

# Potential seed dispersal distances of native and non-native fleshy fruiting shrubs in the South African Mediterranean climate region

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**Abstract** Bird flight distances for the small *Zosterops capensis*, the medium-size *Pycnonotus capensis* and the large *Colius striatus* were extracted from these birds' initial ring and subsequent recapture locations and expressed on equivalent per km bases. The products of the bird-ring recapture records in nine different flight distance categories and daily consumption rates by these birds of seeds of two native (*Chrysanthemoides monilifera* and *Olea europaea* spp. *africana*) and two alien (*Lantana camara* and *Solanum mauritianum*) shrubs were used to construct seed dispersal curves. The dispersal distances to which ingested seeds were theoretically restricted were computed from the product of the retention time of seed in the birds' guts and their flight speeds using published functions. All three bird species displayed thin long-tailed seed dispersal curves characterized by peaks at distances below 1 km which declined progressively with increasing distances, the tails extending to distances of up to 400 km. Flight distances corresponding with predicted seed gut retention times were 9.4 km in the small *Z. capensis*,

17.8 km in the medium size *P. capensis* and 21.2 km in the large *C. striatus*. These potential seed dispersal distances were much greater than the frequently reported long distance seed dispersal threshold of 1 km by frugivorous birds in fragmented landscapes.

**Keywords** Frugivorous birds · Seed dispersal distance · Alien shrubs · Competition · Fleshy fruits

## Introduction

The dispersal of seeds ingested by frugivorous birds over long distances from maternal plants (Van Der Pijl 1982; Higgins et al. 2003; Schurr et al. 2009; Whelan et al. 2008) provide essential genetic links between disconnected plant communities (Nathan et al. 2008; Schupp et al. 2010) by facilitating the formation of new self-sustaining populations in different landscapes (Sakai et al. 2001; Schurr et al. 2007; Nathan et al. 2008; Tsoar et al. 2011). For these reasons, knowledge of bird-mediated seed dispersal is important for predicting future plant distribution ranges (Sakai et al. 2001; Nathan et al. 2008; Tsoar et al. 2011) and in screening potential invasiveness of alien plants in novel environments (Tucker and Richardson 1995; Pheloung et al. 1999; Nel et al. 2004). This is especially pertinent in the South African Mediterranean climate region where alien plants constitute a major threat to the native plant communities (Roura-Pascual et al. 2009), and heavy habitat fragmentation

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renders the region more vulnerable to extinctions associated with long distance dispersal limitations under global climate change (Schurr et al. 2007; Lenz et al. 2010).

Plant fruit, bird and habitat attributes interact to provide resultant dispersal distance patterns and effectiveness (Gosper and Vivian-Smith 2010; Wotton and Kelly 2012). Different models have been applied to predict seed dispersal distances (Higgins et al. 2003), though all are constrained by inconsistent bird movements (Russo et al. 2006; Gomes et al. 2008), differential gut retention times of seeds by captive and free roaming birds (Levey and Martinez del Rio 2001; Kays et al. 2011; Tsoar et al. 2011) and by birds of different body mass (Schurr et al. 2009; Tsoar et al. 2011). Gut retention time of seeds is influenced by seed size with large seeds consumed by bigger birds generally expelled more rapidly than small seeds (Whittaker and Jones 1994; Levey and Martinez del Rio 2001; Charalambidou et al. 2003; Nathan 2007). Moreover, fruit components such as high concentrations of sucrose and glycoalkaloids have a laxative effect on several monophyletic bird lineages, including starlings, mimids and thrushes which consequently cause seeds to be expelled more rapidly (Murray et al. 1994; Malcarney et al. 1994; Cipollini and Levey 1997). Nevertheless, fruits with high monosaccharide content and small seeds are generally preferred by birds and their seeds are more likely to be dispersed than those of contrasting fruit types (Jordano 2000; Gosper et al. 2005; Gosper and Vivian-Smith 2010; Schupp et al. 2010; Aslan and Rejmanek 2012), such as those with a high lipid content which are difficult to process in bird guts (Fuentes 1994).

There are limited data on how far seeds are dispersed by birds (Nathan 2001) and consequent effects on the recruitment of different plant communities (Wang and Smith 2002; Hyatt et al. 2003; Godinez-Alvarez and Jordano 2007). This is attributed to inconsistent bird flight patterns, imprecise technologies for tracking bird movements (Nathan 2001; Schupp et al. 2002; Russo et al. 2006) and altered seed dispersal patterns induced by defaunation and habitat fragmentation (Herrera 1995; Muller-Landau and Hardesty 2005). It has been reported that habitat fragmentation promotes long distance dispersal by frugivorous birds in Manaus, Brazil, with long distance dispersal probabilities however decreasing with diminished size of habitat fragments, reduced

density of fruiting plants and avian dispersers (Uriarte et al. 2011).

