Frugivorous birds visit fruits of emerging alien shrub species more frequently than those of native shrub species in the South African Mediterranean climate region

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We compared daily visitation frequency indices by 4 large (>150 g), 7 medium-size (50–150 g), 5 small (30–50 g) and 8 tiny (<30 g) frugivorous bird species on fleshy fruits of two native shrubs (Aloe europaea subsp. africana and Chrysanthemoides monilifera subsp. monilifera), two established alien shrubs (Solanum mauritianum and Lantana camara) and two emerging alien shrubs (Myoporum tenuifolium and Pittosporum undulatum) at nine different sites in the Cape Floristic Region. Large, medium-size and tiny birds as groups displayed significantly higher visitation frequency indices on fruits of both emerging alien shrub species than the other shrub species. Small birds as a group displayed insignificantly different visitation frequency indices on fruits of both emerging and established alien shrub species but significantly higher visitation frequency indices on fruits of both emerging and established alien shrub species than on fruits of the native shrub species. However, there were significant differences in foraging frequency indices of the bird species included within each of these body size groups on fruits of the different shrub species. Among the large birds, Columba guinea and the medium size birds Sturnus vulgaris, Streptopelia senegalensis, Turdus olivaceus and Onychognathus morio all exhibited significantly higher visitation frequency indices on fruits of both emerging alien shrub species than on fruits of the other shrub species. These findings indicate that alien plant control measures should be focused on eradicating localised populations of emerging aliens to limit preferential consumption of their fruits by birds and consequent dispersal of their seeds that germinate readily into natural areas.

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1. Introduction

Globally, many fleshy-fruited plants rely on birds and other vertebrates for dispersal of their seeds (Howe and Smallwood, 1982; Jordano, 2000). It has been estimated that vertebrates disperse about 90% of trees and shrubs in tropical regions, 50% in neo-tropical regions, 20–60% in Mediterranean-climate regions and about 40% in temperate regions with birds being the predominant vertebrate dispersal agents (Willson et al., 1989; Jordano, 2000). The different proportions are associated with variation in fruit production in different regions although there are some overlaps between sub-regions and regions (Jordano, 2000; Herrera, 2002). According to Knight and Siegfried (1983), 52% of the 1340 species of indigenous angiosperm trees in southern Africa produce fleshy fruits with 23% predominately relying on birds for dispersal of their seeds. In the South African Mediterranean-climate region, it has been estimated that 80% of the fleshy-fruited woody species in succulent karroid scrubland, dune thicket and afromontane forests, 28% of true fynbos shrubs and 46% of renosterveld shrubs rely on birds for dispersal of their seed (Le Maître and Midgley, 1992).

