experimental chapters (chapters 2 to 5) which can be read independently. Each chapter is prepared for publication in relevant peer-reviewed journals and therefore some overlap and repetitions were unavoidable.

Chapter 2. Effect of invasive and indigenous avian species on seed germination of fleshy-fruited invasive alien plants in South Africa

Chapter 3. Invasive rose-ringed parakeets as seed predators of indigenous fig trees in South Africa: effects of their feeding behaviour on seed survival and germination.

Chapter 4. Digestive efficiency of indigenous and invasive avian species fed fruit of invasive alien plants in South Africa

Chapter 5. Seasonal effects on the thermoregulation of invasive rose-ringed parakeets (*Psittacula krameri*).

Chapter 6 is a general conclusion that summarizes the whole study and presents some valuable recommendations for the implementation of effective management strategies of existing invasive alien plant populations. This chapter also highlights the effects of invasive rose-ringed parakeets on indigenous plants and recommendations for future conservation purposes.

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**CHAPTER 2: Effect of invasive and indigenous avian species on seed germination of
fleshy-fruited invasive alien plants 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. This study 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 invasive rose-ringed parakeets (*Psittacula krameri*). Seed retention time was determined as this may influence both seed dispersal and germination. Germination success of ingested seeds was compared to that of manually pulp-removed 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 to seeds from whole fruits. Germination success of manually pulp-removed 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 reproductive success of these plants, it is unlikely that this seed

predator suppresses the population of these invasive alien plants in South Africa as the plants are already well established. Furthermore, they can facilitate dispersal by regurgitation and dropping uneaten fruits away from the parent plant.

Keywords Avian species · Pulp removal · Seed dispersal · 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). 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 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 may 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 Högstedt 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 (Jordaan et al. 2011a; 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 at all on germination success (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 may 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) and reduce seed viability (Westcott and Fletcher 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). These occur 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 extremely invaded by fleshly-fruited invasive plants (Henderson 2001; van Wilgen 2001; Nel 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 these 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 disperse, 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, the aim of this study 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 pulp removed seeds and seeds from the whole fruits. It was 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 x 2.12 x 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 g and 310 g respectively) frugivorous bird species indigenous to South Africa (Sinclair and Ryan 2003). The rose-ringed parakeet 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). Turacos and rose-ringed parakeets eat fruits of both invasive and indigenous plants. These frugivorous bird species were selected as they co-occur in the same habitats in Durban (KwaZulu-Natal) South Africa, however little is known about their effect on the dispersal and germination of invasive plants and their contribution to the rapid invasion rate of alien plants in South Africa.

Plant species

Fruits of four invasive alien plant species, namely bugweed (*Solanum mauritianum*), camphor (*Cinnamomum camphora*), guava (*Psidium guajava*), and mulberry (*Morus alba*) were used 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 48h 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 with a crown diameter of up to 3 m (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, 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

Birds were moved to a constant environment room with a 12L:12D photoperiod at 25 ± 1 °C two weeks before trials were conducted and were housed individually in cages (42.7×43×59.3 cm). Clean plastic trays, the same size as the cage's base were placed in each cage to facilitate removal of faeces. Water was provided *ad libitum*.

The fruit species of each specific trial was incorporated into the maintenance diet two days prior to the sampling day. On the experimental day, birds were fed a specific invasive alien fruit species either whole or cut up and water was provided *ad libitum*. Each trial was run for 12 h (from 06h00 to 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 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

Seed retention time was determined 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. 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. Seed retention time was measured in order to determine the potential effect on germination success and potential seed dispersal distance.

Germination trials

Seeds were removed from each individual bird's excreta or regurgitation and planted in separate trays (265×180×75 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 pulp-removed and whole fruit seeds 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, manually pulp-removed and whole fruits seeds for each fruit species. The time taken from the time of sowing to first seedling emergence for each plant species was analyzed using Kruskal–Wallis ANOVA tests. The germination success of ingested, pulp-removed seeds and seeds in the whole fruit was 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. One-way analysis of variance (ANOVA) was used to compare germination success of seeds

ingested by turacos and rose-ringed parakeets to seeds from manually pulp-removed fruits 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 min and 12-19 min respectively) when fed *M. alba* seeds than rose-ringed parakeets (31-46 min, 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). Seeds 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* seed 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 and c). All *M. alba* ingested by avian species germinated after ca. 5 days (Fig. 2a), which was not significantly earlier than manually pulp-removed 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 pulp-removed seeds (Fig. 3d) but significantly sooner than whole fruit seeds, 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 pulp-removed 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 a significantly slower germination rate than ingested and manually pulp-removed seeds (Fig. 3b and d), while seeds contained in whole fruit of *C. camphora* emerged at approximately the same time with ingested and manually pulp-removed seeds (Fig. 3a and c).

Germination success

Seeds ingested by Knysna and purple-crested turacos had higher germination percentage 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 pulp-removed seeds (Table 1; Fig. 3). These germination percentages were significantly higher than there were 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 turacos ingested and manually pulp-removed (Table 1; Fig. 3a and b). Furthermore, germination percentages of seeds passed through the digestive tract of this species was significantly lower than that of seeds from whole fruits (Table 1). Rose-ringed parakeets *C. camphora* regurgitated seeds had higher germination percentage than seeds contained in whole fruit (Table 1; Fig. 3c), this was not significant different to manually pulp-removed and turacos ingested seeds (Table 1).

Discussion

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. 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 clearly reduced the 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 trait of the avian species' digestive tracts (Barnea et al. 1991; Traveset and Willson 1997; Yagihashi et al. 1999).

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; Jordaan et al. 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 suggest 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 pulp-removed 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 pulp-removed 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 pulp-removed 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. mauritanu* 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.

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 of 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 and 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 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. This study suggests that some indigenous frugivores may be facilitating the spread of many of the most problematic invasive plants in South Africa. Invasive rose-ringed parakeets destroyed many seeds of these plants, suggesting that this bird has a negative impact on the reproductive success of the invasive plant species studied. However, rose-ringed parakeets can facilitate dispersal by dropping uneaten fruits away from the parent plant. Seed dispersal by birds, combined with the ability of seeds to germinate from uneaten fruits may enhance the spread of these invasive alien plant species.

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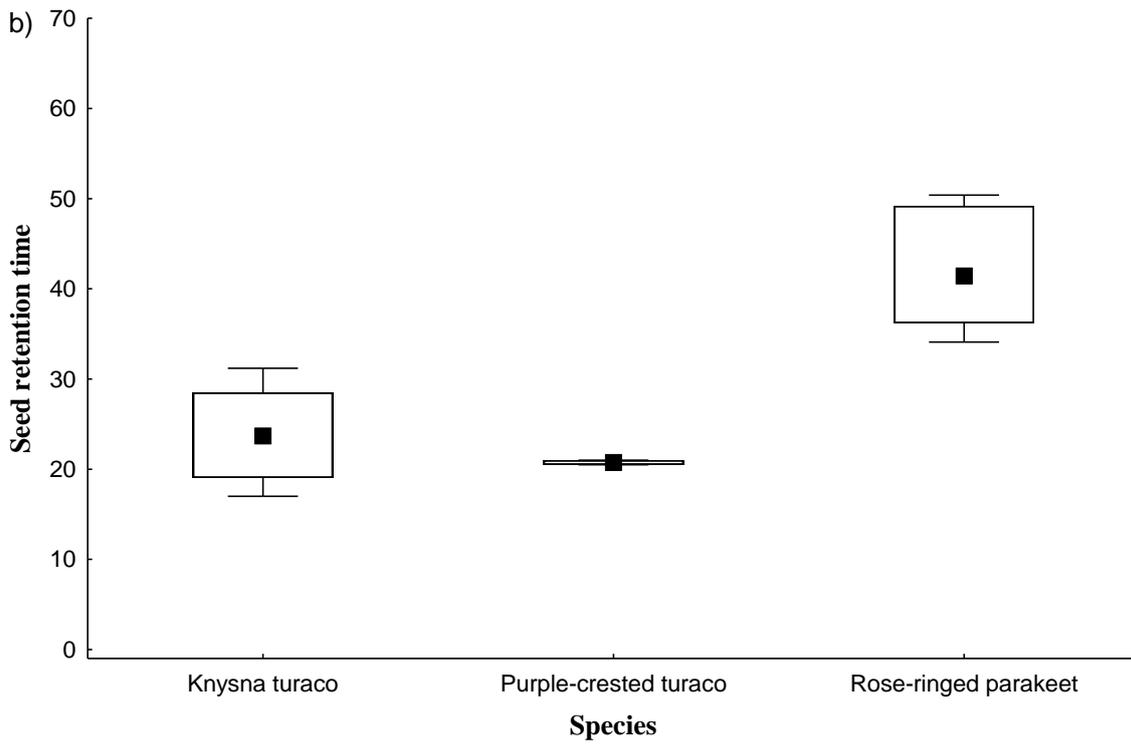
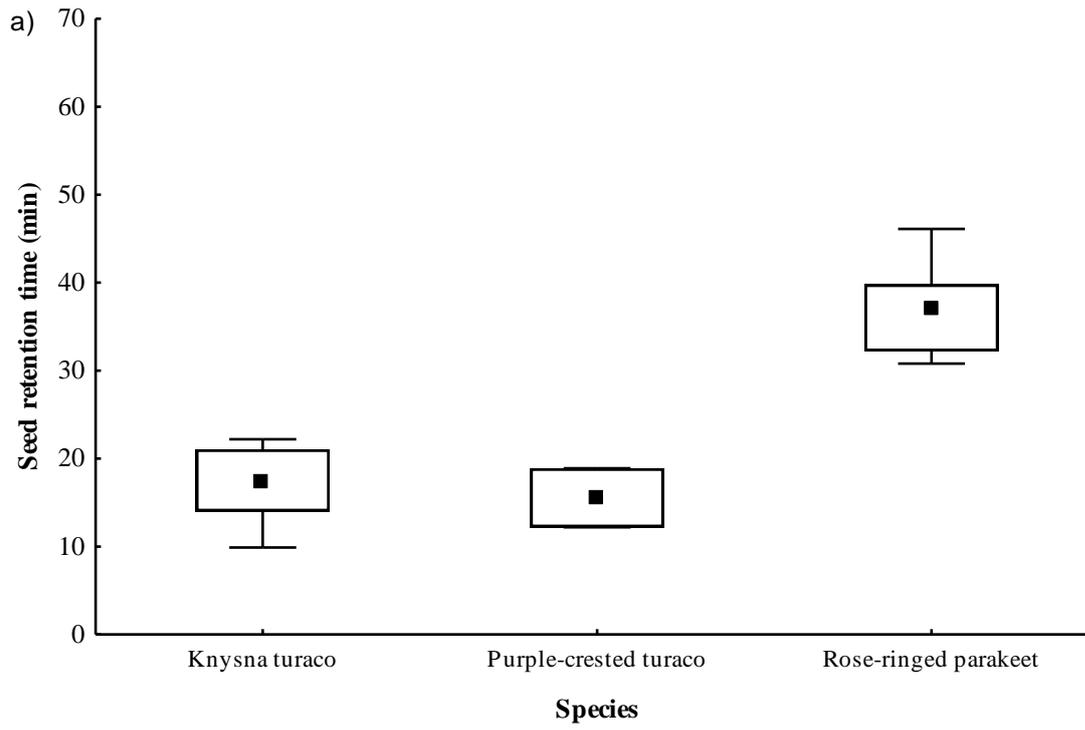
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Table 1 Difference between percentage germination of ingested seeds and that of manually pulp-removed seeds, whole fruits and ingested seeds, for rose-ringed parakeets fed fruits of four invasive alien plant species

Plant species	Avian species	<u>Germination percentage of seeds from</u>					
		Manually pulp-removed fruit compared to ingested seeds			Whole fruit compared to ingested seeds		
		F ₁	P		F ₁	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



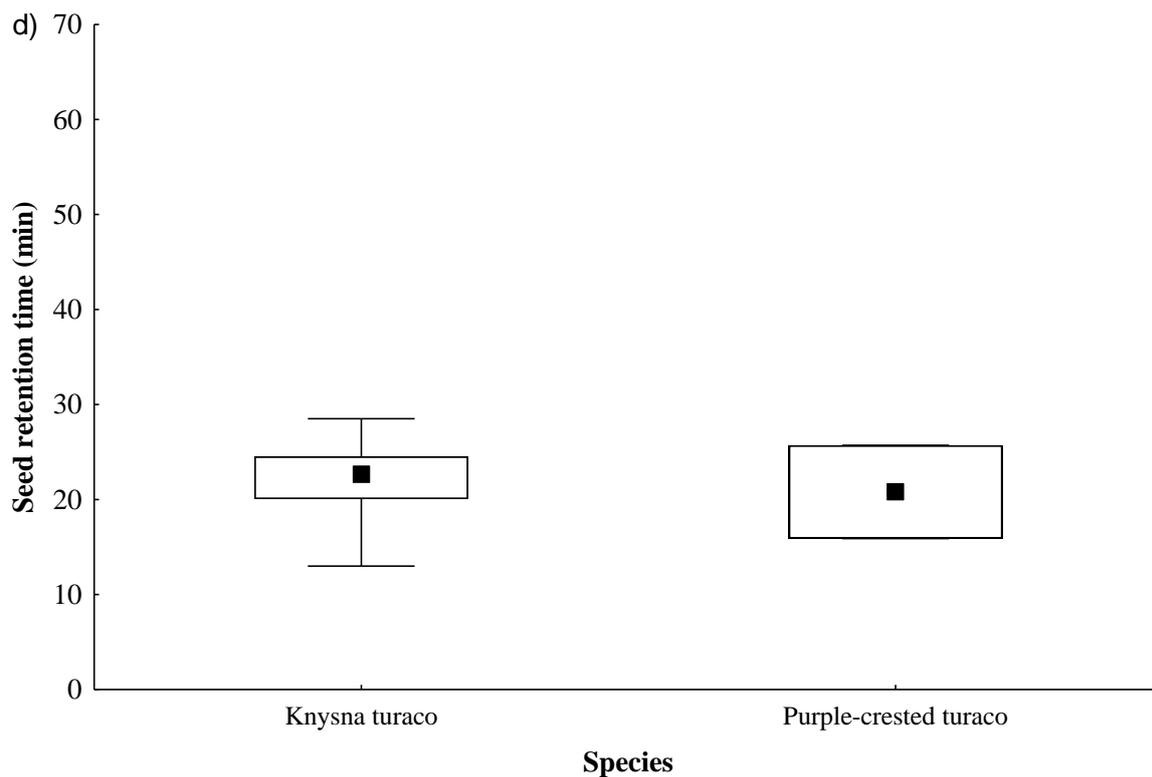
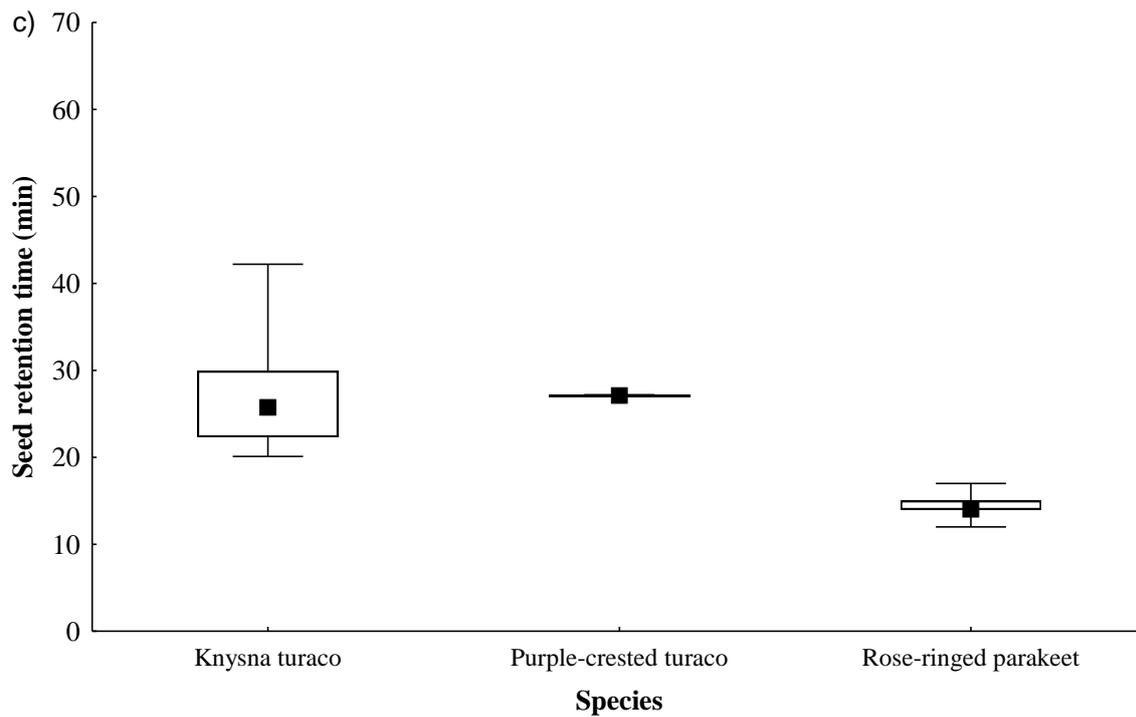
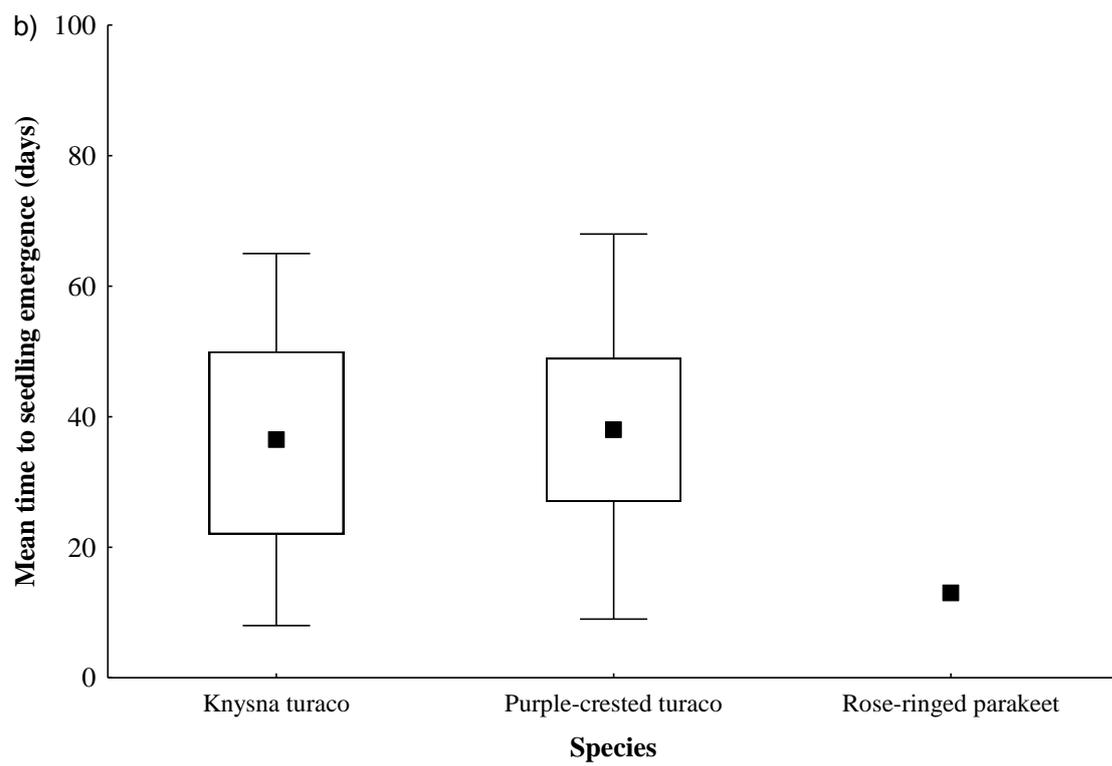
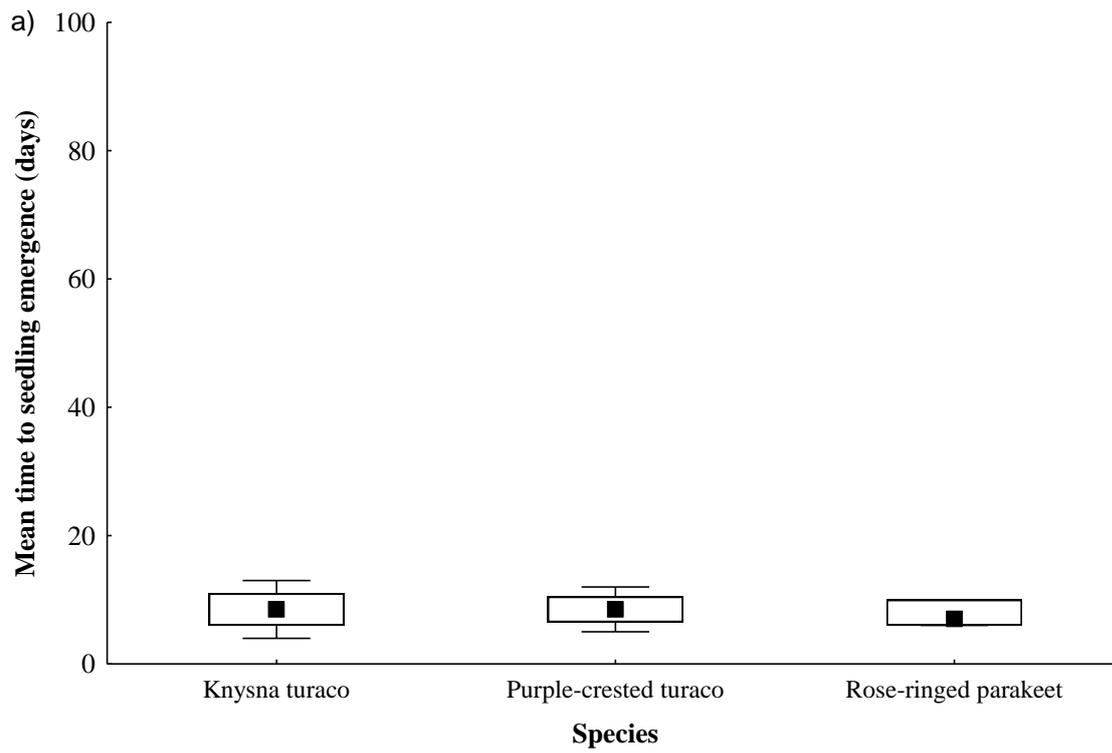