Many past field studies have reported relatively short seed dispersal distances by birds of less than 1 km (Wenny and Levey 1998; Wenny 2000; Levin et al. 2003; Jordano et al. 2007), though longer seed dispersal distances by birds have more recently been reported. Examples include *Onychognathus tristramii* (Tristram grackle) with an observed foraging range of 14.2–28.3 km in the Negev desert of Israel (Spiegel and Nathan 2007), the dispersal of *Virola nobilis* seeds over average distances of 1.8 km per day by wild *Ramphastos* toucans in the Soberania National Park in Panama (Kays et al. 2011) and reported flight distances of up to 14.5 km by *Ceratogymna* hornbills in West Africa (Holbrook and Smith 2000; Holbrook 2011) and trumpeter hornbills *Bicanistes bucinator* in eastern South Africa forests during their foraging bouts (Lenz et al. 2010).

Both bird flight speeds and retention times of seeds in bird guts have been applied to estimate potential seed dispersal distances. An example is the application of measured gut retention times and flight speeds of the fruit pigeon *Ducula pacifica* to compute potential distances that *Myristica hypagyrta* seeds are dispersed in Tonga in Western Polynesia (McConkey et al. 2004). Schurr et al. (2009) in an analysis of published records found a high correlation between bird body mass, flight speed, seed load and seed passage time through the gut. Large birds retained seeds for longer periods in their guts and flew longer distances than small birds (Jordano et al. 2007; Tsoar et al. 2011). However, small frugivorous birds do also tend to cover large distances when avoiding dangerous events such as fires (Wilms and Kappelle 2006; Gomes et al. 2008) and when tracking fruit resources (Berthold 1999; Saracco et al. 2004; Telleria et al. 2008). A typical example is that of the tiny (13–26 g) territorial European robin (*Erithacus rubecula*), which tracks spatially variable fruit over extensive distances in the Spanish Mediterranean scrubland (Telleria et al. 2008). Indeed, such small birds with occasionally extended gut retention times of ingested seeds (Shilton et al. 1999; Spiegel and Nathan 2007) may emulate seed distance dispersal potentials of large birds. In view of these anomalies, we examined how far seeds of fleshy-fruited native and alien shrubs are potentially dispersed by different size bird species in the South Africa Mediterranean climate region. Our hypothesis

was that seeds of both native and alien shrubs are potentially dispersed by frugivorous birds over much greater distances than the frequently reported long distance seed dispersal threshold of 1 km in fragmented landscapes.

## Methods and materials

### Seed dispersal potential

We used spatial distributions for bird-ring recapture frequency as a proxy of foraging movement behaviour (Cain et al. 2000; Tsoar et al. 2011), and a theoretical vector-based model, based on published allometric equations (Schurr et al. 2009; Tsoar et al. 2011), to establish seed dispersal distances by local bird species. Frequency of bird-ring recapture records provided spatial patterns of bird flight distances (Nathan and Muller-Landau 2000; Nathan et al. 2003). These records were extracted from the South African Bird Atlas Project (SABAP 1 & 2) databases (Animal Demography Unit, University of Cape Town) for three different size frugivorous bird species, namely the small *Zosterops capensis* (Cape white-eye), the medium size *Pycnonotus capensis* (Cape bulbul) and the large *Colius striatus* (Speckled mousebird) with different gape dimensions (Ally 2010; Chama 2012). These frugivorous bird species were representative in terms of their size, abundance and contribution to seed dispersal in the study region (Knight 1988; Cowling et al. 1997; Hockey et al. 2005; Mokotjomela et al. 2013b). From the bird-ring recapture records, flight distances were derived from the initial ring location and subsequent recapture locations, these calculated geo-spherically with flight distance measures based on the earth's contour rather than on direct vectors. The total numbers of bird-ring recapture records were extracted for nine different flight distance categories, namely 0–1 km, 1–2.5 km, 2.5–5 km, 5–10 km, 10–50 km, 50–100 km, 100–200 km, 200–300 km, 300–400 km. They were expressed on equivalent per km bases by dividing the numbers of bird-ring recapture records in each category by the distance. The product of the recorded numbers of bird-ring recaptures per km in each flight distance category and previously published records of the average numbers of seeds of two common native (*Chrysanthemoides monilifera* and *Olea europaea* spp. *africana*) and two