Habitat disturbance and importation of alien plants for horticultural purposes has resulted in the invasion of natural habitats by fleshy-fruited alien plants in many global ecosystems (Rejmánek, 1996; Richardson and Rejmánek, 2011). This is assisted by bird-mediated seed dispersal of fleshy-fruited invasive alien plants which, is well-documented globally (Traveset and Richardson, 2011; Richardson and Rejmánek, 2011). It has been reported that birds disperse 25% of the 199 globally representative invasive species (Cronk and Fuller, 1995), 43% of the invasive alien trees and 61% of invasive alien shrubs in 15 distinct global geographical regions (Richardson and Rejmánek, 2011). The extra-tropical regions such as the temperate and Mediterranean-climate regions, except those in the Mediterranean Basin, seem more vulnerable to invasion by alien plants (Rejmánek, 1996; Rejmánek et al., 2005) due to massive habitat fragmentation (Herrera, 1995). Presently, the Mediterranean-climate region of South Africa ranks second to Australia in terms of numbers of invasive fleshy-fruited woody alien species (Richardson and Rejmánek, 2011), many of which possess fruit attributes attractive...
to birds (Vittoz and Engler, 2007). Initial assessments indicate that 51 of the 1698 alien plant species introduced into southern Africa possess fleshy fruits dispersed by birds (Knight, 1986) with these numbers increasing (Richardson and Rejmánek, 2011). It is presumed that migration of about 63 of the 224 terrestrial bird species present in southern Africa into the Mediterranean-climate region of South Africa (Cowling and Richardson, 1995) has been associated with the introduction for commercial, horticultural and forestry purposes of alien trees and shrubs with fleshy fruit displays (Richardson and Rejmánek, 2011). These migrant birds have presumably contributed to the expansion of alien plant infestations in the Cape Floristic Region through dispersal of their seeds (Cowling and Richardson, 1995; Richardson and Van Wilgen, 2004). This is typified by the reported dispersal of Acacia cyclops by the Onychognathus morio (Phyids et al., 1981; Richardson et al., 1992). Although frugivorous birds are effective seed dispersers of fleshy-fruiting alien plants most probably owing to their occasionally nutritious fruits (Jordaen and Downs, 2012; Mokotjomela et al., 2013), recent studies generally suggest that passage of seeds through guts of these frugivores does not increase germination of invasive alien plants (e.g. Solanum mauritianum, Cinnamomum camphora, Lantana camara and Psidium guajava) in South Africa yet their removal of fruit pulp does (Jordaen et al., 2011). In this way, a major role of the avian frugivores remains as dispersal of seeds to distant micro sites of which Sakai et al. (2001) indicated that this leads to establishment of multiple population foci that rapidly expand to homogenise the environment. Nevertheless, there are no comparative studies on the frequency of visitations by different frugivorous bird species on fruits of alien and indigenous plants in the Cape Floristic Region, a global biodiversity hotspot (Myers et al., 2000) characterised by its exceptionally high species richness (9086 species in an area of 87,892 km²) and high fraction (68.2%) of endemic species (Cowling et al., 1989). The foraging visitation frequency of birds on fruits is associated with seed dispersal potential with high visitation indicative of greater chances of seeds being removed and dispersed (Vazquez et al., 2005; Schupp et al., 2010; Mokotjomela, 2012). Past studies have merely identified individual species of birds observed foraging on fruits of alien plants (Myphils et al., 1981; Knight, 1988; Underhill and Hofmeyr, 2007) and how these related to fruiting displays and fruiting phenoLOGY (Knight, 1988).

Frugivorous birds concentrate their activities where fruit resources are most visible and abundant (Saracco et al., 2005; Blendiger et al., 2008; Aslan and Rejmánek, 2012; Mokotjomela et al., 2013) and consequently alien plants with colourful fruit displays, high fruit abundance and nutritional content (Saracco et al., 2005; Carlo et al., 2007; Jordaen and Downs, 2012) may be presumed to attract a greater diversity of frugivorous bird species more frequently than fruits of native plants. Also, the established stands, widely distributed, high density populations of alien plants that offer numerous perching opportunities and food resources for foraging birds, especially in the Cape Floristic Region (Knight, 1988; Maders and Richardson, 1992; Mokotjomela et al., 2013), may be presumed to be more attractive to frugivorous birds than populations of emerging aliens with limited distributions. In view of these presumptions, we predicted that fleshy fruits of established alien shrub species will be visited more frequently by frugivorous birds than those of emerging alien and native shrub species.