Fig. 1 Seed retention time for three avian species feeding on fruits of (a) *M. alba*, (b) *P. guajava*, (c) *C. camphora*, and (d) *S. mauritanum*, where boxes are 25 and 75% quartiles, the solid black squares within the boxes indicate the medians, bars show 10 and 90% values.



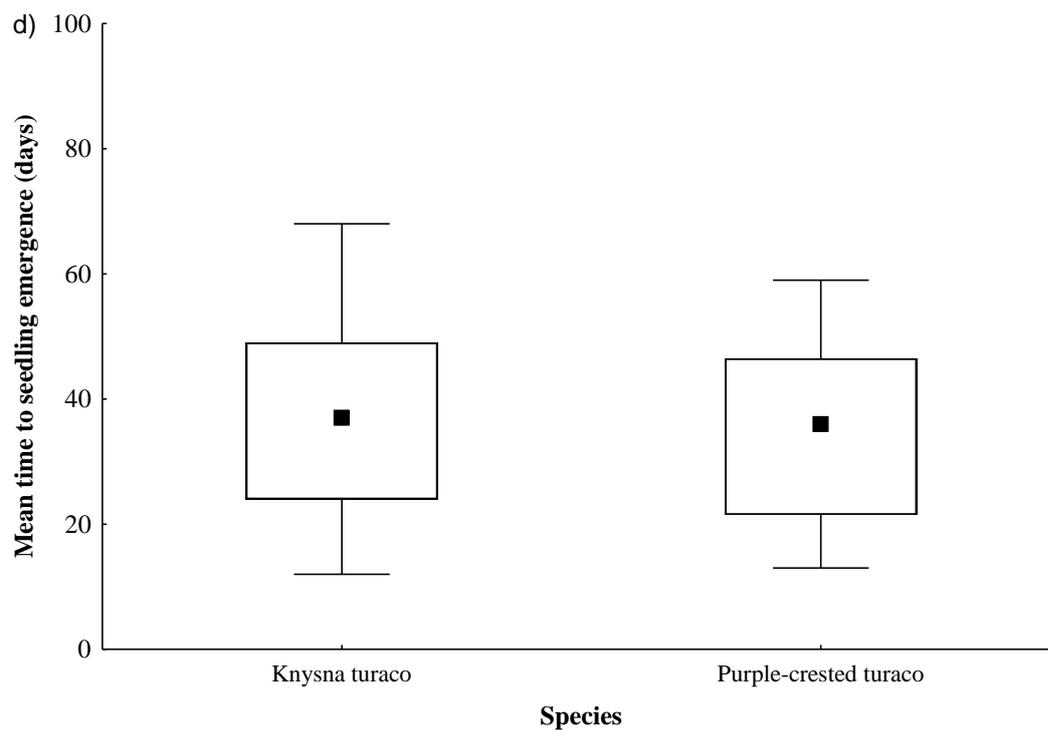
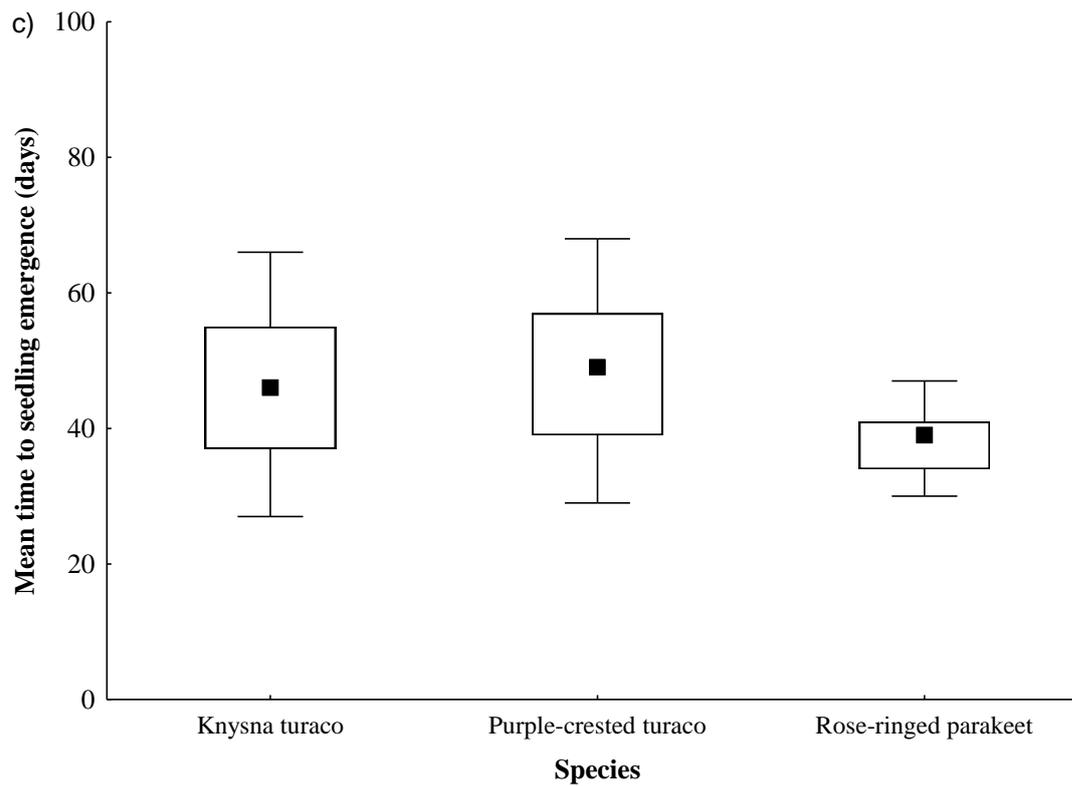
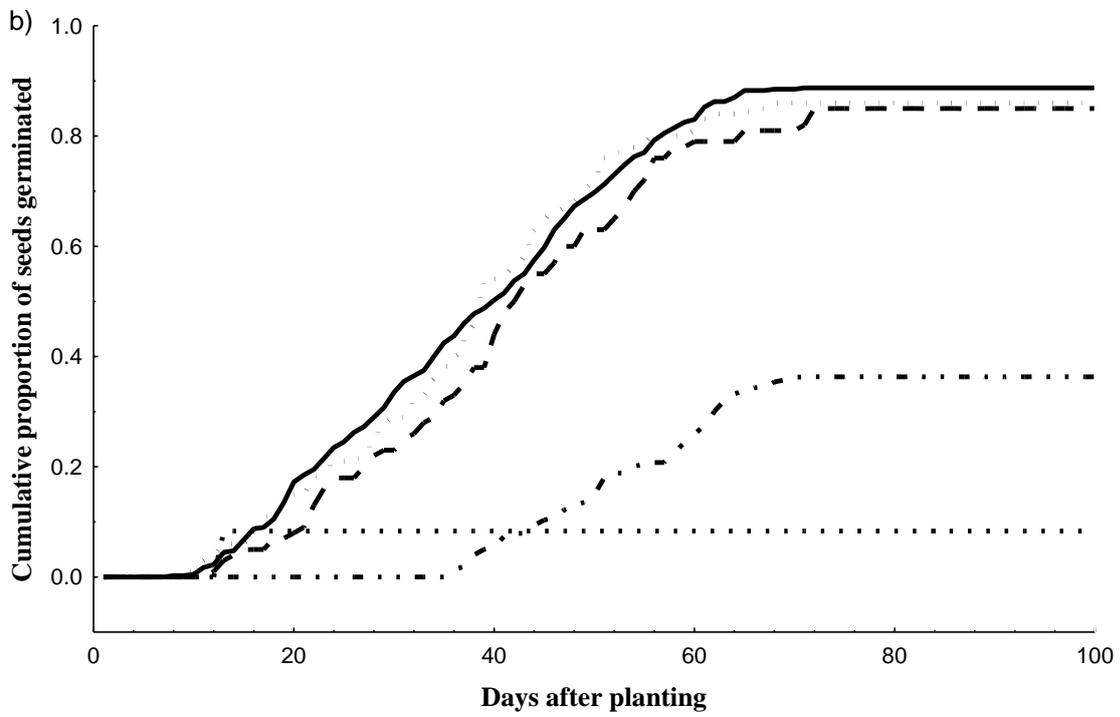
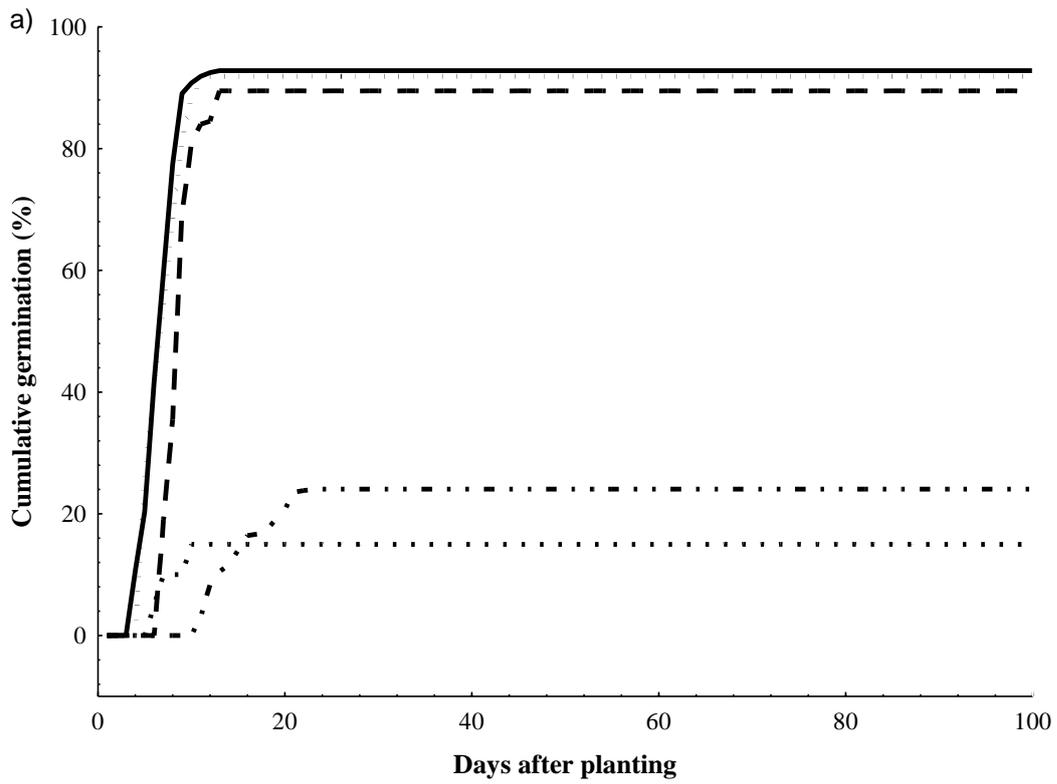


Fig. 2 Mean time to first seedling emergence of seeds ingested by three avian species (or regurgitation by rose-ringed parakeet in the case of *C. camphora*) for (a) *M. alba*, (b) *P. guajava*, (c) *C. camphora*, and (d) *S. mauritianum*, where boxes are 25 and 75% quartiles, the solid black squares within the boxes indicate the medians, bars show 10 and 90% values.