common alien (*Lantana camara* and *Solanum mauritianum*) shrubs consumed per day by the three different size bird species (Mokotjomela et al. 2013a) were used to construct seed dispersal distance curves as suggested by Cain et al. (2000). The distances on the constructed seed dispersal curves to which seeds were theoretically restricted due to their retention time in bird guts were estimated from the product of the predicted retention time of seed in the birds' guts and their displacement velocities (flight speeds) which have both been expressed as functions of bird body mass (Schurr et al. 2009; Tsoar et al. 2011) as follows:

$$\text{GRT} = 1.6\{\text{BM}\}^{0.33} \quad (1)$$

where GRT is mean gut retention time in hours for ingested seed (h), BM is body mass (kg) and 1.6 and 0.33 are allometric constants

$$\text{FS} = 15.7\{\text{BM}\}^{0.17} \quad (2)$$

where FS is flight speed ( $\text{m s}^{-1}$ ), BM is body mass (kg) and 15.7 and 0.17 are allometric constants.

### Statistical analyses

A non-parametric Kruskal–Wallis  $H$  test tested for differences in the computed numbers of seeds of the four shrub species dispersed per km by the three different size frugivorous bird species at a flight distances of one km which is generally presumed the threshold for long distance dispersal in fragmented habitats (Schurr et al. 2009). Significantly different ranked means at  $P \leq 0.05$  were separated with a Dunnett multiple comparisons test using mean ranks (UNISTAT ver. 6.0). Differences between shrub species in the numbers of their seeds dispersed per km were compared with their previously published fruit and seed attributes (Mokotjomela et al. 2013a).

## Results

### Seed dispersal potential

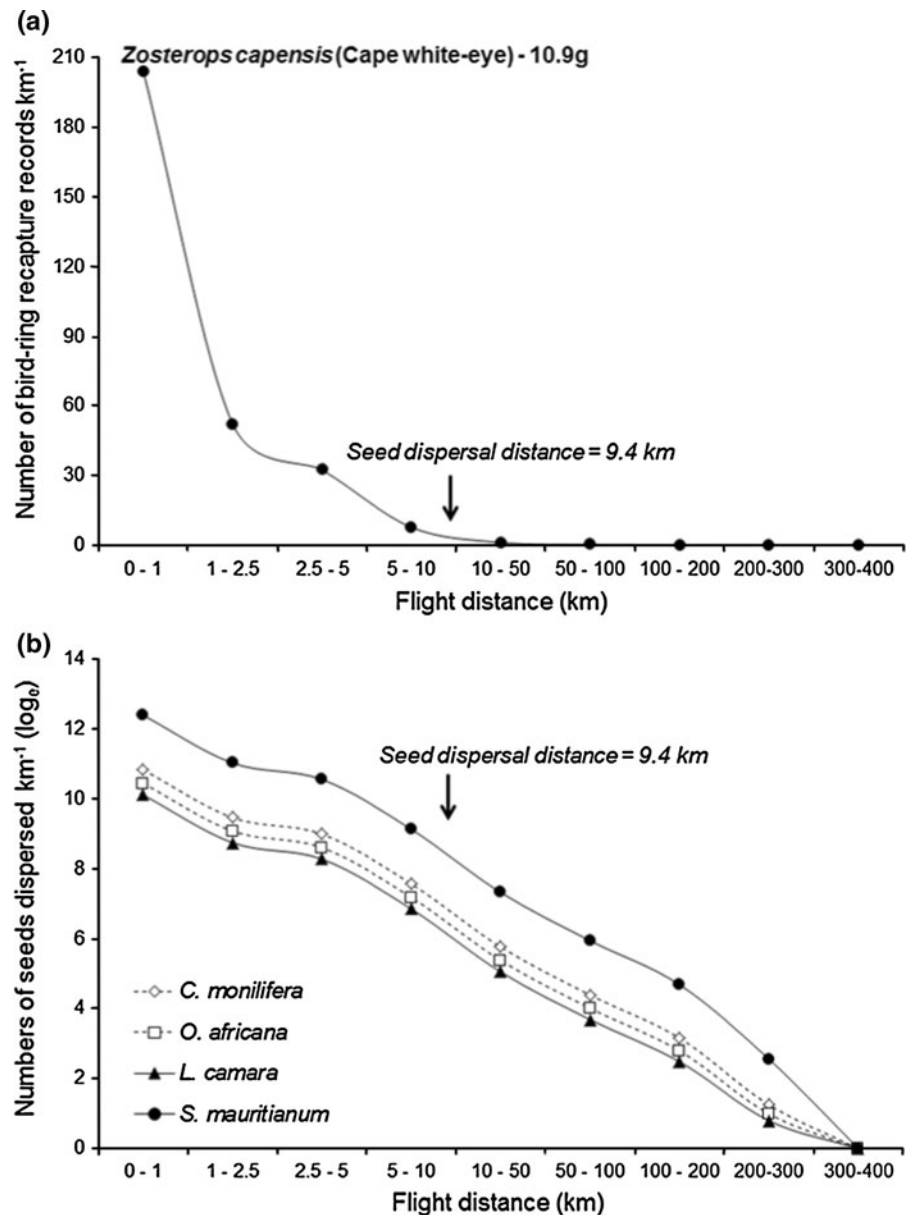
All three bird species displayed typical thin long-tailed flight distance curves characterized by peaks at flight distances below 1 km which declined progressively with increasing bird flight distances with tails extending to distances of up to 400 km in *Z. capensis* and *C. striatus* and 200 km in *P. capensis* (Figs. 1a, 2a, 3a).

