A comparison of bird foraging preferences for fruits of indigenous and alien shrubs and seed dispersal potentials in the Cape Floristic Region

by

THABISO MICHAEL MOKOTJOMELA

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Department of Conservation Ecology and Entomology
Faculty of AgriSciences
Stellenbosch University

Supervisors
Prof. Charles F. Musil
Prof. Karen J. Esler

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Declaration

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FULL NAME: **THABISO MICHAEL MOKOTJOMELA**   DATE: **MARCH 2012**

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Abstract

This study tested the proposal that fleshy-fruited alien shrubs competed more effectively for avian dispersal services than indigenous shrubs. Several different quantitative measures of increasing complexity were applied to test bird foraging preferences for fruits of two established alien shrubs (*Lantana camara, Solanum mauritianum*), two emergent alien shrubs (*Myoporum tenuifolium, Pittisporum undulatum*) and two indigenous shrubs (*Chrysanthemoides monilifera, Olea europaea* subsp. *africana*). Overall the simplest quantitative measure, namely that of bird visitation frequency identified foraging preferences of individual bird species for fruits of alien and indigenous shrubs. Moreover, even the more complex measures of numbers of foraging birds, foraging times and products of these in the computed consumption intensity and seed dispersal efficiency were positively correlated to visitation frequency. There was a distinct preference of several, especially heavily fugivorous, bird species for fruits of established alien than indigenous shrubs and several moderately fugivorous bird species preferred fruits of emergent than established alien shrubs.

Intricate photographic and experimental approaches were applied to obtain precise numerical data on seed removal rates by birds from the alien and indigenous shrubs. Deficiencies associated with the experimental approach included its inability to discriminate between asynchronous fruit production and fruit ripening, individual foraging bird species, and fruit consumption by other fruit foraging vertebrates. The advantages of the photographic approach were in its provision of a detailed permanent record of individual foraging bird species, their total numbers and precise foraging times and the proportions of whole fruits consumed, as well as other behavioural foraging traits. Tested also was the proposal that frugivorous birds remove larger amounts of fruits from plants with high fruit production and nutritional contents and that the germination of the bird-ingested seeds is enhanced. In compliance with this proposal, canopy fruit mass and monosaccharide content were all positively correlated with the total numbers of seeds removed by birds and viable seeds excreted by birds. Only defecated seeds of the indigenous C. *monilifera* and alien *L. camara* displayed enhanced germination following their ingestion by birds

Seed dispersal distances of alien and indigenous shrubs by birds were estimated from published records of bird body masses, gut retention times of consumed seed and flight speeds. Estimated seed dispersal distances ranged between 0.41 and 0.81 km for the subset of heavily and moderately frugivorous bird species examined. However, their foraging distances derived from bird-ring recapture records were much greater, these peaking between 2.5 and 50 km in some heavily frugivorous bird species.

It is concluded 1. that bird visitation frequency be applied as the most efficient and practical quantitative measure for gauging bird foraging preferences in future surveys which should involve large complements of indigenous, emergent and established alien species, 2. that flight speeds and

gut passage times of ingested alien and indigenous seeds need to be measured in local bird species so long distance seed dispersal potentials can be more precisely determined and 3. that control measures should be focused on eradicating especially emergent alien species with fleshy fruits from urban environments to prevent their transport by birds into adjacent natural areas.

Opsomming

Hierdie studie het die voorstel getoets dat uitheemse vlesige-vrug struike meer effektief kompeteer vir voël verspreidingsdienste as inheemse vlesige-vrug struike. Verskeie kwantitatiewe maatstawwe van toenemende kompleksiteit was toegepas om die voedingsvoorkeure van voëls vir vrugte van twee gevestigde uitheemse struike (*Lantana camara, Solanum mauritianum*), twee ontluikende uitheemse struike (*Myoporum tenuifolium, Pittisporum undulatum*) en twee inheemse struike (*Chrysanthemoides monilifera, Olea europaea* subsp. *africana*) te toets. Algeheel het die eenvoudigste kwantitatiewe maatstaf, naamlik voël besoek frekwensie, voedingsvoorkeure van individuele voël spesies vir vrugte van uitheemse en inheemse struike geïdentifiseer. Addisioneel het die meer komplekse maatstawwe soos voël getalle, voedings tye, asook produkte hiervan in die berekende verbruiks intensiteit en saadverspreiding effektiwiteit almal positiewe korrelasies met besoek frekwensie. Predominant vrugtevretende voël spesies het 'n duidelike voorkeur getoon vir vrugte van gevestigde uitheemse eerder as inheemse struike. Verskeie meer gematigde vrugtevretende voël spesies het egter vrugte van ontluikende eerder as gevestigde uitheemse struike verkies.

Ingewikkelde fotografiese en eksperimentele benaderings was gebruik om presiese numeriese data van saad verwyderingstempo's deur voëls vanaf die bestudeerde struike te bekom. Tekortkominge geassosieerd met dié eksperimentele benadering sluit in die onvermoë om te onderskei tussen asinkrone vrug produksie en vrug rypwording, individuele kos soekende voël spesies, asook vrug verbruik deur ander vrugvretende werweldiere. Die voordele van die fotografiese benadering was die verskaffing van 'n gedetailleerde permanente rekord van individuele kos soekende voël spesies, hul totale getalle, presiese voedingstye, proporsie heel vrugte verbruik, asook ander voedingsgedrag eienskappe. Ook getoets was die voorstel dat vrugtevretende voëls groter hoeveelhede vrugte verwyder van plante met hoë vrugproduksie en hoë nutriënt inhoud, en dat ontkieming van voëlingeneemde sade verhoogd is. In nakoming met die voorstel, was blaredak vrugte massa en monosakkaried inhoud albei positief gekorreleer met totale aantal sade verwyder deur voëls en lewensvatbare sade uitgeskei deur voëls. Slegs sade van die inheemse *C. monilifera* en die uitheemse *L. camara* het verhoogde ontkieming gewys na inname deur voëls.

Saadverspreiding afstande van uitheemse asook inheemse struike deur voëls was bepaal vanaf gepubliseerde rekords van liggaams massa, saad behoud tye in die maag na inname, en vliegspoed. Beraamde saadverspreiding afstande het gestrek tussen 0.41 en 0.81 km vir dié subgroep van predominant en gematigde vrugtevretende voël spesies bestudeer. Nogtans was voedings afstande, afgelei van geringde voël hervangs rekords, veel groter, en het gepiek tussen 2.5 en 50 km vir sommige predominant vrugtevretende spesies.

Gevolglik weet ons nou dat 1) voël besoek frekwensie toegepas kan word as die mees effektiewe en praktiese kwantitatiewe maatstaf vir die bepaling van voël voedings voorkeure in toekomstige opnames waar komplementêre groepe inheemse, ontluikende en gevestigde uitheemse spesies bestudeer word; 2) vliegspoed en maag passeer tye van ingeneemde uitheemse en inheemse sade gemeet moet word in plaaslike voël spesies sodat langafstand saadverspreiding potensiaal meer presies bepaal kan word; en 3) beheer maatstawwe moet fokus op die verwydering van spesifiek ontluikende uitheemse vlesige-vrug spesies vanuit stedelike omgewings, om sodoende saad vervoer deur voëls na naasliggende natuurlike areas the verhoed.

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Chapter 1

Literature review, rationale and hypotheses

1.1. Evolution of bird-plant mutualisms

Mutualisms between birds and plant fruits and seeds emerged in the Tertiary (Ericson et al. 2003), as a cost exchange between nutritional supply and seed dispersal service (van der Pijil 1972; Mckey 1975). This was evident from the presence of seeds of a variety of unidentified plant species in bird stomach contents (Zhou & Zhang 2002). Mutualisms between birds and fleshy-fruited plant taxa seemingly coevolved, since specialist frugivores have gut systems that allow passage of ingested seeds in an undamaged state (Howe & Estabrook 1977). Coevolution between frugivorous birds and fruits of the three plant families, Lauraceae, Burseraceae and Palmae are common in the American tropics and Australasia that but not in African tropical forests where such plants and mutualistic frugivorous birds are presently extinct (Snow 1981). In addition, seed dispersal agents in Mediterranean-type shrublands seem evolutionarily younger than the plants whose seeds they disperse (Herrera 1984). For southern Africa, including the southwestern Cape (Knight 1986), there exist similar ratios of fleshy to non-fleshy fruits of both natural and alien species which could be evidence of diffuse relationship between birds and plants. Contrastingly, disproportionate ratios would suggest firm relationships between fleshy-fruited plants and birds that disperse their seeds. Individual interactions between specific birds and fruits are rare (Bond 1995) because several dispersal agents and vice-versa (Dennis & Westcott 2006; Nathan 2007; Carlo et al. 2007) may disperse seeds of fleshy-fruited plant species. Furthermore, Richardson et al. (2000b) showed that the rapidity at which fleshy-fruited alien plants secure vertebrate dispersal agents (e.g. birds) in new habitats is indicative of a diffuse relationship between birds and the fruits they consume. However, most mutualisms between birds and plants whose fruits and seeds they disperse seem obscure with the exception of a few specialised mutualisms between specific birds and fleshy-fruited plant species (Wenny 2001; Tiffney 2004).

1.2. The ecology of bird-plant mutualisms

1.2.1. Introduction

Globally, approximately 50% of fleshy-fruited plants rely on birds and other vertebrates for dispersal of their seed (Binggeli 1996). If this proportion is distributed across distinct climatic zones, seed dispersal by birds and other vertebrates account for 70-94% of the neotropical trees and shrubs, 80-82% of Australian and African rain forests, 50% of trees and shrubs in Mediterranean scrublands, 80% in tropical woodlands and 30-40% in temperate forests (Jordano 2000). The different proportions associated with variation in fruit production in different regions with some overlaps between sub-regions and regions (Jordano 2000). According to

Knight and Siegfried (1983), 52% of the 1340 species of indigenous angiosperm trees in the southern African region produce fleshy fruits with 23% predominantly relying on birds for seed dispersal. In this 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 (le Maitre & Midgley 1992) rely on birds for dispersal of their seed. The lower percentage of bird-dispersed plants in fynbos is partly due to the presence of regular fires, nutrient-poor soils, and large-scale clearing of indigenous forest for agricultural land use (Oatley 1984, Knight 1988; le Maitre & Midgley 1992; Richardson et al. 1992; Bond 1995).

1.2.2. Ecological benefits

The ecological benefits of bird-mediated seed dispersal for plant species include escape, colonisation and focused distribution (Howe & Smallwood 1982; Wenny 2001; Robertson et al. 2006; Schurr et al. 2009). Dispersal of seeds away from parents assists in seedling escape from competition by adults and siblings (Howe & Smallwood 1982; Schupp 1993; Godinez-Alvarez & Jordano 2007), as well as seed predators and parasites, which focus their activities in close proximity to parents where resources are abundant (Willson & Traveset 2000). The dispersed seeds allow plant colonisation of new areas given that these are suitable for seed germination and seedling establishment and that the seeds survive secondary predators at seed deposition sites dependent on bird flight patterns (Howe & Smallwood 1982; Manders & Richardson 1992; Wenny 2001; Russo & Augspurger 2004; Carlo et al. 2007). In addition, bird flights between diverse habitats provide essential genetic links between habitat fragments that facilitate species coexistence (Godoy & Jordano 2001; Opdam & Wascher 2004; Schupp et al. 2010).

1.2.3. Specialist versus non specialist frugivores

Frugivorous birds may be classified into two groups, namely specialist (obligate) frugivores that forage on large highly nutritious fruits rich in proteins and fats, and non-specialist (facultative) frugivores, which forage on small fruits with high carbohydrate contents (Mckey 1975; Snow 1981). Specialised frugivores possess gut systems adapted for digestion of fruits to maximise energy uptake and passage of seeds in an undamaged state (Howe & Estabrook 1977; Snow 1981; Jordano 2000). Usually, such birds have shorter intestines and gut retention times that allow rapid passage of seeds in a viable state (Fuentes 1994; Jordano 2000; Herrera 2002). Snow (1981) defined such specialist frugivores as legitimate dispersers, and considered non-specialist frugivores as mainly seed predators due to their less specialised gut system for effective dispersal of undamaged viable seeds (Stiles & Rosselli 1993; Gopser 2004). Nevertheless, non-specialised frugivores are usually more abundant than specialised frugivores and thus are more reliable dispersal agents for many plants (Snow 1981; Carlo et al. 2003; Carlo et al. 2007).

1.2.4. Effects of bird foraging behaviour on seed dispersal

The foraging behaviour of frugivorous birds is a major factor influencing the quantities of seeds dispersed (Schupp 1993; Jordano & Schupp 2000; Vazquez et al. 2005; Schupp et al. 2010). Flocking bird species usually remove larger number of fruits and seeds than solitary bird species during one foraging visit (Schupp 1993; Chavez-Ramirez & Slack 1994; Vazquez et al. 2005). However, it has been argued that solitary bird species or those foraging in smaller groups may also disperse large numbers of seeds through their high foraging visitation frequency (Jordano & Schupp 2000; Vazquez et al. 2005; Schupp et al. 2010). According to Vazquez et al. (2005), vertebrate seed dispersal agents with high foraging frequency usually contribute substantially to a plant's reproductive success even if their effectiveness is relatively low. This finding was supported by Carlo et al. (2003) who noted that the repeated preference in Puerto Rico by two frugivores, namely the Antillean euphonia *Euphonia musica* and the black-whiskered vireo *Vireo altiloquous,* for fleshy fruits of *Cecropia, Guarea, Schefflera, Miconia* species increased seed dispersal effectiveness.

The manner in which frugivorous birds consume fruits, and seed passage times through bird guts determine the quality of seed dispersal (Schupp 1993). Frugivorous birds are divided into swallowers, mashers and biters depending on how they consume fruits (Jordano 2000; Luck & Daily 2003). Swallowers generally ingest the whole fruit including the seeds (Jordano 2000) and then extract the fruit pulp in the gizzard or gut (Traveset et al. 2001). Mashers chew fruits and ingest both the fruit pulp and seeds whereas biters remove portions of the fruit pulp by biting or pecking (Levey 1987; Jordano 2000; Luck & Daily 2003).

The length of the digestive tract, gizzard, and gut retention times and the corrosiveness of digestive fluids (Traveset et al. 2001; Nogales et al. 2005; Traveset et al. 2008) may alter the dormancy of ingested seeds (Schupp 1993; Samuels & Levey 2005; Traveset et al. 2001; Robertson et al. 2006) through physical and chemical effects on seed coat permeability (Wenny 2001; Traveset et al. 2001; Traveset et al. 2008). Scarification of the seed coat through physical damage during fruit consumption and through chemical damage by digestive fluids during seed ingestion often promotes seed germination (Barnea et al. 1990; Traveset & Wilson 1997; Traveset et al. 2001; Robertson et al. 2006). However, the magnitude of bird-mediated effects on germination of ingested seeds differs with bird and plant species. Traveset et al. (2001) for example, showed that *Rubus* and *Rubia* seeds ingested by the blackbird *Turdus merula* displayed different germination rates to those ingested by the Sardinian warbler *Sylvia melanocephala* in the western Mediterranean. In contrast, Bartuszevige and Gorchov (2006) reported that the germination of seeds of the bush honeysuckle *Lonicera maackii* was inhibited by their passage through the gut of the cedar waxwing *Bombycilla cedrorum* in the United States.

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1.2.5. Effects of bird size on seed dispersal

Bird body size determines the quantities of seeds dispersed by birds (Jordano 2000; Schurr et al. 2009; Tsoar et al. 2011) with for example, the average numbers of fruits of the mahaleb cherry *Prunus mahaleb* ingested by birds reported positively correlated to their body size (Jordano 2000). Small seeds are mostly ingested in larger numbers than large seeds and retained in larger quantities and for longer periods in the disperser's gut than large seed (Crawley 2000; Kitamura et al. 2002; Schurr et al. 2009). In Southeastern Queensland in Australia, 81% of fleshy-fruited invasive alien species possess smaller seeds than indigenous species (Gosper & Vivian-Smith 2010), which might account for their successful establishment and spread. The negative relationship between seed mass and dispersal distance also highlighted as an attribute of the invasiveness of *Pinus* species (Rejmanek & Richardson 1996) which may apply to other angiosperms (Gosper et al. 2005). Indeed, seed mass also accounts for 20% of the variation in dispersal distance among the 31 vertebrate-dispersed fleshy-fruited woody species in Panama (Muller-Landau & Hardesty 2005). Longer visitations by foraging birds is also likely to result in the removal of greater numbers seeds than shorter visitations although deposition of seeds under maternal fruiting trees is more likely (Pratt & Stiles 1983). Visitation times by foraging birds are influenced by environmental factors and bird metabolic demands with bird body size rather than foraging period limiting seed loads (Wheelwright 1991; Jordano 2000).

1.2.6. Effects of timing of fruit maturation on seed dispersal

Fruiting phenology plays an important role in maintaining interactions between dispersal agents and fruits (Snow & Snow 1988; Carlo et al. 2007). The timing of fruit maturation must be such that ripe fruits are present when dispersal agents occur in high abundance (Herrera 1984; Snow & Snow 1988). Opportunistic and prolonged winter fruiting of many alien species offer them greater access to dispersal services since many indigenous tree species are out of fruits at this time (Greenberg et al. 2010). However, this is not pertinent in southern African Mediterranean-climate ecosystem where the highly variable fruit production of native species is a mechanism ensuring overlapping of fruiting times for different resident avian seed dispersers (Knight 1988). Plant species with similar fruiting times consequently compete for the same suite of dispersal agents (Snow & Snow 1988; Carlo 2005; Carlo et al. 2007), especially if dispersal agents are limited. However, better fruit presentation and manipulation of fruiting time by a plant may help avoid competition for dispersal agents occurring in the same habitat (Snow & Snow 1988; Gosper et al. 2006).

1.2.7. Effects of fruit variety on seed dispersal

Fruit variety affects interactions between dispersal agents and fruits with several studies demonstrating that neighbouring fruiting trees influence fruit removal (Foster 1990; Garcia et al.

2010; Saracco et al. 2005; Carlo et al. 2007; Carlo & Morales 2008). For instance, bird foraging on *Juniperus commnunis* fruits increases significantly with the high density of neighbouring fruiting trees (Garcia et al. 2010). A comprehensive test of the impacts of neighbouring fruiting trees on bird frugivory was conducted in Puerto Rico where populations of *Solanum americanus* were experimentally manipulated and avian fruit removal between monospecific populations and one neighbouring *Cestrum diurnum* were monitored (Carlo 2005). The results showed that neighbouring trees increased fruit removal due to more bird visitations to a mixed population. Similarly, the presence of alien fruits of invasive plants might change the nature of native plant species stands and thus increase or decrease bird foraging visitation (Saracco et al. 2005; Carlo 2005). For example, Gleditsch and Carlo (2010) showed that invasion by *Lonicera* in central Pennsylvania had positive facilitative effects on seed dispersal of indigenous plants with invaded areas experiencing increased fruit removal from indigenous plants and increased relative abundance of birds which in turn enhanced fruit removal (Carlo & Morales 2008).

1.2.8. Effects of fruit abundance on seed dispersal

Fruit abundance (crop size) influences fruit choice by birds (Herrera 1984; Jordano 2000; Izhaki 2002; Gosper et al. 2005; Deckers et al. 2008). Foster (1990), for example, examined 27 different fruit characteristics of *Allophylus edulis* associated with fruit removal by birds and found that crop size was most positively correlated with fruit removal and foraging visitations by birds in Paraguay. Similarly, Denslow (1987) reported a positive correlation between larger fruit crop sizes and higher removal rates in *Sambucus pubens,* and Sargent (1990) found faster fruit removal from isolated *Viburnum dentatum* plants with large crop sizes than small crop sizes in New York. Likewise, Saracco et al. (2005) reported a positive correlation between the crop size of the dwarf umbrella tree *Schefflera morototoni* and avian visitation rate in central Puerto Rico, though this finding was inconsistent among focal trees. Therefore, fruiting alien plant species with relatively high fruit abundance are likely to attract more birds than indigenous species (Izhaki 2002; Laska & Stiles 1994; Pysek & Richardson 2008) because frugivorous birds often concentrate their activities where resources are most abundant (Willson & Traveset 2000; Hulme 2002; Saracco et al. 2005; Blendinger et al. 2008). In this regard, Gosper (2004) found that the presence of multiple large fruit crops throughout the year rendered the invasive bitou bush *Chrysanthemoides monilifera* more preferential to vertebrate dispersers than the co-existing indigenous species in New South Wales, Australia. Contrastingly, in the southwestern Cape Region of South Africa, Knight (1988) found that *C. monilifera* has a larger fruit crop size than some alien shrubs yet not locally invasive.

1.2.9. Effects of fruit nutritional content on seed dispersal

Birds select fruits based on the nutritional quality of the pulp (Schaefer et al. 2003) with several studies demonstrating that high fruit nutritional quality is associated with high

consumption rates by birds (Fuentes 1994; Jordano 2000; Witmer 2001; Izhaki 2002; Gosper & Vivian-Smith 2010). Alien fruits with high water contents and concentrations of simple sugars such as glucose and fructose (Martinez del Rio & Restrepo 1993; Jordano 2000; Izhaki 2002; Kueffer et al. 2009; Gosper & Vivian-Smith 2010) but low lipid and protein contents (Jordano 2000; Gosper & Vivian-Smith 2010) are often preferred by birds, which lack enzymes for cleaving fruit sucrose into readily assimilated glucose and fructose (Martinez del Rio & Restrepo 1993; Malcarney et al. 1994). It has been shown that several monophyletic bird lineages, including starlings, mimids, and thrushes, display sucrose-intolerance as their low intestinal maltase activity correlate with a lack of sucrase activity (Malcarney et al. 1994). Gray catbirds (*Dumetella carolinensis*, Mimidae) and purple-headed glossy-starlings (*Lamprotornis purpureiceps*, Sturnidae), for example, exhibit depressed ingestion and increased faecal sugar contents when shifted from solutions of glucose and fructose to sucrose. In addition, these species show no increases in plasma glucose after ingestion of sucrose, but an increase in plasma glucose after ingestion of equicaloric doses of a mixture of glucose and fructose. Furthermore, in vitro measurements of intestinal disaccharidase activities in *D. carolinensis* have revealed insignificant sucrase activity, and low levels of maltase activities (Malcarney et al. 1994). In this regard, Gosper and Vivian-Smith (2010) concluded from an analysis of 34 fleshy-fruited vertebrate-dispersed alien species that the concentrations of simple sugars in their fruit pulps were relatively higher than that of indigenous species in southeastern Queensland, Australia and, therefore, critical for their effective dispersal by birds. Similarly, measures of fruit nutritional quality in some invasive fleshy-fruited woody species in the Seychelles showed higher values than in many native species (Kueffer et al. 2009) and in Durban, South Africa, Jordaan et al. (2011) reported that frugivorous birds selectively utilise highly nutritional fleshy fruits of alien plants to maintain their energy requirements. Some specialist frugivores have been reported to prefer fruits with high protein and fat content (Snow 1981; Howe 1993), though such fruits are avoided by birds in Spanish scrubland due to the long time required to process these fruits in their guts (Fuentes 1994).