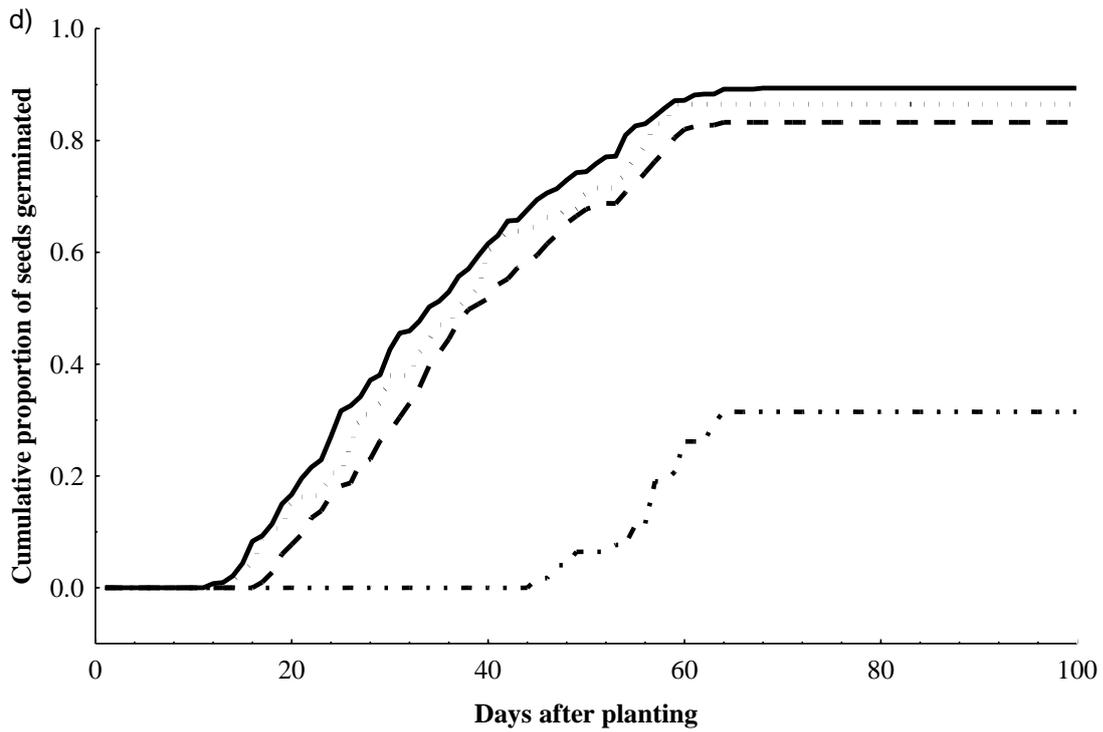
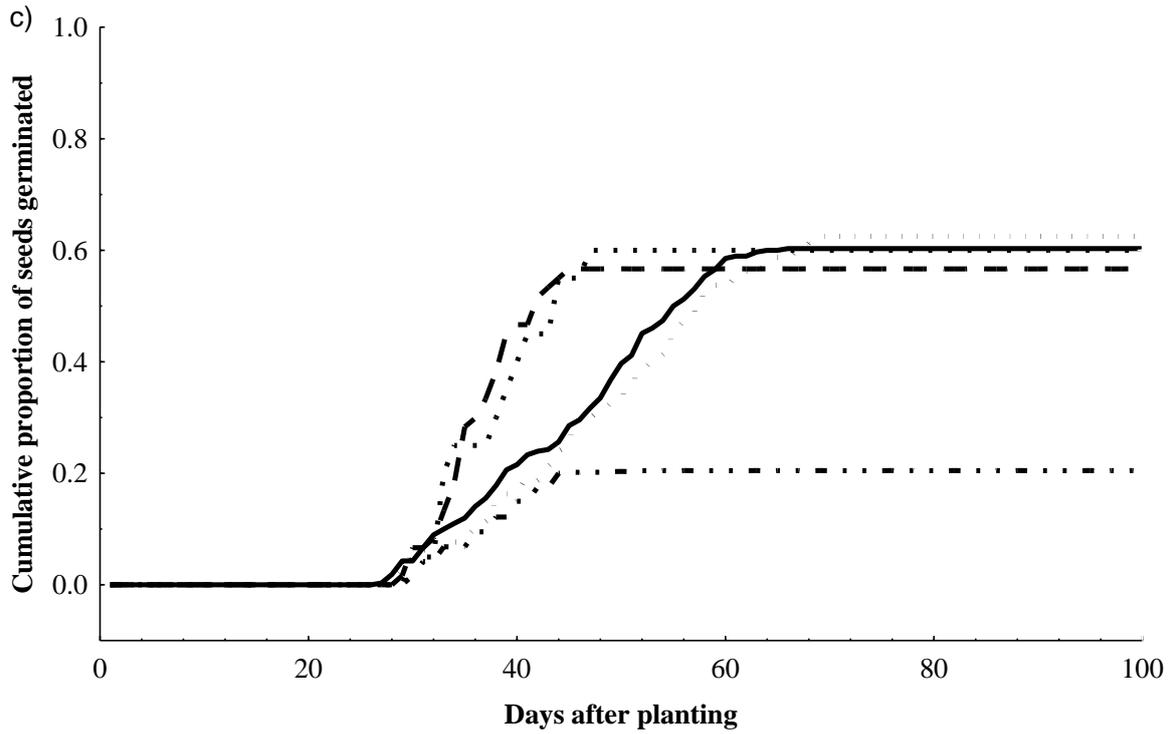


Fig. 3 Cumulative proportion of seeds germinated for Knysna turaco (.), purple-crested turaco (- · - · -), rose-ringed parakeet (- - -), pulp-removed (— —), and whole fruit (— - -) seeds from (a) *M. alba*, (b) *P. guajava*, (c) *C. camphora*, and (d) *S. mauritianum*.

**CHAPTER 3: Invasive rose-ringed parakeets as seed predators of indigenous fig trees
in South Africa: effects of their feeding behaviour on seed germination**

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Abstract

Parrots are considered important seed predators of *Ficus* species worldwide, but there is little information regarding the influence of seed ingestion by parrots on the germination success of figs. This study investigated the impact of fig consumption by the invasive rose-ringed parakeet (*Psittacula krameri*) on *Ficus* species namely *F. lutea*, *F. burkei*, *F. sur* and *F. natalensis* in South Africa. Fruits of these *Ficus* species were fed to rose-ringed parakeets, which have been observed feeding on them in the wild. Seeds removed from excreta, regurgitated seeds, seeds from manually de-pulped, and whole fruit were planted in soil trays housed in a greenhouse. Germination success of whole seeds following ingestion and regurgitation was quantified. Rose-ringed parakeets destroyed ca. 90% of ingested seeds, while only a few (ca. 10%) of the seeds remained intact. However, none of these seeds germinated. This could be as a result of mechanical and chemical digestive processes in the rose-ringed parakeets' digestive tract. Only a few regurgitated seeds managed to germinate. Manually pulp removed seeds resulted in earlier germination, as well as higher seed germination percentages than seeds from whole fruit and regurgitated seeds for all fig species. Our results suggest that invasive rose-ringed parakeets are mainly seed predators of *Ficus* species and rarely seed dispersers. Rose-ringed parakeets directly affect plant reproductive success by reducing the total number of seeds

that could germinate. An increase in the population of rose-ringed parakeets may have several negative impacts on indigenous fruiting tree species recruitment.

Keywords: *Ficus* sp; Invasive rose-ringed parakeets; Seed germination; Seed predation; Feeding behaviour

Introduction

Figs are one of the most important plant species worldwide (Bleher et al., 2003; Tello, 2003; Sreekar et al., 2010; Parr et al., 2011). These species provide a reliable food resource to frugivorous animals, particularly in periods of general fruit scarcity due to their year-round fruiting (Shanahan et al., 2001; Kirika et al., 2008; Lomascolo, 2008; Munin et al., 2011). *Ficus* tree species perform a critical function in the forest ecosystem by sustaining many native frugivorous animals (Ragusa-Netto, 2002; Sreekar et al., 2010; Munin et al., 2011; Parr et al., 2011). Consequently, fruiting figs are regarded as a keystone resource for many frugivores animals in tropical habitats worldwide (Lambert, 1989; Lambert and Marshall, 1991; Bleher et al., 2003).

Many of these frugivores are in turn important seed dispersers for fig trees (Shanahan et al., 2001; Wenny, 2001; Lomáscolo et al., 2010). Frugivorous birds in particular are the main seed dispersal agents of fig trees (Ragusa-Netto, 2002). The process of seed dispersal by birds usually involves ingestion (seeds passed through digestive tract) or regurgitation of viable seeds (Jordaan et al., 2011). The ingestion of seeds by birds often increases the germination rate and success of plants (LaFleur et al., 2009; D'Avila et al., 2010; Reid and Armesto, 2011; Czarnecka et al., 2012; Jordaan et al., 2011; Wilson and Downs, 2012). Regurgitated seeds may also increase germination probably due to pulp removal (Wilson and Downs, 2012). Seed ingestion by dispersers helps seeds escape

predation, competition, and fungal attack under the parent tree, thereby increasing the chance of survival (Jordaan et al., 2012).

The ingestion of seeds by birds is not always beneficial to plants and studies have found that ingested seeds may lose viability, thus reducing germination success (Renton, 2001; Francisco et al., 2008). Some bird species act as predators by killing the seed embryo (Oliveira et al., 2012). These species have the capacity to digest both seeds and fruit pulp or crush seeds before ingestion (Bonal et al., 2007; Burgos et al., 2008; Francisco et al., 2008). Seed predation may reduce or even stop expansion of plant species through reduction of seed survival and abundance (Combs et al., 2011; Carrión-Tacuri et al., 2012). Parrots are considered to be the most important predators worldwide (Sinclair and Ryan, 2000). Prior research provides some evidence demonstrating that seed predators cause significant declines in fig tree fitness (Crawley, 2000; Francisco et al., 2008). However, seed predation is not always detrimental (Young et al., 2012). Seed predators may act as primary seed dispersers by removing fruits from parent plants and carrying them away to feeding roosts for later consumption where seeds are regurgitated or dropped and then germinate (Sazima, 2008). In most cases, the negative effect of seed predation outweighed any positive effects in terms of dispersal (Janzen, 1981; David et al., 2015).

The rose-ringed parakeet (*Psittacula krameri*), is a medium sized parrot that has been widely introduced and naturalized in many countries throughout the world, including South Africa (Butler, 2003; Sinclair and Ryan, 2003; Hart and Downs, 2014). Rose-ringed parakeet is now considered as invasive species in South Africa (Thabethe et al. 2013; Hart and Downs, 2014). This species is regarded as one of the major destructive crop pests attacking a variety of grain products and fruit in its native range and is regarded as primary seed predators (Butler, 2003). Rose-ringed parakeets either prey on seeds by extracting seeds directly from the fruit and crack them or digest both pulp and seeds (Butler, 2003). The

feeding habit of this species potentially reduces effective plant dispersal and recruitment but this is poorly understood especially in terms of how seed predation influence seed germination rate and percentage as has been found in a Neotropical species *Brotogeris tirica* (Sazima, 2008).

Despite the potential impacts of seed predators on plant fitness, very few studies have been done on the intensity of seed predation by rose-ringed parakeets. This study assessed the amount of seed predation by invasive rose-ringed parakeets on seed germination success of fig species in South Africa. Germination success of whole seeds following ingestion and regurgitation was quantified. The objective of this research was to compare the germination success of fig seeds contained within whole fruits and pulp-removed seeds with ingested and regurgitated seeds. Numbers of rose-ringed parakeets have increased markedly in South Africa in recent years and are expected to continue to increase if not managed (Roche and Bedford-Shaw, 2008; Thabethe et al., 2013). Thus information on their role as seed predators or dispersers of native plants and their effect on germination success would be useful for future conservation and management purposes.

Methods

Maintenance of birds

This study was conducted at University of KwaZulu-Natal (UKZN), Pietermaritzburg, South Africa (29°37'0"S; 30°23'0"E) between January and June 2014. Ten captive-bred rose-ringed parakeets were housed in outside aviaries (1 x 2.12 x 2.66 m) at the UKZN animal house prior to experiments. Birds were fed a maintenance diet of pears, apples, bananas and oranges and sunflower seeds (*Helianthus spp.*) daily. AviPlus Softbill/Mynah pellets and crumble (Avi-products, Durban, South Africa), were added to the maintenance diets. Water was provided *ad libitum*.

Experiments

During experiments, birds were kept individually in cages (42.7 × 43 × 59.3 cm) in a constant environment room with 12L:12D photoperiod at 25 ± 1 °C for two weeks prior to trials being conducted. Clean plastic trays were placed under each cage to facilitate the removal of seeds from the excreta. Food was removed at 18h00 prior to trials which commenced the following morning at 06h00. All birds were weighed prior to (06h00) and after (18h00) for each trial. Fresh, ripe fig fruits were collected randomly from trees around UKZN and offered to the birds within 24 h of collection. Experimental fruits were incorporated into the maintenance diet two days prior to trial days. Only one fruit species was incorporated at a time. On the trial day, birds were fed a specific indigenous fruit species either cut or whole and water was provided *ad libitum*. Fruits were weighed to 0.01 g at the start and again at the end of each trial to determine the amount of food eaten per day. Control fruits were placed in the trial room and weighed before and after each trial to estimate evaporative water loss from uneaten fruits. Birds were observed at the start of each experiment to record feeding behaviour of an individual bird. At the end of each trial, excreta and regurgitated seeds were collected from the plastic trays.

Germination trial

Seeds were extracted from individual bird's excreta from each fruit treatment and planted within 24h of collection. Seeds were planted in separate plastic trays (265 × 180 × 75 mm) containing standard soil. The same soil type was used for all plant species. Seeds were covered with a potting soil layer c. 0.5 cm deep. All trays were then housed in a greenhouse and watered daily. Regurgitated seeds, de-pulped seeds and whole fruits were planted in the same manner for each species concurrently. Germination was considered as when the

seedlings first emerged through the soil surface. Once germinated, seedlings were counted and removed from the germination trays. Number of germinated seeds was recorded daily for 90 days.

Data analyses

The mean cumulative germination percentage was calculated for ingested, regurgitated, de-pulped and whole fruit seeds for each fruit species. The time taken from the time of sowing to first seedling emergence for each plant species was analyzed using Kruskal–Wallis ANOVA tests. The germination success of ingested, regurgitated, pulp-removed and whole fruit seeds was compared using Kruskal–Wallis ANOVA tests. One-way analysis of variance (ANOVA) was used to compare germination success of seeds ingested and regurgitated by rose-ringed parakeets to seeds from de-pulped fruits 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

General observation

Rose-ringed parakeets opened *Ficus* fruit with their beaks, tearing away pieces of the fruit wall and exposing the seeds for consumption. This species crushed most seeds before consumption but also consumed undamaged seeds together with pulp. They also dropped partially consumed fruit and regurgitated a few whole seeds while feeding.

Germination percentage

Most ingested *Ficus* seeds (ca. 90%) were damaged or destroyed by rose-ringed parakeets, thus not viable for planting (Fig. 1). Few whole seeds escaped digestion and were found in the excreta of a few (ca. five) individuals; however none of these seeds germinated after 90 days of planting (Fig. 1). The rose-ringed parakeets regurgitated a small number of seeds, some of which germinated while others were physically damaged (cracked open) (Figs. 1). Percentage germination of regurgitated seeds varied significantly between the tree species (Kruskal–Wallis ANOVA $H_3 = 290$, $n = 720$, $p = 0.00$) (Table 1). Mean regurgitated seed percentage germination ranged from 0.0 ± 0.0 (*F. natalensis*) to $26.7 \pm 1.9\%$ (*F. lutea*), which was different to pulp removed seeds (Table 1). Germination percentages of seeds from pulp removed fruit were higher than regurgitated seeds and seeds from whole fruit in all fig tree species (Fig. 1.). Pulp-removed seeds germination percentage varied significantly between species (Kruskal–Wallis ANOVA $H_3 = 360$, $n = 50.84$, $p = 0.00$) (Fig. 1). Mean percentage germination of pulp-removed seeds ranged from 43.1 ± 3.7 (*F. burkei*) to $62.1 \pm 4.1\%$ (*F. sur*), which was significantly different to regurgitated seeds (Table 1). Seed ingestion by rose-ringed parakeets had a significant negative effect on seed germination percentage in all *Ficus* species (Fig. 1).

Mean time to first seedling emergence

Seedling emergence time from regurgitated seeds varied significantly between *Ficus* species (Kruskal–Wallis ANOVA $H_3 = 11.5$, $n = 20$, $p = 0.0095$) (Fig. 1). The mean time for emergence of seedlings from regurgitated seeds ranged from 0.00 ± 0.00 (*F. natalensis*) to 27.4 ± 1.3 (*F. lutea*) days (Fig. 1). *F. lutea* and *F. burkei* regurgitated seeds germinated earlier than seeds from intact fruits (Fig. 1a and 1b) while *F. sur* regurgitated seeds germinated at the same time as seeds from intact fruit (Fig. 1c). *F. natalensis* regurgitated

seeds did not germinate at all (Fig. 1d). Pulp-removed seeds emerged earlier than whole fruit and regurgitated seeds in all species, while excreted (ingested) seeds did not germinate at all (Fig. 1, Table 1).

Discussion

Our results suggest that rose-ringed parakeets are mainly seed predators of *Ficus* fruit. Rose-ringed parakeets destroyed ca. 90% of ingested seeds, while only a few (ca. 10%) of the seeds remained intact. However, none of these seeds germinated. Parakeets crushed most seeds before consumption. These results are similar to those obtained by Jordano (1983) who documented that seed predators (especially parrots) destroyed about 78% of *F. continifolia* seeds in Costa Rica thus decreasing the survival of this species. Similarly, seed predation by orange-chinned parakeets (*Brotogeris jugularis*) damaged 77% of *F. ovalis* seeds in Costa Rica (Janzen, 1981). Janzen (1971) reported that orange-chinned parakeet extract seeds directly from the fig and crack them thus acting as seed predators. Lambert (1989) suggested that rose-ringed parakeets have grit in their muscular gizzard and long small intestines that may assist destruction of ingested seeds, hence decreasing or inhibiting germination strength. Seed predation directly affects plant reproductive success by reducing the total number of seeds that may germinate (Francisco et al., 2002). However, seed predation is not always detrimental.

Although the preyed upon seeds have little chance of survival, and thus do not often germinate, seed predation does not always result in death of the seed (Jordano, 1983; Castro et al., 1999; Wenny, 2000; Sazima, 2008; Young et al., 2012). For instance, some predators regurgitate few intact seeds, thus allowing successful germination (Moles et al., 2003; Guerrero and Tye, 2009; Young et al., 2012). Rose-ringed parakeets regurgitated few intact seeds that managed to germinate in this study. Seed regurgitation by seed predators is not

new, both the rock pigeon (*Columba livia*) and the Eurasian collared dove (*Streptopelia decaocto*) are said to regurgitate seeds (Cowles and Goodwin, 1958; Corlett, 1998). David et al., (2015) reported that although parakeets may regurgitate viable seeds they are not seed dispersers, as they usually regurgitate these seeds below parental trees and thus do not aid seed dispersal. These regurgitated or dropped seeds below the parent trees may be later eaten by post-dispersal seed predators or attacked by fungi and thus not germinate (David et al., 2015).