*P. capensis* also displayed a secondary dispersal peak evident at a flight distance of between 2.5 and 5 km. However, computed flight distances corresponding with seed gut retention times did in all three bird species exceed the distances corresponding with their primary dispersal peaks (Figs. 1a, 2a, 3a) and in *P. capensis* even the distance corresponding with its secondary dispersal peak (Fig. 2a).

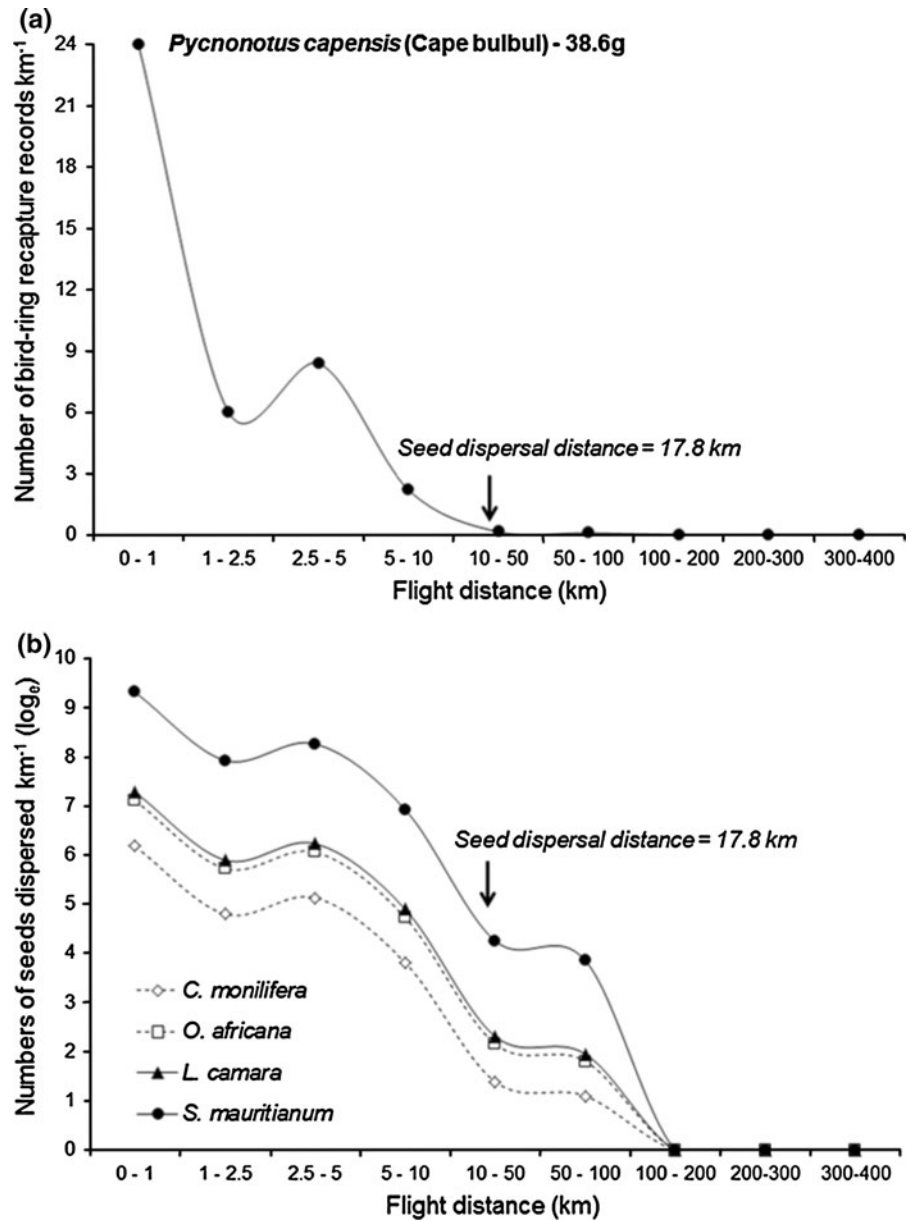
At flight distances between 0 and 1 km, all three bird species dispersed significantly ( $P \leq 0.001$ )