1.2.10. Seed dispersal distances

In most plant species, the majority of seeds are dispersed over relatively short distances by birds, the distances rarely exceeding a few dozen meters from original seed sources (Willson 1993). The bulk of locally dispersed seeds generate a spatial template that often moulds the local dynamics of plant populations and communities (Howe & Smallwood 1982; Levine et al. 2003). It has been shown that long-distance dispersal (LDD) events are typically rare, yet play a major role in determining large-scale processes such as population spread, the flow of individuals between populations, the colonization of unoccupied habitats and the assembly of local communities from the metacommunity (Levine & Murrell 2003; Nathan et al. 2008; Schurr et al. 2009). In addition, LDD rather than local dispersal may determine the spread of invasive

plants, range shifts following climate change and the persistence of species in fragmented landscapes (Trakhtenbrot et al. 2005). Consequently, despite immense difficulty in measurement and prediction seed dispersal distances (Cain et al. 2000; Nathan et al. 2003), LDD research is currently experiencing an upsurge of general interest (Nathan 2005), especially in plant ecology (Levine et al. 2003; Nathan 2005; Munoz et al. 2004), and understanding of spread invasive alien plants (Tsoar et al. 2011).

Reliable estimates of dispersal distances of seed ingested by birds are restricted by erratic bird flight patterns (Nathan 2001a; Schupp et al. 2002; Muller-Landau & Hardesty 2005; Russo et al. 2006), and distorted plant-animal mutualisms induced by habitat fragmentation and defaunation (Herrera 1995; Opdam & Waschar 2004; Muller-Landau & Hardesty 2005). Some studies have applied various analytical models (mechanistic and phenomenological) to predict seed dispersal distances. However, these models do not fully incorporate all the complexities of long-distance seed dispersal (Nathan & Muller-Landau 2000; Russo et al. 2006) and bird behavioural dynamics such as fruit tracking (Sarraco et al. 2004; Telleria et al. 2005) and changes in bird flight patterns due to habitat disturbance and fruit preferences (Wilms & Kappelle 2006; Gomes et al. 2008). An alternate vector-based approach has been proposed, based on the assumption that seed dispersal distance is directly proportional to the body size of the disperser in flying vertebrates, since large birds often disperse seeds to more distant microsites than smaller birds during habitat exploitation (Jordano 2000; Bowman et al. 2002; Jenkins et al. 2007; Schurr et al. 2009; Tsoar et al. 2011). Examples include the observed greater dispersal distance of seeds of the fleshy-fruited shrub *Ochradenus baccatus* by large Tristram's grackles *Onychognathus tristramii* than by smaller bulbuls *Pycnonotus xanthopygos* in Israel (Spiegel & Nathan 2007). However, smaller birds may also disperse seeds to distant sites in their movement between intermittently fruiting populations along geographical gradients (fruit tracking), and occasionally through extended seed gut retention times (Shilton et al. 1999; Saracco et al. 2004; Telleria et al. 2008). The territorial European robin *Erithacus rubecula,* for example, tracks spatially variable fruit availability in the Spanish Mediterranean scrubland (Telleria et al. 2008), which overrides the constraints of body size on dispersal distances of seeds ingested by mammals (Bowman et al. 2002).

Seed dispersal distance is a function of seed retention time in the bird gut, flight distance and flight speed (Fukui 1996; Sun et al. 1997; Holbrook & Smith 2000; Higgins et al. 2003; Westcott & Graham 2000; McConkey et al. 2004; Schurr et al. 2009). McConkey et al. (2004) for example, determined the dispersal distances of *Myristica hypagyria* seeds ingested by the fruit pigeon *Ducula pacifica* in Tonga, Western Polynesia from the product of this bird's gut retention time of seed and its flight speed. Similarly, the gut passage time of seeds and measurements of foraging ranges of *Ceratogymna* hornbills and trumpeter hornbills *Bycanistes bucinator* were used to estimate potential dispersal distances of ingested seeds in Cameroon and South African forests (Holbrook & Smith 2000; Lenz et al. 2010). Retention times of seed in bird guts are positively correlated with bird body mass (Schurr et al. 2009; Tsoar et al. 2011).

This feature and the tendency for large birds to fly more rapidly over larger distances may potentially allow large birds to disperse seed over greater distances than small birds (Schurr et al. 2009). However, gut retention time of seeds is also influenced by seed size. Large seeds consumed by bigger birds do tend to be expelled more rapidly than small seeds (Whittaker & Jones 1994; Martinez del Rio 2001; Charalambidou et al. 2003). Moreover, high concentrations of sucrose and glycoalkaloids in some fruit types have a laxative effect causing seeds also to be expelled more rapidly (Murray et al. 1994; Malcarney et al. 1994). Empirical data on movement of frugivorous birds can provide estimates of seed dispersal distances from maternal plants (Nathan 2001b; Levine & Murrell 2003; Westcott et al. 2005; Holbrook 2010).

1.3. Disruption of bird-plant mutualisms by aliens

1.3.1. Global perspective

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 (Rejmanek 1996; Richardson & Rejmanek 2011). This assisted by bird-mediated seed dispersal of fleshy-fruited invasive alien plants which is well-documented globally (Dean et al. 1986; William & Karl 1996; Dean & Milton 2000; Richardson et al. 2000b; Gosper et al. 2005; Milton et al. 2007; Vittoz & Engler 2007; Traveset & Richardson 2011; Richardson & Rejmanek 2011). It has been reported that birds disperse 25% of the 199 globally representative invasive species (Cronk & Fuller 1995) and 43% of the invasive alien trees and 61% of invasive alien shrubs in 15 distinct global geographical regions (Richardson & Rejmanek 2011). The extra-tropical ecosystems such as the temperate and Mediterranean climate ecosystems, except those in the Mediterranean Basin, seem more vulnerable to this invasion (Rejmanek 1996; Rejmanek et al. 2005) due to the massive habitat fragmentation (Herrera 1995). Typical examples include the spread of aliens *Cinnamomum camphora* and *Ligustrum lucidum* by frugivorous birds in a subtropical rainforest in New South Wales associated with habitat loss and indigenous fruit-bearing trees (Richardson et al. 2000b). The alien forests unfavourable to indigenous birds have also proliferated due to the increased dispersal of fleshy-fruited alien shrubs by alien birds in Nelson, New Zealand (Williams & Karl 1996).

Lack of indigenous fruits has resulted in birds consuming and dispersing seeds of alien plants species in many parts of the world (Oatley 1984; LaFleur et al. 2007; Quix 2007). However, undisturbed continental tropical areas with the highest abundance (e.g. 80%) of fleshy fruits (Jordano 2000) have relatively fewer numbers of alien plant species than extra-tropical habitats (Rejmanek 1996; Rejmanek et al. 2005) probably due to tight coevolved indigenous bird-plant relationships which limit penetration by alien species (Snow 1981). For example, the fruiting phenologies of 18 species in the tropical laurel family (Lauraceae) dictate the timing and direction of seasonal movements by the resplendent quetzal *Pharomachrus mocinno* (Wheelwright 1983). Also, it has been observed that counter-competition by 65 native plant

species bearing fleshy fruits for vertebrate seed dispersal agents has prevented the spread of 19 alien fleshy-fruited species in Montpellier, France (Desbussche & Isenmann 1990). Despite this, many introduced fleshy-fruited alien species for horticultural purposes do possess attributes attractive to birds such as large fruit crop sizes, prolonged and attractive fruit displays (Richardson & Rejmanek 2011) which facilitate dispersal seed dispersal and invasiveness (Tucker & Richardson 1995; Murray & Phillips 2010). For example, it has been shown that the prolonged availability of fruits of the alien shrub *Chrysanthemoides monilifera* (bitou) of South African origin renders it more preferential to native vertebrate dispersers than indigenous fruiting species in Australia (Gosper 2004).

Different mechanisms of disruption of plant-seed disperser interactions have been reviewed in Traveset and Richardson (2006). The presence of alien fruits in the habitat can lead to reduction of numbers of disperser's visits to native fruit or seeds removed by native avian dispersers of which reduce the effectiveness (e.g. quantity, Schupp 1993) of seed dispersal and plant population growth. For instance, the ingested seeds of native plants are likely to be deposited under alien trees and shrubs canopies where their germination may be retarded by allelopathic effects to the advantage of the alien seeds (Gosper 2004; Sun et al. 2006). In addition, if fruit resources accumulate locally, the disperser's behaviour (e.g. foraging movements) can be changed to being territorial and thus, promote inbreeding and reduction of population of native seed dispersers. Long-term effects of increased dispersal of alien fruit/seeds may entail change in the native plant community structure and associated fauna (Sallabanks 1993; William & Karl 2002).

1.3.2. Regional perspective

Alien tree species were introduced into southern Africa in the middle of the seventeenth century for commercial, horticultural and forestry purposes (Macdonald et al. 1986; Richardson 1998; Richardson & Rejmanek 2011). Presently, southern Africa ranks second to Australia as a global region with the largest numbers of invasive fleshy-fruited woody alien species (Richardson & Rejmanek 2011) many of which possess fruit attributes attractive to birds (Vittoz & Engler 2010). Initial assessments indicate that 51 of the 1 698 alien plants introduced into southern Africa possess fleshy fruits dispersed by birds (Knight 1986) with these numbers increasing (Richardson & Rejmanek 2011). Currently, the most prominent fleshy-fruited alien species dispersed by birds in southern Africa include the widely distributed established species *Lantana camara*, *Opuntia ficus-indica* (sweet prickly-pear), *Rubus fruticosa* (blackberry) and *Solanum mauritianum* (bugweed) and the more localised emergent species *Myoporum tenuifolium* (manataka) and *Pittosporum andulatum* (Australian cheesewood) (Knight 1986; Rejmanek & Richardson 1996; Henderson 2007). It has been proposed that the presence of these flesh-fruited alien plants in local habitats could change bird frugivory patterns and disrupt seed dispersal services for native plants (Knight 1986; Richardson et al. 2000b; Traveset &

Richardson 2006; Traveset & Richardson 2011). This proposal is corroborated by the observed altered feeding ecology of *Columba arquatrix* (African olive-pigeon) by the presence of the invasive alien shrub *Solanum mauritianum* whose fruits attract large numbers of local avian dispersers (Oatley 1984; Geldenhuys et al. 1986). Also, Milton et al. (2007) reported that fleshy fruits of the aliens *Shinus molle*, *Rhus pendulina* and *Celtis* species attract local birds due their similar fruit characteristics as those of indigenous plant species thereby reducing the seed dispersal potential of indigenous species. However, the provision of supplementary food sources by flesh fruited aliens may assist in maintaining populations of native bird species (Buckley et al. 2006; Aslan & Rejmanek 2010; Jordaan et al. 2011) as demonstrated in three important native frugivores, namely red-winged starling *Onychognathus morio*, speckled mousebird *Colius striatus* and dark-capped bulbul *Pycnonotus tricolor* which depend on alien fruits to meet their daily energetic requirements in Durban, South Africa (Jordaan et al. 2011). This preferential consumption of fleshy fruits of alien species by birds has direct implications for natural ecosystems, since the dispersed seeds contribute to the expansion of the alien populations (Rejmanek & Richardson 1996; Murray & Phillips 2010).

1.4. Study rationale, hypotheses and thesis content

The infiltration by alien species of ecological networks in novel environments may disrupt existing mutualisms between birds and plants (Geldenhuys et al. 1986; Richardson et al. 2000; Traveset and Richardson 2006; Milton et al. 2007). Where co-fruiting alien and indigenous shrubs share similar avian dispersal assemblages, competition for dispersal agents may result (Terborgh & Diamond 1970, Geldenhuys et al. 1986; Gosper et al. 2006; Carlo et al. 2007). Swaying of avian dispersers' attention from native to alien fruits may alter seed dispersal systems and eventually vegetation structure of the invaded habitat (Carlo et al. 2003; Williams 2006; Bascompte & Jordano 2007; Green 2007). Also, the more attractive and rewarding fruits of alien invasive plant species over their native counterparts (Rejmanek & Richardson 1996; Reichard et al. 2001; Traveset & Richardson 2006; LaFleur et al. 2007; Pysek & Richardson 2008) might attract larger numbers of foraging birds, and lead to prolonged foraging periods. Consequently, foraging by birds in larger numbers and over longer periods on alien fruits might increase their fruit/seed removal to the detriment of the native species (Courtney & Sallabanks 1992; Schupp 1993; Jordano & Schupp 2000; Trakhtenbrot et al. 2005; Traveset & Richardson 2006). Previous studies on fleshy-fruited alien plants merely identified which bird species disperse seeds of woody alien species (Glyphis et al. 1981; Oatley 1984; Geldenhuys et al. 1986; Manders & Richardson 1992; Underhill & Hofmeyr 2007) as a means of determining potential invasiveness (e.g. *Shinus molle*, Iponga 2009). Other studies on primary seed dispersal process of fleshy-fruited plants by birds in South Africa (e.g. Phillips 1927, Glyphis et al. 1981; Cowling et al. 1997, Jordaan et al. 2011) have demonstrated that ingestion of seeds by birds improve their germination (Figure 1.1). However, these studies have disregarded the consequences of avian seed dispersal process on plant fitness (Wang & Smith 2002) and

skewed competitive interactions between indigenous and aliens species as a threat to native biodiversity. The only comparative studies between alien and indigenous tree and shrub species in southern Africa are those on fruit phenology and fruit displays (Knight 1986, 1988). Recent reviews (Gopser et al. 2005; Buckley et al. 2006) emphasised that comparative studies between fleshy-fruited alien and indigenous species might strengthen management protocols of invasive alien trees and shrubs dispersed by birds, and improve understanding of invasion dynamics (Tsoar et al. 2011). For example, knowledge of the interactions between alien and indigenous species and their potential effects on seed dispersal may assist in replacing alien species with suitable indigenous fruiting species without negatively affecting bird diet and consequent seed dispersal by birds (Buckley et al. 2006; Gosper et al. 2006; Tsoar et al. 2011). In view of these knowledge deficiencies, the numbers and composition of bird species, their visitation frequencies and foraging periods on fruits of neighbouring alien and indigenous shrubs were quantified in this study. The findings whose contribution to the different processes in the seed dispersal cycle according to Wang & Smith (2002) are shown in Figure 1.1 and presented in Chapters 3 and 4. The following hypotheses were tested namely: (i) that fruits of alien shrubs are visited more frequently and by a larger complement of foraging bird species than those of indigenous shrubs, and (ii) that fruits of alien shrubs are foraged by larger numbers of individual bird species and for longer periods than those of indigenous shrubs. In addition, various multiples of foraging bird numbers, foraging times and visitation frequencies were applied as determinants of bird consumption intensities and in combination with measures of seed size in determining proxies of potential dispersal capacities of indigenous and alien seeds ingested by birds. These complex measurements are presented in Chapter 5. Their effectiveness, relative to simpler visitation frequency, foraging number and foraging time measurements, in discriminating between bird foraging activities on fruits of alien and native plants, are evaluated in the general discussion in Chapter 9.

High reproductive output is generally associated with increased fitness in natural plant populations (Kelly & Sork 2002) and invasiveness in alien plant species (Richardson & Rejmanek & Richardson 1996; Levine et al. 2003; Milton et al. 2007). Alien plant species with relatively high fruit abundance are likely to attract more birds (Izhaki 2002; Laska & Stiles 1994) because frugivorous birds concentrate their activities where resources are most abundant (Willson & Traveset 2000; Hulme 2002; Saracco et al. 2005; Blendinger et al. 2008). Also, fruit choice by birds is driven by the nutritional quality of the pulp, especially high concentrations of simple sugars such as glucose and fructose (Martinez del Rio & Restrepo 1993; Jordano 2000; Izhaki 2002; Kueffer et al. 2009; Gosper & Vivian-Smith 2010). However, the few studies that have compared bird fruit preferences between alien invasive and native plants have producing conflicting results (Daehler 2003; Levine et al. 2003; Buckley et al. 2006; Kueffer et al. 2009). Knowledge of fruit dietary components may therefore assist identifying functionally similar avian frugivores and thus predict the key seed dispersers of invasive species (Gosper et al. 2005, 2008). In addition, the viability of seeds contained in fruits consumed by birds may also be

altered by the manner in which birds consume fruits, the length of their digestive tracts, gizzard and gut retention times and the corrosiveness of their digestive fluids (Traveset et al. 2001; Nogales et al. 2005; Traveset et al. 2008). Consequently, fruit production and nutritional contents were quantified in neighbouring alien and indigenous shrubs in this study and compared with the amounts of fruits and associated seeds removed by birds and the viability of the ingested seeds. Tsoar et al. (2011) suggested that invasion success depends of post-dispersal processes (Wang & Smith 2002) as they determine survival and establishment of seeds deposited in different microsites. These measurements, whose contribution to the different processes in the seed dispersal cycle according to Wang & Smith (2002) are shown in Figure 1.1 and presented in Chapter 6. The following hypothesis were tested, namely: (i) that frugivorous birds remove larger amounts of fruits and seeds from especially alien plants with high fruit production and nutritional contents, (ii) that the germination of the seeds ingested by the birds is enhanced.

Several studies have examined the effectiveness of different empirical approaches for measuring the quantities of fruits and associated seeds removed by birds (Nathan & Muller-Landau 2000; Nathan 2001b; Bullock et al. 2006). However, the different methods applied have yielded contrasting results for comparable environmental conditions, plant and bird species (Nathan & Muller-Landau 2000; Nathan 2001b; Bullock et al. 2003, 2006). Experimental approaches applied in determining seed removal rates by birds have entailed direct counts of the numbers of fruits consumed by birds over specific time intervals coupled with placement of fruit traps underneath the plant canopies to measure fruit loss by abscission (Sallabanks 1993; Korine et al. 2000; Bache & Kelly 2004). Photographic approaches have entailed the use of digital camcorders to photograph birds consuming fruits (Spiegel & Nathan 2007), these providing permanent visual and time-lapse records for individual foraging bird species. Also, knowledge of the distances that seeds of alien and native species are dispersed by birds is essential in predicting future distribution ranges and in selecting suitable management strategies to limit the spread of aliens (Sakai et al. 2001; Tsoar et al. 2011). In most plant species, the majority of seeds are dispersed over relatively short distances by birds, the distances rarely exceeding a few dozen meters from original seed sources (Willson 1993). The bulk of locally dispersed seeds generate a spatial template that often moulds the local dynamics of plant populations and communities (Howe & Smallwood 1982; Levin et al. 2003). Long-distance dispersal (LDD) events are typically rare, yet play a major role in determining large-scale processes such as population spread, the flow of individuals between populations, the colonization of unoccupied habitats and the assembly of local communities from the metacommunity (Levine & Murrell 2003). Improved measurements of the foraging movements (e.g. home range, Bowman et al. 2002) of a disperser may therefore assist in predicting spatial distribution of alien plants (Buckley et al. 2006; Richardson & Rejmanek 2011; Tsoar et al. 2011). Consequently, rates of fruit and seed removal by birds from neighbouring alien and native plants were quantified and compared using both experimental and photographic

approaches in this study. In addition, seed dispersal distance limits were quantified for different species of birds foraging on fruits of neighbouring alien and native plants using initial capture and recapture ring locations extracted from the South African Bird Atlas Project database and published records of seed gut retention times and flight speeds. These measurements, whose contribution to the different processes in the seed dispersal cycle according to Wang & Smith (2002) are shown in Figure 1.1 and presented in Chapter 7. The following hypotheses were tested, namely (i) that larger quantities of seeds are removed by birds from alien than indigenous shrubs and (ii) that seeds of alien shrubs are dispersed to greater distances than those of indigenous shrubs.

Fleshy-fruited alien plants may be classified into established or emergent groups (Henderson 2001; Nel et al. 2004), the former comprising widely distributed populations of high density introduced in the distant past and the latter comprising more recently introduced isolated populations of low density and restricted distribution (Nel et al. 2004). The greater number of perches for foraging birds provided by established alien populations and their consequentially higher fruit abundance are likely to attract more birds than populations of emergent aliens with relatively smaller fruit abundance (Knight 1988; Manders & Richardson 1992; Izhaki 2002). This premise concurs with the fruit crop hypothesis, which asserts that predators concentrate their activities where resources are most abundant (Hulme 2002; Saracco et al. 2005; Blendinger et al. 2008). Consequently, visitation frequencies of identical complements of bird species foraging on fruits of disparate populations of established and emergent aliens were quantified in this study. These measurements, whose contribution to the different processes in the seed dispersal cycle according to Wang & Smith (2002) are shown in Figure 1.1 and presented in Chapter 8. The following hypothesis was tested, namely: (i) that fruits established alien shrubs are visited more frequently by foraging birds than those of emergent aliens.

A critical evaluation of all the study's findings, their contribution to management protocols, recommendations for future research and conclusions are presented in Chapter 9.