2. Methods and materials

2.1. Study sites and shrub species selection

There were nine study sites located in different natural vegetation units (Mucina and Ruthcrford, 2006) within the Cape Floristic Region, each comprising mixed populations of native and alien shrubs bearing fleshy fruits frequently consumed by local frugivorous birds (Richardson and Fraser, 1995). The sites comprised Hout Bay (34° 00′ 44.84 S 18° 23′ 55.49 E), Constantia (33° 49′ 30.26 S 18° 47′ 37.64 E), Silvermine (37° 41′ 41.20 N 024° 01′ 09.48 E), Kalk Bay (34° 07′ 40 S 18° 26′ 54 E), Simons Town (34° 16′ 22.30 S 18° 42′ 94.20 E) all located on Peninsula Granite Fynbos; Paarl (33° 45′ 27.22 S 19° 01′ 32.86 E) located on Swartland Shale Renosterveld; Franshoek (33° 53′ 57.6 S 19° 06′ 10.5 E) located on Boland Granite Fynbos; Swellendam (34° 02′ 27.09 S 20° 33′ 03.06 E) located on Breede Shale Renosterveld and Hermanus (34° 24′ 01.06 S 19° 12′ 42.49 E) located on Overberg Sandstone Fynbos. Two native shrub species, two established alien shrub species and two emerging alien shrub species with overlapping fruiting periods (Knight, 1988; Van Wyk and Van Wyk, 1997) and distribution ranges were selected for comparisons of bird visitation frequencies on their fleshy fruits. Distribution ranges were based on records extracted from PRECIS (Germishuizen et al., 2006), ACKDAT (Mucina and Rutherford, 2006) and SAPIA (Henderson, 2011) databases. The native shrubs comprised Chrysanthemoides monilifera subsp. monilifera (L) Norlindh. (Asteraceae) and Olea europaea subsp. africana Mill (Oleaceae), commonly referred to as O. africana. The established alien shrubs comprised L. camara L. (Verbenaceae) and S. mauritianum Scopoli (Solanaeceae) and the emerging alien shrubs comprised Myoporum tenufolium Auct. (Myoporaceae) and Pittosporum undulatum Vent. (Pittosporaceae). C. monilifera, O. africana, L. camara and M. tenufolium produce small fruits (drupes) each containing a single nutlet (seed), except L. camara whose drupes contain two nutlets, the fruits turning purplish or black when ripe. In contrast, S. mauritianum produces clusters of yellow fruit, about 10 mm in diameter (Henderson, 2001), each containing up to 193 seeds (Witkowski and Garner, 2008) and P. undulatum produces globe-shaped fruit capsules about 16 mm long, each containing 20–40 sticky orange seeds ingested by frugivores (Binggeli et al., 1998).

2.2. Bird species and visitation frequencies

Bird observations were restricted to the peak fruiting season (i.e. autumn to spring of 2009 and 2010) of the native, established alien and emerging alien shrub species and was done daily to 3 h early morning and 3 h late afternoon periods of maximum bird activity (La Rosa et al., 1985; Bibby et al., 2000). Bird species identifications were aided by descriptions and keys presented in Sinclair and Ryan (2003) and Hickey et al. (2005). Measurements of bird foraging activity on randomly selected reproductively mature individuals of each shrub species at each site were performed with binoculars (8 × 42 magnification) at a distance of about 30 m from each shrub, and simultaneously recorded with a digital camcorder (Kodak C813: 8.2 megapixel, ISO 1250, digital IS) for a permanent photographic record (Spiegal and Nathan, 2007). Five days of bird observations were conducted on each of the six shrub species, the fruit crop sizes of the individual shrub species differing between sites and consequently included as a source of variation. Only one shrub species was monitored at a time over each daily observation period at each site. At each site, all frugivorous bird species (Hickey et al., 2005) that were observed actively consuming fruits of the native, established alien and emerging alien shrub species were recorded. Each visitation comprised an arrival and departure time of an individual foraging bird species, irrespective of visitation length, with the numbers of recorded visitations for each frugivorous bird species summed for each 6-h daily observation period.

2.3. Data synthesis and statistical analysis

Recorded foraging bird species were classified into four body mass groups defined by Dennis and Westcott (2007), namely large birds (>150 g), medium size birds (50–150 g), small birds (30–50 g) and tiny birds (<30 g). A nested analysis of variance (bird species nested within each shrub species) tested for differences in daily visitation frequencies by birds of different body mass and species on fruits of the native, established alien and emerging alien shrub species. Also,
3. Results

There was no statistical significant (P ≤ 0.05) difference in the average numbers of bird species per site observed foraging on fruits of the native, established alien and emerging alien shrubs (Fig. 1). However, the total number of bird species observed foraging on fruits of both native shrubs over all sites were higher than the total numbers observed foraging on fruits of the established alien and emerging alien shrubs (Fig. 1). Large, medium-size and tiny birds as groups displayed significantly higher (P ≤ 0.001) visitation frequency indices on fruits of both emerging alien shrub species than the other shrub species (Table 1). Small birds as a group displayed insignificantly (P ≤ 0.05) different visitation frequency indices on fruits of both emerging and established alien shrub species but significantly (P ≤ 0.01) higher visitation frequency indices on fruits of both emerging and established alien shrub species than on fruits of the native shrub species (Table 1).