greater numbers of seeds of the alien *S. mauritianum* than seeds of the alien *L. camara* and the two native shrubs *O. africana* and *C. monilifera* (Table 1). Up to 10, 23 and 35 times greater numbers of *S. mauritianum* seeds were dispersed by the small *Z. capensis*, the medium-size *P. capensis* and the large *C. striatus* respectively than seeds of the other three shrub species. In fact, consistently greater numbers of *S. mauritianum* seeds were dispersed at all flight distances (Figs 1b, 2b, 3b), this was corresponding

**Fig. 1** **a** Numbers of bird-ring recapture records per km in different flight distance categories for the small *Z. capensis* (Cape white-eye) and **b** numbers of seeds per km ( $\log_e$ ) of two native shrubs (*C. monilifera*, *O. africana*) and two alien shrubs (*L. camara*, *S. mauritianum*) dispersed by *Z. capensis* with increasing flight distances. Seed dispersal distance is the product of the predicted gut retention time and flight speed



**Fig. 2** **a** Numbers of bird-ring recapture records per km in different flight distance categories for the medium size *P. capensis* (Cape bulbul) and **b** numbers of seeds per km ( $\log_e$ ) of two native shrubs (*C. monilifera*, *O. africana*) and two alien shrubs (*L. camara*, *S. mauritianum*) dispersed by *P. capensis* with increasing flight distances. Seed dispersal distance is the product of the predicted gut retention time and flight speed



with *S. mauritianum*'s significantly ( $P \leq 0.001$ ) greater fruit mass and energy (monosaccharide) content and seed numbers per  $m^2$  canopy area than that of the other alien and native shrub species (Table 1).

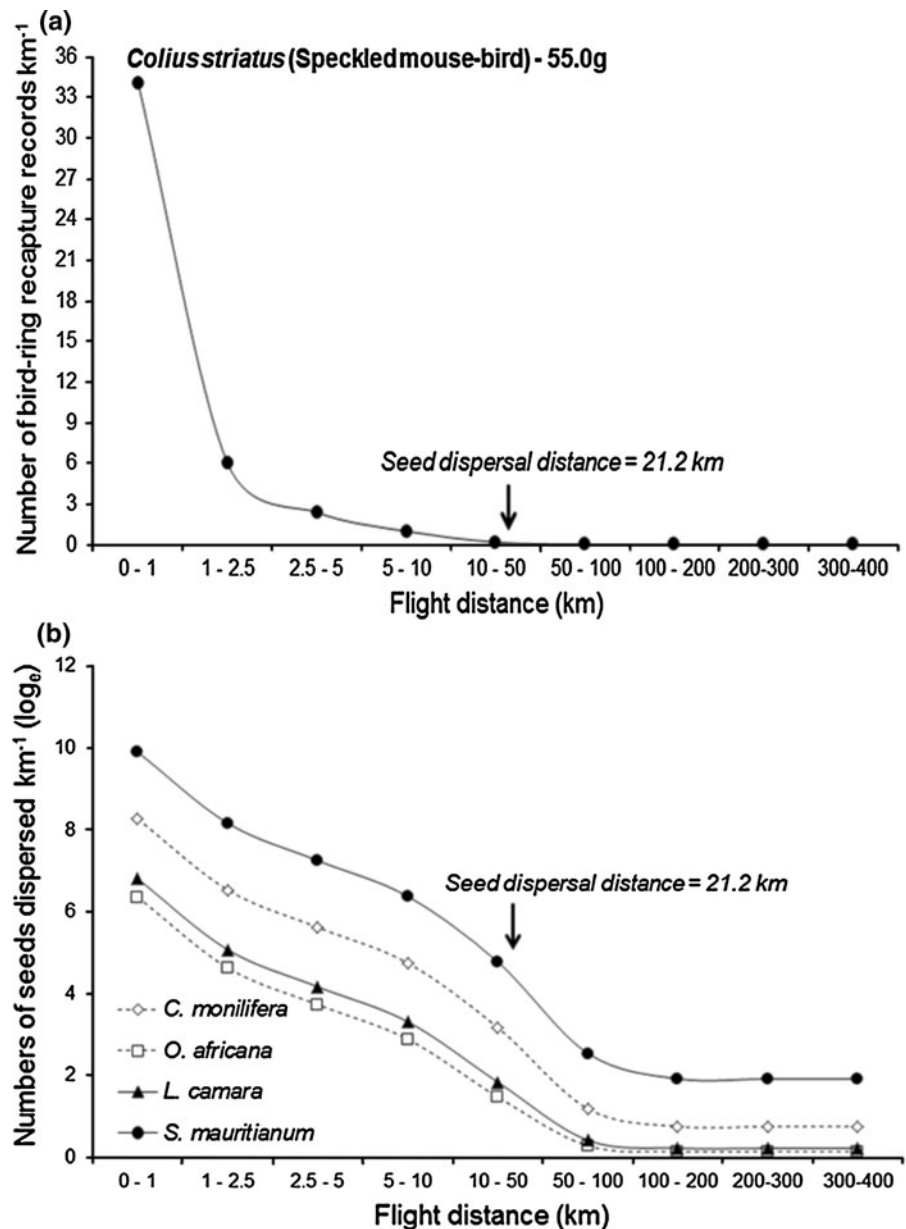
The medium-size *P. capensis* also consumed and dispersed significantly ( $P \leq 0.001$ ) greater numbers of seeds of the alien shrub *L. camara* than seeds of the native shrub *C. monilifera* but not seeds of the native shrub *O. africana* at flight distances between 0 and 1 km (Table 1). In contrast, the large *C. striatus* consumed and dispersed significantly ( $P \leq 0.001$ ) greater numbers of