31
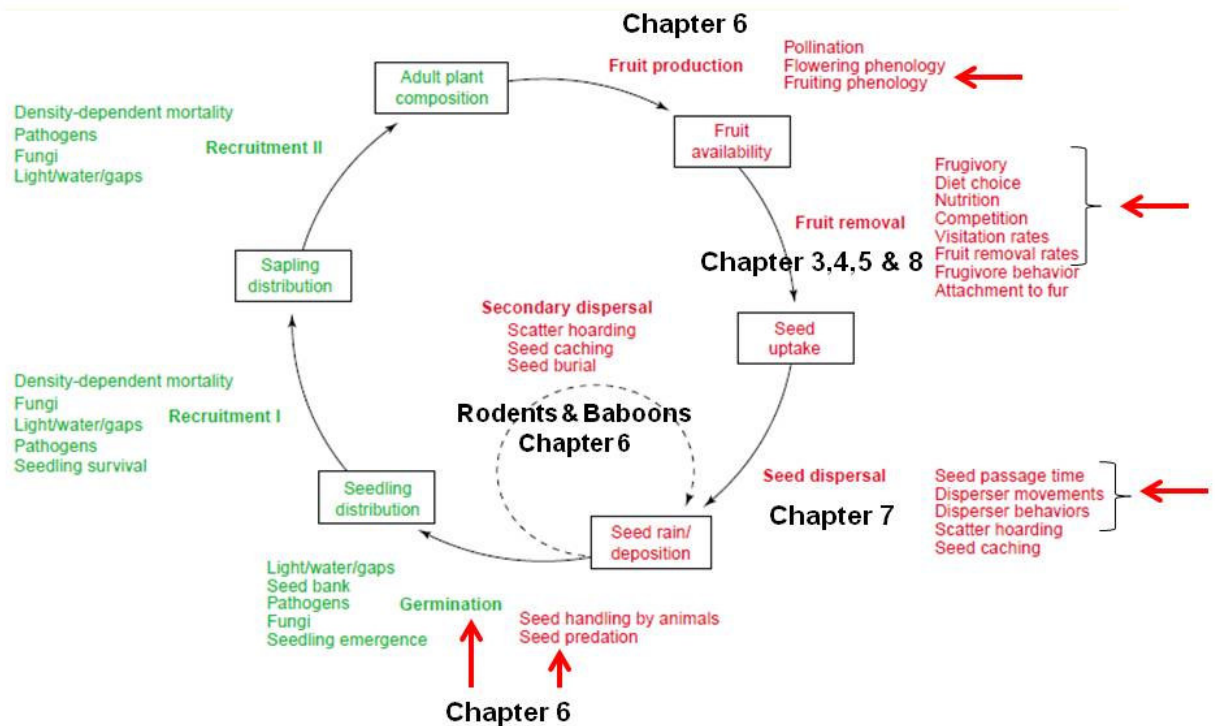
Figure 1.1. Schematic representation of a typical seed dispersal cycle according to Wang & Smith (2002) with the different processes examined in this study indicated by arrows

1.6. Reference list

Aslan, C.E. & Rejmanek, M. (2010) Avian use of introduced plants: ornithologist records illuminate interspecific associations and research needs. *Ecological Applications*, **20**, 1005-20.

Barnea, A., Yom-Tov, Y. & Friedman, J. (1990) Differential germination of two closely related species of Solanum in response to bird ingestion. *OIKOS*, **57**, 222-228.

Bartuszevige, A.M. & Gorchov, D.L. (2006) Avian seed dispersal of an invasive shrub. *Biological invasions,* **8**, 1013–1022.

Bascompte, J. & Jordano, P. (2007) The structure of plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **38**, 567-593.

Beater, M.M.T., Garner, R.D. & Witkowski, E.T.F. (2008) Impacts of clearing invasive alien p lants from 1995 to 2005 on vegetation structure, invasion intensity and ground cover in a temperate to subtropical riparian ecosystem. *South African Journal of Botany*, **74**, 495-507.

Binggeli, P. (1996) A taxonomic, biogeographical and ecological overview of invasive woody plants. *Journal of Vegetation Science*, **7**, 121-124.

Blendinger, P.G., Loiselle, B.A. & Blake, J.G. (2008) Crop size, plant aggregation, and microhabitat type affect fruit removal by birds from individual melastome plants in the Upper Amazon. *Oecologia*, **158**, 273-283.

Blossey, B. & Notzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887-89.

Bond, W. J. & Breytenbach, G. J. (1985) Ants, rodents and seed predation in Proteaceae. *South African Journal of Zoology*, **20,** 150-154.

Bond, W.J. (1994) Do mutualisms matter – assessing the impact of pollinator and disperser disruption on plant extinction? Philosophical Transactions of the Royal. *Society of London Series B-Biological Sciences*, **344**, 83-90.

Bond, W.J. (1995) Effects of global change on plant-animal synchrony: implications for pollinitation and seed dispersal in Mediterranean habitats. *Global Change and Mediterranean-Type Ecosystems*. (eds. Moreno, J.M. & Oechel, W.C.) pp. 181–202. Springer-Verlag, New York.

Bowman, J., Jaeger, J. A.G. & Fahrig, L. (2002) Dispersal distance of mammals is proportional to home range size. *Ecology,* **83**, 2049–2055.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., Ditomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. (2004) Effects of invasive alien plants on fire regimes. *BioScience*, **54**, 677-688.

Buckley, Y.M., Anderson. S., Catterall, C.P., Corlett, R.T., Engel, T., Gosper, C.R., Nathan, R., Richardson, D.M., Setter, M., Spiegel, O., Vivian-Smith, G., Voigt, F.A., Weir, J.E.S. & Westcott, D.A. (2006) Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology,* **43**, 848–857.

Carlo, T.A. & Morales, J.M. (2008) Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. *Journal of Ecology*, **96**, 609–618.

Carlo, T.A. (2005) Interspecific neighbors change seed dispersal pattern of an avian-dispersed plant. *Ecology*, **86**, 2440-2449.

Carlo, T.A., Aukema, A.G. & Morales, J.M. (2007) Plant-frugivore interactions as spatially explicit networks: integrating frugivore foraging with plant spatial patterns. *Seed dispersal: theory and its application in a changing world*. (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 369-390. Reading: Biddles Ltd.

Carlo, T.A., Collazo, J.A. & Groom, M.J. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia*, **134**, 119–131.

Christian, C.E. (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* **413**, 635-639.

Crawley, M.J. (2000) Seed predators and plant population dynamics. *Seeds: the ecology of regeneration in Plant Communities*. (ed. Fenner, M.) pp. 167–182. CABI Publishing, Oxford.

D'Antonio, C.M. & Meyerson, L.A. (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology*, **10**, 703-713.

Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics,* **34**, 183-211.

Dean, S.J., Holmes, P.M. & Weiss, P.J. (1986) Seed biology of invasive alien plants in South African and South West Africa/Namibia. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 157-170. Oxford University Press, Cape Town.

Dean, W.R.J. & Milton, S.J. (2000) Directed dispersal of *Opuntia* species in the Karoo, South Africa: are crows the responsible agents? *Journal of Arid Environments*, **45**, 305–314.

Debussche, M. & Isenmann, P. (1989) Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean region. *OIKOS*, **56**, 327-338.

Deckers, B., Verheyen, K., Vanhellemont, M., Maddens, E., Muys, B. & Hermy, M. (2008) Impact of avian frugivores on dispersal and recruitment of the invasive *Prunus serotina* in an agricultural landscape. *Biological Invasions*, **10**, 717–727.

Dennis, A. & Westcott, D. (2006) Reducing complexity when studying seed dispersal at community scales: a functional classification of vertebrate seed dispersers in tropical forests. *Oecologia,* **149**, 620-634.

Dennis, A.J. & Westcott, D.A. (2007) Estimating dispersal kernels produced by diverse community of vertebrates. *Seed dispersal: theory and its application in a changing world* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 201-228. Reading: Biddles Ltd.

Downey, P.O., Scanlon, T.J. & Hosking, J.R. (2010) Prioritising alien plant species based on their ability to impact on biodiversity: a case study from New South Wales. *Plant Protection Quarterly,* **25**, 111-126.

Dukes, J.S. & Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology and Evolution*, **14**, 135-139.

Ferguson, R.N. & Drake D.R. (1999) Influence of vegetation structure on spatial patterns of seed deposition by birds. *New Zealand Journal of Botany*, **37**, 671 - 677.

Figueroa, J.A. & Castro, S.A. (2002) Effects of bird ingestion on seed germination of four woody species of the temperate rainforest of Chiloe Island, Chile. *Plant Ecology*, **160**, 17-23.

Foster, M.S. (1990) Factors influencing bird foraging preferences among conspecific fruit trees. *The Condor*, **92**, 844-854.

Fuentes, M. (1994) Diets of fruit-eating birds: What are the causes of interspecific differences? *Oecologia,* **97**, 134-142.

Galatowitsch, S. & Richardson, D.M. (2005) Riparian scrub recovery after clearing of invasive alien trees in headwater streams of the Western Cape, South Africa. *Biological Conservation*, **122**, 509-521.

Garcia, D., Zamora, R. & Amico, G.C. (2010) Birds as suppliers of seed dispersal in temperate ecosystems: eonservation guidelines from real-world Landscapes. *Conservation Biology* **24**, 1070-1079.

Garcia, D., Zamora, R., Gomez, J.M. & Hodin, J.H. (2001) Frugivory in *Juniperus communis* depends more on population characteristics than on individual attributes. *Journal of Ecology,* **89**, 639–647.

Geldenhuys, C.J., le Roux, P.J. & Cooper, K.H. (1986) Alien invasions in indigenous evergreen forest. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 119-131. Oxford University Press, Cape Town.

Glyphis, P.J., Milton, J.S. & Siegfried, R.W. (1981) Dispersal of *Acacia cyclops* by birds. *Oecologia*, **48**, 138-141.

Godinez-Alvarez, H. & Jordano, P. (2007) An empirical approach to analysing the demographic consequences of seed dispersal by frugivores. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.) pp. 391-406. Reading: Biddles Ltd.

Godoy, J.A. & Jordano, P. (2001) Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. *Molecular Ecology*, **10**, 2275-2283.

Gosper, C.R. (2004) Consequences of weed invasion and control on plant-bird interactions and bird communities. Ph.D. Thesis, Department of Biological Sciences, University of Wollongong, Wollongong.

Gosper, C.R. (2004) Fruit characteristics of invasive bitou bush, *Chrysanthemoides monilifera* (Asteraceae), and a comparison with co-occurring native plant species. *Australian Journal Botany*, **52**, 223 –230.

Gosper, C.R., Stansbury, C.D. & Vivian-Smith, G. (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distributions*, **11**, 549-558.

Gosper, C.R., Whelan, R.J. & French, K. (2006) The effect of invasive plant management on the rate of removal of vertebrate-dispersed fruits. *Plant Ecology*, **184**, 351 –363.

Green, R.J. (2007) Refining the conservation management of seed-dispersing frugivores and their fruits: examples from Australia. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 579-598. Reading: Biddles Ltd.

Greenberg, C.H., Smith, L.M. & Levey, D.J. (2001) Fruit fate, seed germination, and growth of an invasive vine: an experimental test of 'sit and wait' strategy. *Biological Invasions,* **3**, 363–372.

Gurevitch, J. & Padilla, D.K. (2004) Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution,* **19**, 470–474.

Herrera, C.M. (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs*, **54**, 1-23.

Herrera, C.M. (1995) Plant-Vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics*, **26**, 705-727.

Herrera, C.M. (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs*, **68**, 511-538.

Herrera, C.M. (2002) Seed dispersal by vertebrates. *Plant animal interactions: an evolutionary approach*. (eds. Herrera, C.M. and Pellmyr, O.) pp. 185-208. Blackwell Science, Oxford, UK.

Higgins, S.I. & Richardson, D.M. (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *The American Naturalist*, **153**, 464-475.

Howe, H.F. & Estabrook, G.F. (1977) On intraspecific competition for avian dispersers in tropical trees. *The American Naturalist*, **111**, 817-832.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review Ecological Systematics*, **13**, 201–228.

Howe, H.F. (1993) Specialized and generalized dispersal systems: where does 'The Paradigm' Stand? *Vegetatio*, **107/108**, 3-13.

Hulme, P.E. (2002) Seed-eaters: see dispersal destruction and demography. *Seeds dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D. J., Silva, R. W. & Galleti, M.) pp. 161-175. Wallingford: CABI Publishing.

Izhaki, I. & Safriel, U.N. (1989) Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *OIKOS*, **54**, 23-32.

Izhaki, I. & Safriel, U.N. (1990) The effect of some Mediterranean scrubland frugivores upon germination patterns. *Journal of Ecology*, **78**, 56-65.

Izhaki, I. (2002) The role fruit traits in determining fruit removal in east Mediterranean ecosystems. *Seeds dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D.J., Silva, R.W. & Galleti, M.) pp. 161-175. Wallingford: CABI Publishing.

Janzen, D.H. (1985) The natural history of mutualisms. *The biology of mutualism: ecology and evolution.* (ed. Boucher, D.H.) pp. 40-99. Croom Helm, London.

Johnson, R.A., Willson, M.F. & Thompson, J.N. (1985) Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology*, **66**, 819–827.

Jordaan, L.A., Johnson, S.D. & Downs, C.T. (2011) Digestion of fruit of invasive alien plants by three southern African avian frugivores. *Ibis*, **153**, 863-867.

Jordano, P. & Schupp, E.W. (2000) Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, **70***,* 591–615.

Jordano, P. (1987) Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology*, **68**, 1711-1723.

Jordano, P. (1993) Geographical ecology and variation of plant-seed disperser interactions: southern Spanish junipers and frugivorous thrushes. *Vegetatio*, **107**/**108**, 85-104.

Jordano, P. (2000) Fruits and frugivory. *Seeds: the ecology of regeneration in natural plant communities.* (ed. Fenner, M.) pp. 125-166. CABI Publishers, Wallingford, UK.

Jordano, P. (2007) Frugivores, seeds and genes: analysing the key elements of seed shadows. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Jordano, P.C. Garcia, J.A. Godoy, & Garcia-Castano, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3278-3282.

Kelly, D. & Sork, V.L. (2002) Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics,* **33**, 427-447.

Knight, R.S. & Siegfried, W.R. (1983) Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia*, **56**, 405-412.

Knight, R.S. (1986) A comparative analysis of fleshy fruit displays in alien and indigenous plants. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 171-178. Oxford University Press, Cape Town.

Knight, R.S. (1988) Aspects of plant dispersal in the south-western Cape with particular reference to the roles of birds as dispersal agents. Ph.D. Thesis, University of Cape Town, South Africa.

Krug, C.B. & Krug, R.M. (2007) Restoration of Old Fields in Renosterveld: a case study in a Mediterranean-type shrubland of South Africa. *Old fields: dynamics and restoration of abandoned farmland.* (eds. Cramer, V.A. & Hobbs, R.J.) pp. 265 - 334. Society for Ecological Restoration International. Island Press.

Kruger, J.F., Breytenbach, G.J., Macdonald, I.A.W. & Richardson, D.M. (1989) The characteristics of invaded Mediterranean-climate regions. *Biological invasions: a global perspective.* (eds. Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., RejmaHnek, M. & Williamson, M.) pp. 181-213. John Willey & Sons Ltd, Chichester.

Kueffer, C. (2006) Impacts of woody invasive species on tropical forests of the Seychelles. Ph.D. Thesis, Swiss Federal Institute of Technology Zurich, Switzerland.

Kueffer, C., Kronauer, L. & Edwards, P.J. (2009) Wider spectrum of fruit traits in invasive than native floras may increase the vulnerability of oceanic islands to plant invasions. *OIKOS*, **118**, 1327-1334.

LaFleur, N.E., Rubega, M.A. & Elphick, C.S. (2007) Invasive fruits, novel foods, and choice: an investigation of European starling and American robin frugivory. *Wilson Journal of Ornithology*, **119**, 429–438.

Laska, M.S. & Stiles, E.W. (1994) Effects of fruit crop size on intensity of fruit removal in *Viburnum prunifolium* (Caprifoliaceae). *OIKOS*, **69**, 199-202.

Latimer, A.M., Silander, J.A., Gelfand, A.E., Rebelo, A.G. & Richardson, D.M. (2004) A method for quantifying the magnitude of threat to plant biodiversity from alien plant invasions and other anthropogenic factors – a case study in the CFR, South Africa. *South African Journal of Science*, **100**, 81–86.

le Maitre, D.C. & Midgley, J.J. (1992) Plant reproductive ecology. *The ecology of fynbos*. (ed. Cowling, R.) pp. 135-174. Oxford University Press: Cape Town.

le Maitre, D.C., Versfeld, D.B. & Chapman, R.A. (2000) The impact of invading alien plants on surface water resources in South Africa. A preliminary assessment. *Water SA*, **26**, 397-407.

Levey, D.J. (1987) Sugar-tasting ability and fruit selection in tropical fruit-eating birds. *The Auk* **104**, 173-179.

Levine, J.M. & Murrell, D.J. (2003) The community-level consequences of seed dispersal patterns. *Annual Review of Ecology and Systematics*, **34**, 549 – 574.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant Invasions. *Proceeding of Royal Society London Botany*, **270**, 775–781.

Luck, G.W. & Daily, G.C. (2003) Tropical countryside bird assemblages: richness, composition, foraging differ by landscape context. *Ecological Applications*, **13**, 235-247.

Macdonald, I.A.W. & Richardson, D.M. (1986) Alien species in the terrestrial ecosystems of the fynbos biome. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 77-91. Oxford University Press, Cape Town.

Malcarney, H.L., Martínez del Rio, C. & Apanius, V. (1994) Sucrose intolerance in birds: simple nonlethal diagnostic methods and consequences for assimilation of complex carbohydrates. *The Auk,* **111**,170-177.

Manders, P.T. & Richardson, D.M. (1992) Colonization of Cape fynbos communities by forest species. *Forest Ecology and Management*, **48,** 277-293.

Marco, A., Lavergne, S., Dutoit, T. & Bertaudiere-Montes, V. (2010) From the backyard to the backcountry: how ecological and biological traits explain the escape of garden plants into Mediterranean old fields. *Biological Invasions,* **12,** 761-779.

Martinez del Rio, C. & Restrepo, C. (1993) Ecological and behavioral consequences of digestion in frugivorous animals. *Plant Ecology*, **107-108**, 205-216.

McConkey, K.R., Meehan M.H. & Drake, D.R. (2004) Seed dispersal Pacific Pigeon *Ducula pacifica* in Tonga, western Polynesia. *Emus*, **104,** 369-376.

McKey, D. (1975) The ecology of coevolved seed dispersal systems. *Coevolution of animals and plants.* (eds. Gilbert, L.E. & Raven,P.H.) pp. 159-191. University of Texas Press, Austin, Texas, USA.

McMahon, L. & Fraser, M. (1988) *A fynbos year.* David Philip, Cape Town

Milton, S.J., Wilson, J.R.U., Richardson, D.M., Seymour, C.L., Dean, W.R.J., Iponga, D.M. & Proches, S. (2007) Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. *Journal of Ecology*, **95**, 648–661.

Mooney H.A. & Cleland, E.E. (2001) The evolutionary impact of invasive species. National Academy of Sciences colloquium. *Proceeding of National Academy of Science USA*, **98**, 5446–5451.

Muller-Landau, H.C. & Hardesty, B.D. (2005) Seed dispersal of woody plants in tropical forests: Concepts, Examples, and Future Directions. *Biotic interactions in the tropics: their role in the maintenance of species diversity*. (eds. Burslem, D., Pinard, M. & Hartley, S.) pp. 267–309. Cambridge University Press, Cambridge, UK.

Muller-Landau, H.C. (2007) Predicting the long-term effects of hunting on plant species composition and diversity in Tropical Forests. *Biotropica*, **39**, 372-384.

Munoz, J., Felicísimo, A.M., Cabezas, F., Burgaz, A.R. & Martínez, I. (2004) Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science*, **304**, 1144–1147.

Murphy, S.R., Reid, N., Yan, Z. & Venables, W.N. (1993) Differential passage time of mistletoe fruits through the gut of honeyeaters and flowerpeckers: effects on seedling establishment. *Oecologia*, **93**, 171-176.

Murray, B. & Phillips, M. (2010) Investment in seed dispersal structures is linked to invasiveness in exotic plant species of south-eastern Australia. *Biological Invasions*, **12**, 2265-2275.

Myers, J.H., Simberloff, D, Kuris, A.M. & Carey, J.R. (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution*, **15**, 8316-320.

Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278-285.

Nathan, R. (2001) The challenges of studying dispersal. *Trends in Ecology & Evolution*, **16**, 481-483.

Nathan, R. (2006) Long-distance dispersal of plants. *Science,* **313**, 786–788.

Nathan, R. (2007) Total dispersal kernels and the evaluation of diversity and similarity in complex dispersal systems. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. (2008) Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution*, **23**, 638-647.

Nel, J.L., Richardson , D.M., Rouget, M., Mgidi, T.N., Mdzeke , N., le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L. & Neser, S. (2004) A proposed classification of invasive alien plant species in South Africa: towards prioritizing species and areas for management action. *South African Journal of Science*, **100**, 53-64.

Nogales, M., Nieves, C., Illera, J.C., Padilla, D.P. & Traveset, A. (2005) Effect of native and alien vertebrate frugivores on seed viability and germination patterns of *Rubia fruticosa* (Rubiaceae) in the eastern Canary Islands. *Functional Ecology*, **19**, 429–43

Oatley, T.B. (1984) Exploitation of a new niche by the Rameron Pigeon *Columba arquatrix* in Natal. *Proceedings of the Fifth Pan-African Ornithological Congress* (ed. Ledger, J.A.*)* pp. 323–330, Southern African Ornithological Society.

Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285-297.

Pratt, K.T. & Stiles, W.E. (1983) How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. *The American Naturalist*, **122**, 797-805.

Pysek, P. & Richardson, D.M. (2008) Invasive Plants. Ecological Engineering Vol **3** of *Encyclopedia of Ecology* (eds. Jorgensen, S.E. & Fath, F.D.) pp. 2011-2020. Oxford: Elsevier.

Quix, J.C. (2007) The role of alien plants in the composition of fruit-eating bird assemblages in Brazilian urban ecosystems. *Orsis*, **22**, 87-104.

Reichard, S.H., Chalker-Scott, L. & Buchaman, S. (2001) Interaction among non-native plants and birds. *Avian ecology and conservation in an urbanising world*. (eds. Marcluff, J.M., Bowman, R. & Donnelly, R.) pp. 179- 223. Kluwer Academic Publishers.

Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 165*5–1660.*

Rejmanek, M. (1996) Species richness and resistance to invasions. Biodiversity and ecosystem processes in tropical forests (ed. Orians, G.H., Dirzo R. & Cushman, J.H.) pp. 153–172, Springer, Berlin.

Rejmanek, M. (2000) Invasive plants: approaches and predictions. *Austral Ecology*, **25**, 497-506.

Rejmanek, M., Richardson, D.M. & Pysek, P. (2005) Plant invasions and invasibility of plant communities. (ed. van der Maarel, E.) pp. 332–355. *Vegetation ecology*, Oxford: Blackwell.

Richardson, D.M. (1998) Forestry trees as invasive aliens. *Conservation Biology* **12**, 18-26.

Richardson, D.M. & Pysek, P. (2006) *Plant* invasions: merging the concepts of species invasiveness and community invisibility. *Progress in Physical Geography*, **30**, 409–431.

Richardson, D.M. & Rejmánek, M. (2011) Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions*, **17**, 788-809.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmanek, M. (2000b) Plant invasions - the role of mutualism. *Biology Reviews*, **75**, 65-93.