Pulp removal resulted in earlier seed germination and improved seed germination success compared with regurgitated seeds and seeds in intact fruits for all fig trees in this study. While ingested seeds did not germinate at all. This suggests that fig species require legitimate seed dispersers for effective dispersal and enhanced percentage germination. Although the present study focuses only on fig tree species, rose-ringed parakeets may consume the seeds of a variety of other native tree species and consequently an increase in the population of rose-ringed parakeets may have several negative impacts on many tree species recruitment. More studies are needed on the effects of invasive seed predators on native plants as the lack of research in this area may underestimate the impact of these predators on seed loss and low recruitment of native plants.

Acknowledgements

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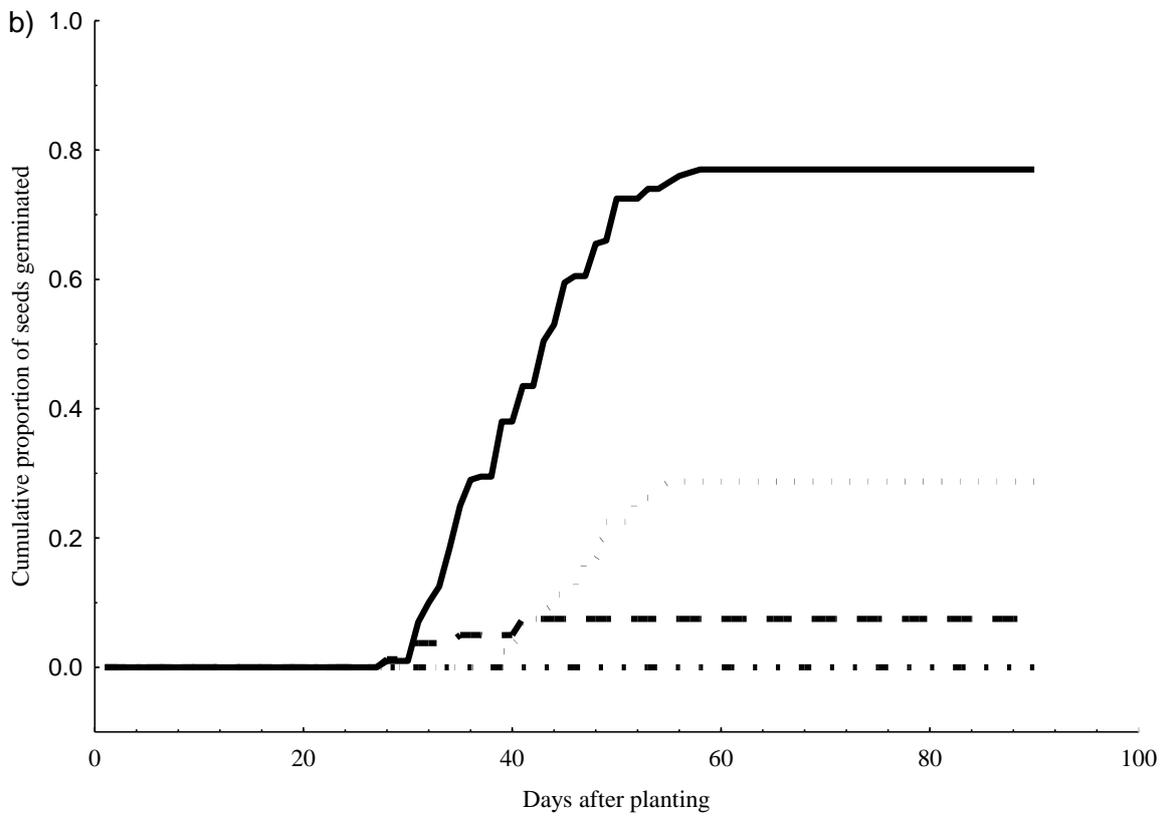
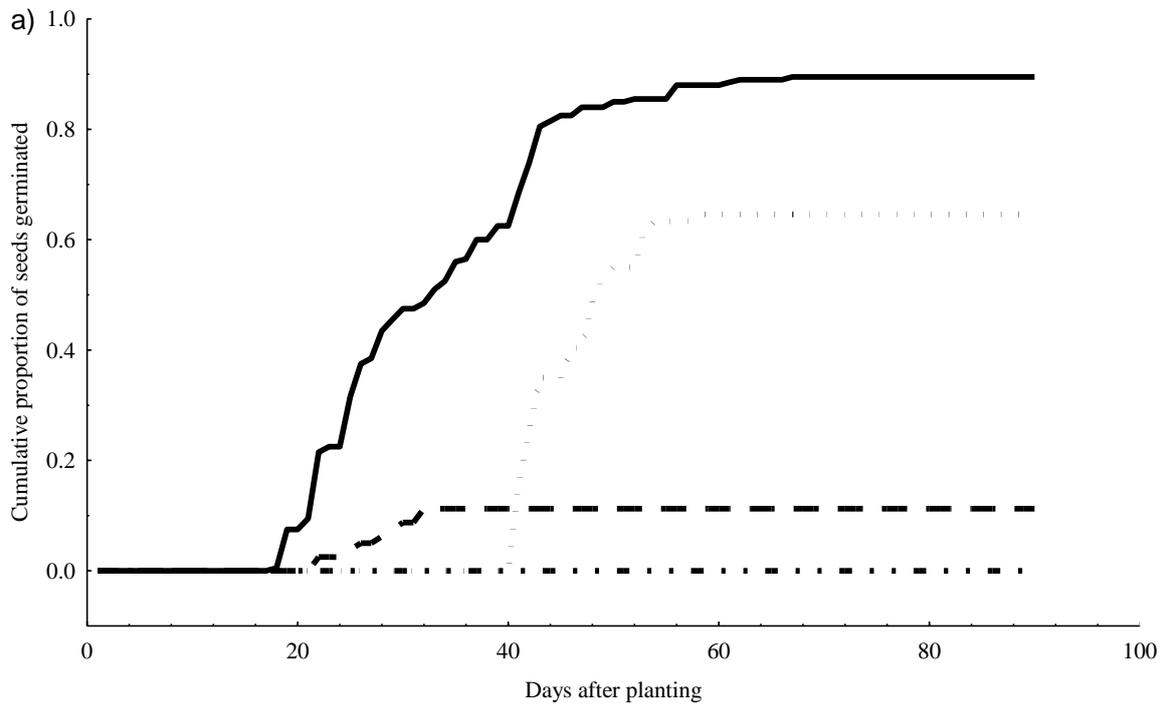
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Table 1 Difference between percentage germination of regurgitated seeds and that of pulp-removed seeds, whole fruits and ingested seeds, for rose-ringed parakeets fed fruits of four *Ficus* species

<i>Ficus</i> species	<u>Germination percentage of seeds from</u>								
	Pulp-removed seeds compared to regurgitated seeds			Whole fruit compared to regurgitated seeds			Ingested seeds compared to regurgitated seeds		
	F ₁	P		F ₁	P		F ₁	P	
<i>F. lutea</i>	31.87	0.00	S	2.67	0.10	NS	205.63	0.00	S
<i>F. burkei</i>	41.74	0.00	S	30.91	0.00	S	163.12	0.00	S
<i>F. sur</i>	67.03	0.00	S	6.16	0.01	NS	228.07	0.00	S
<i>F. natalensis</i>	302.1	0.00	S	129.68	0.00	S	N/A	N/A	N/A

N/A both treatment treatments did not germinate at all

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



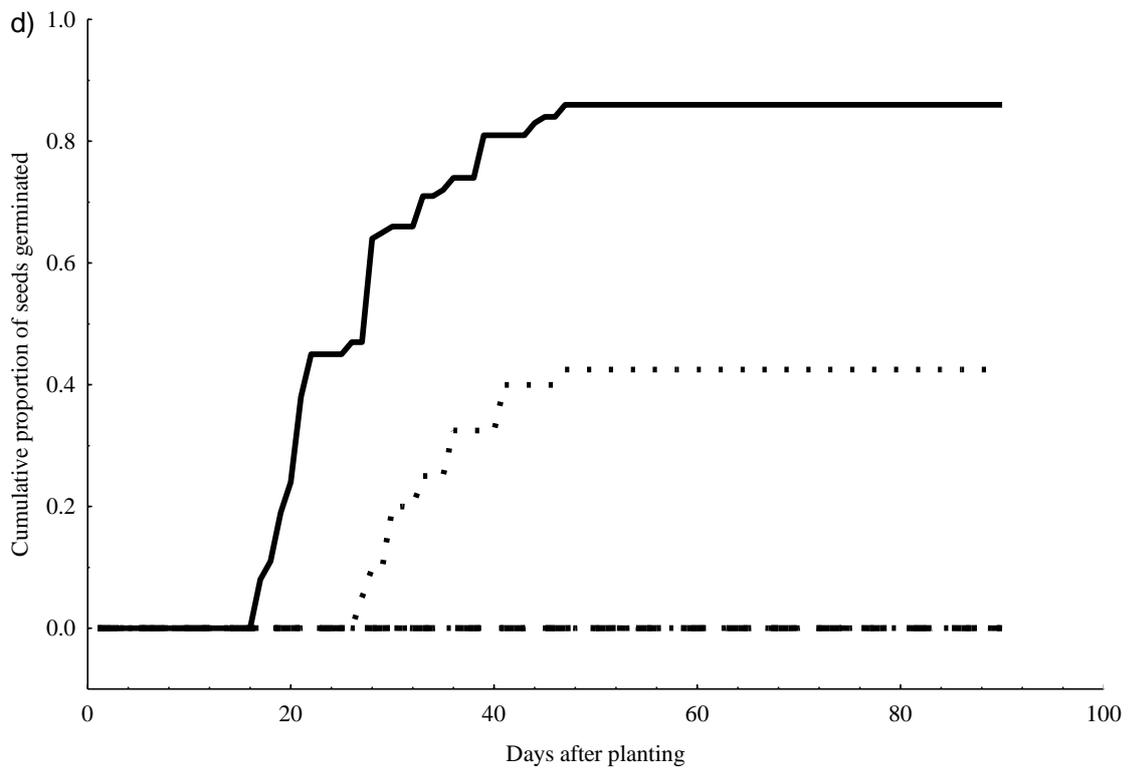
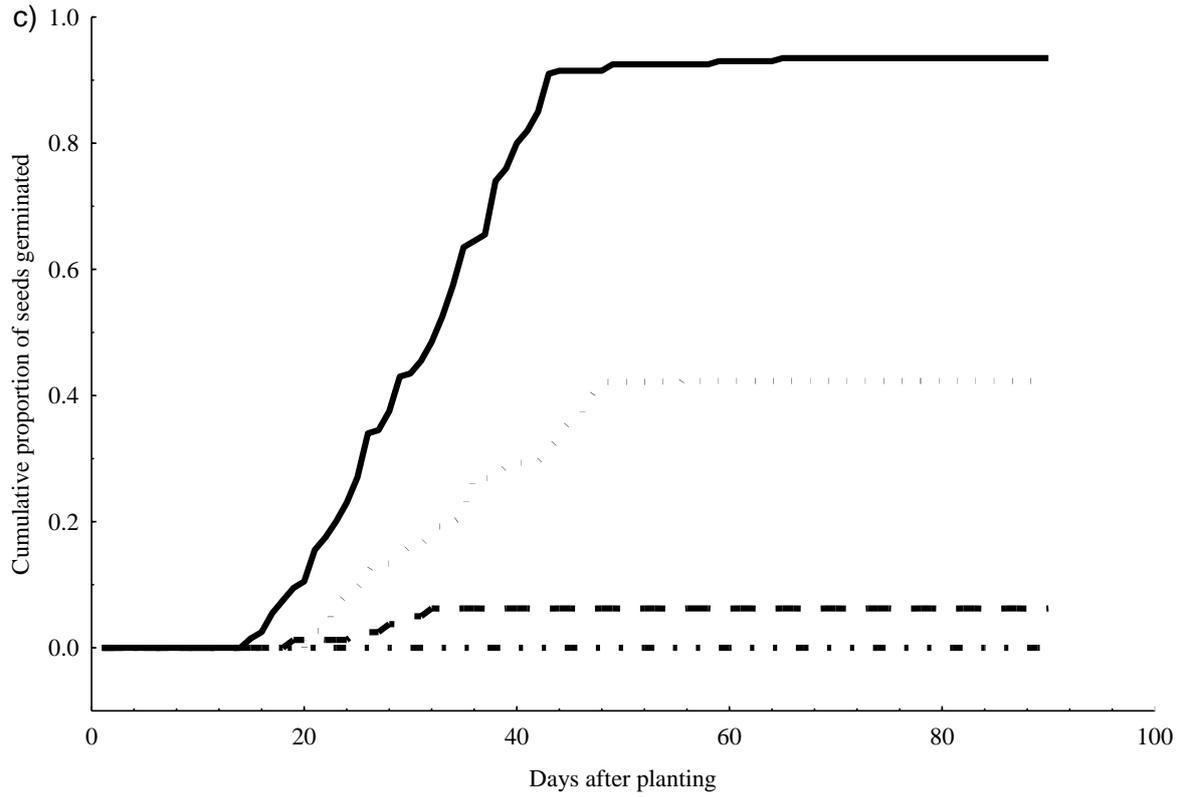


Figure 1: Mean cumulative proportion of seeds germination for ingested (---), regurgitated (···), pulp removed (—), and whole fruit (-·-·) seeds from (a) *F. lutea*, b) *F. burkei*, c) *F. sur* and d) *F. natalensis*.

**CHAPTER 4: Digestive efficiency of indigenous and invasive avian species fed fruit of
invasive alien plants in South Africa**

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Abstract

Many highly invasive plant species produce fleshy fruit that are consumed and dispersed by frugivorous birds. However, little is known about assimilation efficiency of many of these fruits by indigenous or invasive avian species in South Africa. We investigated whether indigenous Knysna (*Tauraco corythaix*) and purple-crested (*Gallirex porphyreolophus*) turacos and alien rose-ringed parakeets (*Psittacula krameri*) can maintain their body mass and meet their energy demands when fed fruits of four fleshy-fruited invasive alien plant species: *Solanum mauritianum*, *Cinnamomum camphora*, *Psidium guajava*, and *Morus alba*. Energetic parameters were calculated for all fruit diets. All avian species maintained their body mass when fed fruits of these invasive alien plants. Our results show that both invasive and indigenous avian species managed to gain their daily energy requirements from all four fruits of invasive plants, suggesting that they can meet their energetic demands by feeding on them only. These findings may explain why fruits of invasive alien plants are attractive to avian frugivores and highlights the role of avian frugivores in their dispersal.

Keywords: Assimilation efficiency, Avian species, Fleshy fruit, Invasive alien plant, South Africa

Introduction

Fleshly-fruited plants provide an important food source for many frugivorous animals worldwide (Corlett 2011; Davis 2011). These plants produce fleshly fruits that are primarily consumed and dispersed by different bird species (Drummond 2005; Davis 2011; Lehouck et al. 2011). It has been widely suggested that the relationship between fleshly-fruited plants and frugivores is mutualistic as frugivores benefit from energetic rewards from nutritious fleshy pulp while plants benefit from seed dispersal away from parent plant (Johnson et al. 1985; Witmer 1998; Lafleur et al. 2007; Gleditsch and Carlo 2011). Fruits differ considerably in their energy rewards (Gosper and Vivian-Smith 2010). Consequently, many avian frugivores show variation in preference among fruits (Izhaki and Safriel 1989; Greenberg and Walter 2010). Fruit preference of birds is influenced by a variety of fruit traits including: fruit nutritional composition, fruit size, fruit colour, seed size, seed load, fruit availability and accessibility (Avery et al. 1995; Greenberg and Walter 2010; Gleditsch and Carlo 2011).

Fruit choice by avian frugivores may also be influenced by the frugivores' ability to digest and assimilate nutrients (such as different sugars) efficiently (Levey and Rio 2001; Brown and Downs 2003; Jordaan et al. 2011b; Wilson and Downs 2011a; Wilson and Downs 2012b). The energy and nutrient content of the fruit does not necessarily reflect the value of that fruit to the frugivore (Levey and Rio 2001). Digestive efficiency is a proportional measure of nutrient extraction from consumed food (Levey and Duke 1992). This is a significant measure in quantifying nutrient utilization and energetic rewards gained by bird (Wilson and Downs 2012a). Digestive efficiency determines how efficiently frugivores digest and absorb nutrients and energy from a particular fruit (Jordaan et al. 2011b; Wilson and Downs 2012a) and depends on different factors such fruit intake rate, gut

size, transit time and the nutritional composition of the fruit (Worthington 1989; Wilson and Downs 2011b).

Fruit-eating birds generally have high energy demands and short gut retention times due to the cost of flight (Witmer 1999; Downs et al. 2012). In previous studies, frugivorous birds were often regarded as inefficient nutrient assimilators (Bosque and Parra 1992; Afik and Karasov 1995; Witmer and Van Soest 1998; Witmer 1999). However, recent studies have found that most of these birds have high apparent assimilation efficiencies (Brown and Downs 2003; Brown et al. 2010). These birds meet their energy demands by relying on high quality, energy rich and low bulk fruits (Wilson and Downs 2011a; Wilson and Downs 2012b). Furthermore, frugivorous birds increase their nutrient and energy uptake by increasing the rate of fruit intake and transit time (Gosper et al. 2005; Wilson and Downs 2012a). Some bird species, especially seed predators, increase their energy assimilation by digesting the seed content together with the fruit pulp (Witmer and Van Soest 1998).