seeds of the native *C. monilifera* than seeds of the native *O. africana* and seeds of the alien shrub *L. camara* at flight distances between 0 and 1 km (Table 1).

**Discussion**

Results conformed to the study hypothesis in that all three bird species displayed potential seed dispersal distances much greater than the frequently reported long distance seed dispersal threshold of 1 km by

**Fig. 3** **a** Numbers of bird-ring recapture records per km in different flight distance categories for the large *C. striatus* (speckled mousebird) and **b** numbers of seeds per km ( $\log_e$ ) of two native shrubs (*C. monilifera*, *O. africana*) and two alien shrubs (*L. camara*, *S. mauritianum*) dispersed by *C. striatus* with increasing flight distances. Seed dispersal distance is the product of the predicted gut retention time and flight speed



frugivorous birds in fragmented landscapes. Potential seed dispersal distances ranged from 9.4 km in the small *Z. capensis*, 17.8 km in the medium size *P. capensis*, to 21.2 km in the large *C. striatus*. With the exception of the seed dispersal distance of up to 12 km reported for *Zosterops lateralis* (silveryeye) in south-western Australia (Stansbury 2001), the seed dispersal distances computed for the different size bird species in this study were all substantially longer than seed dispersal distances of less than 1 km reported for

small and medium size passerine birds in Costa Rica (Wenny 2000) and in Spain (Jordano et al. 2007) and the frequently observed long distance dispersal threshold of 1 km for frugivorous birds in fragmented landscapes (Nathan et al. 2003; Schurr et al. 2009). Indeed, recent studies by Lenz et al. (2010) and Kays et al. (2011) have concluded from GPS tracking of birds in South Africa and Panama that long distance dispersal by flying vertebrates is more common than previously envisaged (Tsoar et al. 2011).



**Table 1** Fruit and seed production and fruit nutritional content of native and alien shrub species and numbers of their seeds consumed and potentially dispersed by three frugivorous bird species of different mass and gape size at flight distances below 1 km