However, there were significant (P ≤ 0.05) differences in foraging frequency indices of the bird species included within each of these size groups on fruits of the different shrub species. Among the large birds, only Columba guinea displayed a significantly (P ≤ 0.001) higher visitation frequency index on fruits of both the emerging alien shrub species than the other species. Among the other large birds, Streptopelia capicola exhibited a significantly (P ≤ 0.05) higher visitation frequency index on fruits of the emerging alien M. tenuifolium only and Columba arquatrix exhibited a significantly (P ≤ 0.05) higher visitation frequency index on fruits of both the emerging alien M. tenuifolium and the established alien S. mauritianum than on fruits of the other shrub species (Table 1). Among the medium size birds, four species, namely Sturnus vulgaris, Streptopelia senegalensis, Turdus olivaceus and Onychognathus morio all exhibited significantly (P ≤ 0.05) higher visitation frequency indices on fruits of both emerging alien shrub species than on fruits of the other shrub species (Table 1). Among the other medium-size birds, Lantarius ferrugineus

Table 1

<table>
<thead>
<tr>
<th>Mass class/scientific name</th>
<th>Nested ANOVA</th>
<th>Bird (shrub)</th>
<th>Native shrubs</th>
<th>Established alien shrubs</th>
<th>Emerging alien shrubs</th>
</tr>
</thead>
<tbody>
<tr>
<td>All birds</td>
<td>F₄₀²₄ = 9.66 □□□</td>
<td>F₁₀₂₄ = 1.08 □□□</td>
<td>1.29 ± 0.34</td>
<td>0.52 ± 0.34</td>
<td>2.09 ± 0.36</td>
</tr>
<tr>
<td>Large birds: &gt;150 g</td>
<td>F₁₈₂₄ = 4.78 □□□</td>
<td>F₁₈₂₄ = 1.15</td>
<td>1.29 ± 0.34</td>
<td>0.52 ± 0.34</td>
<td>2.09 ± 0.36</td>
</tr>
<tr>
<td>Medium birds: 50–150 g</td>
<td>F₁₃₂₄ = 1.93 □□□</td>
<td>F₁₃₂₄ = 2.23 □□□</td>
<td>1.42 ± 0.34</td>
<td>0.52 ± 0.34</td>
<td>2.09 ± 0.36</td>
</tr>
<tr>
<td>Small birds: 30–50 g</td>
<td>F₁₃₂₄ = 3.95 □□□</td>
<td>F₁₃₂₄ = 0.98</td>
<td>1.29 ± 0.34</td>
<td>0.52 ± 0.34</td>
<td>2.09 ± 0.36</td>
</tr>
<tr>
<td>Tiny birds: &lt;30 g</td>
<td>F₁₃₂₄ = 4.39 □□□</td>
<td>F₁₃₂₄ = 2.23 □□□</td>
<td>1.42 ± 0.34</td>
<td>0.52 ± 0.34</td>
<td>2.09 ± 0.36</td>
</tr>
</tbody>
</table>