Many highly invasive plant species have fleshy fruits that are consumed by frugivorous birds (Spotswood et al. 2013). Studies of frugivore preference for native and invasive fruits have found that many frugivores prefer invasive fruits to those of native plants and therefore may significantly influence the spread of invasive plant species worldwide (Sorensen 1984; Panetta and McKee 1997; Mokotjomela et al. 2013; Spotswood et al. 2013). These preferences may be due to the fact that fleshy fruits of some invasive plants have higher nutrient contents and energetic values than native species (Jordaan et al. 2011b; Jordaan and Downs 2012; Spotswood et al. 2013).

Fruits of invasive plants can have higher sugar content, more variable nitrogen amounts and smaller seed loads when compared with indigenous species (Willson and Harneson 1973; Wheelwright 1985; Stanley and Lill 2002; Gosper et al. 2005). These plants usually fruit year round and have longer fruiting periods (Gosper et al. 2005).

Invasive plants may therefore benefit both invasive and indigenous bird species by providing them with a valuable food source especially during times of fruit scarcity (Jordaan 2011b; Jordaan and Downs 2012). However, the increased consumption of invasive fruit by frugivores can accelerate the spread of invasive species and may have major negative implications for indigenous frugivorous animals and native plant species (Buckley et al. 2006). Both indigenous and invasive frugivores have shown a preference for invasive alien fruits suggesting that they may be able to efficiently process and assimilate energy from them (Gosper et al. 2005; Buckley et al. 2006; Jordaan et al. 2011b).

Despite the fact that some of the most damaging invasive plants are consumed by birds, few studies have focused on the consumption and digestive efficiency of invasive fleshy fruits by indigenous and invasive birds simultaneously in one study leading to ineffective management of these plants (Gosper et al. 2005). Consequently this study aimed to determine the digestive efficiency of invasive and indigenous avian frugivores feeding on the same. The second aim was to determine whether these birds are able to maintain their body mass and meet their energy demands while feeding on invasive fruits only. The bird species considered in this study were invasive rose-ringed parakeets (*Psittacula krameri*), and indigenous Knysna turacos (*Tauraco corythaix*) and purple turacos (*Gallirex porphyreolophus*). Knowledge of digestive efficiency of invasive alien fruits by frugivorous bird species will improve our understanding of the interaction of frugivores and invasive plants, which in turn would facilitate the development of improved management strategies for bird-dispersed invasive plant species in South Africa and globally

Methods

Maintenance of study animals

This study was conducted at the University of KwaZulu-Natal (UKZN), Pietermaritzburg campus, South Africa between March 2013 and April 2014. Ten rose-ringed parakeets, eight Knysna turacos and two purple-crested turacos were housed in outside aviaries (1 x 2.12 x 2.66 m), before the experiments were conducted. All species were long-term captive-bred individuals and thus acclimated to the local conditions.

Birds were fed a maintenance diet of fresh fruits including pears, apples, bananas and oranges daily. All fruits were either grated or chopped. 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 (*Helianthus spp.*) daily. Water was provided *ad libitum*.

Study species

Purple-crested and Knysna turacos are relatively large (c. 300 g and 310 g respectively) fairly common forest frugivorous birds that are indigenous to South Africa (Sinclair and Ryan 2003). The rose-ringed parakeet is a medium-sized (c. 116 g to 140 g) most widely introduced parrot that has managed to establish feral populations in at least 35 countries on five continents, including South Africa (Sinclair and Ryan 2003; Tayleur 2010). Rose-ringed parakeets and turacos eat fruits of both invasive and indigenous plants. However, rose-ringed parakeet also eat seeds and are therefore more of seed predators rather than frugivores. These bird species were chosen as they co-occur in the same habitats in Durban (KwaZulu-Natal), however little is known about their digestive efficiency while feeding and energy assimilation on invasive fruits in South Africa.

Alien fruit species

Fruits of five invasive alien plant species, namely: yellow guava (*Psidium guajava*), camphor (*Cinnamomum camphora*), mulberry (*Morus alba*) and bugweed (*Solanum mauritianum*) were investigated. These fruiting plants are some of the worst invasive plants in South Africa, especially in KwaZulu-Natal (Henderson 2007) and were chosen as the bird species in this study have been observed or reported to feed on these fruits in the wild. All ripened fruits were collected from naturalized plants in Pietermaritzburg, KwaZulu-Natal and offered to birds within 48 h of collection.

Experiments

During the experimental period, birds were moved from their outdoor maintenance aviaries and housed in a constant environment room set at 25 ± 1 °C on a 12:12 light dark cycle. Birds were acclimatized for two weeks prior to onset of the experiments and fed the maintenance diet daily during acclimatization. Birds were held individually in cages (42.7 × 43 × 59.3 cm) with a wooden perch, and were weighed before 06:00 h and after 18:00 h on sampling days. Removable plastic trays were placed below each cage prior to experimentation to facilitate excreta collection.

Prior to each experiment, sample fruit either whole or chopped was incorporated in the maintenance diet to ensure that birds were familiar with the particular fruit species and observed to feed on it. On the experimental day, birds were offered a specific single-species invasive fruit diet with water provided *ad libitum*. Fruits were weighed before and after each experiment to quantify the consumption of each fruit. Control fruits for each experiment were weighed prior to and after experimentation to estimate evaporative water loss from uneaten fruit. Food intake rates were corrected for evaporative water loss. Each specific

fruit species was fed for consecutive days. The first day of the experiment for each fruit species served to remove non-experimental food from the digestive tract and thus no excreta material was collected. All excreta for each individual bird were collected on the second day of the experiments.

Excreta were scraped off the tray into glass vials at the end of each sample day and weighed to determine wet mass. Excreta were then oven dried at 60 °C to constant mass and re-weighed. Control fruits were also oven dried at 60 °C to constant mass and re-weighed. Gross energy (GE) in food and excreta samples was measured with a bomb calorimeter and analysed at the Animal Science Department, UKZN.

Daily food intake (DFI) was quantified by correcting the amount of fruit eaten for evaporative water loss. DFI was then converted to a dry weight based on water content of the fruit and multiplied by the energy content of the fruit eaten to get the gross energy intake (GEI). To calculate the excreta energy loss (EE), the amount of dried excreta was multiplied by its dry weight energy value. Daily apparent energy assimilation (DEA) was calculated by subtracting EE from GEI. Apparent energy assimilation (AEA) was calculated as DEA divided by GEI and converted to a percentage. Finally, DFI, GEI, EE, DEA and AEA were all divided by mean body mass to convert to per gram individual body mass. The above procedure was repeated for each invasive fruit species and each bird species.

Analyses

All analyses were conducted using STATISTICA version 7 (Statsoft Inc, Tulsa, USA). General Linear Model Repeated Measures of Analysis Variance (GLM RMANOVA) was used to compare transit time, body mass, food intake rate and energy assimilation parameters.

Results

Body mass

There were no significant changes in mean body mass of rose-ringed parakeets ($F_{2,18} = 0.94$, $P = 0.41$, Table 1) Knysna turacos ($F_{3,21} = 0.58$, $P = 0.64$) and purple-crested turacos ($F_{3,3} = 0.88$, $P = 0.54$) respectively (Table 1) when fed the four invasive alien fruit diets during the experiments. All avian species maintained body mass on the respective fruit diets.

Daily food intake and energy assimilation

Knysna turacos and rose-ringed parakeets ingested significantly different amounts of the fruit diets respectively ($F_{3,25} = 12.54$, $P < 0.05$ and $F_{2,18} = 18.19$, $P < 0.05$, Table 1). While purple-crested turacos ingested similar amounts of the four fruit diets ($F_{3,3} = 3.57$, $P = 0.16$, Table 1). Knysna turacos consumed a greater amount of *M. alba* (0.35 ± 0.03 g g⁻¹ BM, $n = 8$) and the lowest amount of *S. mauritianum* (0.18 ± 0.02 g g⁻¹ BM, $n = 8$). Rose-ringed parakeets also ingested greater amounts of *M. alba* (0.54 ± 0.03 g g⁻¹ BM, $n = 10$) but ingested the lowest amount of *C. camphora* (0.25 ± 0.3 g g⁻¹ BM, $n = 10$), while they did not eat *S. mauritianum* at all. There was a significant difference in GEI of the four fruit diets for Knysna and purple-crested turacos respectively ($F_{3,21} = 57.95$, $P < 0.05$ and $F_{3,3} = 18.27$, $P < 0.05$, Table 1). However, there was no significance difference in GEI of three fruit diets for rose-ringed parakeets ($F_{2,18} = 1.46$, $P = 0.27$, Table 1). All avian species had the highest GEI on *M. alba* while the lowest on *S. mauritianum* for both species of turacos and *C. camphora* for rose-ringed parakeets (Table 1). There were significant differences in excreta energy loss in all avian species between the respective fruit diets, with the highest excreta loss on *M. alba* for all avian species while the lowest on *S. mauritianum* for both species of turacos and *C. camphora* for rose-ringed parakeets (Table 1). Furthermore, DEA of Knysna and purple-crested turacos was significantly different between fruit species, while DEA of rose-ringed

parakeets was not significantly different. All avian species had a highest DEA on *M. alba* while the lowest on *S. mauritianum* for both species of turacos and *P. guajava* for rose-ringed parakeets (Table 1). AE of Knysna turacos and rose-ringed parakeets was significantly different between the respective fruit species diets ($F_{3,21} = 20.97, P < 0.05$ and $F_{2,18} = 5.15, P < 0.05$, Table 1). AE of purple-crested turacos was not significantly different between the respective fruit species diets ($F_{3,3} = 2.54, P = 0.23$, Table 1). AE was high for all fruit diets; Knysna and purple-crested turacos had the highest AE on *M. alba* and lowest on *S. mauritianum*. Rose-ringed parakeets had the highest AE on *C. camphora* and lowest on *P. guajava* (Table 1).

Discussion

Bosque and Parra (1992) suggested that many avian species that include fruit in their diet are unable to maintain body mass when fed fruit only. Contradicting this, all avian species maintained their body mass when fed fruit of invasive alien plants in the current study, indicating that they obtained adequate energy from all fruits of studied invasive alien plants. These results were similar to those obtained by Jordaan et al. (2011b) who found that three frugivorous species managed to maintain their body mass on fruit of several invasive alien plants in South Africa.

Apparent assimilation efficiency is defined as how well a bird is able to digest a particular diet (Witmer 1998). In this study, both species of turacos and rose-ringed parakeets efficiently assimilated nutrients from all fruit of invasive alien plants eaten. Apparent assimilation efficiencies obtained in this study were relatively high (82-95%) and comparable to those of other frugivorous birds. For instance, our results were similar to obtained by Worthington (1989) who found high assimilation efficiencies ranging from 86-97.6% in two manakin species (*Manacus vitellinus* and *Pipra mentalis*). These results were

also comparable to those obtained by Jordaan et al. (2011b) who reported high apparent assimilation efficiencies (77-88%) of fruit of invasive alien plant fed to three indigenous avian species in South Africa. Furthermore, Witmer and Van Soest (1998) also obtained similar assimilation efficiencies in American robins (*Turdus migratorius*) that were maintained on fruit. Apparent assimilation efficiencies in this study were higher than those obtained by Wilson and Downs (2012a) for Knysna turacos when fed fruits of indigenous plants, which ranged from (15-84%). The lower assimilation efficiencies for Knysna turacos when fed indigenous fruit may be due to the fact that fruits of invasive alien plants have higher nutrient contents (e.g sugar) and energetic values when compared with indigenous fruits (Jordaan and Downs 2012; Wilson and Downs 2012a). This further supports speculation that a lower sugar concentration in the fruit may result in low assimilation efficiencies (Castro et al. 1989).

Fruits of invasive alien plants used in this study (i.e. *M. alba*, *P. guajava* and *S. mauritianum*) have higher sugar content and lower lipid content when compared with indigenous fruits (Jordaan and Downs 2012), while *C. camphora* fruit are relatively lower in sugar and higher in lipid content (Jordaan et al. 2011b). All avian species in this study were observed to have highest intake rate on *M. alba* diet, where they had the highest energy intake. Knysna and purple-crested turacos also had the highest apparent energy assimilation on the *M. alba* diet while rose-ringed parakeets had the highest apparent energy assimilation on the *C. camphora* diet. The high apparent energy assimilation of *M. alba* fruit may be a consequence of higher concentration of hexose sugars as suggested by Brown et al. (2010) that avian frugivorous prefers and efficiently assimilate hexose sugar than sucrose sugar. Jordaan and Downs (2012) found that *S. mauritianum* consist of relatively higher amount of sucrose sugars when compared to other fruits of invasive alien plants used in this study, this

may be the reason of low apparent energy assimilation of *S. mauritianum* fruits in the present study.

Our results show that both invasive and indigenous avian species are able to efficiently process all four fruits of invasive plants, suggesting that they can meet their energetic demands by feeding on invasive alien fruit only. These results may explain why fruits of invasive alien plant are attractive to frugivores. Ingestion of fruits of invasive plants by avian frugivores leads to the rapid spread and establishment of these plants and so has major negative implications on indigenous plant species. Future studies of visitation and feeding rates on invasive alien plants may give insight into avian frugivore behaviour in terms of seed dispersal and of fruit preference.

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Table 1: Mean \pm SE of amount eaten, gross energy intake, excreta energy, daily energy assimilated and apparent assimilation efficiency of rose-ringed parakeet, Knysna and purple-crested turacos when fed fruits from four invasive alien species

	<i>M. alba</i>	<i>P. guajava</i>	<i>C. camphora</i>	<i>S. mauritanium</i>
Knysna turaco				
Body mass (g)	272.8 \pm 7.10 ^a	273.4 \pm 6.29 ^a	271.1 \pm 6.43 ^a	273.18 \pm 6.79 ^a
Amount eaten (gg ⁻¹ BM)	0.35 \pm 0.03 ^a	0.34 \pm 0.02 ^a	0.31 \pm 0.04 ^a	0.18 \pm 0.02 ^b
Gross energy intake (kJg ⁻¹ BM)	4.15 \pm 0.34 ^a	1.30 \pm 0.08 ^b	1.99 \pm 0.24 ^{ab}	0.75 \pm 0.07 ^b
Excreta energy (kJg ⁻¹ BM)	0.44 \pm 0.03 ^a	0.24 \pm 0.02 ^c	0.30 \pm 0.03 ^c	0.16 \pm 0.02 ^d
Daily energy assimilated (kJg ⁻¹ BM)	3.71 \pm 0.31 ^a	1.06 \pm 0.08 ^b	1.68 \pm 0.21 ^b	0.75 \pm 0.07 ^c
Apparent assimilation efficiency (%)	94.1 \pm 0.15 ^b	90.3 \pm 0.89 ^d	91.9 \pm 0.33 ^d	89.1 \pm 0.43 ^d
Purple-crested turaco				
Body mass (g)	246.0 \pm 14.8 ^a	248.5 \pm 15.3 ^a	245.0 \pm 5.07 ^a	267.7 \pm 8.85 ^a
Amount eaten (gg ⁻¹ BM)	0.39 \pm 0.02 ^a	0.33 \pm 0.04 ^a	0.24 \pm 0.10 ^a	0.09 \pm 0.04 ^a
Gross energy intake (kJg ⁻¹ BM)	4.59 \pm 0.24 ^b	1.24 \pm 0.13 ^c	1.56 \pm 0.67 ^c	0.37 \pm 0.17 ^d
Excreta energy (kJg ⁻¹ BM)	0.45 \pm 0.01 ^d	0.24 \pm 0.04 ^a	0.25 \pm 0.07 ^a	0.07 \pm 0.01 ^c
Daily energy assimilated (kJg ⁻¹ BM)	4.14 \pm 0.25 ^c	1.00 \pm 0.17 ^a	1.31 \pm 0.60 ^a	0.31 \pm 0.16 ^d
Apparent assimilation efficiency (%)	95.0 \pm 0.33 ^d	89.2 \pm 3.06 ^d	90.5 \pm 1.25 ^d	88.7 \pm 4.33 ^d
Rose-ringed parakeet				
Body mass (g)	131.9 \pm 1.27 ^a	133.0 \pm 1.33 ^a	131.8 \pm 1.49 ^a	
Amount eaten (gg ⁻¹ BM)	0.54 \pm 0.03 ^b	0.32 \pm 0.04 ^a	0.25 \pm 0.3 ^a	
Gross energy intake (kJg ⁻¹ BM)	2.31 \pm 0.14 ^a	1.81 \pm 0.23 ^a	1.95 \pm 0.22 ^a	
Excreta energy (kJg ⁻¹ BM)	0.72 \pm 0.05 ^c	0.57 \pm 0.07 ^b	0.43 \pm 0.06 ^b	
Daily energy assimilated (kJg ⁻¹ BM)	1.59 \pm 0.09 ^a	1.24 \pm 0.17 ^a	1.52 \pm 0.18 ^a	
Apparent assimilation efficiency (%)	83.1 \pm 0.31 ^d	82.9 \pm 1.59 ^b	87.8 \pm 1.39 ^a	

BM, body mass

Treatments with the same transcript letter are not significant different at the 5% level

**CHAPTER 5: Seasonal effects on the thermoregulation of invasive rose-ringed
parakeets (*Psittacula krameri*)**

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Abstract

Invasive species are a major threat to global biodiversity. Rose-ringed parakeets (*Psittacula krameri*) are widely established outside their native range and are successful invaders in many countries, including South Africa. Physiological and behavioral responses to environmental conditions are considered to be major factors that influence the abundance and distribution of birds. As rose-ringed parakeets are able to tolerate a wide range of climatic conditions as invaders, it is important to understand their physiological responses to these. This study examined the effects of seasonal changes in ambient temperatures (T_a) on metabolic rate and body temperature (T_b) of captive-bred rose-ringed parakeets. Resting metabolic rate at various T_a and basal metabolic rate were significantly lower in winter compared to summer, and the thermo-neutral zone was broader in winter than in summer. There was no significant difference in body mass (M_b) between seasons. These parakeets showed seasonal thermoregulatory responses that represented energy conservation as expected, rather than cold tolerance. They were relatively tolerant of low T_a and showed no hypothermia at 5 °C. Our results suggest that this species is physiologically and behaviorally equipped to cope with a range of climatic situations and this partly explains its global success as an invader species.