Richardson, D.M., Cowling, R.M. & Lamont, B.B. (1996) Non-linearities, synergisms and plant extinctions in South African fynbos and Australian kwongan. *Biodiversity and Conservation*, **5**, 1035-1046.

Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P., Pyšek, P. & Hobbs, R.J. (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Diversity and Distributions*, **13**, 126-139.

Richardson, D.M., Macdonald, I.A.W. & Forsyth, G.G. (1989) Reductions in plant species richness under stands of alien trees and shrubs in the fynbos biome. *South African Forestry Journal*, **149**, 1-7.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H. & Henderson, L. (1997) Alien plant invasions. (eds. Cowling, R.M., Richardson, D.M & Pierce S.M.) pp. 534-570, *Vegetation of Southern Africa.* Cambridge, UK: Cambridge University Press.

Richardson, D.M., Macdonald, I.A.W., Holmes, P.M. & Cowling, R.M. (1992) Plant and animal invasions. *The ecology of fynbos: nutrients, fire and diversity* (ed. Cowling, R.M.) pp. 271–308. Oxford University Press, Cape Town.

Richardson, D.M., Pysek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000a) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions,* **6**, 93-107.

Robertson, A.W., Trass, A. Ladley, J.J. & Kelly, D. (2006) Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Functional Ecology*, **20**, 58–66.

Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation,* **112**, 63-85.

Roura-Pascual, N., Richardson, D.M., Krug, R.M., Brown, A., Chapman, A.R., Forsyth G.G., le Maitre, D.C., Robertson, M.P., Stafford, L., Van Wilgen, B.W., Wannenburgh, A. & Wessels, N. (2009) Ecology and management of alien plant invasions in South African fynbos: Accommodating key complexities in objective decision making. *Biological Conservation*, **142**, 1595–1604.

Russo, S.E. & Augspurger, C.K. (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters*, **7**, 1058–1067.

Russo, S.E., Portnoy, S. & Augspurger, C.K. (2006) Incorporating animal behaviour into seed dispersal models: implications for seed shadows. *Ecology*, **87**, 3160-3174.

Sakai, A.K., Weller, S.G., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A, Baughman, S, Cabin, R.J, Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M. & Thompson, J.N. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–32.

Sallabanks, R. (1993) Fruiting plant attractiveness to avian seed dispersers: native vs. invasive Crataegus in western Oregon. *Madrono*, **40**, 108–16.

Sallabanks, R. & Courtney, S.P. (1993) On fruit-frugivore relationships: variety is the spice of life. *OIKOS*, **68**, 567-570.

Samuels, I.A. & Levey, D.J. (2005) Effects of gut passage on seed germination: do experiments answer the questions they ask? *Functional Ecology*, **19,** 365–368.

Saracco, F.J., Collazo, J.A., Groom, M.J. & Carlo, T.A. (2005) Crop size and fruit neighbourhood effects on bird visitations to fruiting *Schefflera mototoni* trees in Puerto Rico. *Biotropica*, **37**, 81-87.

Saracco, J.F., Collazo, J.M. & Groom, M.J. (2004) How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia*, **139**, 235-245.

Sargent, S. (1990) Neighborhood effects on fruit removal by birds: A field experiment with *Viburnum Dentatum* (Caprifoliaceae). *Ecology* **71**, 1289-1298.

Schaefer, H.M., Schmidt, V. & Bairlein, F. (2003) Discrimination abilities for nutrients: which difference matters for choosy birds and why? *Animal Behaviour*, **65**, 531–541.

Schupp, E.W. (1993) Quantity, quality and effectiveness of seed dispersal by animals. *Vegetatio*, **107**/**108**, 12-29.

Schupp, E.W., Jordano, P. & Gomez, J.M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, **188**, 333-353.

Schupp, E.W., Milleron, T. & Russo, S.E. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. *Seed dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D.J., Silva W.R. & Galetti, M.) pp. 19-33. Wallingford, UK: CAB International.

Schurr, F.M., Midgley, G.F., Rebelo, A.G., Reeves, G., Poschlod, P. & Higgins, S.I. (2007) Colonization and persistence ability explain the extent to which plant species fill their potential range. *Global Ecology and Biogeography*, **16**, 449–459.

Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar A. & Nathan, N. (2009) Long-distance seed dispersal. *Annual Plant Reviews*, **38,** 204–237.

Simberloff, D. & Holle, V.B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Snow, B. & Snow, D. (1988) *Birds and berries.* T. & A.D. Poyser, Calton, UK.

Snow, D.W. (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica*, **13**, 1-14.

Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, **10**, 718–728.

Steadman, D.W. (1997) The historic biogeography and community ecology of Polynesian pigeons and doves. *Journal of Biogeography*, **24**, 737-753.

Stiles, E. (1980) Patterns of fruit presentation and seed dispersal in bird-mediated woody plants in the eastern deciduous forest. *The American Naturalist*, **16**, 670-688.

Stiles, E.W. (2000) Animals as seed dispersers. *Seeds: the ecology of regeneration in plant communities.* (ed. Fenner, M.) pp. 111-124. CABI Publishing: Wallingford.

Stiles, F.G. & Roselli, L. (1993) Consumption of fruits of the Melastomataceae by birds; how diffuse is coevolution? *Vegetatio*, **107/108**, 57-73.

Sun, B., Tan, J., Wan, Z., Gu, F. & Zhu, M. (2006) Allelopathic effects of extracts from *Solidago canadensis* L. against seed germination and seedling growth of some plants. *Journal of Environmental Sciences*, **18**, 304-318.

Sun, B.Y., Tan, J.Z., Wan, Z.G., Gu, F.G. & Zhu, M.D. (2006) Allelopathic effects of extracts from *Solidago canadensis* L. against seed germination and seedling growth of some plants. *Journal of Environmental Sciences*, **18**, 304-309.

Sun, C., Ives, A.R., Kraeuter, H.J. & Moermond, T.C. (1997) Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia*, **112**, 94-103.

Telleria, J.L., Ramirez, A. & Perez-Tris, J. (2005) Conservation of seed-dispersing migrant birds in Mediterranean habitats: Shedding light on patterns to preserve processes. *Biological Conservation*, **124**, 493–502.

Tiffney, B.H. (2004) Vertebrate dispersal of seed plants through time. *Annual Review of Ecology, Evolution and Systematics,* **35**, 1-29.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173–181.

Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecology & Evolution*, **21**, 208–216.

Traveset, A. & Richardson, D.M. (2011) Mutualisms: key drivers if invasion …key casualties of invasions. *Fifty years of invasion ecology. The legacy of Charles Elton* (ed. Richardson, D.M.) pp. 143-157, Wiley-Blackwell, Oxford.

Traveset, A., Riera, N. & Mas. R.E. (2001). Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology,* **15**, 669-675.

Traveset, A., Rodriguez-Perez, J. & Pias, B. (2008) Seed trait changes in dispersers' guts and consequences for germination and seedling growth. *Ecology*, **89**, 95-106.

Tsoar, A., Shohami, D. & Nathan, R. (2011) A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats. *Fifty years of invasion ecology. The legacy of Charles Elton* (ed. Richardson, D.M.) pp. 103-119, Wiley-Blackwell, Oxford.

Tucker, K.C. & Richardson, D.M. (1995) An expert system for screening potentially invasive alien plants in South African fynbos. *Journal of Environmental Management*, **44**, 309-338.

van der Pijil, L. (1972) *Principles of dispersal in higher plants*. Springer, New York.

van Wilgen, B.W., de Wit, M.P., Anderson, H.J., le Maitre, D.C., Kotze, I.M., Ndala, S., Brown B. & Rapholo, M.B. (2004) Costs and benefits of biological control of invasive alien plants: case studies from South Africa South African. *Journal of Science*, **100**, 113-122.

van Wilgen, B.W., le Maitre, D.C. & Cowling, R.M. (1998) Ecosystem services, efficiency, sustainability and equity: South Africa's Working for Water programme. *Trends in Ecology and Evolution*, **13**, 378.

van Wilgen, B.W., Richardson, D.M., le Maitre, D.C., Marais, C., & Magadlela, D. (2001) The economic consequences of alien plant invasions: examples of impacts and approaches to sustainable management in South Africa. *Environment, Development and Sustainability*, **3**, 145-168.

Vitousek, P.M., D'Antonio, C., Loope, L.L., Rejmanek, M. & Westbrook, R. (1997) Introduced species: a significant component of human-caused global. *New Zealand Journal of Ecology,* **21***,* 1-16.

Vittoz, P. & Engler, R. (2007) Seed dispersal distances: a typology based on dispersal modes and plant traits. *Botanica Helvetica*, **117**, 109-124.

Walther, G-R., Roques, A., Hulme, P.E., Sykes, M.T., Pysek, P., Kuhn, I., Zobel, M., Bacher, S., Botta Dukat, Z., Bugmann, H., Czucz, B., Dauber, J., Hickler, T., Jarosik , V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vila, M., Vohland, K. & Settele, J. (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology Evolution*, **24**, 686–693.

Wenny, D.G. (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research*, **3**, 51–74.

Wheelwright, N. T. (1983) Fruits and the ecology of resplendent quetzals. *The Auk*, **100**, 286-301.

Wheelwright, N.T. (1991) How long do fruit-eating birds stay in the plants where they feed? *Biotropica*, **23**, 29-40.

Whelan, C.J., Wenny, D.G. & Marquis, R.J. (2008) Ecosystem services provided by birds. *Annals of the New York Academy of Sciences*, **1134**, 25–60.

Whittaker, R.J. & Jones, S.H. (1994) The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography*, **21**, 245-258.

Williams, P. (2006) The role of blackbirds (*Turdus merula*) in weed invasion in New Zealand. *New Zealand Journal of Ecology*, **30**, 285-291.

Williams, P.A. & Karl, B.J. (1996) Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. *New Zealand Journal of Ecology*, **20**, 127-145.

Williams, P.A. and Karl, B.J. (2002) Birds and small mammals in kanuka (Kunzea ericoides) and gorse (*Ulex europaeus*) scrub and the resulting seed rain and seedling dynamics. *New Zealand Journal of Ecology,* **26**, 31–41.

Willson, M. & Traveset, A. (2000) The ecology of seed dispersal. *The ecology of regeneration in plant communities*. (ed. Fenner, M.) pp. 85-110. CAB International, Wallingford, UK.

Willson, M.F., Irvine, A. K. & Walsh, G.N. (1989) Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica,* **21**, 133-147.

Witmer, M.C. (2001) Nutritional interactions and fruit removal: *Cedar Waxwing* consumption of *Viburnum opulus* fruits in spring. *Ecology*, **82**, 3120-3130.

Zhou, Z. & Zhang, F. (2002) A long-tailed, seed-eating bird from the early Cretaceous of China. *Nature*, **418**, 405-409.

Chapter 2
Study area, sites and species

2.1. Study area

The study area was the Cape Floristic Region (CFR), recognised as one of the most biologically diverse regions on earth (Goldblatt & Manning 2002). Considered as one of six global Floral Kingdoms, this relatively small region of approximately 90 000 km^2 situated at the southwestern tip of Africa is home to about 9 000 vascular plant species, 69 percent of which are endemic (Cowling et al. 1996; Holmes 2001). The CFR covers the Mediterranean climate region of South Africa's Western Cape Province and extends eastward into the Eastern Cape Province, a transitional zone between the winter-rainfall region to the west and the summer-rainfall region to the east (Cowling et al. 1996).

The predominant vegetation in the Cape Floristic Region is a shrubland known as fynbos, which comes from an Afrikaans word meaning "fine bush". Fynbos primarily comprises four growth forms namely proteoid, ericoid, restoid and geophyte (Cowling et al. 1996; Rebelo 1996). Fynbos occurs predominantly on well-leached, infertile soils (Rebelo 1996; Cowling & Holmes 1992), but in areas of high rainfall (600 to 800 mm per annum), granites and even shales become sufficiently leached to support Asteraceous fynbos (Cowling & Richardson 1995). Below 200 mm fynbos is replaced by arid Succulent Karoo vegetation (Rebelo 1996). Fire frequencies range between 6 and 45 years and are necessary to sustain plant species diversity (Moll & Bossi 1983; Moll et al. 1984; Cowling & Richardson 1995). In the absence of fire, fynbos becomes senescent and forest and thicket elements begin invading. Moll & Bossi (1983) described four distinctive fynbos vegetation types, namely renosterveld, western strandveld, mesic mountain fynbos and sandplain fynbos, though more recently fynbos has been reclassified into more detailed vegetation units based on their floristic composition and underlying geology (Mucina & Rutherford 2006).

Generally, the whole CFR is threatened by human activities that have reduced renosterveld and sandplain fynbos to 48% (Rouget et al. 2003). Even in less accessible mountainous areas, farming based on indigenous crops such as rooibos tea (*Aspalathus linearis*), honeybush tea (*Cyclopia* spp.) and cut flowers (mainly Proteaceae) is rapidly encroaching on natural habitats. Nonetheless, the greatest threat to the Cape Flora overall is undoubtedly its invasion by alien plants (Richardson et al. 1992; Rouget et al. 2003), these originating mainly from other Mediterranean-type climate regions such as southern Australia, the Mediterranean Basin and California (Richardson & Rejmanek 2011).

Historically, bird diversity in the CFR is low because of the relatively few forested habitats and limited sources of food, such as fleshy fruits and large insects (Cody 1983; McMahon & Fraser 1988). There exists an east-west decline in avian species richness corresponding with a westerly decline in forested habitats (Cody 1983) and scarcity of fruit

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resources, especially in fynbos (McMahon & Fraser 1988) where frequent fires destroy the seed of fleshy-fruited species thereby retarding the regeneration (le Maitre & Midgley 1992). Of the approximately 600 terrestrial bird species in southern Africa, only 14% are frugivorous (Snow 1981; Knight 1988). These include introduced generalist species such as the common starling *Sturnus vulgaris* and house sparrow *Passer domesticus,* as well as the Acacia pied barbet *Tricholaema leucomelas* that exhibited rapid expansions in their distribution ranges (Macdonald 1986; Macdonald & Richardson 1986). These increases in numbers of generalist birds and expansions in their distribution ranges have probably altered natural patterns of frugivory and contributed to the spread of fleshy-fruited invasive alien shrubs and trees. Currently about 244 native bird species (excluding seabirds) have been recorded in the CFR of which about 63 bird species occur specifically in habitats transformed by invasive alien trees and large shrubs, their recorded presence coinciding with the alien plant introductions (Richardson et al. 1992; Cowling & Richardson 1995). Strictly the only endemic bird species occurring in fynbos forested habitats is the forest canary *Serinus scotops* whereas in lowland fynbos and renosterveld shrublands six endemic birds are found, namely the victorin's warbler *Bradipterus victorini*, Cape rock-jumper *Chaetops frenatus*, orange-breasted sunbird *Nectarina violacea*, Cape sugarbird *Promerops cafer* and Cape siskin *Serinus totta* (Cowling & Richardson 1995). Important avian frugivores in the fynbos biome are indigenous bird species namely, the Cape robin-chat *Cossypha caffra,* southern boubou *Laniarius ferrugineus,* African olive-pigeon *Columba arquatrix,* red-winged starling *Onichognathus morio,* mousebirds *Colius* species, sombre greenbul *Andropadus importunus,* olive thrush *Turdus olivaceus,* Cape bulbul *Pycnonotus capensis,* fiscal flycatcher *Sigelus silens* and Cape white-eye *Zosterop capensis* (Glyphis et al. 1981; Knight 1988; Manders & Richardson 1992; Cowling et al. 1997).

2.2. Study sites

There were seven study sites, four primary and three secondary sites. The four primary sites comprised Hout Bay located on Peninsula Granite Fynbos, Paarl located on Swartland Shale Renosterveld near, Hermanus located on Overberg Sandstone Fynbos and Swellendam located on Breede Shale Renosterveld near (Figure 2.1). The fynbos and renosterveld vegetation classifications according to Mucina and Rutherford (2006). These sites comprised mixed populations of indigenous and established alien shrubs, namely the indigenous *Chrysanthemoides monilifera* (L) Norlindh. (Asteraceae), *Olea europaea* subsp. *africana* Mill (Oleaceae), hereafter referred to as *O. africana,* and the established aliens *Lantana camara* L (Verbenaceae) and *Solanum mauritianum* Scopoli (Solanaceae). The co-occurring established alien and indigenous shrubs at these four primary sites possessing overlapping spring to autumn fruiting periods (Van Wyk & Van Wyk 1997), though the length of their fruiting periods differ (Knight 1988), similar fruit architectures (black single-seeded drupes, except *S. mauritianum* which produces yellow berries) with regular consumption of their fruits by local frugivorous birds (Richardson & Fraser 1995). The three secondary sites comprised

Simonstown located on Peninsula Sandstone Fynbos and Franshoek and Jonkershoek located on Boland Granite Fynbos (Figure 2.2). These three sites comprised mixed populations of indigenous species and the aliens *Myoporum tenuifolium* Auct (Myoporaceae) and *Pittosporum undulatum* Vent (Pittosporaceae) designated as emergent aliens due to their more recent introductions and less expansive distributions in the Cape Floristic Region. These emergent aliens possess a high invasive potential based on their propagule-pool size and history of weediness elsewhere in the world (Nel et al. 2004).

2.3 Description of study species

2.3.1. Indigenous plants

Chrysanthemoides monilifera is commonly referred to as Bietou or boneseed (Figure 2.2A). It produces between autumn and spring fleshy, ovoid to round, purple-black fruits approximately 6 mm in diameter, each containing a single egg-shaped seed 5 – 7 mm long that is dark brown to black when dry. This species' fruits are attractive to birds, rabbits, and other vertebrates, and even some insects such as ants, and because seeds are tough and difficult to digest they are often dispersed in animal droppings (Parsons 1973; Emert 2001). Seed production is prolific, with up to 50 000 seeds produced by a mature plant per annum, about 60% of which are viable (CRC Weed Management 2003), though high flower mortality during the dry season does substantially reduce total seed production (Knight 1988; Scott 1996). Seeds germinate with difficulty and often require scarification, as occurs with passage through bird gut, to germinate effectively. The high fruit and coupled seed production and effective seed dispersal by birds and other vertebrates have rendered *C. monilifera* as an invasive alien in Australia (Scott 1996; Gosper 2004a).

Olea europaea subsp. *africana* is commonly referred to as the African/wild olive (Figure 2.2B). It forms one of 33 species and nine subspecies included in the genus *Olea* which has a wide geographic range in diverse habitats (Coates Palgrave 1983; Cuneo & Leishman 2006). This species occurs in several environments including Hawaii, Australia, Norfolk Island and eastern Africa (Cuneo & Leishman 2006). Flowering occurs between October and December followed by prolonged and variable fruiting period during which single-seed-bearing fleshy, ovoid fruits, 4-7 mm diameter are produced that turn brown to black at maturity (Cuneo & Leishman 2006). Fruit production follows a supra-annual cycle of 2 or 3 years, depending on climatic conditions (Rey & Alcantara 2000). Trees at the early mature stage are capable of producing more than 25 000 fruits and fruit maturation within stands is asynchronous with ripe fruits produced on individual trees from June – September (Cuneo & Leishman 2006), but extends into summer autumn depending on climatic conditions. Fruits are foraged by important prominent avian and vertebrate dispersers (Knight 1986; Richardson & Fraser 1995) with seeds remaining dormant for around 20 months during which time they become susceptible to predation by rodents (Rey & Alcantara 2000). Although Cuneo and Leishman (2006) pointed out

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that *O. africana* is a native of the eastern African countries including South Africa, the origin of *O. africana* is not well known since there is genetic overlap between African species and South European Mediterranean cultivated types (Besnard et al. 2002). It is thought that African/wild olives might have their ancestry in the cultivated olives of southern Europe Mediterranean areas as both possess similar chromosomal numbers (Angiolillo et al. 1999; Lumaret et al. 2004). Also, there is evidence of hybridisation between commercial and wild olive species which may have provided wild olives with typical alien characteristics (Lumaret et al. 2004).

2.3.2. Established alien plants

Lantana camara is commonly referred to as lantana (Figure 2.2C). It was introduced into South Africa as an ornamental and hedging plant from central tropical America in 1858 (Cillier & Neser 1991; Bromilow 2010). It is an aggregate species or species complex with several natural variants across its presumed native range in the tropical Americas. In addition, some hundreds of horticultural colour and habit varieties have been developed around the world, with over 650 varietal names coined (Howard, 1969; Smith & Smith 1982). Most variants produce small amounts of viable fruit and all are probably capable of contributing viable pollen to other variants, both factors increasing the likelihood of further feral genotypes. *Lantana* is prominent in the western Cape and Kwazulu Natal and flowers all year round under adequate moisture and light (Henderson 2001; Sharma et al. 2005; Bromilow 2010), but in cooler and drier regions flowering is restricted to warm wet times due to this species vulnerability to frost and drought. Fruit-set rates in weedy forms range from 37% to 85% (Swarbrick et al. 1995). Mature plants produce up to 12,000 single seed bearing fruits annually and up to several thousand per m^2 (Day et al. 2003). Fruits are greenish to blue-black in colour, approximately 5 mm in diameter. In South Africa, *L. camara* produces fruits throughout the year round, setting an average of 856 seeds/plant/year (see Jordaan et al. 2011). Seed dispersal is primarily by fruit-eating birds and to a lesser degree by other frugivorous vertebrates (Day et al. 2003; Sharma et al. 2005). Seed longevity in the soil is not well documented, but 50% seed viability after 6 months dry shelf-storage has been recorded and seeds are thought to remain viable for several years under natural conditions (Weiss et al. 2008). Germination rates are reported as being increased by removal of fruit pulp, as occurs with passage through bird gut (Day et al. 2003), and by warm temperatures, light, and high soil moisture. However, Vivian-Smith et al. (2006) reported that responses to fruit and seed damage are biotype-dependent and in some cases, seedling emergence improves with seed damage. Germination rates even under favourable conditions are sometimes reported as low *i.e.* <45% or less (Day et al. 2003). There is a strong correlation between seedling establishment and soil disturbance (Stock & Wild 2002; Stock 2004; Marco et al. 2010); with critical factors being disturbance-mediated increases in light and available soil nutrients (Gentle & Duggin 1998) and the competitive advantage of lantana seedlings relative to many native species (Stock 2004). Detailed investigations on dispersal of *L. camara* are

required since it is reported to decrease diversity of ground dwelling invertebrates, suppresses regeneration via allelopathy and poisons livestock in different parts of South Africa (van Wilgen et al. 2001). Conceivably, further spread of lantana stands may increase the harm on native biodiversity.