Fig. 1. Average numbers of frugivorous bird species per site ± standard errors foraging on fruits of native (C. monilifera-C. mon and O. africana-O. afr.), established alien (L. camara-L. cam and S. mauritianum-S. maur) and emerging alien (M. tenuifolium-M. ten and P. undulatum-P. und.) shrub species.
exhibited a significantly ($P \leq 0.05$) higher visitation frequency index on fruits of the emerging alien P. undulatum only and Colius striatus exhibited a significantly ($P \leq 0.05$) higher visitation frequency index on fruits of only the established alien S. mauritianum than on fruits of the other shrub species (Table 1). Among the tiny birds, Cosyptha caffra displayed a significantly ($P \leq 0.05$) higher visitation frequency index on fruits of the emerging alien M. tenuifolium only and Passer domesticus and Serinus canicollis have significantly ($P \leq 0.05$) higher visitation frequency indices only on fruits of the emerging alien P. undulatum than the other shrub species (Table 1). The tiny Zosterops pallidus differed in exhibiting a significantly ($P \leq 0.05$) higher visitation frequency index on fruits of only the established alien S. mauritianum than the other shrub species (Table 1). Among the small birds, Ploceus velatus displayed a significantly ($P \leq 0.001$) higher visitation frequency index on fruits of the established alien S. mauritianum and L. camara, but displayed a significantly ($P \leq 0.05$) higher visitation frequency index on fruits of only the established alien S. mauritianum than on fruits of the native shrub species (Table 1).

### 4. Discussion

The quantity and variety of seeds dispersed by birds have been positively correlated with frugivore bird species richness (Garcia and Martinez, 2012), an important determinant of population dynamics in diverse plant communities (Dennis and Westcott, 2007). Although fleshy fruits of alien plants are an important supplemental fruit source for native avian frugivore species (Mokotjomela et al., 2009; Gleditsch and Carlo, 2010; Jordaan et al., 2011), we observed no statistically significant difference in the average numbers of bird species per site species observed foraging on fruits of the native, established alien and emerging alien shrub species in this study. This is possibly a consequence of the relatively few endemic frugivorous bird species and fleshy fruit resources in the South African Mediterranean climate region (Cody, 1983).

In contrast, several of the large, medium-size and tiny bird species displayed significantly higher visitation frequency indices on fruits of either one or both of the two emerging alien species than the other shrub species. A meta-analysis of published data and fruit choice-tests using caged birds (Aslan and Rejmánek, 2012) concluded that bird preferences for alien fruits was due to their greater visibility and attractiveness. This premise may have potentially applied to the large conspicuous orange coloured fruits of P. undulatum (Binggeli et al., 1998) but not necessarily to the smaller purplish coloured fruits of M. tenuifolium (Bornhorst, 1996) whose colouring and architecture was similar to the fruits produced by the two native shrub species C. monilifera and O. africana (Scott, 1996; Rey and Alcantara, 2000) and the established alien shrub species L. camara (Day et al., 2003). P. undulatum fruits contain numerous sticky orange seeds likely attractive to granivorous birds such as the large C. guinea, the medium-size S. senegalensis, the tiny P. domesticus and S. canicollis which all displayed significantly higher visitation frequency indices on fruits of the emerging alien P. undulatum. Also, it has been reported that frugivorous birds do prefer foraging at the margins of forest gaps (Restrepo et al., 1999; Carlo et al., 2007) where emerging alien trees are more prolific in the Cape Floristic Region (Bond, 1995). The edges of forest gaps are characterised by diverse fruit resources and high habitat heterogeneity which are targeted by a large array of bird species during breeding seasons (Restrepo et al., 1999; De La Montana et al., 2006), and consequently fruiting plants established in these habitats experience frequent visitations by frugivorous birds. Such habitats also preferred by bird species in Spanish Mediterranean woodlands (De La Montana et al., 2006). In contrast, dense stands of established alien trees are often less rich in plant species and fruit resources, which in Spanish Mediterranean scrubland were observed to attract fewer bird species (De La Montana et al., 2006). This feature also evident in this study where slightly fewer bird species on average were observed visiting fruits of the established alien than emerging alien shrub species. Another potential explanation for the significantly higher visitation frequency indices displayed by most large and medium-size birds as well as some tiny birds on fruits of the two emerging alien species is the opportunistic foraging behaviour displayed by frugivorous birds on fruits of novel alien plants (Mandon-Dalger et al., 2004; LaFleur et al., 2007; Kueffer et al., 2009). Many foraging birds tend to prefer new fruits which are often more attractive than their customary fruits (Knight, 1986; LaFleur et al., 2007) as they provide a means of maximising energy acquisition (Kueffer et al., 2009; Gosper and Vivian-Smith, 2010). Also, local frugivorous birds in the Cape Floristic Region display a higher preference for alien fruits where large scale habitat modification has reduced the variety of native fruits (Oatley, 1984). Therefore, the close association of birds with human settlements which are rich in emerging alien fruit resources (Cowling and Richardson, 1995; Reichard et al., 2001; Aslan and Rejmánek, 2010) and the relatively close proximity of several of the study sites possessing emerging aliens to urban areas may explain the observed higher visitation frequency indices by frugivorous birds on fruits of the emerging alien group. There was no clear explanation for the significantly higher visitation frequency indices displayed by several different size bird species, such as the large S. capicola and C. arquatrix, the medium-size S. vulgaris, O. morio and T. olivaceus and C. caffra on fruits of the emerging alien M. tenuifolium. One possible explanation is the heavy and continuous year round fruit production by M. tenuifolium occurring in areas of low vegetation density and high habitat heterogeneity which experience frequent visitations by frugivorous birds. This suggestion was supported by previous reports of the attraction of the C. caffra to the dense thickets of natural vegetation (Manders and Richardson, 1992) and thus true for thick stands of M. tenuifolium. Also it has been reported that heavily fruiting Sambucus nigra attracts large flocks of the European starling (S. vulgaris) in New Zealand (Williams and Karl, 1996) and the heavily fruiting Juniperus ashei attracts large flocks of the American robin (Turdus migratorius) in Texas (Chavez-Ramirez and Slack, 1994). Furthermore, bird foraging behaviour profiles are shaped by factors such as predation and competition for limited fruit resources (Knight, 1988; Manders and Richardson, 1992). As a consequence, birds tend to congregate on and forage on fruits of less known emerging shrubs rather than recognised established alien and native shrubs species where there is a higher likely interference from other bird species thereby minimising their exposure to predators and competition for available fruit resources (Martin, 1985; Saracco et al., 2004).