Keywords: Invasive, Bird, Parrot, Rose-ringed parakeets, Summer, Thermoregulation,

Winter

Introduction

Invasive species are considered to be a serious ecological threat worldwide (Clavero and Garcia-Berthou, 2005). The spread of invasive alien species is now recognized as one of the greatest threats to ecological and economic security as they have an effect on native species through competition for resources and predation (Pithon and Dytham, 1999; Butler, 2005; Shwartz et al., 2009). In addition, invasive species not only pose a threat to biodiversity, but can also endanger human health by introducing diseases (Strubbe and Matthysen, 2007) and many are considered to be serious agricultural pests in many countries (Krishnaprasadan et al., 1988; Manchester and Bullock, 2000). Some invasive species succeed particularly well and manage to establish feral populations across a wide variety of regions and climatic conditions (Shwartz et al., 2009). Therefore, identifying the mechanisms that enable these species to establish viable populations in their new environments is vital for future management strategies. The range of climatic conditions a species is able to tolerate can be important in determining whether it establishes a self-sustaining population (Shwartz et al., 2009). Invasive species may become more successful when they are introduced to areas with climates that are similar to those of their native range (Shwartz et al., 2009).

Many birds tolerate a wide variety of environmental conditions as a result of their ability to undergo physiological, morphological and behavioral adaptations, which helps them to maintain a constant internal environment (White et al., 2007; Bush et al., 2008a, b; McKechnie, 2008). These adaptations include changes in metabolic rate, body mass, torpor, migration, fat content, burrowing, bill size and insulation capacity (Kaňuščák et al., 2004). For birds to survive in areas with considerable seasonal variation in ambient temperature,

they need to acclimatize to different seasonal temperatures (Chamane and Downs, 2009).

In this study, thermoregulatory metabolic responses of a medium-sized bird, the rose-ringed parakeet (*Psittacula krameri*), were investigated over two seasons to determine seasonal effects on thermoregulation. The invasive rose-ringed parakeet has managed to establish feral populations in at least 35 countries on five continents (Shwartz et al., 2009), including European countries, the USA, the United Kingdom and South Africa (Butler, 2005). This species is native to India and Asia, where it is considered to be one of the most significant agricultural pests of fruits and grains (Krishnaprasadan et al., 1988; Manchester and Bullock, 2000). Rose-ringed parakeets experience a wide range of climatic conditions in their native habitats ranging from cool and wet (e.g. northern India winter) to hot and dry (e.g. the savannas of Africa in summer) (Butler, 2005). Such a broad tolerance for climatic conditions suggests that climate matching would be of little relevance to this species; therefore, it is important to determine the factors that encourage their invasion. Rose-ringed parakeets may compete with native hole-nesters for nest sites, and they have relatively high reproductive success, facilitating their spread (Krishnaprasadan et al., 1988). They are one of the few parrot species that adapt to disturbed habitats.

Anthropogenic habitats are linked with biological invasions, and have certainly played a part in the spread of the rose-ringed parakeet (Czajka et al., 2011). Rose-ringed parakeet populations are increasing at an average of about 25% per annum in many non-native countries (Butler, 2005). Numbers of rose-ringed parakeets have increased markedly in South Africa in recent years and are expected to continue increasing (Butler, 2005; Roche and Bedford-Shaw, 2008). This invasive alien species has become established in various cities around South Africa (e.g. Durban, Johannesburg, etc.; Roche and Bedford-Shaw, 2008). Given their increase in numbers, their potential impacts on cavity nesting birds and other frugivores (Strubbe and Matthysen, 2007; Roche and Bedford-Shaw, 2008; Shwartz

et al., 2009), as well as their effect on agricultural crops are of concern.

Despite the fact that the rose-ringed parakeet is widely introduced, the ecology and the biology of this invasive species remain largely unstudied (Pithon and Dytham, 1999; Butler, 2005; Shwartz et al., 2009). The objectives of this study were to determine the rose-ringed parakeets T_b and oxygen consumption in summer and winter at different ambient temperatures. Further objectives were to determine their changes in resting metabolic rate at different T_a (RMR_{T_a} , see Zungu et al., 2013), BMR and the TNZ in two seasons (summer and winter). The hypothesis that rose-ringed parakeet thermoregulation is affected by season was tested, and it was predicted that BMR and RMR_{T_a} would decrease in winter for birds to conserve energy. In addition, it was predicted that M_b would increase in winter. This species offers an opportunity to determine whether a possible reason for its success as an invasive species is its ability to alter its physiology in a manner which makes it suitable to survive in new environments. Furthermore, as this species appears to be increasing in South Africa, information on their physiological capabilities would be useful for future management of this invader, particularly in terms of predicting future invasion pathways/areas.

Methods

Study animal and maintenance

The study was conducted at the University of KwaZulu-Natal (UKZN), Pietermaritzburg, South Africa (29°37'0"S; 30°23'0"E) between February and August 2012. Ten captive-bred rose-ringed parakeets from a breeder in Pietermaritzburg (so acclimatized to local conditions) were sourced and housed in two outdoor aviaries (1.0 x 2.1 x 2.7 m³) for the duration of the study. Five birds were kept in each aviary for 2-3 weeks before the experiments began. Birds were fed daily between 08:00 and 09:00 on a maintenance diet of fruits and vegetables, including bananas, apples, pears, pawpaws, spinach, carrots and

beetroot, supplemented with AviPlus Softbill/Mynah pellets and crumble (Avi-products, Durban, South Africa). All fruits and vegetables were either grated or chopped. Sunflower seeds and water were provided *ad libitum*.

Ambient temperature measurements (T_a)

T_a was measured using two *i-Buttons*® (Model DS 1922L \pm 0.5 °C, Dallas semiconductor, USA) placed inside a Stevenson's screen to record T_a in the outside aviary; one *i-Buttons*® was programmed to record summer (February–March) data and another one to record winter (July–August) data. T_a for other months (April–June) were acquired from the UKZN, Agrometeorology website for Pietermaritzburg, KwaZulu-Natal, South Africa (29° 37' 39.72" S, 30° 24' 09" E).

Body temperature (T_b) measurements

The core T_b of rose-ringed parakeets was measured using surgically implanted thermocron *i-Buttons*®. *i-Buttons*® were covered with paraffin wax and one of them was surgically implanted anaesthetically into the peritoneal cavity of each bird by a veterinarian. *i-Buttons*® were implanted on the 15th of February 2012 for summer measurements and on the 28th of June 2012 for winter measurements. All *i-Buttons*® were programmed to record T_b every 15 min for both summer and winter measurements. At the end of respirometer trials for each season (summer and winter) *i-Buttons*® were surgically removed from the birds by the same veterinarian.

Metabolic rate measurements

Metabolic measurements were tested over two treatments: summer acclimatization

(last week of February–March 2012) and winter acclimatization (last weeks of July–August 2012). Birds were fed during the day prior to the VO_2 measurements and fasted overnight during (and for 3 h prior to) testing, to ensure post-absorptive conditions. Oxygen consumption (VO_2) was used as an indirect measure of metabolic rate using a computerized open flow-through circuit respirometer system with an Ametek (model S-3A/l, Pittsburgh, PA, USA) oxygen analyzer to measure oxygen concentration. Effluent air was passed through a water condenser and then silica gel to remove water vapor, and soda lime to remove carbon dioxide. For metabolic rate measurements, birds were weighed and placed individually in transparent Perspex respirometer (35 X 20 X 25 cm³) with a wooden perch. Five respirometers (four experimental and one control chamber) were placed into a 1 m³ conviron that controlled $T_a \pm 0.1$ °C, with 12L:12D.

The respirometer system was switched on at least 2 h prior to the start of respirometry trials. Birds were placed in their respective respirometers between 15:30 and 16:00 and allowed to acclimate to the chamber for at least 2 h prior to testing. Lights were set to switch off at 18:00 and on at 06:00 the following day. Each VO_2 trial was conducted at a different T_a (5, 10, 15, 20, 25, 30, and 35 °C) in a random order. Flow rate of each chamber was measured using a Brooks thermal mass flow meter (Model 580E, Hatfield, PA, USA) with flow rates between 0.88 and 1.16 l min⁻¹. Flow rate was adjusted to maintain less than 1% change in concentration of O_2 in respirometers (compared with the baseline chamber where O_2 was set at 20.94%). A VO_2 recording was made every 6 min for each individual as described in Lindsay et al. (2009a, b) with 10 readings per individual per hour. Measurements of the various parameters for each chamber (T_a , flow rate and fractional O_2 concentrations) were recorded at the end of each 45 s sampling interval. Lowest mean hourly VO_2 for each rose-ringed parakeet at each T_a was taken as the RMR_{T_a} (Smit et al., 2008; Zungu et al., 2013). The following morning, birds were removed from the chambers

at ca. 07:00, except at 35 °C, where birds were removed at ca. 21:00 to avoid excessive evaporative water loss and to prevent thermal stress. Birds were reweighed and returned to the outdoor aviaries.

Comparative analyses

In this study, a non-phylogenetic regression (least squares regression (OLS)) was performed using the StigmaPlots® (Systat Software Inc., version 8.0) based on the data obtained from Lovegrove et al. (2011) to compare observed with expected based on body size of the species. The BMR and M_b of rose-ringed parakeets were added to the OLS regression to determine whether they fell within or above the 95% confidence intervals or within 95% prediction interval based on parrot allometric data (Lovegrove et al., 2011).

Data analyses

Data were analyzed using STATISTICA version 7 (Statsoft Inc, Tulsa, USA). Generalized Linear Models (GLIM) Repeated Measures Analysis of Variance (RMANOVA) was used to analyze RMR_{T_a} (expressed as mass specific values at each T_a because of individual variation in body mass) to determine change with temperature as each bird was subjected to seven different T_a in a particular season. Post-Hoc Tukey HSD tests were used to determine significant differences in RMR_{T_a} at various T_a . Therefore, these results were used to determine the width of the TNZ in both summer and winter. M_b , and T_b data were analyzed similarly. BMR was determined by taking the lowest RMR_{T_a} per individual across the range of T_a that lay within the TNZ.

Results

Ambient temperature (T_a)

Mean daily T_a were higher in summer (25.31 ± 5.53 °C; mean \pm S.E) than in winter (11.14 ± 5.30 °C, Fig. 1). Both minimum and maximum daily T_a were significantly higher in summer than in winter. There was a significant difference in average T_a between months, in summer (January, February and March) and winter (June, July and August; GLIM RMANOVA, $F_{5, 175} = 95.59$, $P < 0.05$, Fig.1). In summer, T_a ranged from 11.96 °C to 39.96 °C (mean minimum and maximum, respectively) while in winter they ranged from -0.29 °C to 29.49 °C (mean minimum and maximum).

Body mass (M_b)

There was no significant difference in M_b of the rose-ringed parakeets between summer and winter at various ambient temperatures (GLIM RMANOVA, $F_{6, 42} = 1.34$, $P = 0.26$, Fig. 2). However, there was a significant difference between initial and final M_b during overnight trials in summer (GLIM RMANOVA, $F_{6, 42} = 3.494$, $P < 0.05$) and winter (GLIM RMANOVA, $F_{6, 48} = 1.19$, $P < 0.05$). Post-Hoc Tukey's HSD test showed that initial M_b was significantly higher than final M_b in both seasons (Post-Hoc Tukey's HSD test, $P < 0.05$).

Metabolic rate

There was a significant difference in RMR_{T_a} at various ambient temperatures for rose-ringed parakeets between seasons. The respective summer RMR_{T_a} were generally higher compared with winter RMR_{T_a} (GLIM RMANOVA, $F_{6, 42} = 39.63$, $P = 0.00$, Fig. 3). Significant differences between the seasons were observed for RMR_{T_a} at 5 and 35 °C (Post-Hoc Tukey's HSD test, $P < 0.05$). However, there were no significant differences observed

from 10 to 30 °C between the seasons (Post-Hoc Tukey's HSD test, $P > 0.05$). In winter, there was no significant difference in RMR_{Ta} between 15 and 35 °C (Post-Hoc Tukey's HSD test, $P > 0.05$), indicating a broad TNZ ranging from 15 to 35 °C. In summer, no significant difference in RMR_{Ta} was observed between 20 and 35 °C (Post-Hoc Tukey's HSD test, $P > 0.05$), and consequently the TNZ in summer was from 20 to 35 °C. Although measurements were not carried out above 35 °C it is likely to be the upper critical temperature of the TNZ here as birds were showing heat stress. The lowest mean minimum VO_2 in the TNZ was taken as BMR and was measured at 30 °C in winter and 20 °C in summer. BMR was significantly higher in summer ($2.04 \pm 0.082 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1}$) than in winter ($1.77 \pm 0.072 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, GLIM RMANOVA, $F_{1,7} = 9.23$, $P = 0.019$, Fig. 3). Rose-ringed parakeets reduced their VO_2 during the scotophase in both summer and winter trials. The reduction in VO_2 was observed in all individuals and it was maintained until ca. 1h before the photophase. The time required to reach a minimum RMR_{Ta} during scotophase varied among individuals, ambient temperatures and seasons. It ranged from 1h (19:00 at 5°C in summer) to 11h (05:00 at 30 °C in winter). Most birds required at least 5h to reach minimum RMR_{Ta} .

Comparative analysis

Both winter and summer BMR data for rose-ringed parakeet (mean mass = 123.45 g and 123.04 g respectively) fell above the 95% confidence interval of the OLS regression but within the upper 95% prediction interval. BMRs in both summer and winter were higher, 10% and 15%, respectively, than those predicted for a parrot of its size.

Body temperature (T_b)

When the minimum and maximum T_b of individual rose-ringed parakeets were compared between summer and winter when birds were in the outdoor aviaries prior to

experimental trials, no significant seasonal differences were found in $T_{b \text{ min}}$ and $T_{b \text{ max}}$ (GLIM RMANOVA $F_{1, 9} = 0.23$, $P > 0.05$ and GLIM RMANOVA $F_{1, 9} = 0.21$, $P > 0.05$ respectively, Fig. 4). While summer $T_{b \text{ min}}$ was slightly higher ($38.06 \pm 0.68^{\circ}\text{C}$) than winter $T_{b \text{ min}}$ ($37.58 \pm 0.75^{\circ}\text{C}$), $T_{b \text{ max}}$ was similar in both summer and winter ($42.87 \pm 0.17^{\circ}\text{C}$ and $42.76 \pm 0.19^{\circ}\text{C}$ respectively).

Significant differences were observed in T_b during trials at the various respirometer temperatures in summer (GLIM RMANOVA $F_{36, 1496} = 14.89$, $P < 0.05$). T_b at 35°C was significantly different from all other temperatures (Post-Hoc Tukey's HSD test, $P < 0.05$). Interestingly, there was also a significant difference in $T_{b \text{ min}}$ at various respirometer temperatures in summer (GLIM RMANOVA $F_{36, 1496} = 14.89$, $P < 0.05$). $T_{b \text{ min}}$ was also significantly different at 35°C than at all the other temperatures (Post-Hoc Tukey's HSD test, $P < 0.05$), indicating the possible effects of higher ambient temperature. However, there was no significant difference $T_{b \text{ max}}$ at various respirometer temperatures in summer (GLIM RMANOVA $F_{6, 30} = 12.202$, $P < 0.05$, Fig. 9).

Although the *i*-Buttons® were set to record T_b during the respirometer trials in both seasons, T_b at T_b at 15°C and 20°C in winter were not recorded, and thus it was not possible to compare $T_{b \text{ min}}$ and $T_{b \text{ max}}$ across all VO_2 trials in winter. However, parakeets generally maintained a constant T_b at different respirometer temperatures in both seasons; T_b at 5 and 10°C in both summer and winter showed similar trend but were lower in winter (Fig. 5). In both seasons, all parakeets steadily reduced their T_b during the onset of the scotophase, then kept T_b fairly constant during the scotophase at about 20h00 and then increased their T_b at least 1 h before the photophase (Fig. 5).

Discussion

Southern hemisphere areas, including South Africa, are generally characterized by mild winters, but have unpredictable climates with daily and seasonal variation in temperatures (Jury and Nkosi, 2000; Wilson et al., 2011). This trend is evident in the temperature data obtained in the current study. Seasonal changes in temperature are known to have several morphological, behavioral and physiological consequences in birds. Climatic conditions can influence birds' ranges directly through impacts on thermo-regulatory processes, and indirectly by affecting food availability (Sheldon and Swanson, 1994). Interestingly, some bird species can tolerate a wide variety of climatic conditions and have established feral populations in non-native environments (Shwartz et al., 2009). Meanwhile other bird species with narrow environmental tolerance are restricted to their native regions (Bonier et al., 2007).

The rose-ringed parakeet is a global invader (Butler, 2005) and as has been highlighted from these results, one major factor that could influence the abundance and distribution of this and other bird species is their physiological response to environmental conditions (Weathers, 1979). Therefore, studies of physiological responses to climatic components of the environment are particularly relevant in the case of invasive species, as this can help us understand their invasion success.