Solanum mauritianum is commonly referred to as bugweed, wild tobacco, kerosene plant, woolly nightshade and flannel weed in English, groot bitterappel or luisboom in Afrikaans and igayintombi, umbanga banga or isigwayana in Zulu (Figure 2.2D). It was introduced into South Africa from South America in 1862. This species is presently distributed along the eastern and western coastal regions of South Africa including inland provinces of Limpopo and Mpumalanga (Bromilow 2010). It is one of the five most invasive alien plant species in the summer rainfall region of South Africa (Henderson 2001; 2007) infesting disturbed forest, savanna grassland, fynbos and riparian ecosystems (Dean et al. 1986; Olckers 1999; Henderson 2001; Richardson et al. 2007; Witkowski & Garner 2008). *Solanum mauritianum* produces purple flowers and fruits during spring and summer approximately 10 mm in diameter containing numerous small seeds that readily germinate under suitable conditions (Campbell & van Staden 1994). *Solanum mauritianum* produces clusters of yellow fruit, about 10 mm in diameter (Henderson 2001), each containing up to 193 seeds (Witkowski & Garner 2008). Smaller plants (1.5–1.8 m) produce 40–70 berries per inflorescence while adult plants (3.3 m) can produce 100,000–200,000 seeds (Witkowski & Garner 2008). The rapid spread and persistence of this species is associated with its high reproductive output (Witkowski & Garner 2008) and dispersal of its seed by bird foraging in large numbers on its nutritious berry fruits (Oatley 1984; Geldenhuys et al. 1986; Olckers 1999; Jordaan et al. 2011). Seeds are 80% viable for a period of two years after which they lose viability (Witkowski & Garner 2008). Invasive *Solanum mauritianum* is reported to decrease diversity of ground dwelling invertebrates, changes in feeding ecology of native birds and out-competes native trees for seed dispersal agents in different parts of southern Africa including the Cape Floristic Region (van Wilgen et al. 2001).

2.3.3. Emergent alien plants

Myoporum tenuifolium is commonly referred to as Naio, Bastard or False Sandlewood (Figure 2.2E). It is indigenous to Hawaii and occurs on Mangaia in the Cook Islands in a variety of habitats including in shoreline vegetation, moist, and wet forests. *Myoporum tenuifolium* was introduced into South Africa's western and Eastern Cape Provinces for shade, windbreak and ornamental purposes (Henderson 2001; Bromilow 2010). It flowers all year round, the 0.3 cm bell-shaped flowers are highly fragrant arranged close to the stems and range in colour from white to pink (Bornhorst 1996; Koob 1998). *Myoporum tenuifolium* produces round, fleshy fruits about 0.3 to 0.6 cm in diameter containing single seed with the fruits when ripe range in colour from greenish white to pinkish or purplish. Fruits are consumed by birds that disperse seeds to different places in southwestern Cape (Knight 1986; 1988). Seed germination times range from

6 to 18 months (Mew 1987) with germination rates varying from 10 to 70% depending on the quality of the seed with unscarified seeds displaying much lower germination rates ranging from 5 to 30% (Obata 1967; Stratton et al. 1998).

Pittosporum undulatum is commonly called Australian cheesewood, mock orange, native daphne, orange or sweet pittosporum, Victorian laurel or Victorian box and wild coffee (Figure 2.2F). It is native to Southeastern Australia, but has now spread to a number of islands in the Pacific and Caribbean, as well as islands in the Atlantic and to South Africa where it was introduced for shade, windbreak and ornamental purposes (Henderson 2001; Bromilow 2010). *Pittosporum undulatum* produces few almost white fragrant flowers borne on the youngest branches in terminal clusters about 2-3 cm long. Due to its attractive flowers, *P. undulatum* is often used as an ornamental tree (Binggeli et al. 1998). Flowering starts at around 5 years of age and fruits take about 6 months to mature. Fruit capsules are globe-shaped, compressed, usually 16 mm long, leathery containing 20-40 sticky orange seeds (Binggeli et al. 1998). A single tree can produce more than 37,500 seeds (Goodland & Healey 1997) which are angular, 3 mm long and 1 mm thick (Pacific Islands Ecosystems at Risk 2003). Seeds are bird-dispersed, with the blackbirds *Turdus merula* and pied currawongs *Strepera graculina* being important vectors in its native Australia (Mullet 2000). Germination of seeds takes place in late autumn to spring with seedling densities reaching 5000 m² in areas with high light intensity (Binggeli et al. 1998). Since this species is an extra-limital invader in Australian forests (Gleadow et al. 1992; Mullet 2000), it has a potential to become a major problem in South Africa where it is currently classified under emerging weeds (Nel et al. 2004). Invasive potential of *P. undulatum* is enhanced by possession of bird-dispersed seeds in South Africa where it invades the tall scrub and riparian forests (Richardson & Brink 1985; Rejmanek & Richardson 1996). This is supported by the fact that the screening protocols suggest *P. undulatum* has high invasion potential in many areas such as Hawaii and Pacific Islands (Daehler et al. 2004).
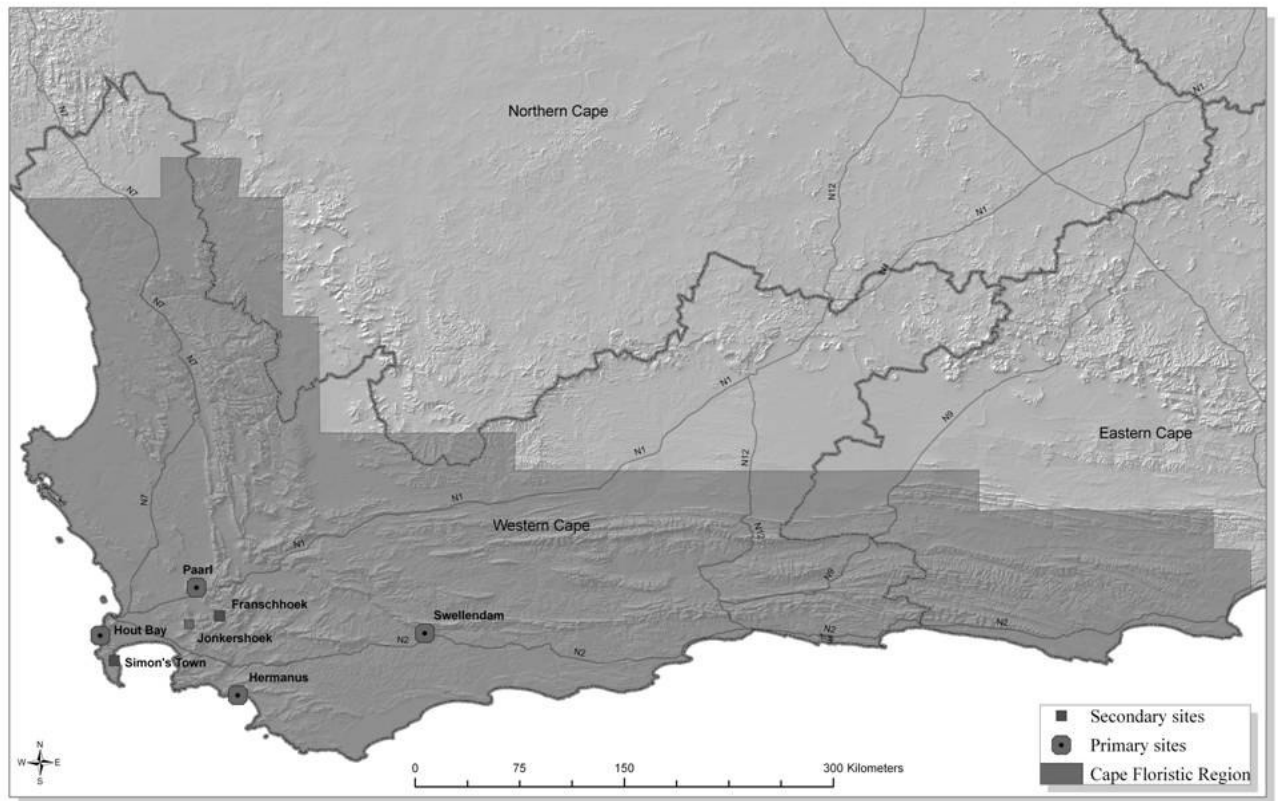
Figure 2.1. Location of four primary study sites (Hout Bay, Paarl, Hermanus & Swellendam) and three secondary study sites (Simonstown, Jonkershoek & Franschhoek) in the Cape Floristic Region
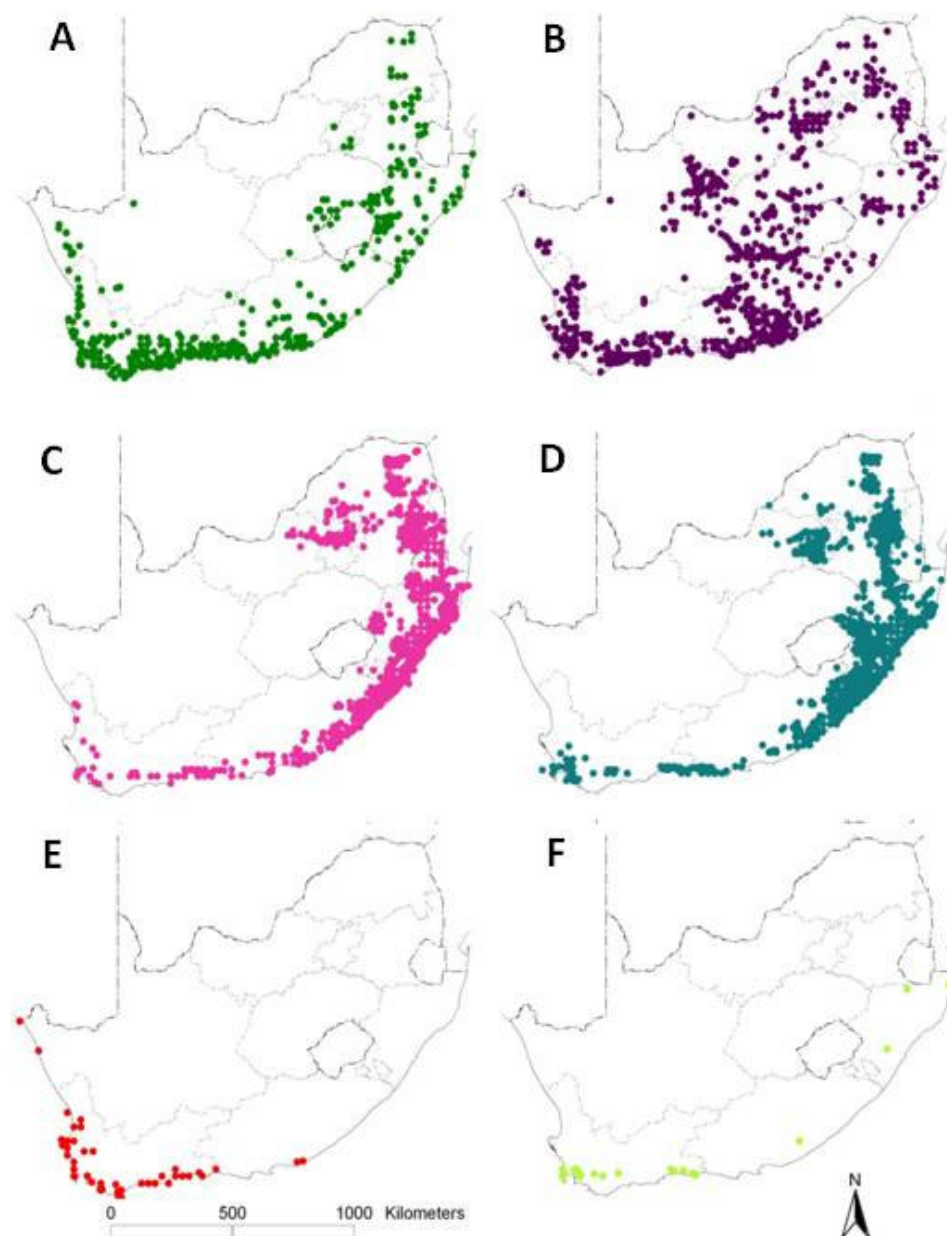
Figure 2.2. Geographical distribution of study species in South Africa A. *Chysanthemoides monilifera* subsp*. monilifera,* B. *Olea europaea* subsp. *africana,* C. *Lantana camara,* D. *Solanum mauritianum,* E. *Myoporum tenuifolium* and F. *Pittosporum undulatum.* Records obtained from PRECIS (Germishuizen et. al. 2003), Acock and National vegetation databases (Mucina et al. 2000).

2.3.4. Frugivorous birds

The multiple diffuse interactions reported between individual bird species and fruiting plant species complicates investigations of individual bird species' potential contribution to plant species fitness (Nathan & Muller-Landau 2000; Muller-Landau & Hardesty 2005; Carlo et al. 2007; Dennis & Westcott 2007; Nathan 2007). Therefore, Dennis & Westcott (2006) proposed

classifying vertebrate dispersers into functional groups in order to obtain estimates that are closer to the total dispersal kernel rather than to fractional contributions by individual species. The fruit foraging birds in the Cape Floristic Region, like those foraging figs in South-eastern Asia (Lambert & Marshall 1991), do display diverse movement patterns influenced by irregular shrub fruiting phonologies, distribution of resources and nature of the habitat (Knight 1988; Hockey et al. 2005). A total of 224 bird species have been reported for the CFR (Richardson et al. 1992) of which a subset of 37 bird species were recorded visiting habitats infested by alien trees and large shrubs in this study (Figure 2.3). These species were classified into several different functional groups based on the proportions of fruit in their diet and body mass (Jordano 2000; Hockey et al. 2005; Dennis & Westcott 2006; Schurr et al. 2009). These two attributes have direct implications on the effectiveness (e.g. quantity of seeds removed and dispersal distances) of seed dispersal by birds (Jordano 2000; Schupp 1993). Two frugivorous groups were identified, namely heavily frugivorous birds with fruits their main source of sustenance according to diet scores presented in Hockey et al. (2005) and moderately frugivorous birds with fruits their secondary or occasional source of sustenance. A third non-frugivorous group was also included whose diet comprised commodities (insects and floral nectar) associated with fleshy fruits of indigenous and alien plants (Hockey et al. 2005) and consequently indirectly with fruit quality and subsequent seed dispersal. It must be noted that the frugivore groups partly apply in the context of this study only because the omnivorous common starling *Sturnus vulgaris* and the granivorous house sparrow *Passer domesticus* (Figure 2.3) were classified as heavily frugivorous due to similar fruit diet proportions with obligate frugivorous bird species (Hockey et al. 2005). Within each frugivorous group, foraging bird species were sub-divided into four functional body mass sub-groups defined by Dennis and Westcott (2005, 2007), namely large birds (> 150 g), medium size birds (50-150 g), small birds (30-50 g) and tiny birds (< 30 g).

Frugivore class	Body mass class	Common name/species
Heavily	Large >150 g	African Olive-pigeon *Columba arquatrix*
	Medium 50- 150 g	Red-winged starling *Onycognathus morio* Speckled mousebird *Colius striatus* Red-faced mousebird *Urocolius indicus* Common starling *Sturnus vulgaris* Olive thrush *Turdus olivaceus*
	Small 30-50 g	Sombre greenbul *Andropadus importanus* Cape bulbul *Pycnonotus capensis*
	Tiny <30 g	Cape Robin-chat *Cossypha caffra* House Sparrow *Passer domesticus* Cape white-eye *Zosterops capensis*
Moderately	Large >150 g	Speckled pigeon *Columba guinea* Cape turtledove *Streptopelia capicola* Red-eyed dove *Streptopelia semtorguata*
	Medium 50- 150 g	Laughing dove *Streptopelia senegalensis* Southern boubou *Laniarius ferrugineus*
	Small 30-50 g	Common fiscal *Lanius collaris* Southern-masked weaver *Ploceus valetus* Cape weaver *Ploceus capensis* Southern tchagra *Tchagra tchagra*
	Tiny <30 g	Yellow canary *Crithagra flaviventris* Cape bunting *Emberiza capensis* Grey tit *Serinus canicollis* Fiscal flighcatcher *Sigelus silens*
Non-frugivorous	Small 30-50 g	Yellow bishop *Euplectes capensis* Less-grey shrike *Lanius minor* Cape sugarbirds *Promerops cafer*
	Tiny <30 g	Lesser swamp-warbler *Acrocephalus gracilirostris* Grey-backed cisticola *Cisticola subruficapilla* Cape siskin *Critahra totta* Cinnamon-breasted bunting *Emberiza tahapisi* Malachite sunbird *Nectarina famosa* Red-headed quelea *Quelea quelea* Orange-breasted sunbird *Anthobaphes violacea* Cape batis *Batis capensis* Southern double-coloured sunbird *Cinnyris chalybeus*

Figure 2.3. Classification system applied to the subset of bird species recorded foraging on fruits and associated dietery commodities on alien (*L. camara* & *S. mauritianum*) and indigenous (*C. monilifera* & *O. africana)* shrub species in the Cape Floristic Region

2.4. Reference list

Aslan, C.E. & Rejmanek M. (2010) Avian use of introduced plants: ornithologist records illuminate interspecific associations and research needs. *Ecological Applications*, **20**, 1005-20.

Binggeli, P., Hall, J.B. & Healey, J.R. (1998) A review of invasive woody plants in the tropics. School of Agricultural and Forest Sciences Publication Number 13. Online publication, University of Wales, Bangor. (http://www.safs.bangor.ac.uk/iwpt).

Bromilow, C. (2010) Problem plants and alien weeds of South Afric*a*. Briza Publications, Pretoria.

Cain, M.L., Milligan, B.G. & Strand, A.E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany*, **87**, 1217-1227.

Campbell, P.L. & van Staden, J. (1994) The viability and germination characteristics of exhumed *Solanum mauritianum* seeds buried for different periods of time. *Plant Growth Regulation*, **14**, 97-108.

Coates Palgrave, K. (1983) *Trees of Southern Africa.* C. Struik, Cape Town.

Cowling, R.M. & Richardson, D.M. (1995) *Fynbos: South Africa's unique floral kingdom.* Fernwood Press, Cape Town.

Cowling, R.M., Rundel, P.W., Lamont, B.B., K. Arroyo, M. & Arianoutsou, M. (1996) Plant diversity in Mediterranean-climate regions. *Trends in Ecology & Evolution*, **11**, 362-366.

Cuneo, P. & Leishman, M.R. (2006) African Olive (*Olea europaea* subsp*. cuspidata*) as an environmental weed in eastern Australia: a review. *Cunninghamia*, **9**, 545-557.

Daehler, C.C., Denslow, J.S., Ansari, S. & Kuo, H.C. (2004) A riskassessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. *Conservation Biology*, **18,** 360–368.

Day, M., Wiley, C.J., Playford, J. & Zalucki, M.P. (2003) Lantana: current management status and future prospects. ACIAR, Canberra, ACT, Australia.

Emert, S. (2001) Gardener's companion to weeds (2nd ed.), Sydney, NSW, Australia: Reed New Holland, p. 100.

Fraser, M.W. & Crowe, T.M. (1990) Effects of alien woody plant invasion on the birds of mountain fynbos in the Cape of Good Hope Nature Reserve. *South African Journal of Zoology*, **25**, 97-108.

Geldenhuys, C.J.. le Roux, P.J. & Cooper, K.H. (1986) Alien invasions in indigenous evergreen forest. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 119-131. Cape Town, Oxford University Press.

Gleadow, R. M. (1982) Invasion by *Pittosporum undulatum* of the forests of central Victoria. II. Dispersal, germination and establishment. *Australian Journal of Botany*, **30**, 185-198.

Goldblatt, P. & Manning, J.C. (2002) Plant Diversity of the Cape Region of Southern Africa. *Annals of the Missouri Botanical Garden*, **89**, 281-302.

Goodland, T. & Healey, J.R. (1997) The effect of *Pittosporum undulatum* on the native vegetation of the Blue Mountains of Jamaica. Report by the Invasive Woody Plants in the Tropics Research Group. School of Agricultural and Forest Sciences, University of Wales, Bangor, UK.

Gosper, C.R., Stansbury, C.D. & Vivian-Smith, G. (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity & Distributions,* **11**, 549-558.

Henderson, L. (2001) *Alien weeds and invasive plants - A complete guide to declared weeds and invaders in South Africa*. Plant Protection Research Institute Hand Book 12 edition. Agricultural Research Council, Pretoria.

Herrera, C.M. (1995) Dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics*, **26**, 705-727.

Holmes, P.M. (2001) Shrubland restoration following woody alien invasion and mining: effects of topsoil depth, seed source, and fertilizer addition. *Restoration Ecology* **9**, 71-84.

Howard, R.A. (1969) A checklist of cultivar names used in the genus *Lantana*. *Arnoldia,* **29**, 73-109.

Jordano, P. (2000) Fruits and frugivory. *Seeds: the ecology of regeneration in natural plant communities*. (ed. Fenner, M.) pp. 125-166. CABI Publishers, Wallingford, UK.

Knight, R.S. & Siegfried, W.R. (1983) Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia*, **56**, 405-412.

Knight, R.S. (1986) A comparative analysis of fleshy fruit displays in alien and indigenous plants. *The ecology and management of biological invasions in Southern Africa*. (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 171-178. Oxford University Press, Cape Town.

Kueffer, C., Kronauer, L. & Edwards, P.J. (2009) Wider spectrum of fruit traits in invasive than native floras may increase the vulnerability of oceanic islands to plant invasions. *OIKOS*, **118**, 1327-1334.

Lambert, F.R. & Marshall, A.G. (1991) Keystone characteristics of bird-dispersed Ficus in a Malaysian lowland rain forest. *Journal of Ecology,* **79**, 793-809.

Loiselle, B.A. & Blake, J.G. (2002) Potential consequences of extinction of frugivorous birds for shrubs of a tropical wet forest. *Seed dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D.J., Silva W.R. & Galetti, M.) pp. 397-406. CABI Publishing, Oxford, UK.

Lumaret, R., Ouazzani, N., Michaud, H., Vivier, G., Deguilloux, M.F. & Di Giusto, F. (2004) Allozyme variation of oleaster populations (wild olive tree) (*Olea europaea* L.) in the Mediterranean Basin. *Heredity*, **92**, 343-351.

Macdonald, I.A.W. (1986) *Range expansion* in the *Pied Barbet* and the spread of alien tree species in southern Africa. *Ostrich,* **57,** 75-94.

Maclean, G.L. (1990) Ornithology for Africa. University of Natal Press, Pietmaritzburg.