The high visitation frequency indices displayed by several different size bird species, such as the large C. arquatrix, the medium-size C. striatus, the small P. velatus and P. capensis and the tiny Z. pallidus on fruits of the established alien S. mauritianum seemed a likely consequence of S. mauritianum’s high fruit mass and energy content in South Africa (Jordaan et al., 2011; Mokotjomela et al., 2013) which have been reported to be directly correlated with measured quantities of fruit pulp consumed by birds (Johnson et al., 1985). Also, since frugivorous birds tend to vary their diet with arthropods (Jordano, 1988) which are abundant on alien plants both in the South African Mediterranean climate region (Proches et al., 2008), as well as in southeast Texas (Hartley et al., 2010), the diverse floral and faunal resources associated with S. mauritianum’s continuous fruit production may have also contributed to the high bird visitation frequency indices.

In conclusion, this study’s findings indicate that the eradication of emerging aliens, whose impacts on natural habitats are likely less
severe during early stages of invasion (Nel et al., 2004; Buckley et al., 2006), should be prioritised (Aslan and Rejmánek, 2010). Also, the suppression of populations of alien birds such as the S. vulgaris and the P. domesticus require prioritisation, since several studies have reported that birds assist the spread and colonisation of natural areas by fleshly-fruited alien plants (Williams, 2006; Vittoz and Engler, 2007; Aslan and Rejmánek, 2012). In particular, Jordaan et al. (2011) demonstrated that seeds of invasive alien shrubs species germinate readily in South Africa and therefore, their effective bird dispersal may lead to rapid population proliferation. This is partly facilitated by the presence of alien mutualistic partners (Mandon-Dalger et al., 2004; Travest and Richardson, 2011). However, alien birds have also been reported to be instrumental in the dispersal of seeds of native plants where native avian dispersers are absent (Foster and Robinson, 2007; Kawakami et al., 2009). Consequently, fleshly-fruited alien plant eradication programmes should be accompanied by propagation of native species with similar growth form and reproductive attributes as the alien species to replace perching, nesting and food sources for the frugivorous birds (Gosper and Vivian-Smith, 2009; Mokotjomela et al., 2009; Gleditsch and Carlo, 2010; Jordaan and Downs, 2012).

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