In general, seasonal patterns of metabolic thermoregulation are more variable in birds than in (Swanson and Weinacht, 1997; Zheng et al., 2008) mammals (Lovegrove, 2005). Variation in an animal's body mass is regulated by several factors such as environmental temperature, food availability and quality, and physiological status (Zheng et al., 2008). In general, many bird species are thought to increase body mass to cope with cold ambient temperature and other climatic conditions in winter (Zheng et al., 2008). Interestingly, this was not the case in this study; there was no significant difference in body

mass of rose-ringed parakeets (medium-sized birds) in winter and summer, in accordance with the findings of Butler (2003), who suggested that rose-ringed parakeets may not associate the cooler temperatures of winter with a reduced food supply. This contrasts with the findings of several studies that have observed higher body masses in winter compared with summer (Chamane and Downs, 2009; Zungu et al., 2013). However, Bush et al. (2008b) and Smit et al. (2008) also observed no significant changes in body mass of some Afrotropical southern hemisphere bird species between seasons. Invasive house sparrows *Passer domesticus* also showed no changes in body mass between seasons (Nzama et al., 2010) in the southern hemisphere. Invasive monk parakeets *Myiopsitta monachus*, also did not change body mass between seasons (Weathers, 1979). This constant body mass in these invasive species suggests that these birds rely mostly on metabolic capacity rather than insulation to maintain their core body temperature, thereby facilitating their establishment in a wide variety of climatic conditions. However, this requires further investigation.

Some birds survive harsh winters by increasing or decreasing their basal metabolic rate (BMR), or by lowering the lower critical limit of the thermo-neutral zone (TNZ). Some studies have found winter reductions in BMR for several species of southern African birds, while others observed no change or an increased BMR in winter (Ambrose and Bradshaw 1988; White et al., 2007; Bush et al., 2008a; McKechnie, 2008; Chamane and Downs, 2009; Nzama et al., 2010; Wilson et al., 2011; Zungu et al., 2013). In endotherms, the capacity for physiological adjustment to winter is often related to body size (Packard and Boardman, 1999). Small birds (< 100 g) have been shown to increase their BMR during winter as a cold defence mechanism (Bush et al., 2008a, b). Some studies on large birds (> 200 g) have shown they decrease BMR in winter (Weathers and Caccamise, 1978; Smit et al., 2008). However, some medium-sized birds (100–200 g) have been shown to exhibit no seasonal flexibility or only slight decreases or increases in BMR (Sheldon and Swanson,

1994; Wilson et al., 2004). Generally seasonal flexibility of metabolic regulation is common in birds (White et al., 2007). In particular, many non-migrant species adjust their BMR seasonally, with some winter-acclimatized birds exhibiting higher BMR than those of summer-acclimatized birds (Zheng et al., 2008; Chamane and Downs, 2009; Nzama et al., 2010). Seasonal thermoregulatory responses that are associated with cold tolerance have been reported for many species that inhabit regions (e.g. Holarctic) where winters are severe, but relatively few studies have focused on species from regions where the climate is more unpredictable (e.g. southern Africa; Chamane and Downs, 2009; Lovegrove et al., 2011; Wilson et al., 2011).

The native range for rose-ringed parakeets includes Afrotropical regions but also the Oriental region (Butler, 2005). Generally, birds residing in Afrotropical regions are expected to reduce their BMR in winter as an energy conservation mechanism (Lovegrove and Smith, 2003). In this study, BMR and RMR_{Ta} were significantly lower in winter than in summer, indicating that the rose-ringed parakeets conserved energy during winter, as expected. Our results are similar to those of Smit and McKechnie (2010), and Zungu et al. (2013), who found decreased BMR in winter in Afrotropical southern hemisphere birds. However, other studies have found increased BMR in winter in Afrotropical southern hemisphere birds (e.g. Chamane and Downs, 2009; Nzama et al., 2010; Wilson et al., 2011). In addition, a few studies have found no seasonal difference in BMR in various Afrotropical southern hemisphere birds (e.g. Bush et al., 2008a, b; Smit et al., 2008). Rose-ringed parakeets displayed seasonal flexibility in BMR, with higher BMRs than predicted by the parrot allometry in both seasons. The winter BMR was 10% higher than predicted while the summer BMR was 15% higher than predicted for a parrot of its size. Both winter and summer BMRs of rose-ringed parakeets fell above the upper 95% prediction but within the upper 95% prediction interval. These contrast with the findings of Zungu et al. (2013),

where both winter and summer BMRs of burrowing parrots *Cyanoliseus patagonus* fell within the predicted intervals and were lower than expected. However, the results are similar to those of Lovegrove et al. (2011), where both winter and summer BMRs of greater vasa parrots *Coracopsis vasa* were higher than expected, although their winter BMR fell within predicted intervals.

Winter in Afrotropical regions is characterized by milder temperatures than that in Holarctic regions (Swanson and Weinacht, 1997). Rose-ringed parakeets are able to inhabit this region and become established as invasive species through physiological mechanisms (results from this study) and the exploitation of resources in urban habitats (Roche and Bedford-Shaw, 2008). Introduced species are more likely to be found in urban areas due to the abundance of food and nesting sites (Yap and Sodhi, 2004). Reductions in BMR facilitate a great energy saving during winter when increased thermoregulatory demands may coincide with low food availability (White et al., 2007). A reduction in BMR could thus aid rose-ringed parakeets during periods when food availability is low or unpredictable during winter. The patterns of seasonal metabolic adjustments in rose-ringed parakeets in the southern hemisphere reflect energy conservation in winter, rather than improved cold defense. This is similar to several southern hemisphere species (rock kestrel (*Falco rupicolis*) (Bush et al., 2008a), Australian silver-eye (*Zosterops lateralis*) (Maddocks and Geiser, 2000), African scops-owl (*Otus senegalensis*), fork-tailed drongo (*Dicrurus adsimilis*), crimson-breasted shrike (*Laniarius atrococcineus*), white-browed sparrow-weaver (*Plocepasser mahali*), and the pearl-spotted owlet (*Glaucidium perlatum*) (Smit et al., 2008) which also show reduced winter BMR, suggesting that winter reductions in maintenance energy requirements may be important components of seasonal acclimatization in some species inhabiting milder environments.

The TNZ of the rose-ringed parakeet is narrower in summer than in winter, which is

consistent with our predictions. These results are similar to other studies of other parrot species and medium to large birds (Bush et al., 2008a; Lovegrove et al., 2011; Wilson et al., 2011; Zungu et al., 2013). In general, birds with a wider TNZ are better adapted to cold environments (Schmidt-Nielsen, 1997). A broad TNZ can serve as an energy saving mechanism, allowing an organism to tolerate a wide range of temperatures without a necessity for increased metabolism (Hill et al., 2004).

We found no significant seasonal variation in T_b for the rose-ringed parakeets in the outdoor aviaries. Similarly several other species in both northern and southern hemispheres maintain a constant T_b , irrespective of changing T_a (Weathers, 1979; Chamane and Downs, 2009; Zungu et al., 2013). Birds have a distinct diurnal cycle in T_b , with higher T_b during the active phase than in the rest phase (Prinzinger et al., 1991). In this study, all rose-ringed parakeets reduced their T_b with the onset of scotophase and maintained this until 1 or 2 h before photophase. The reduction of T_b during the scotophase indicates that this species conserves energy at night since they are inactive. $T_{b\ min}$ was significantly higher at 35 °C in summer, indicating that this species increased their $T_{b\ min}$ at the highest T_a , but maintained a constant T_b at all other T_a 's. Rose-ringed parakeets were able to maintain a constant T_b under hot conditions so appear efficient at offloading excess heat. This, combined with their use of bird-feeders in urban areas (Butler 2003) and of cavities at night, may promote their success as invaders species.

In summary, BMR and RMR_{T_a} of the rose-ringed parakeets were significantly lower in winter than in summer. This decrease can be seen as an energy saving mechanism allowing this species to reduce energy costs in colder winter months. Therefore, the seasonal thermoregulatory adjustments in the rose-ringed parakeets are indicative of improved energy conservation, as expected for a bird that inhabits an unpredictable environment. M_b of rose-ringed parakeets did not change significantly between seasons but the TNZ was broader in

winter than in summer. The broader TNZ served as an energy saving mechanism, allowing this invasive species to tolerate a wider range of temperatures without increasing its metabolism. This species maintained fairly constant T_b 's in both summer and winter, indicating that they can tolerate low and high T_a 's irrespective of seasons. Therefore, this species seems physiologically and behaviorally equipped to occupy most climatic conditions. Other characteristics of rose-ringed parakeets which could contribute to their success as an invasive species may include their tolerance of man, their highly varied omnivorous diet, their high reproductive rate, and their ability to inhabit urban environments, such as the cities of Durban and Johannesburg, where they are mainly found in South Africa (Roche and Bedford-Shaw, 2008). These characteristics, combined with the phenotypic flexibility exhibited by rose-ringed parakeets in this study, may explain their global success as an invader species.

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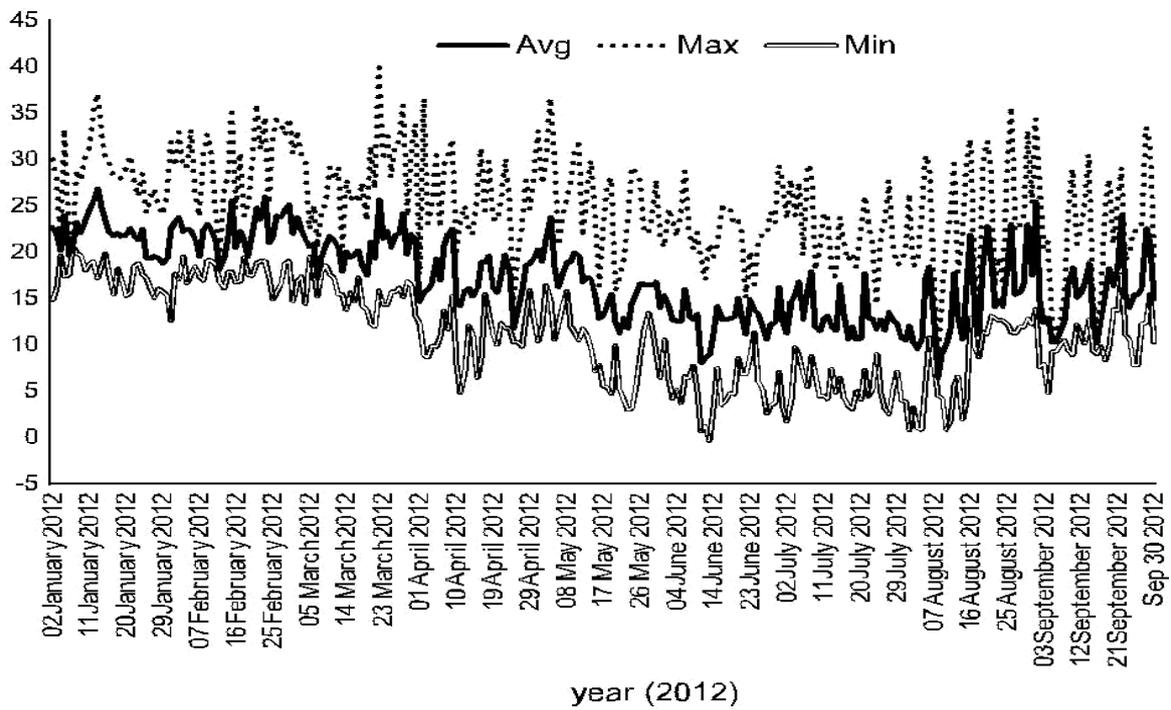


Fig. 1. Minimum (T_{\min}), maximum (T_{\max}) and average ambient (T_{avg}) daily temperatures for Pietermaritzburg from January to September 2012.

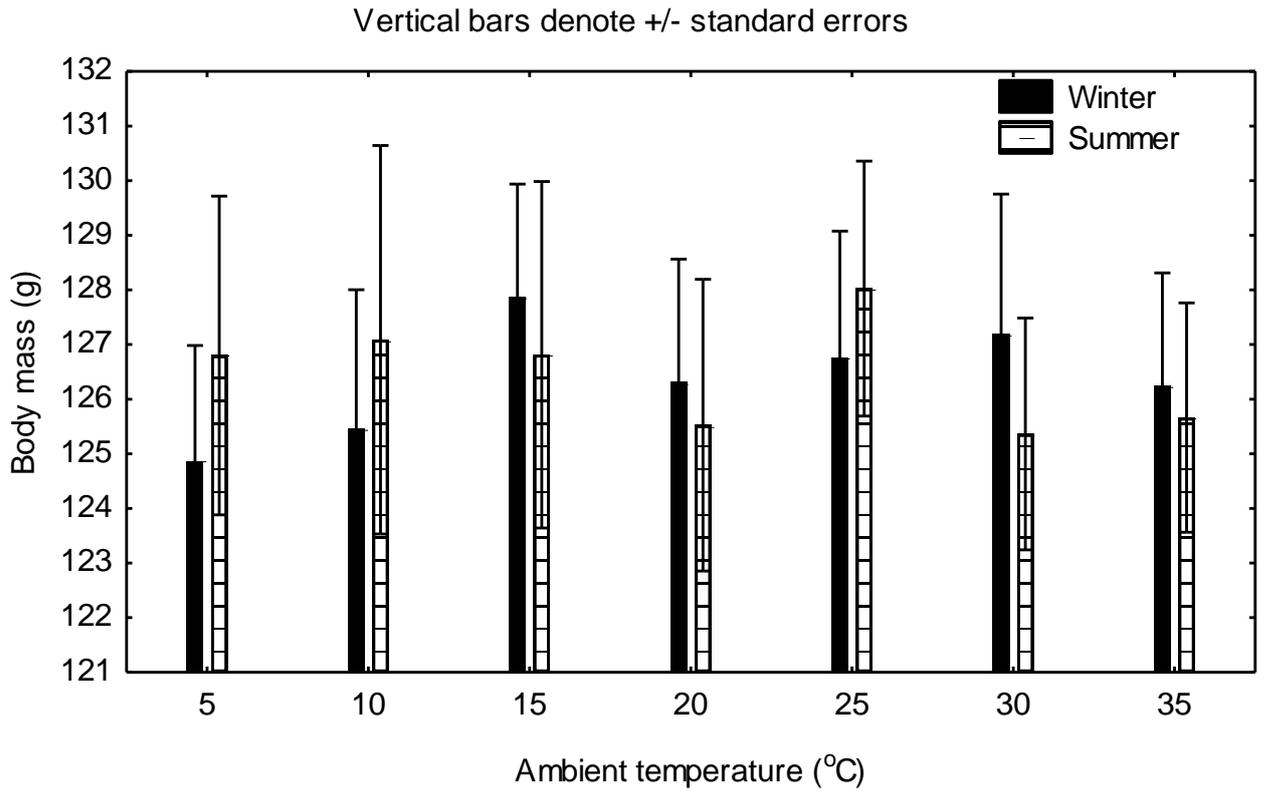


Fig. 2. Body mass (g; mean \pm S.E.) of rose-ringed parakeets at various ambient temperatures (°C) in summer and winter measurements were carried out.