Parameter	Native shrubs		Alien shrubs		Kruskal–Wallis	
	<i>Chrysanthemoides monilifera</i>	<i>Olea africana</i>	<i>Lantana camara</i>	<i>Solanum mauritianum</i>	H statistic	Probability
Fruit type	Drupe	Drupe	Drupe	Berry		
Fruit colour	Purple-black	Brown-black	Blue-black	Yellow		
Fruit dimensions (mm)	6–7	8–10	3–6	10–15		
Seeds per fruit	1	1	1–2	60		
Seed dimensions (mm)	5	6	1.5	1.5–2.0		
Fruit numbers m <sup>-2</sup> plant canopy <sup>+</sup>	489.8 <sup>a</sup>	357.3 <sup>b</sup>	1,386.4 <sup>c</sup>	216.7 <sup>d</sup>	$H_{(3,2492)} = 368.9$	$P \leq 0.001$
Fruit mass g m <sup>-2</sup> plant canopy <sup>+</sup>	20.9 <sup>a</sup>	61.4 <sup>b</sup>	47.0 <sup>a</sup>	139.2 <sup>c</sup>	$H_{(3,2492)} = 960.6$	$P \leq 0.001$
Fruit monosaccharide mg m <sup>-2</sup> plant canopy <sup>+</sup>	110.4 <sup>a</sup>	351.1 <sup>b</sup>	180.8 <sup>a</sup>	876.0 <sup>c</sup>	$H_{(3,2492)} = 1210.1$	$P \leq 0.001$
Seed numbers m <sup>-2</sup> plant canopy <sup>+</sup>	489.8 <sup>b</sup> ± 15.7	357.3 <sup>a</sup> ± 17.0	1,386.4 <sup>b</sup> ± 73.4	14,425.5 <sup>c</sup> ± 321.6	$H_{(3,2492)} = 1551.5$	$P \leq 0.001$
<i>Zosterops capensis</i> (Cape white-eye)						
Bird mass = 10.9 g						
Gape size = 6.76 ± 0.09 mm						
Seeds consumed per day <sup>+</sup>	249.8 <sup>a</sup>	169.8 <sup>a</sup>	121.8 <sup>a</sup>	1,191.7 <sup>b</sup>	$H_{(3,54)} = 27.9$	$P \leq 0.001$
Numbers of seeds dispersed km <sup>-1</sup> (0–1 km)	50,959.2 <sup>a</sup>	34,639.2 <sup>a</sup>	24,848.2 <sup>a</sup>	243,106.8 <sup>b</sup>	$H_{(3,54)} = 27.9$	$P \leq 0.001$
<i>Pycnonotus capensis</i> (Cape bulbul)						
Bird mass = 38.6 g						
Gape size = 12.15 ± 0.16 mm						
Seeds consumed per day <sup>+</sup>	20.1 <sup>a</sup>	51.0 <sup>ab</sup>	60.6 <sup>b</sup>	462.3 <sup>c</sup>	$H_{(3,42)} = 15.4$	$P \leq 0.001$
Numbers of seeds dispersed km <sup>-1</sup> (0–1 km)	482.4 <sup>a</sup>	1,224.0 <sup>ab</sup>	1,454.4 <sup>b</sup>	11,095.2 <sup>c</sup>	$H_{(3,42)} = 15.4$	$P \leq 0.001$
<i>Colius striatus</i> (Speckled mousebird)						
Bird mass = 55.0 g						
Gape size = 15.54 ± 0.14 mm						
Seeds consumed per day <sup>+</sup>	115.2 <sup>b</sup>	17.1 <sup>a</sup>	26.7 <sup>a</sup>	589.3 <sup>c</sup>	$H_{(3,34)} = 14.4$	$P \leq 0.001$
Numbers of seeds dispersed km <sup>-1</sup> (0–1 km)	3,916.8 <sup>b</sup>	581.4 <sup>a</sup>	907.8 <sup>a</sup>	20,036.2 <sup>c</sup>	$H_{(3,34)} = 14.4$	$P \leq 0.001$

Means ± standard errors in each row with different superscript letters significantly different at  $P \leq 0.05$

+ Data extracted from Mokojomela et al. (2013a)

In addition, fruit resource tracking by frugivorous birds in highly fragmented natural habitats may also explain dispersal of seed to distances longer than anticipated 1 km thresholds. Fruit tracking has been observed in the territorial *E. rubecula* (European robin) in the Spanish Mediterranean scrubland (Telleria et al. 2008), in flocks of wintering frugivorous thrushes *Turdus torquatus* and *T. viscivorus* in south-eastern Spain, which fly between isolated fruiting populations of the *Juniperus communis* (Garcia and Ortiz-Pulido 2004) as well as in *T. albicollis* (white-throated thrush) which disperse seeds over longer distances in fragmented habitats in Brazil (Uriarte et al. 2011). Although Perez-Tris and Telleria (2002) reported that only wintering migrant bird species display extensive spatial fruit tracking movements in Spanish shrublands, altitudinal migrations of sedentary bird species driven by resource dynamics are also known (Johnson 1992; Berthold 1999). However, the distribution of bird ring-recapture records in our study with long tails extending up to 400 km do imply that some sedentary bird species may also track fruits beyond their daily range. Furthermore, bird flights to distant patches to avoid fires which occasionally occur in the natural vegetation of the South African Mediterranean climate region (Cowling et al. 1989) may also facilitate long distant seed dispersal.