Magill, R.E., Russell, G.E., Morris, J.W. & Gonsalves, P. (1983) PRECIS, the Botanical Research Institute herbarium data bank. *Bothalia,* **14**, 481-495.

Manders, P.T. & Richardson, D.M. (1992) Colonization of Cape fynbos communities by forest species*. Forest Ecology and Management*, **48,** 277-293.

Marco, A., Lavergne, S., Dutoit, T. & Bertaudiere-Montes, V. (2010) From the backyard to the backcountry: how ecological and biological traits explain the escape of garden plants into Mediterranean old fields. *Biological Invasions,* **12,** 761-779.

McMahon, L. & Fraser, M. (1988) *A fynbos year*. David Philip, Cape Town

Milton, S.J., Wilson, J.R.U., Richardson, D.M., Seymour, C.L., Dean, W.R.J., Iponga, M. & Proches, S. (2007) Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. *Journal of Ecology*, **95**, 648-661.

Moll, E.J. & Bossi, L. (1983) Assessment of the extent of the natural vegetation of the Fynbos biome of South Africa. *South African Journal of Science*, **80**, 355-358.

Moll, E.J., Campbell, B.M., Cowling, R.M., Bossi, L. M. Jarman, L. & Boucher, C. (1984) A description of major vegetation categories in and adjacent to the Fynbos Biome. pp. 12-14. *South African nation scientific programmes report* No 83, CSIR, Pretoria.

Mucina, L. & Rutherford, M.C. (eds.) (2006) *The vegetation of South Africa, Lesotho and Swaziland.* Strelitzia 19, South African National Biodiversity Institute, Pretoria.

Mucina, L., Bredenkamp, G.J., Hoare, D.B. & McDonald, D.J. (2000) A national vegetation database for South Africa. *South African Journal of Science*, **96**, 497, 498.

Muller-Landau, H.C. & Hardesty, B.D. (2005) Seed dispersal of woody plants in tropical forests: Concepts, examples and future directions. *Biotic interactions in the tropics: their role in the maintenance of species diversity*, (eds. Burslem, D., Pinard, M. & Hartley, S.) pp. 267–309. Cambridge University Press, Cambridge, UK.

Mullett, T.L. (2000) The ecology of *Pittosporum undulatum* Vent. (Pittosporaceae) an environmental weed in south east Australia. Ph.D. Thesis. Deakin University, Australia.

Nathan, N. (2006) Long distance dispersal of plants. *Science*, **313**, 786- 789.

Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278-285.

Nathan, R. (2007) Total dispersal kernels and the evaluation of diversity and similarity in complex dispersal systems. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Nel, J.L., Richardson, D.M., Rouget, M., Mgidi, T.N., Mdzeke, N., le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L. & Neser, S. (2004) A proposed classification of invasive alien plant species in South Africa: towards prioritizing species and areas for management action. *South African Journal of Science*, **100**, 53-64.

Oatley, T.B. (1984) Exploitation of a new niche by the Rameron Pigeon *Columba arquatrix* in Natal. *Proceedings of the Fifth Pan-African Ornithological Congress* (Ed. Ledger, J.A.), pp. 323-330, Southern African Ornithological Society.

Olckers, T. (1999) Biological control of *Solanum mauritianum* Scopoli (Solanaceae) in South Africa: a review of candidate agents, progress and future prospects. *African Entomology Memoir*, **1**, 65–73.

Parsons, W.T. (1973) Noxious weeds of Victoria, Melbourne, Vic., pp. 100–101. Australia: Inkata Press.

Quix, J.C. (2007) The role of alien plants in the composition of fruit-eating bird assemblages in Brazilian urban ecosystems. *Orsis*, **22**, 87-104.

Rebelo, A.G. (1996) West Coast Renosterveld. *Vegetation of South Africa, Lesotho and Swaziland: a companion to the vegetation map of South Africa, Lesotho and Swaziland.* (eds. Low, A.B. & Rebelo, A.G.). Department of Environmental Affairs and Tourism, Pretoria.

Reichard, S.H. & Hamilton, C.W. (1997) Predicting invasions of woody plants introduced into North America. *Conservation Biology*, **11**, 193 - 203.

Reichard, S.H. & White, P. (2001) Horticulture as a pathway of invasive plant introductions in the United States. *BioScience*, **51**, 103-113.

Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655-1661.

Rey, P.J. & Alcantara, J.M. (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology*, **88**, 622-633.

Richardson, D.M. & Brink, M.P. (1985) Notes on *Pittosporum undulatum* in southwestern Cape. *Veld and Flora*, **71**, 75-77.

Richardson, D.M. & Fraser, M.W. (1995) Birds of Swartboskloof, Jonkershoek Valley, Stellenbosch: a mountain fynbos ecosystem. *Southern Birds*, **18**, 1-44.

Richardson, D.M. & Rejmánek, M. (2011) Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions*, **17**, 788-809.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmanek, M. (2000) Plant invasions: the role of mutualisms. *Biological Reviews*, **75**, 65-93.

Richardson, D.M., Cowling R.M. & Lamont, B.B. (1996) Non-linearities, synergisms and plant extinctions in South African fynbos and Australian kwongan. *Biodiversity and Conservation*, **5**, 1035-1046.

Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P., Pyšek, P. & Hobbs, R.J. (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Diversity and Distributions*, **13**, 126-139.

Richardson, D.M. & Rejmánek, M. (2011) Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions*, **17**, 788-809.

Rutherford, M.C., Powrie, L.W., Midgley, G.F. (2003) ACKDAT: A digital spatial database of distributions of South African plant species and species assemblages. *South African Journal of Botany*, **69**, 99-104

Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar A. & Nathan, N. (2009) Long-distance seed dispersal. *Annual Plant Reviews*, **38,** 204–237.

Sekercioglu, C.H. (2006) Increasing awareness of avian ecological function. *Trends in Ecology and Evolution*, **21**, 464-471.

Sharma, G.P., Raghubanshi, A.S. & Singh J.S. (2005) Lantana invasion: an overview. *Weed Biology and Management*, **5**, 157-165.

Stock, D. (2004) The dynamics of *Lantana camara* L. invasion of subtropical rainforest in southeast Queensland. Ph.D. Thesis, School of Environmental and Applied Sciences, Griffith University, Queensland.

Stock, D.H. & Wild, C.H. (2002) The capacity of lantana (*Lantana camara* L.) to displace native vegetation. *13th Australian Conference: weeds "threats now and forever?"* (eds. Jaco, H.S., Dodd, J., Moore, J.H.) pp. 104-107. Sheraton Perth Hotel, Western Australia, September.

Swarbrick, J.T., Willson, B.W. & Hannan-Jones, M.A. (1995) The biology of Australian weeds 25. *Lantana camara L. Plant Protection Quarterly*, **10,** 82-95.

Traveset, A. & Richardson, D.M. (2011) Mutualisms: key drivers if invasion …key casualties of invasions. *Fifty years of invasion ecology. The legacy of Charles Elton* (ed. Richardson, D.M.) pp. 143-157, Wiley-Blackwell, Oxford.

Van Wyk, B. & van Wyk, P. (1997) *Field guide to trees of southern Africa*. Struik Publishers: Cape Town.

Vivian-Smith, G., Gosper, C.R., Wilson, A. & Hoad, K. (2006) *Lantana camara* and the fruit- and seed-damaging fly, *Ophiomyia lantanae* (Agromyzidae): seed predator, recruitment promoter or dispersal disrupter? *Biological Control*, **36,** 247-257.

Weiss, P.W., Adair, R.J., Edwards, P.B., Winkler, M.A. & Downey, P.O. (2008) *Chrysanthemoides monilifera* subsp. *monilifera* (L.) T.Norl. and subsp. *rotundata* (DC.) T.Norl. *Plant Protection Quarterly*, **23**, 3-14.

Witkowski, E.T.F. & Garner, R.D. (2008) Seed production, seed bank dynamics, resprouting and long-term response to clearing of the alien invasive *Solanum mauritianum* in a temperate to subtropical riparian ecosystem. *South African Journal of Botany*, **74**, 476-484.

Chapter 3

Bird species richness and visitation frequencies on alien and indigenous shrubs in the South African Cape Floristic Region

3.1. Abstract

The hypothesis that fleshy fruits of alien shrubs are visited more frequently and by a larger complement of foraging bird species than those of indigenous shrubs was tested. This was achieved by comparing bird species richness in heavily, moderately and non-frugivorous groups and their visitation frequencies on fleshy fruits of two alien (*Lantana camara* and *Solanum mauritianum*) and two indigenous (*Olea europaea* subsp*. africana* and *Chrysanthemoides monilifera*) shrubs at four diverse sites (Hout Bay, Paarl, Hermanus and Swellendam) in the Cape Floristic Region. The 592 surveillance records yielded 37 bird species included in 32 genera and 17 families with 25 bird species observed consuming fruits of the alien and indigenous shrubs. Overall, 21 bird species were observed foraging on *C. monilifera* fruits, 20 species on *O. africana* fruits, 17 species on *L. camara* fruits and 15 species on *S. mauritianum* fruits. The highest total visitations by foraging birds were on *S. mauritianum* (374 visitations) followed by *L. camara* (204 visitations), *O. africana* (176 visitations) and *C. monilifera* (132 visitations). The differences in visitation frequencies between the alien and indigenous shrubs were mostly apparent among the heavily frugivorous birds, particularly the small and tiny birds. More heavily than moderately frugivorous bird species foraged on fruits of the alien shrubs but this was not apparent in the indigenous shrubs. Also, the heavily frugivorous bird group more frequently visited fruits of the two alien shrubs than the two indigenous shrubs but this was not apparent among the moderately and non-frugivorous bird groups. Only four heavily frugivorous bird species *(Columba arquatrix, Colius striatus, Pycnonotus capensis* and *Zosterops capensis)* and two moderately frugivorous bird species (*Ploceus velatus a*nd *Serinus canicollis)* displayed significantly higher visitation frequencies on *S. mauritianum* than the two indigenous shrubs. This fruit preference by several foraging bird species for *S. mauritianum* fruits partly supported the study hypothesis. It could potentially enhance the amount of seed dispersal of *S. mauritianum* to the disadvantage of co-occurring indigenous shrubs.

Keywords fleshy fruits, seed dispersal, bird species, frugivory, bird mass, competition.

3.2. Introduction

It has been proposed that the ability of alien species to infiltrate ecological networks in novel environments may disrupt reproductive mutualisms, particularly seed dispersal by birds (Geldenhuys et al. 1986; Richardson et al. 2000; Traveset and Richardson 2006; Milton et al. 2007). For instance, introduction of fleshy-fruited alien species with more attractive fruit displays than indigenous species may change birds' foraging behaviour and fruit preferences (Knight 1986, 1988; LaFleur et al. 2007). Previous studies suggest that alien fruits have more conspicuous fruit displays (Knight 1986) and higher nutritional quality than indigenous (Gosper et al. 2005; Kueffer et al. 2009; Gosper & Vivian-Smith 2010). If the co-fruiting alien and indigenous shrubs share similar avian dispersal assemblages, competition for dispersal agents may result (Terborgh & Diamond 1970, Geldenhuys et al. 1986; Gosper et al. 2006). Swaying of avian dispersers' attention from native to alien fruits may be detrimental as it may change seed dispersal systems and eventually vegetation structure of the invaded habitat (Carlo et al. 2003; Williams 2006; Bascompte & Jordano 2007; Green 2007).

Globally, approximately 50% of fleshy-fruited trees and shrubs (Binggeli 1996; Williams 2006; Quix 2007) and more than 90% of tropical trees and shrubs plants are vertebrate-dispersed (Howe & Smallwood 1982; Jordano 2000; Reichard et al. 2001) with bird-dispersal dominating (Willson et al. 1989). At least 23% of southern Africa fleshy-fruited woody plants species also rely on bird-mediated seed dispersal (Knight & Siegfried 1983). In the CFR, about 80% of trees species in succulent karroid scrubland, dune thicket and afromontane forests are bird dispersed, though le Maitre and Midgley (1992) estimated lower percentages for renosterveld (46%) mountain fynbos (28%) and lowland fynbos (3%). Since a high percentage (between 20-95%) of fleshy-fruited tree and shrub species in Mediterranean-climate ecosystems are bird-dispersed (Herrera 1995), the CFR is no exception. Bird-mediated seed dispersal determines spatial structure, dynamics and composition of plant communities (Herrera 1995; Jordano 2000; Muller-Landau & Hardesty 2005; Spiegel & Nathan 2007; Godinez-Alvarez & Jordano 2007).

Although bird-mediated seed dispersal is important, frugivorous bird species are rare in the South African fynbos (Knight 1986, 1988; le Maitre & Midgley 1992) due to limited preferential forest habitats for frugivorous birds (Cody 1983). However, the invasion of fynbos by alien trees and shrubs with fruits and seeds attractive account for migration of about 36 of the 224 bird species of the terrestrial birds occurring in the fynbos biome (Macdonald & Richardson 1986; Richardson et al. 1992; Cowling & Richardson 1995). This has contributed to the expansion of alien plant infestations through bird mediated seed dispersal (Williams 2006). A typical example is the reported dispersal by the red-winged starling *Onychognathus morio* of *Acacia cyclops* in South African mountain fynbos (Glyphis et al. 1981, Richardson et al. 1992). Examples in other ecosystems include the dispersal by the introduced red-whiskered bulbul *Pycnonotus jocosus* of over 24 fleshy-fruited alien plant species in Florida and La Reunion, the dispersal by exotic birds of 37% of 90 major weeds in Hawaii, and the dispersal by the

introduced European blackbird *Turdus merula* of alien plants in New Zealand (Simberloff & Holle 1999; Mandon-Dalger et al. 2004; Williams 2006). Indeed, some invaders are successful in the novel habitats through interactions with the fellow alien species – invasion meltdown (Simberloff & Holle 1999). Although alien bird species also disperse indigenous fruit (Richardson et al. 2000b) and assist reestablishment of collapsed mutualisms (Kawakami et al. 2009), the increasing rates of invasion by fleshy-fruited plant species suggest that alien fruits are more preferential than indigenous fruits.

Conservation of important native mutualisms must identify key participant species in the mutualism (Green 2007; Jordano 2007); since the decline of each could have substantial negative effects on local and regional plant diversity and distribution (Williams & Karl 1996; Alcantara et al. 1997; Levine & Murrel 2003; Telleria et al. 2005; Nathan 2007). However, the multiple interactions between one vertebrate disperser and many fruiting trees and *vice versa* complicates investigations of the individual species' role (Nathan & Muller-Landau 2000; Muller-Landau & Hardesty 2005; Carlo et al. 2007; Dennis & Westcott 2007; Nathan 2007). Comparison of bird species assemblages foraging fleshy-fruited alien and indigenous shrubs could effectively elucidate whether seed dispersal of indigenous species are disrupted by presence of neighbouring fleshy-fruited alien species.

There are no existing studies that compare the richness and composition of bird species foraging on fruits of alien and indigenous shrubs in the Cape Floristic Region. Previous studies merely identified which bird species that disperse seed of alien species (Glyphis et al. 1981; Oatley 1984; Geldenhuys et al. 1986; Knight 1988; Manders & Richardson 1992; Underhill & Hofmeyr 2007) as a means of determining potential invasiveness (e.g. *Shinus molle*, Iponga 2009). The comparative study between alien and indigenous trees and shrubs species was conducted on fruit phenology and fruit displays in southern Africa by Knight (1986, 1988). Although competition for dispersal agents between alien and indigenous shrubs was recognised (Kruger et al. 1986; Knight 1986; Traveset & Richardson 2006), bird foraging behaviour on alien and indigenous shrubs was not compared. This is an essential requirement for effective management of alien species and decision-making process on resources allocation (Byers et al. 2002; Gooden et al. 2009; Roura et al. 2009). In fact, there are limited data on avian seed dispersal in the Cape Floristic Region compared with other global Mediterranean climate areas (Herrera 2002), yet fleshy-fruited alien tree and shrub species dispersed by birds are an important threat to the biodiversity of this region. In view of these knowledge deficiencies, this study compared the richness of bird species and their foraging visitation frequencies on fleshy fruits of alien and indigenous shrubs in the Cape Floristic Region.

3.3. Methods and materials

3.3.1. Experimental design, study sites and species

The experimental design comprised 4 study sites, each comprising mixed populations of alien and indigenous shrubs located on Peninsula Granite Fynbos (Hout Bay site in Cape Town), Swartland Shale Renosterveld site (Paarl site), Overberg Sandstone Fynbos (Hermanus site) and Breede Shale Renosterveld site (Swellendam site). The fynbos and renosterveld vegetation classifications were according to Mucina and Rutherford (2006). Within each site, there were intermixed populations of four different shrub species with fleshy fruit displays, namely the indigenous *Chrysanthemoides monilifera* and *Olea europaea* subsp. *africana* (hereafter called *O. africana*) and the aliens *Lantana camara* and *Solanum mauritianum*. Since vegetation composition strongly influences fruit and seed removal by birds (Garcia et al. 2001; Carlo et al. 2007), all shrub species were selected based on their co-occurrence over a wide range of natural vegetation types, their overlapping fruiting times (Van Wyk & Van Wyk 1997) and consumption of their fruit by local frugivorous birds (Richardson & Fraser 1995). *Lantana camara, C. monilifera* and *O. africana* possess similar fruit architectures, namely single-seeded drupes that turn black when ripe, whereas *S. mauritianum* produces green multi-seeded berry turning yellowish when ripe.

3.3.2. Foraging bird species diversity and frequency

At each site, bird surveillances were conducted during the peak fruiting periods of the alien and indigenous shrub species and restricted to 6 h daily periods of peak bird activity, namely a 3 h period after sunrise and a 3 h period before sunset (Howe 1977; Snow & Snow 1988; McNamara et al. 1994; Bibby et al. 2000). Individual shrubs that are reproductively mature were randomly selected for bird surveillances, which were conducted at approximately 30m distance from each shrub during the peak fruiting periods namely, spring and autumn of 2008 and 2009 (Knight 1988). The bird surveillances were performed manually with binoculars (8 x 42 magnification) and simultaneously recorded with a digital camcorder (Kodak C813: 8.2 megapixel, ISO 1250, digital IS) for a permanent record (Spiegel & Nathan 2007). Five days of bird surveillances were conducted on each of the four shrub species at each site (80 day surveillance period overall). All bird species that were observed either directly consuming the fruits of the alien and indigenous shrubs or feeding on nectar and/or insects present on their fruits and inflorescences were recorded. Each visitation comprised an arrival and departure time of a foraging bird species, with the numbers of recorded visitations summed for the 5-day observation periods at each site. Bird species were identified with the aid of descriptions and keys presented in Sinclair and Ryan (2003) and Hockey et al. (2005). Plots of the cumulative numbers of foraging bird species against surveillance days (Figure 3.1) showed that the 20 days on each shrub species provided adequate samples of total foraging bird species complements.
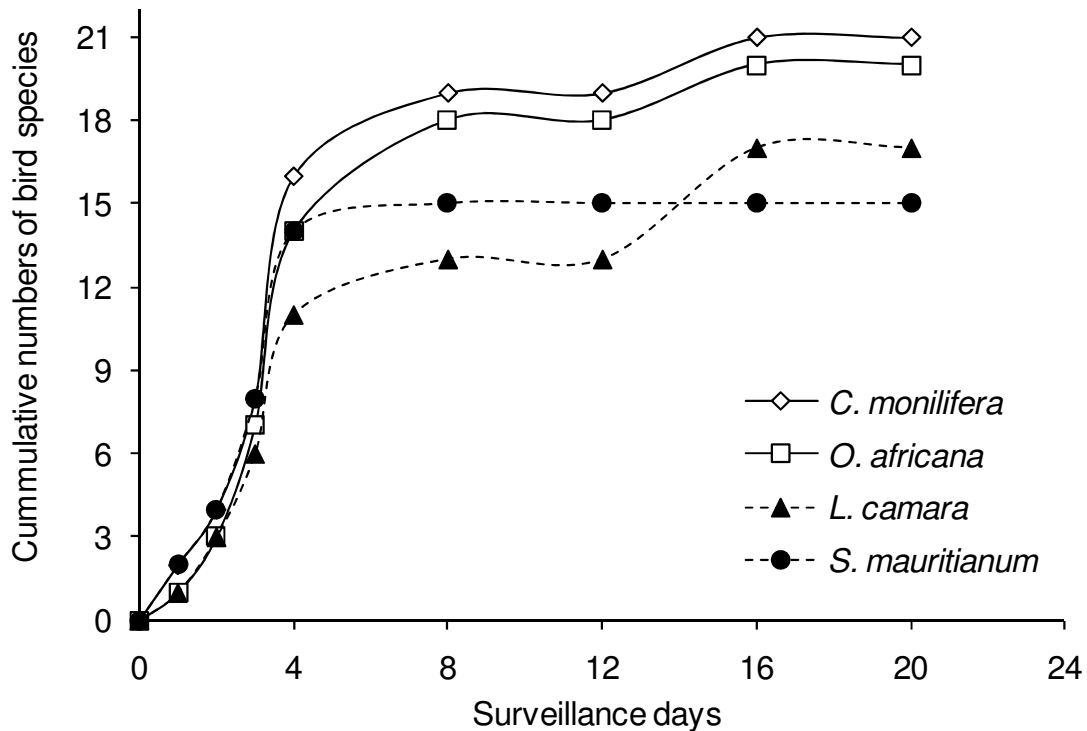
Figure 3.1. Plots of the cumulative numbers of recorded bird species against surveillance days foraging on fruits of four shrub species (indigenous *C. monilifera* and *O. africana* and alien *L. camara* and *S. mauritianum*) at four diverse sites

3.3.3. Data synthesis and statistical analysis

3.3.3.1. Variance components analysis

The recorded foraging bird species were classified into two frugivorous groups namely heavily frugivorous birds with fruits their main source of sustenance and moderately frugivorous birds with fruits their secondary or occasional source of sustenance. A third non-frugivorous group was also included whose diet comprised commodities (insects and floral nectar) associated with fleshy fruits of indigenous and alien plants (Hockey et al. 2005) and consequently indirectly with fruit quality and subsequent seed dispersal. Within each frugivorous group, foraging bird species were sub-divided into four functional body mass sub groups defined by Dennis and Westcott (2005), namely large birds (> 150 g), medium size birds (50-150 g), small birds (30-50 g) and tiny birds (< 30 g).

All measurements were $\log_e$ transformed before statistical analysis to reduce the inequality of variance in the raw data (Figure 3.2). The experimental design was unbalanced due to unequally replicated frequency measurements on each bird species at each site.