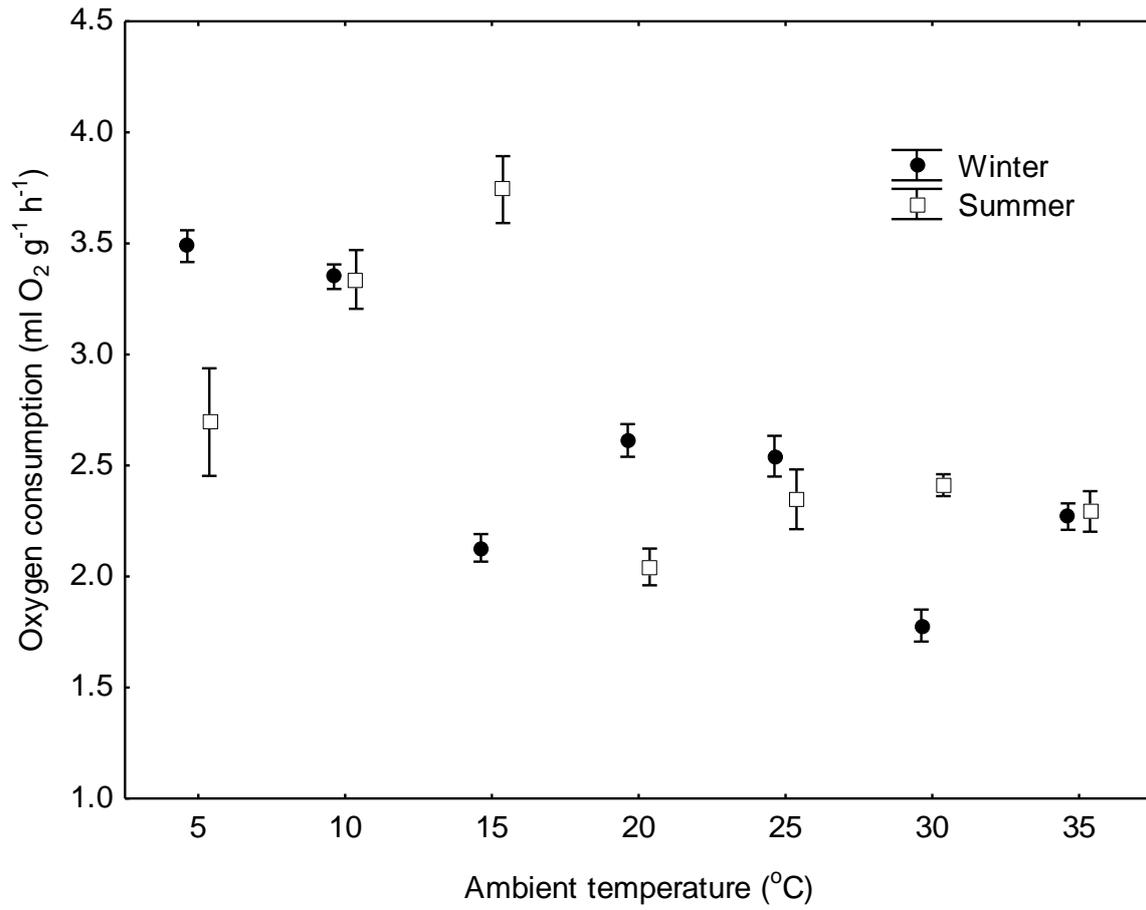
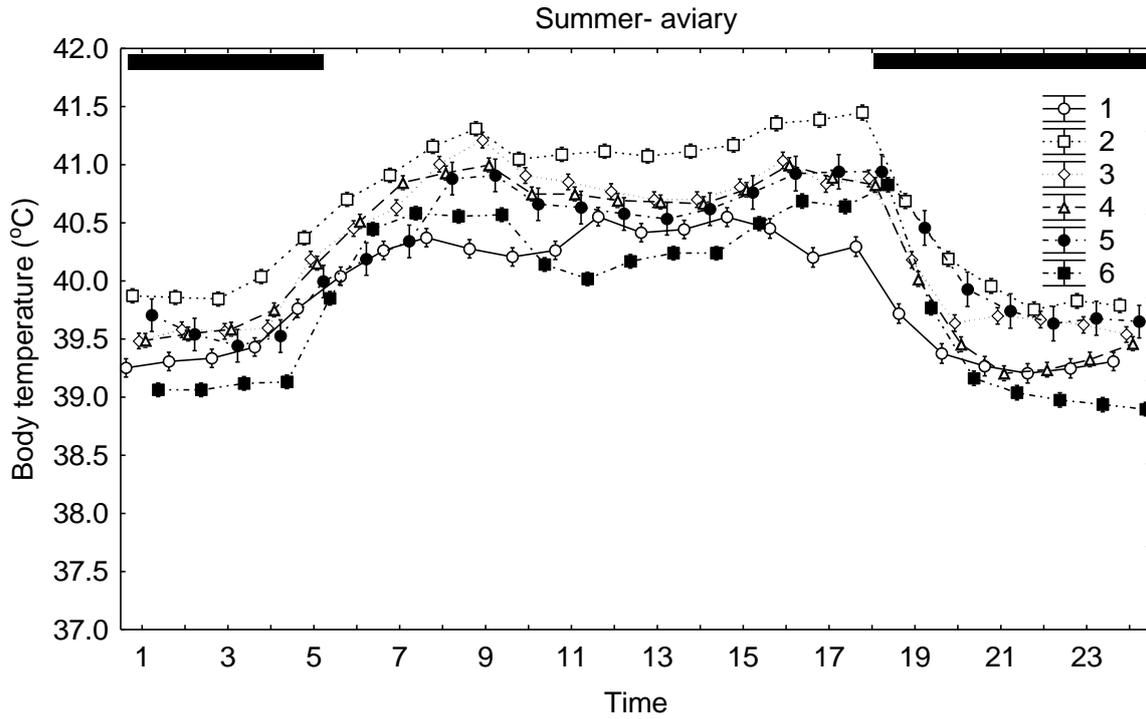


Fig. 3. Oxygen consumption (mean \pm S.E.) of rose-ringed parakeet at various ambient temperatures in summer and winter ($n = 10$).

a



b

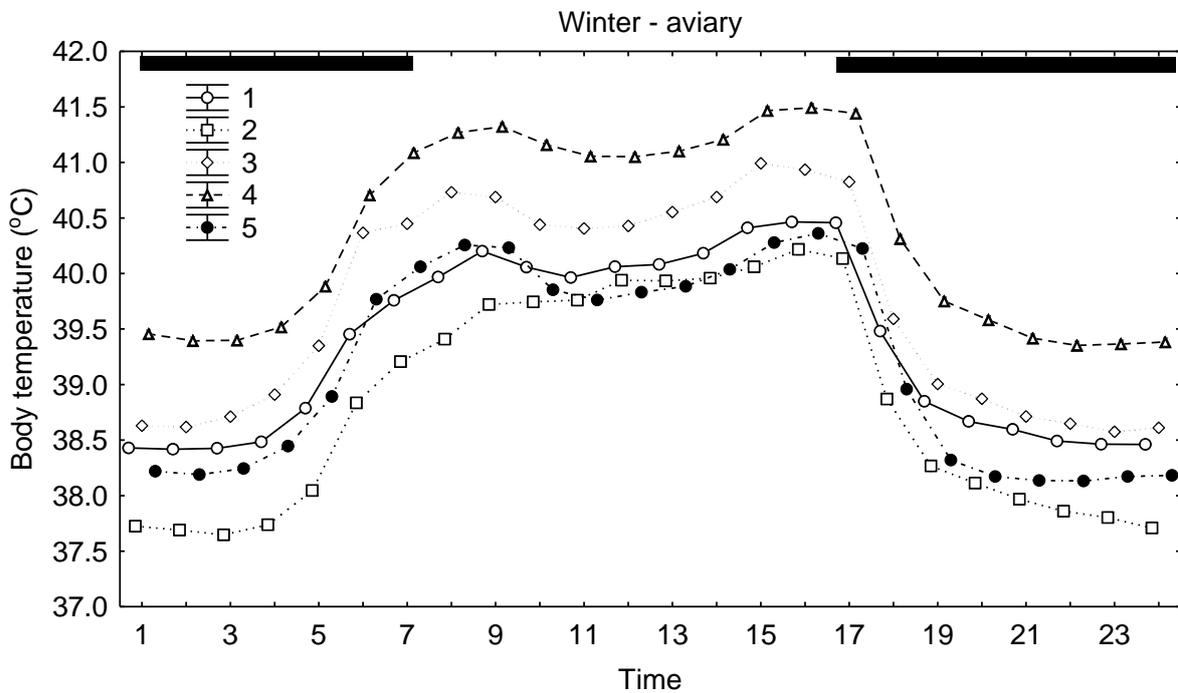
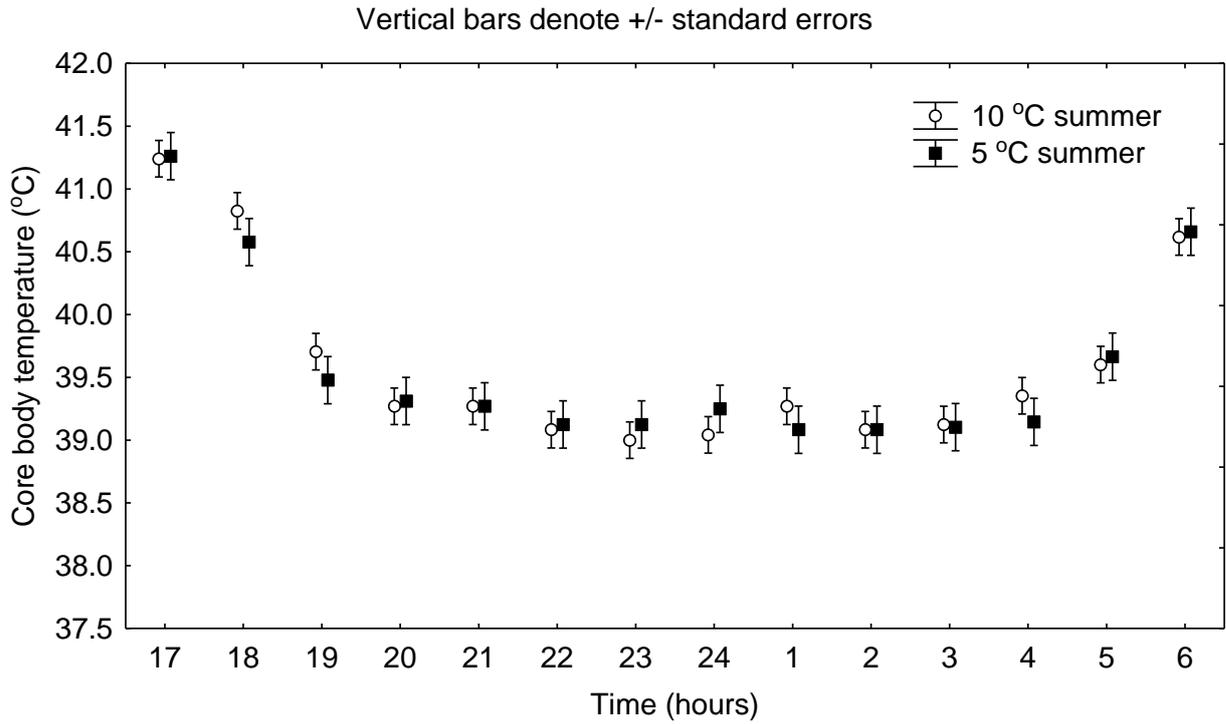


Fig. 4. Core body temperature (T_b) of rose-ringed parakeets over time (hours) in summer (a) and winter (b), when in outside aviaries. Each line represents an individual bird. Horizontal bars represent the scotophase.

a)



b)

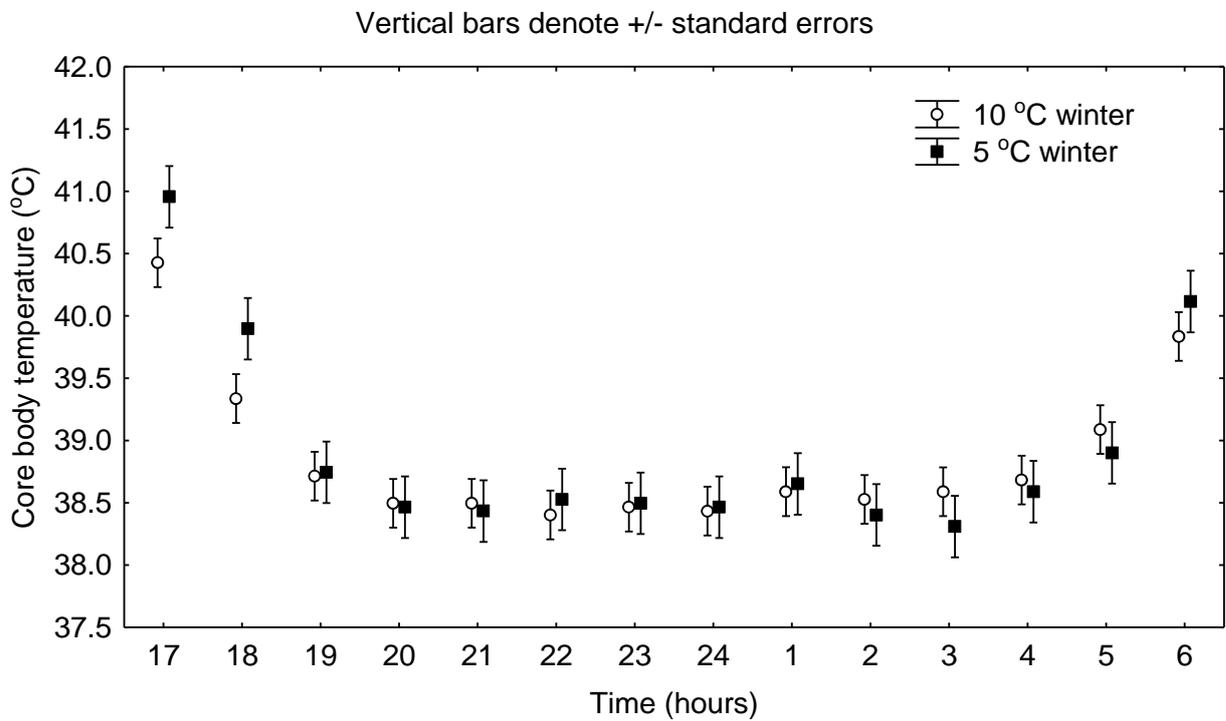


Fig. 5. Core body temperature (T_b) of rose-ringed parakeets with time (h ours) in a. summer ($n = 6$) and b. winter ($n = 4$) during respirometry trials at an ambient temperature of 5°C and 10°C respectively.

CHAPTER 6: Conclusion

Results obtained from this study suggests that indigenous Knysna and purple-crested turacos are the most efficient legitimate seed dispersers of the studied invasive alien plant species, while invasive rose-ringed parakeets are mainly seed predators (Chapter 2). Germination success of manually pulp-removed seeds did not differ from that of all invasive plant seeds ingested by turacos (Chapter 2). This suggests that seed coat abrasion is not important for germination of these plant species. However, since the germination success of seeds from whole fruit was significantly lower, we suggest that pulp-removal is needed for enhanced germination of these plants (Chapter 2). Thus frugivores may facilitate the establishment of fleshy-fruited invasive plants not only through seed dispersal, but also through seed processing that enhances germination and reduces the germination time (Chapter 2). Rose-ringed parakeets preyed heavily on seeds of the invasive alien plants in this study (Chapter 2). Germination percentage was very low, with a maximum value of ca. 20% and a minimum of ca. 10% for the seeds passed through the digestive tracts of rose-ringed parakeets (Chapter 2). Although the reproductive success of invasive plants may be negatively affected by invasive rose-ringed parakeets, it is unlikely that this species suppresses the population of these plants as they are already well established.

While it is important to understand the role of avian species on the germination of invasive plants it is also important to understand their role on germination of indigenous plants. It has been suggested that many indigenous plant species rely on frugivorous bird species for seed dispersal and recruitment. However, the type and quality of frugivory determines whether or not a seed is successfully dispersed (Jordano, 1983; Bleher et al., 2003; Vaz Ferreira et al., 2011). Some frugivores are legitimate disperses and successfully disperse ingested seeds, while other species are seed predators feeding on the embryo of the seed and thus rarely act as seed dispersers (Yagihashi et al., 1999; Crawley, 2000). Parrots

are among the most important seed predators of indigenous tree species worldwide (Jordano, 1983; Shwartz et al., 2009), however few studies have quantified the damage they cause to seeds. Rose-ringed parakeets are a highly invasive parrot species worldwide and its effects on indigenous trees seed dispersal and germination is of interest (Shwartz et al., 2009). Knowledge on the process of seed dispersal, seed predation and germination of indigenous plants is crucial for achieving sustainable forest management (Vaz Ferreira et al., 2011).

It is therefore essential that we gain an understanding as to the relationship between avian species and indigenous fruits. This thesis therefore also aimed to determine the amount of seed predation by rose-ringed parakeets of four indigenous *Ficus* species, in South Africa (Chapter 3). In addition, germination success of whole seeds following ingestion and regurgitation was quantified. Rose-ringed parakeets destroyed ca. 90% of ingested seeds, while only a few (ca. 10%) whole seeds escaped predation. However none of the seeds that escaped predation germinated (Chapter 3), suggesting that ingestion of seeds by this species is disadvantageous and has the potential to severely reduce recruitment rates of fig species.

Both native and invasive avian species have been shown to prefer fruit of invasive plant species over those of indigenous species (Mokotjomela et al., 2013). The amount of available energy in each fruit determines the amount of food that an individual will consume (Jordaan et al., 2011a; Wilson and Downs, 2012). It has been suggested that avian species tend to reduce food intake as energy level increases (Jordaan et al., 2011b). In general, fruits of invasive plants often offer greater nutritional rewards than those of indigenous plants (Jordaan et al., 2011b), suggesting that avian species may be able to efficiently process and assimilate energy from these fruit species. In this study, all avian species managed to meet their energetic demands by feeding on invasive alien fruit only (Chapter 4). These avian species also maintained their body mass when fed invasive alien plants only, suggesting that invasive alien plants may sustain both invasive and indigenous avian species during periods

of food scarcity, especially winter, as they have a longer fruiting period (Chapter 4). Fleshly-fruited invasive alien plants may thus facilitate the establishment and persistence of invasive bird species by providing a reliable food source (Chapter 4).

It is of importance to consider how the energy requirements of invasive avian species feeding on invasive fleshly-fruited plants differ seasonally. Rose-ringed parakeets have managed to establish feral populations in at least 35 countries on five continents (Shwartz et al., 2009) including South Africa (Thabethe et al., 2013). As this species is able to tolerate wide varieties of environmental conditions, it is vital to understand its physiological responses to various environmental conditions (Weathers and Caccamise, 1978; Bonier et al., 2007; Zheng et al., 2008; Thabethe et al., 2013; Zungu, et al. 2013). Rose-ringed parakeets were found to significantly reduce their resting metabolic rate (RMR) and basal metabolic rate (BMR) in winter (Chapter 5). They were also found to have a broader thermo-neutral zone (TNZ) in winter than in summer (Chapter 5) indicating a seasonal thermoregulatory response of energy conservation as expected, rather than cold defense. The body mass of this species did not vary between seasons. White et al. (2007) suggested that a reduction in BMR during winter (which is the period of low food availability) facilitates energy saving, this could explain the ability of rose-ringed parakeets to survive harsh conditions. Results obtained from this study suggest that this species is physiologically and behaviourally equipped to cope with a range of environmental conditions and this may explain its global success as an invader species.

Knowledge from this thesis will improve our understanding of the interaction of avian species and invasive and indigenous plants, which in turn would facilitate the development of improved management strategies for bird-dispersed invasive plant species in South Africa and globally. Furthermore, information on invasive rose-ringed parakeet's physiological capabilities would be useful for future management of these invaders,

particularly in terms of predicting future invasion pathways. Further studies should determine feeding behaviour as well as feeding rates of avian 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 seeds processed, should not be underestimated in the process of invasion. Additional studies are needed in order to clarify the role of rose-ringed parakeets on indigenous fruiting plants in South Africa.

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