The thin long-tailed dispersal curves displayed by all three bird species in this study, which extended to distances of up to 400 km were indicative of a high potential for long distance dispersal (Portnoy and Willson 1993; Gomez and Espadaler 1998; Nathan et al. 2008). This is because the seed retention time by a dispersal vector or the vector displacement velocity or both may be occasionally high and consequently contribute prolonged transport of even small seed loads (Nathan et al. 2008). Such long-tailed dispersal curves are important for maintenance of metapopulations (Cain et al. 2000; Nathan et al. 2008), since they allow for a high diversity of movement of seeds from distant plant communities (Gomez and Espadaler 1998; Klein et al. 2006). They have been implicated in large-scale changes in natural plant communities, plant range shifts following climate change and persistence of species in fragmented landscapes (Levin et al. 2003; Schurr et al. 2007; Nathan et al. 2008; Lenz et al. 2010) and consequently may likely explain the rapid spread of fleshy fruited invasive alien plants in the South African Mediterranean climate region.

Noteworthy also in this study's findings was that greater quantities of *S. mauritanum* than *L. camara*, *C. monilifera* and *O. africana* seeds were consumed and dispersed by all three different size frugivorous bird species. *S. mauritanum* possessed the largest most conspicuous, abundant and nutritious fruits which concurred with foraging theory that proposes that fruit size plays an important role in fruit conspicuousness and thus selection by birds (Johnson et al. 1985; Sallabanks 1993; Carlo and Morales 2008). Indeed, Knight (1988) found that fruit consumption by birds in the south-western Cape, South Africa was mostly dependent on abundance and availability. Also, fruit pulp mass has been reported as the principal determinant of fruit choice by *T. migratorius* (American robins) in western Oregon of the USA (Sallabanks 1993) and fruit abundance the best predictor of fruit removal by birds from *Phillyrea latifolia* trees growing in Spanish scrublands (Herrera et al. 1994). Similarly, large berries such as those of *S. maritimum* are often preferred by birds over other fruit types in southern Africa (Knight and Siegfried 1983) as they produce copious amounts of small seeds which increases their probability of removal and dispersal by birds (Murray 1987; Knight 1988; Herrera et al. 1994). In this regard, Gosper and Vivian-Smith (2010) demonstrated that invasive alien plants dispersed by birds in Australia possess small numerous fruits/seeds and nutritious pulp. Small seeds are ingested in large numbers and retained for prolonged periods in the gut of birds (Levey and Martinez del Rio 2001; Spiegel and Nathan 2007), which might account for the relatively higher dispersal potential of seeds of *S. mauritanum* than other shrub species in this study.

Aslan and Rejmanek (2010) proposed that native fruiting shrubs can compete as effectively for seed dispersal agents if they possess similar visual and nutritional fruit attributes as those of alien species. This proposal was partly supported by this study's finding as seeds from the purple-black, brown-black and blue-black fruits of *C. monilifera*, *O. africana* and *L. camara* respectively were consumed and dispersed in insignificantly different quantities by the small *Z. capensis*. Indeed, the predominance of red and black fleshy fruits in the wild and trends in frugivorous feeding habits (Knight 1988; Fischer and Chapman 1993) tend to support the proposition that these fruit colours are more preferential than other colours to foraging birds (Knight and Siegfried 1983; Willson and Whelan



1990; Burns 2005). However, our findings partly contrasted this proposition as the yellowish fruits of *S. mauritianum* were consumed in significantly greater quantities by all three bird species than the fruits of *C. monilifera*, *O. africana* and *L. camara* respectively. In this regard, Ally (2010) also found that *C. striatus* given equal access to six different colours of artificial fruits of equal nutritional value displayed no significant preference for black and/or red fruits, though green fruits were eaten less frequently than preferred orange and yellow coloured fruits. Consistently, the large yellow coloured fruits of *S. mauritianum* likely augmented their conspicuousness and detection by avian frugivores, since fruit encounter rates are related to fruit detection ability (Knight and Siegfried 1983; Cazetta et al. 2009) which is partly enhanced by fruit colours (Willson and Whelan 1990; Burns et al. 2009). Brightly coloured fruits increase detectability by their colour contrast/conspicuousness against background (Knight and Siegfried 1983; Willson and Whelan 1990; Burns 2005; Cazetta et al. 2009).

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