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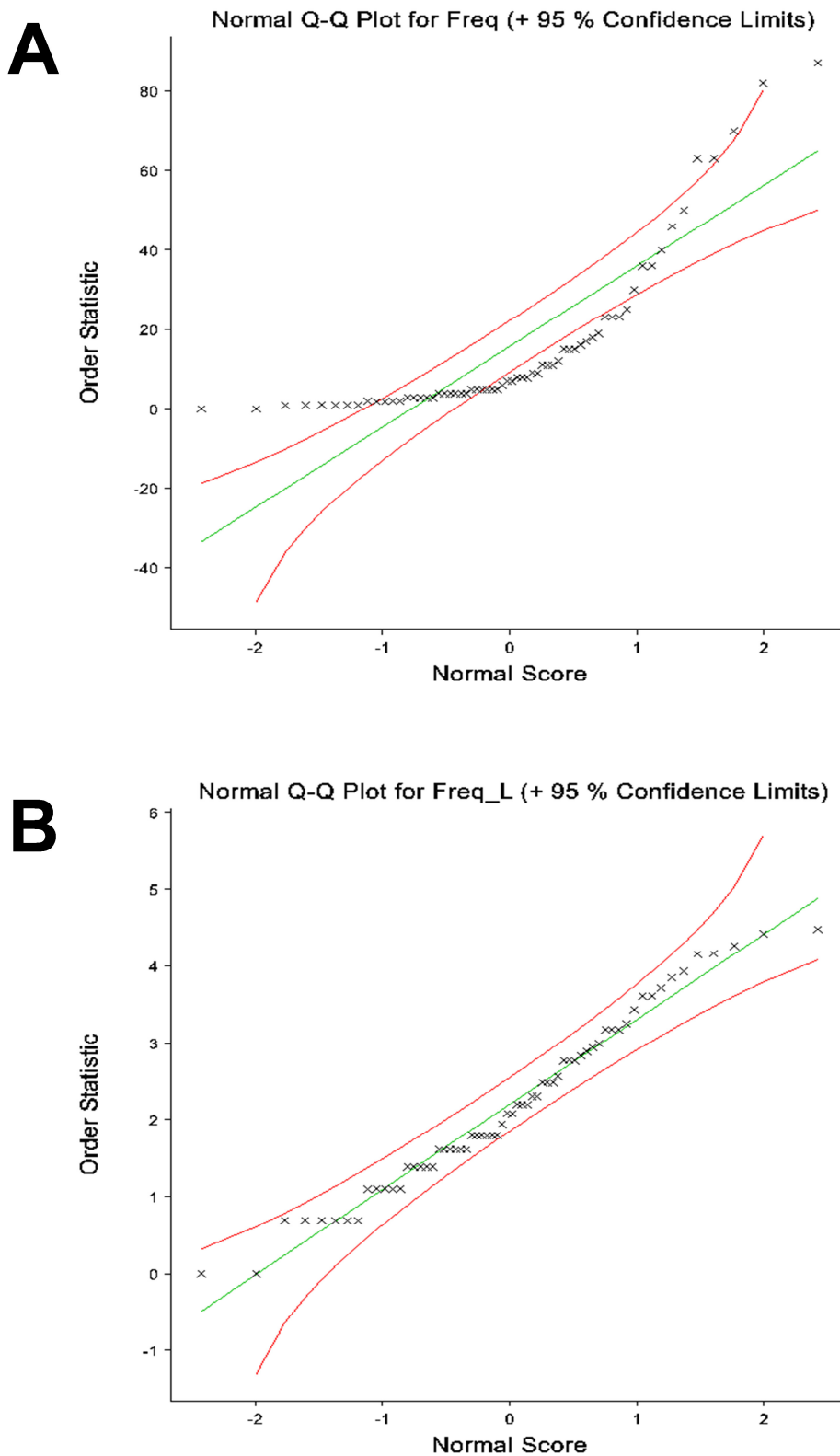
Figure 3.2. Normal distribution plots for A. untransformed and B. log$_e$ transformed bird visitation frequencies on fleshy fruits of indigenous (*C. monilifera* and *O. africana)* and alien (*L. camara* and *S. mauritianum*) shrubs.

Consequently, a residual maximum likelihood (REML) variance component analysis (linear mixed model) was applied to test for differences in visitation frequencies and species richness of birds foraging on fleshy fruits of the alien and indigenous shrubs. Four separate REML analyses were conducted using the Wald X^2 statistic generated by the REML (GENSTAT Discovery Edition 3, VSL Lty, UK). The first REML tested for differences in visitation frequencies and species richness of birds included in heavily, moderately and non-frugivorous groups foraging on fleshy fruits of the alien and indigenous shrubs. The second REML tested for differences in visitation frequencies of bird species included in the heavily frugivorous group foraging on fleshy fruits of the alien and indigenous shrubs. The third REML tested for differences in visitation frequencies of bird species included in the moderately frugivorous group foraging on fleshy fruits of the alien and indigenous shrubs. The fourth REML tested for differences in visitation frequencies of bird species included in the non-frugivorous group foraging on the alien and indigenous shrubs. In the first REML, bird frugivore group and shrub species variables were fitted in the fixed model and site, shrub and frugivore group factors in the random model. In the second, third and fourth REML, bird species and shrub species variables were fitted in the fixed model and site, shrub and bird species factors in the random model. Differences exceeding twice the mean standard error of differences were used to separate significantly different treatment means at P ≤ 0.05. This was based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is two.

3.3.3.2. Multiple correspondence analysis

Multiple correspondence analysis (MCA) was applied to determine associations between frugivorous bird species, fruiting shrub species and sampling sites. It is an extension of correspondence analysis which allows analysis of the pattern of relationships of several categorical dependent variables (Abdi & Valentin 2007). Its major premise is that strongly related categorical variables are closely associated (Hoffman & Leeuw 1992). In the application of MCA in this study, species exclusion criteria were applied by placing thresholds on recorded foraging bird visitation frequencies to exclude bird species with frequently low or absent values. The exclusion criteria applied were the omission of those foraging bird species whose total visitation frequencies were below values of 20. Computed standardized deviates and a correspondence map of the first two dimensions identified the degree of association between different species of birds, alien and indigenous shrub species and sites. Large and positive values of standardized deviates indicated better than expected associations between bird species and shrub species or sites whereas the converse applied to large negative values of standardized deviates.

3.4. Results

3.4.1. Variance components analysis

The 592 surveillance records yielded 37 foraging bird species included in 32 genera and 17 families, of which 21 bird species were observed foraging on *C. monilifera*, 20 species foraging on *O. africana*, 17 species on *L. camara* and 15 species foraging on *S. mauritianum* fleshy fruits (Table 3.1). The highest total visitations by foraging birds were on the alien *S. mauritianum* (374 visitations) followed by the alien *L. camara* (204 visitations), indigeneous *O. africana* (176 visitations) and the endemic *C. monilifera* (132 visitations), the differences between the alien and indigenous shrubs mostly apparent among the heavily frugivorous, the small and tiny bird groups (Table 3.1). There were significant ($P \leq 0.001$) interactions between shrub species and frugivore group for both bird species richness and visitation frequency (Table 3.2). Significantly ($P \leq 0.05$) more heavily than moderately fugivorous bird species foraged on fruits of the alien shrubs but not those of the indigenous shrubs (Figure 3.3). Also, the heavily fugivorous bird group more frequently ($P \leq 0.05$) visted fruits of the two alien shrubs than the two indigenous shrubs but this was not apparent among the moderately and non frugivorous bird groups (Figure 3.4). In addition there were significant ($P \leq 0.001$) interactions between shrub species and bird species included in the heavily the moderately and non-frugivorous groups frugivorous group on bird visitation frequencies (Table 3.2). Among the heavily frugivorous bird species, only the African olive-pigeon *Columba arquatrix*, speckled mousebird *Colius striatus*, Cape bulbul *Pycnonotus capensis* and Cape white-eye *Zosterops capensis* displayed significantly ($P \leq 0.05$) higher visitation frequencies on the alien *S. mauritianum* than the two indigenous shrubs (Table 3.3). Among the moderately frugivorous bird species, only the southern masked-weaver *Ploceus velatus* and Cape canary *Serinus canicollis* (Tabel 3.4) and among the non-frugivorous bird species only the Cape sugarbird *Promerops cafer* and the yellow bishop *Euplectes capensis* displayed significantly ($P \leq 0.05$) higher visitation frequencies on the alien *S. mauritianum* than the two indigenous shrubs (Table 3.5).

3.4.2. Multiple correspondence analysis

The multiple correspondence analysis map and table of standardized deviates indicated that positive associations between bird species and shrub species in terms of visitation frequency (Figure 4.3) were site specific. Four bird species were positively associated with the indigenous *O. africana*. These included the southern masked-weaver *P. velatus* and Cape canary *S. canicollis* association with *O. africana* at the Paarl site, the red-winged starling *O. morio* association with *O. africana* at the Cape Town site and the common starling *S. vulgaris* association with *O. africana* at the Cape Town site Sweelendam site (Figure 4.3). Three bird species were positively associated with the alien *L. camara*. These included the speckled mousebird *C. striatus* and red-faced mouse bird *U. indicus* association with *L. camara* at the Swellendam site and Cape white-eye *Z. capensis* association with *L. camara* equally at Paarl

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and Hermanus sites (Figure 4.3). Only the African olive-pigeon *C. arquatrix* displayed a positive association with *S. mauritianum*, this restricted to the Cape Town site. Similarly, only the Cape bulbul exhibited a positive association with the indigenous *C. monilifera*, this restricted to the Swellendam site (Figure 4.3).

Table 3.1. Bird foraging visitation frequency and species richness totals in parenthesis for different frugivorous and mass groups of indigenous (*C. monilifera* and *O. africana)* and alien (*L. camara* and *S. mauritianum*) shrubs

Bird Group	Indigenes		Aliens	
	C. monilifera	*O. africana*	*L. camara*	*S. mauritianum*
Heavily Frugivorous	83 (8)	111 (10)	168 (9)	278 (7)
Moderately Frugivorous	38 (8)	65 (10)	34 (7)	55 (5)
Non-Frugivorous	11 (5)	0 (0)	2 (1)	41 (3)
Large: >150 g	19 (3)	21 (4)	14 (3)	60 (1)
Medium: 50 g – 150 g	29 (5)	49 (5)	62 (5)	60 (4)
Small: 30 g -50 g	31 (5)	40 (5)	38 (4)	111 (5)
Tiny: < 30 g	53 (8)	66 (6)	90 (5)	143 (5)
Totals	**132 (21)**	**176 (20)**	**204 (17)**	**374 (15)**

Table 3.2. Wald χ² statistics derived from three separate REML'S (linear mixed models) which tested for differences in species richness and foraging visitation frequencies by birds (different frugivorous groups and species) on fruits of indigenous (*C. monilifera* and *O. africana)* and alien (*L. camara* and *S. mauritianum*) shrubs. Significant at *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

MAIN EFFECTS AND INTERACTIONS	df	Wald X² statistic	
		Bird species numbers	Bird visitation frequencies
REML 1		Figure 3.3	Figure 3.4
Shrub species	3	0.69	17.11***
Frugivore Group	2	139.10***	88.91***
Shrub species x Frugivore Group	6	23.97***	23.61***
REML 2			Table 3.3
Shrub species	3	-	17.30***
Heavily Frugivorous spp	10	-	279.00***
Shrub species x Heavily Frugivorous species	30	-	127.81***
REML 3			Table 3.4
Shrub species	3	-	2.64
Moderately Frugivorous	13	-	84.09***
Shrub species x Moderately Frugivorous species	39	-	59.44*
REML 4			Table 3.5
Shrub species	3	-	11.69**
Non Frugivorous	12	-	28.84**
Shrub species x Non Frugivorous species	32	-	72.77***

70
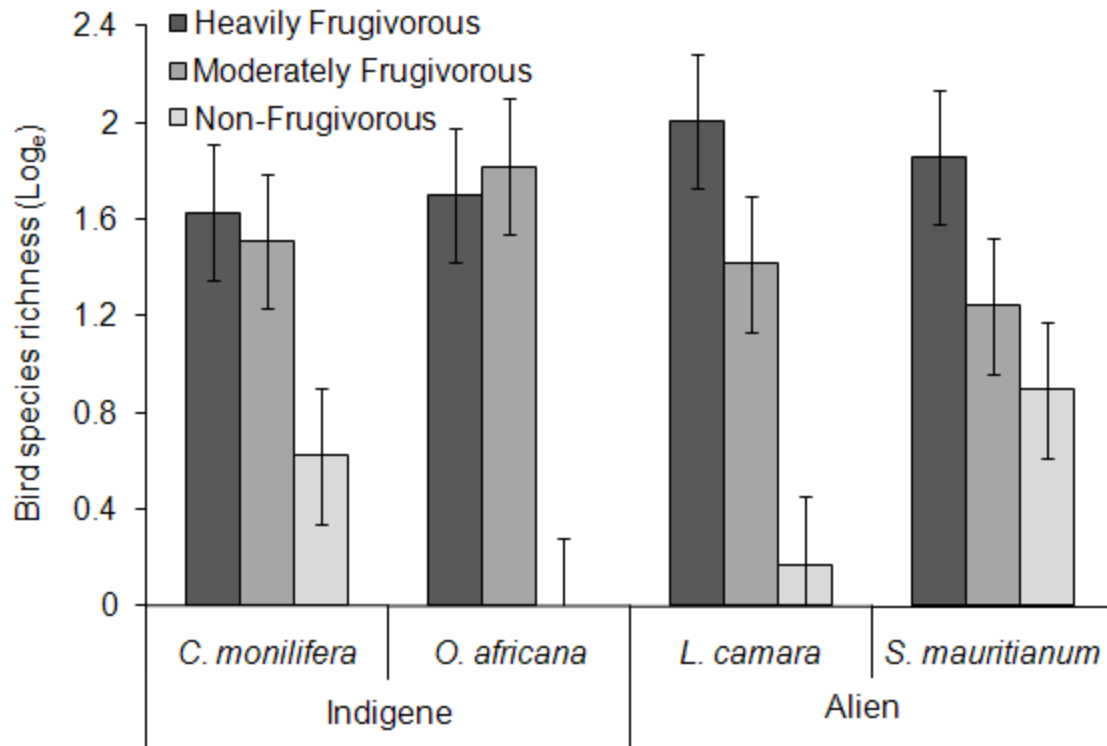
Figure 3.3. Average numbers of bird species in different frugivore groups observed foraging on fleshy fruits of indigenous (*C. monilifera* and *O. africana)* and alien (*L. camara* and *S. mauritianum*) shrubs. Average standard error of differences shown by bars
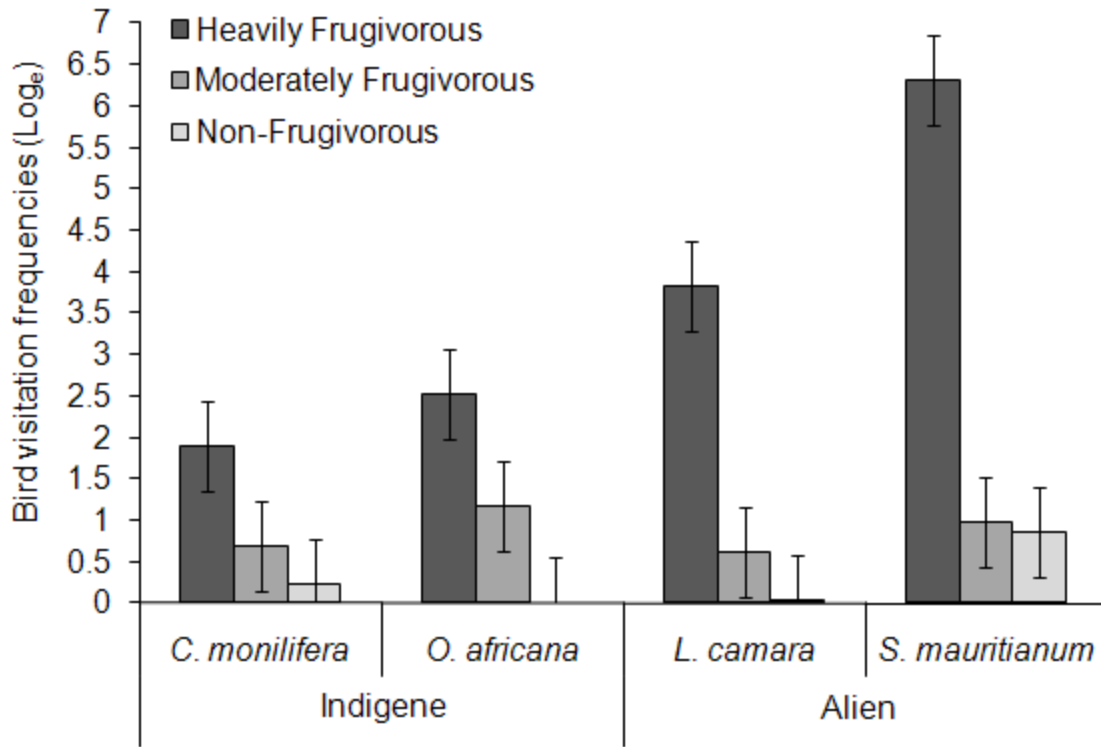
Figure 3.4. Average foraging visitation frequencies per site for birds in different frugivore groups foraging on fleshy fruits of two alien (*L. camara* and *S. mauritianum*) and two indigenous (*C. monilifera* and *O. africana*) shrub species. Average standard error of differences shown by bars

Table 3.3. REML predicted mean foraging visitation frequencies ($\log_e$) per site for heavily frugivorous bird species in different mass groups foraging on fruits of *C. monilifera (C. mon), O. africana* (*O. afr*), *L. camara (L. cam)* and *S. mauritianum (S. mau)*. Significantly (P ≤ 0.05) different means with uncommon letters shown in bold; se is mean standard error of difference; * show alien birds

Scientific Name	Common Name	Family	Indigenes		Aliens	
			C. mon	*O. afr*	*L. cam*	*S. mau*
Heavily Frugivorous						
>150 g			se differences = 2.52			
Columba arquatrix	African olive-pigeon	Columbidae	**1.75a**	**0.50a**	**1.25a**	**15.00b**
50-150 g						
Colius striatus	Speckled mousebird	Collidae	**0.75a**	**5.50a**	**6.75a**	**12.25b**
Onychognathus morio	Red-winged starling	Sturnidae	1.75a	2.75a	2.00a	0.00a
*Sturnus vulgaris	Common starling	Sturnidae	0.00a	0.75a	0.00a	0.00a
Urocolius indicus	Red-faced mousebird	Collidae	1.75a	0.00a	2.75a	1.00a
Turdus olivaceus	Olive thrush	Turdidae	1.25a	1.25a	2.50a	1.50a
30-50 g						
Andropadus importunus	Sombre bulbul	Pycnonotidae	0.00a	0.25a	0.25a	0.00a
Pycnonotus capensis	Cape bulbul	Pycnonotidae	**4.25a**	**5.00a**	**7.25ab**	**11.50b**
<30 g						
*Passer domesticus	House sparrow	Passeridae	0.00a	1.25a	0.00a	0.00a
Cossypha caffra	Cape robin-chat	Muscicapidae	2.25a	1.25a	2.25a	1.50a
Zosterops capensis	Cape white-eye	Zosteropidae	**7.00a**	**9.25a**	**17.00b**	**26.75c**

Table 3.4. REML predicted mean foraging visitation frequencies ($\log_e$) per site for moderately frugivorous bird species in different mass groups foraging on fruits of *C. monilifera (C. mon), O. africana* (*O. afr*), *L. camara (L. cam)* and *S. mauritianum (S. mau)*. Significantly (P ≤ 0.05) different means with uncommon letters shown in bold; se is mean standard error of difference

Scientific Name	Common Name	Family	Indigenes		Aliens	
			C. mon	*O. afr*	*L. cam*	*S. mau*
Moderately Frugivorous						
>150 g			se differences = 1.16			
Columba guinea	Speckled pigeon	Columbidae	1.00a	0.75a	1.25a	0.00a
Streptopelia capicola	Cape turtledove	Columbidae	**2.00ab**	**3.75b**	**1.00a**	**0.00a**
Streptopelia semitorquata	Red-eyed dove	Columbidae	0.00a	0.25a	0.00a	0.00a
50-150 g						
Streptopelia senegalensis	Laughing dove	Columbidae	0.00a	0.00a	0.00a	0.00a
Laniarius ferrugineus	Southern boubou	Malaconotidae	1.75a	2.00a	1.50a	0.25a
30-50 g						
Lanius collaris	Common fiscal	Laniidae	0.00a	0.00a	0.00a	0.00a
Ploceus velatus	Southern masked-weaver	Ploceidae	**1.50c**	**4.00b**	**1.50c**	**6.50a**
Ploceus capensis	Cape weaver	Ploceidae	1.00a	0.25a	0.00a	0.50a
Tchagra tchagra	Southern tchagra	Malaconotidae	0.50a	0.50a	0.50a	0.00a
<30 g						
Crithagra flaviventris	Yellow canary	Fringillidae	1.00a	0.00a	0.00a	0.00a
Emberiza capensis	Cape bunting	Fringillidae	0.00a	1.75a	0.75a	0.00a
Parus afer	Grey tit	Paridae	0.00a	0.00a	0.00a	2.00a
Serinus canicollis	Cape canary	Fringillidae	**0.75b**	**2.75ab**	**2.00b**	**4.50a**
Sigelus silens	Fiscal flycatcher	Muscicapidae	0.00a	0.25a	0.00a	0.00a

Table 3.5. REML predicted mean foraging visitation frequencies ($\log_e$) per site for non-frugivorous bird species whose diet comprised commodities (insects and floral nectar) associated with fleshy fruits of *C. monilifera (C. mon)*, *O. africana* (*O. afr*), *L. camara (L. cam)* and *S. mauritianum (S. mau)*. Significantly ($P \leq 0.05$) different means with uncommon letters shown in bold; se is mean standard error of difference

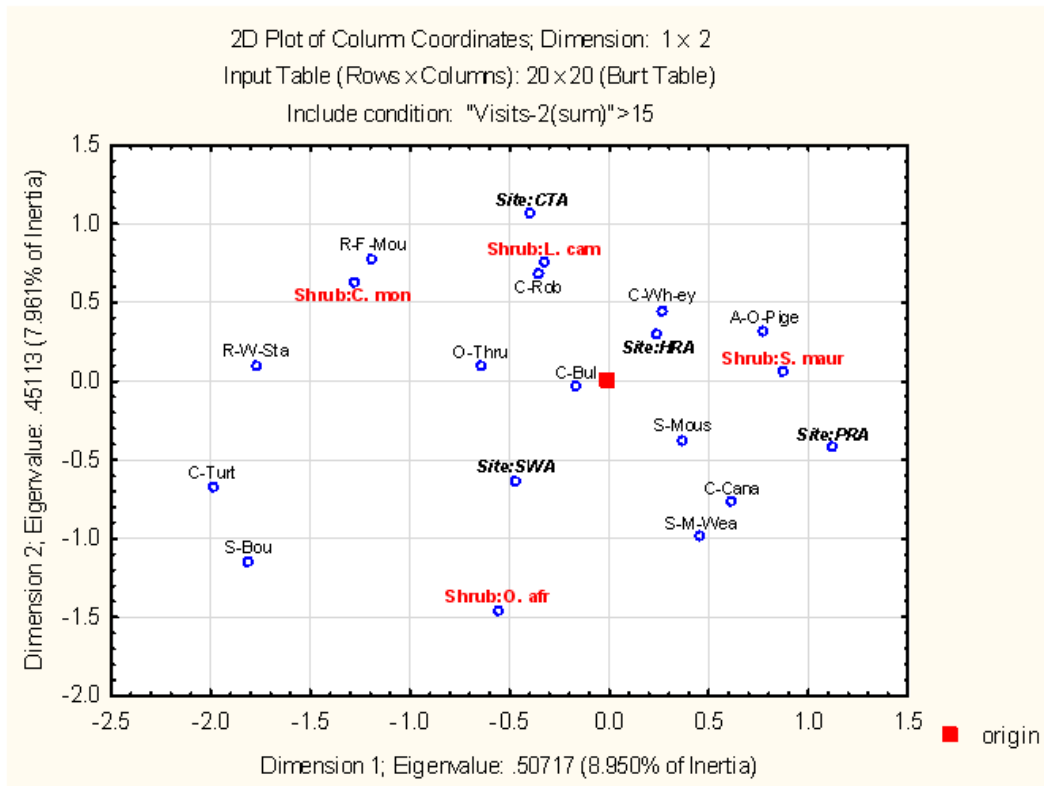| Scientific Name	Common Name	Family	Indigenes		Aliens	
			C. mon	*O. afr*	*L. cam*	*S. mau*
Non Frugivorous **30-50 g**			se differences = 0.95			
Euplectes capensis	Yellow bishop	Ploceidae	**0.00b**	**0.00b**	**0.00b**	**2.50a**
Lanius minor	Lesser grey shrike	Laniidae	0.00a	0.00a	0.00a	0.00a
Promerops cafer	Cape sugarbird	Promeropidae	**0.50b**	**0.00b**	**0.00b**	**6.75a**
<30 g						
Acrocephalus gracilirostris	Lesser swamp-warbler	Sylviidae	0.00a	0.00a	0.00a	0.00a
Cisticola subruficapilla	Grey-backed cisticola	Cisticolidae	0.00a	0.00a	0.00a	0.00a
Crithagra totta	Cape siskin	Fringillidae	0.00a	0.00a	0.00a	0.00a
Emberiza tahapisi	Cinnamon-breasted bunting	Fringillidae	0.00a	0.00a	0.00a	0.00a
Nectarinia famosa	Malachite sunbird	Nectariniidae	0.75a	0.00a	0.00a	0.00a
Quelea erythrops	Red-headed quelea	Ploceidae	0.00a	0.00a	0.00a	0.00a
Anthobaphes violacea	Orange-breasted sunbird	Nectariniidae	0.25a	0.00a	0.00a	0.00a
Batis capensis	Cape batis	Malaconotidae	0.50a	0.00a	0.00a	0.00a
Cinnyris chalybeus	Southern double-collared sunbird	Nectariniidae	0.75a	0.00a	0.50a	1.00a

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2D Plot of Column Coordinates; Dimension: 1 x 2
Input Table (Rows x Columns): 20 x 20 (Burt Table)
Include condition: "Visits-2(sum)">15

Species	Code
African Olive-Pigeon	A-O-Pige
Speckled Mousebird	S-Mous
Red-winged Starling	R-W-Sta
Common Starling	C-Star
Red-faced Mousebird	R-F-Mou
Olive Thrush	O-Thru
Cape Bulbul	C-Bul
House Sparrow	H-Spa
Cape Robin-Chat	C-Rob
Cape White-eye	C-Wh-ey
Speckled Pigeon	S-Pige
Laughing Dove	C-Turt
Southern Boubou	S-Bou
Southern Masked-Weaver	S-M-Wea
Cape Weaver	C-Weav
Southern Tchagra	S-Tchag
Cape Bunting	C-Bun
Grey Tit	G-Tit
Cape Canary	C-Cana
Cape Town	CTA
Paarl	PRA
Hermanus	HRA
Swellendam	SWA
C. monilifera	C. mon
O. africana	O. afr
L. camara	L. cam
S. mauritianum	S. maur

(Heavilly Frugivorous: African Olive-Pigeon through Cape White-eye; Moderately Frugivorous: Speckled Pigeon through Cape Canary)

Standardized Deviates

	A-O-Pige	S-Mous	R-W-Sta	R-F-Mou	O-Thru	C-Bul	C-Rob	C-Wh-ey	C-Turt	S-Bou	S-M-Wea	C-Cana
CTA	0.66692	-0.51937	**1.60357**	-2.26338	-0.02208	-0.99478	0.47990	0.6841	**2.27835**	-0.93793	-0.16198	-1.08598
PRA	-1.45473	**0.43136**	-2.16224	-1.98897	0.15017	-1.36811	**2.09550**	1.0417	-2.20343	-1.48620	**2.66029**	**2.16532**
HRA	-0.89608	-0.36383	0.47432	1.36962	-1.17912	0.75465	-0.59798	**1.3574**	-0.43712	-0.87723	-1.76548	0.33197
SWA	**1.19663**	0.39931	-0.13616	**2.13645**	**0.84141**	**1.16664**	-1.38983	-2.3525	0.07032	**2.49069**	-0.35276	-0.91660
C. mon	-1.01334	-2.93672	1.79276	2.26622	0.73852	**0.38014**	2.48846	-0.9059	2.20492	**2.26622**	-0.53942	-1.07812
O. afr	-3.29029	0.48013	2.60381	-2.07990	-0.04978	-0.43114	-0.29416	-1.4837	**4.20578**	1.76643	**1.65152**	**1.11767**
L. cam	-3.10675	0.40916	0.62166	**2.38645**	**1.41073**	0.25206	0.68528	**1.1296**	-1.03426	0.24192	-2.01020	-0.59914
S. maur	**5.22939**	**1.04626**	-3.29608	-1.71268	-1.47574	-0.11687	-1.75744	0.6706	-3.35887	-2.70214	0.72334	0.31453

Figure 3.5. Two-dimensional multiple correspondence analysis map and tabulated standardized deviates showing relationships between foraging bird visiation frequencies, shrubs and sites. Standardized deviates in bold indicating the most positive associations of individual bird species with shrub species and sites. Shaded bird species names those dispaying REML derived significant differences between shrub species (Table 3.3 - 3.4)

3.5. Discussion

The insignificantly different numbers of heavily and moderately frugivorous bird species observed foraging fruits of the indigenous and alien shrub species pointed to diet generalist behaviour among frugivorous birds in the Cape Floristic Region. Therefore, in compliance with the "specialisation disturbance hypothesis" (Vazquez & Simberloff 2002), changes in ecosystem fruit composition induced by alien plant invasions may not substantially influence avian dispersers in the Cape Floristic Region. Alien fruits are an important resource for bird conservation in the USA (Aslan & Rejmanek 2010) and Australia (Buckley et al. 2006), and also may be considered critical for survival of non-fynbos-endemic bird species in the Cape Floristic Region (Richardson et al. 1992; Cowling & Richardson 1995; Jordaan et al. 2011). In fact, the continuous fruiting patterns displayed by fleshy-fruited alien and indigenous shrubs in the southwestern Cape (Knight 1988), the abundance of arthropods on their flowers and fruits (Geldenhuys et al. 1986; Proches et al. 2008), and their nectar (Waring et al. 1993) have resulted in foraging niche overlaps between, for example, frugivorous, nectarivorous and insectivorous birds (Terborgh & Diamond 1970; Geldenhuys et al. 1986; Jordano 1987).

Tightly coevolved dispersal systems between birds and fleshy fruits (Howe 1977) are rare among heavily frugivorous birds (Bond 1994; Herrera 1995; Kollmann 2000). Knight (1986) concluded that no fixed relationships exist between fleshy fruit type and avian frugivores in the south-western Cape due to the existence of similar ratios of indigenous and alien fruits. Generally, low visitation frequencies were observed among heavily frugivorous flocking birds, such as the red-winged starling *Onychognathus morio,* the common starling *Sturnus vulgaris* and the red-faced mousebird *Urocolius indicus* (Chapman & Reiss 1999; Hockey et al. 2005) on *C. monilifera* and *O. africana* fruits. However, this flocking feature might allow greater removal of fruits and seeds per visitation (Chavez-Ramirez & Slack 1994; Vazquez et al. 2005). In contrast, discriminatory foraging by the heavily frugivorous African olive-pigeon *Columba arquatrix*, speckled mousebird *Colius striatus*, Cape bulbul *Pycnonotus capensis* and the Cape white-eye *Zosterops capensis* was observed on *S. mauritianum* fruits which concurred with Fleming's (1979) observation that tropical plants competing for dispersal agents have evolved fruits that target specific dispersers. *Solanum mauritianum's* large fruits especially allow for maximisation of energy intake (Sallabanks & Courtney 1993; Sallabanks 1993), a feature also exhibited by the American robin *Turdus migratorius*, which preferentially forages large fruits of the hawthorn *Crataegus monogyna* in western Oregon (Sallabanks & Courtney 1993).

Similarly, *L. camara* was found to be sustaining several endangered bird species in Australia, a feature attributed to its aseasonal fruiting phenology (Sharma et al. 2005; Buckley et al. 2006; Turner & Downey 2008) of which may be true in South Africa (Jordaan et al. 2011). High foraging frequency of heavily frugivorous birds on *L. camara* might be associated with low human disturbance of the riparian areas and forests that birds might prefer to exploit during foraging (Wilms & Kappelle 2006; Gomes et al. 2008). In addition, other studies of zoochorous seed dispersal and forest recruitment found that the frugivorous birds strongly discriminate

foraging environments. The moderately frugivorous southern boubou *Laniarius ferrugeneus* and the Cape bunting *Emberiza capensis*, for example, forage indiscriminately on fynbos shrubs with relatively low fruit quality to birds and *O. africana* with its prolonged fruit displays (Castley et al. 2001; Knight 1986, 1988). Conversely, heavily frugivorous bird species such as the African olive-pigeon *C. arquatrix*, olive thrush *Turdus olivaceous* and Cape robin-chat *Cossypha caffra* chose distinct patches with best fruit resources (Castley et al. 2001; Manders & Richardson 1992) which suggests that metabolic demands are likely to influence foraging dynamics in the birds (McNamara et al. 1994).

Body mass among avian seed dispersal agents is an important determinant of the quantities of fruits removed and seed dispersal distance (Schupp 1993; Jordano 2000; Speigel & Nathan 2007; Schurr et al. 2009; Tsoar et al. 2011). The low visitation frequencies observed especially by the large African olive-pigeon *C. arquatrix* on fruits of the two indigenous shrubs suggests that seeds of fleshy-fruited fynbos shrubs may have limited long distance seed dispersal opportunities (Kruger et al. 1986; Knight 1988; Herrera 1995). In addition, the fact that pigeons and doves do grind seeds may compound this problem even though Lambert (1989) reported that some seeds are dispersed in an intact and viable state over long distances. Seed dispersal by large birds is important for connecting fragmented indigenous populations in highly transformed Mediterranean-climate ecosystems (Herrera 1995) and on Pacific islands (Steadman 1997). In fact, poor regeneration of indigenous taxa in degraded renosterveld transformed by agriculture and alien grasses in the Cape Floristic Region (Musil et al. 2005) has been attributed to limited seed dispersal from pristine renosterveld fragments (Kemper et al. 1999; Krug & Krug 2007). The inherently rare dispersal of seeds over long distances in the Mediterranean climate ecosystems has been attributed to the prevalence of medium size birds as dispersal agents (Herrera 1995). This feature was also apparent in the present study where species richness among medium size birds and their visitation frequencies on fruits of the two indigenous shrubs were approximately double that of large birds.

Whereas alien birds increase fitness of alien plants by consuming and dispersing their seeds (Simberloff & Holle 1999), fruit foraging bird species, such as the common starling *S. vulgaris* and the house sparrow *P. domesticus,* which are strictly alien to southern Africa were not observed visiting the established alien *L. camara* and *S. mauritianum* at all study sites. A possible explanation could be the presence of alternative preferential food resources at the study sites (Knight 1986; Schaefer et al. 2003), since these heavily frugivorous bird species are not completely obligate frugivores (Hockey et al. 2005). Many bird species include arthropods associated with fruits as a dietary supplement due to the high nutritional demand during breeding periods (Hockey et al. 2005). In addition, Lafleur et al. (2007) reported that the European starling *S. vulgaris* selected fruits that it was most familiar with during fruit choice trials in Connecticut, which may partly explain why novel alien fruits might not be preferred by the common starling *S. vulgaris* as observed in this study.

The multiple correspondence analyses (MCA) map and tabulated standardized deviates indicated that positive associations between foraging bird species based on their visitation frequencies and shrub species were site specific. The positive associations between the African olive-pigeon *Columba arquatrix*, speckled mousebird *Colius striatus* the alien *S. mauritianum* and based on their visitation frequencies was also reflected in the significantly higher visitation frequencies given by the variance components analysis for these two bird species on the alien *S. mauritianum.* However, there were exceptions with respect to the other bird species. For example, the red-faced mousebird *U. indicus* and the olive thrush *T. olivaceous* according to the MCA map and computed standardized deviates displayed a high positive association with the alien *L. camara* but only at the Swellendam site. This was in contrast to the variance components analysis, which found no significantly different visitation frequencies by these two bird species on *L. camara* to the other shrub species over all sites. The MCA derived site-specific associations between these two bird species and the alien *L. camara* might be possibly due to a lower level of human activity at the remote Swellendam site. This suggestion is supported by reports that human disturbance activity negatively influences foraging activity of frugivorous birds in Costa Rica (Wilms & Kappelle 2006; Gomes et al. 2008). Similarly, forest patches in fynbos that are less disturbed by human activity and fire (Knight 1988; Manders & Richardson 1992; Cowling et al. 1997) are visited more frequently by birds due to the higher levels of fruit diversity than in disturbed patches (Kollmann 2000).

Non-frugivorous bird species, which comprised 21.5% of the total bird species complement, were also observed visiting some alien shrubs more frequently than indigenous shrubs suggesting that alien trees and shrubs may also be more effective competitors for pollinators. Noteworthy in this regard is that the primarily insectivorous black-whiskered vireo *Vireo altiloquous* was found to be a more reliable dispersal agent of many fruiting plants than obligate frugivores due to its regular opportunistic foraging on fruits and its local abundance in Puerto Rico forests (Carlo et al. 2003). In this study, the nectarivorous Cape sugarbird *Premerops cafer* and the broad diet spectrum yellow bishop *E. capensis* displayed substantially higher foraging visitation frequencies on *S. mauritianum* than the indigenous shrubs, which may however associated with nectar and frugivorous insects in this case. Similarly, heavily frugivorous bird species that are also nectar feeders such as the speckled mousebird *C. striatus,* Cape bulbul *P. capensis* and Cape white-eye *Z. capenisis,* and the moderately frugivorous southern masked-weaver *P. velatus* also exhibited relatively high visitation frequencies on *S. mauritianum.* Such focus by frugivorous, nectivorous and insectivorous birds (Johnson et al. 2006) on an alien shrub *S. mauritianum* could lead to disruption of reproduction of indigenous taxa (Johnson & Bond 1992; Larson & Barrett 2000; Donaldson et al. 2002) and altered native community structure and composition (Ghazoul et al. 2004; Traveset & Richardson 2006).

In conclusion, the higher visitation frequencies observed by specifically in heavily frugivorous birds on the *S. mauritianum* and *L. camara* fruits partly supported the study

hypothesis. The findings concur with previous reports (e.g. Geldenhuys et al. 1986; Jordaan et al. 2011) showing that local frugivorous bird species use alien fruits to meet their daily energy demands thereby potentially enhancing the seed dispersal of these two alien species to the disadvantage of co-occurring indigenous shrubs.

3.6. Reference list

Abdi, H. & Valentin, D. (2007) Multiple correspondence analysis. *Encyclopedia of Measurement and Statistics.* (ed. Salkind, N.) pp. 651-657. Thousand Oaks (CA): Sage.

Alcantara, J., Rey, P.J., Valera, F., Sanchez-Lafuente, A.M., & Gutierrez, J.E. (1997) Habitat alteration and plant intra-specific competition for seed dispersers. an example with *Olea europaea* var*. sylvestris. OIKOS*, **79**, 291–300.

Aslan, C.E. & Rejmanek, M. (2010) Avian use of introduced plants: ornithologist records illuminate interspecific associations and research needs. *Ecological Applications,* **20**, 1005-1020.

Bascompte, J. & Jordano, P. (2007) The structure of plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 567-593.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. (2000) *Bird census techniques.* Academic Press, London.

Binggeli, P. (1996) A taxonomic, biogeographical and ecological overview of invasive woody plants. *Journal of Vegetation Science,* **7**, 121-124.

Bond, W.J. (1994) Do mutualisms matter -assessing the impact of pollinator and disperser disruption on plant extinction? Philosophical Transactions of the Royal. *Society of London Series B-Biological Sciences,* **344**, 83-90.

Buckley, Y.M., Anderson, S., Catterall, C.P., Corlett, R.T., Engel, T., Gosper, C.R., Nathan, R., Richardson, D.M., Setter, M., Spiegel, O., Vivian-Smith, G., Voigt, F.A., Weir, J.E.S. & Westcott, D.A. (2006) Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology*, **43**, 848–857.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hayes, D. (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology,* **16**, 630-640.

Carlo, T.A. (2005) Interspecific behaviour change seed dispersal pattern of an avian-dispersed plant. *Ecology*, **86**, 2440-2449.

Carlo, T.A., Aukema, A.G. & Morales, J.M. (2007) Plant-frugivore interactions as spatially explicit networks: integrating frugivore foraging with plant spatial patterns. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 369-390. Reading: Biddles Ltd.

Carlo, T.A., Collazo, J.A. & Groom, M.J. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia*, **134**, 119–131.

Castley, J.G., Bruton, J-S., Kerley, G.I. & McLachlan, A.H. (2001) The importance of seed dispersal in the Alexandria coastal dunefield. S*outh Afric*a *Journal of Coastal Conservation*, **7**, 57-70.

Chapman, J.L. & Reiss, M.J. (1999) *Ecology: Principles and Applications.* Cambridge University Press, UK.

Chavez-Ramirez, F. & Slack, D.R. (1994) Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe Juniper. *OIKOS*, **71**, 40-46.

Cody, L.M. (1983) Bird diversity and density in South African forests. *Oecologia*, **59**, 201-215.

Cowling, R.M. & Richardson, D.M. (1995) *Fynbos: South Africa's unique floral kingdom*. Fernwood Press, Cape Town.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M. & Arianoutsou, M. (1996) Plant diversity in Mediterranean-climate regions. *Trends in Ecology & Evolution*, **11**, 362-366.

Dennis, A.J. & Westcott, D.A. (2007) Estimating dispersal kernels produced by diverse community of vertebrates. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 201 – 228. Reading: Biddles Ltd.

Donaldson, J., Nanni, I., Costas, Z. & Kemper, J. (2002) Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa. *Conservation Biology*, **16**, 1267-1276.

Fleming, T.H. (1979) Do tropical frugivores compete for food? *American Zoologist,* **19**, 1157–1172.

Garcia, D., Zamora, R., Gómez, J.M. & Hodin, J.H. (2001) Frugivory in *Juniperus communis* depends more on population characteristics than on individual attributes. *Journal of Ecology*, **89**, 639–647.

Geldenhuys, C.J., le Roux. P.J. & Cooper, K.H. (1986) Alien invasions in indigenous evergreen forest. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 119–131. Cape Town, Oxford University Press.

Ghazoul, J. (2004) Alien abduction: disruption of native plant-pollinator interactions by invasive species. *Biotropica*, **36**, 156-164.

Glyphis, P.J., Milton, J.S. & Siegfried, R.W. (1981) Dispersal of *Acacia cyclops* by birds. *Oecologia*, **48**, 138-141.

Godinez-Alvarez, H. & Jordano, P. (2007) An empirical approach to analysing the demographic consequences of seed dispersal by frugivores. *Seed dispersal: theory and its application*

in a changing world. (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 391-404. Reading: Biddles Ltd.

Goldblatt, P. & Manning, J.C. (2002) Plant diversity of the Cape Region of Southern Africa. *Annals of the Missouri Botanical Garden,* **89**, 281–302.

Gomes, L.G.L., Oostra, V. Nijman, V., Cleef, A.M. & Kappelle, M. (2008) Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. *Biological Conservation*, **141**, 860-871.

Gooden, B., French, K., Turner, P.J. & Downey, P.O. (2009) Impact threshold for an alien plant invader, *Lantana camara* L., on native plant communities. *Biological Conservation,* **142**, 2631-2641.

Gosper, C.R., Whelan, R.J. & French, K. (2006) The effect of invasive plant management on the rate of removal of vertebrate-dispersed fruits. *Plant Ecology*, **184**, 351 –363.

Green, R.J. (2007) Refining the conservation management of seed-dispersing frugivores and their fruits: examples from Australia. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 579-598. Reading: Biddles Ltd.

Herrera, C.M. (1995) Plant-vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics,* **26**, 705-727.

Herrera, C.M. (2002) Seed dispersal by vertebrates. *Plant animal interactions: an evolutionary approach*. (eds. Herrera, C.M. and Pellmyr, O.) pp. 185-208. Blackwell Science, Oxford, UK.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (eds) (2005) *Roberts' birds of Southern Africa*, 7th edn. John Voelcker Bird Book Fund, Cape Town.

Hoffman, D.L. & Leeuw, J. (1992) Interpreting multiple correspondence analysis as a multidimensional scaling method. *Marketing Letters,* **3,** 259-272.

Holmes, P.M. (2001) A comparison of the impact of winter versus summer burning of slash fuel in alien-invaded fynbos areas in the Western Cape. *Southern African Forestry Journal,* **192**, 41–49.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review Ecological Systematics*, **13**, 201–228.

Howe, H.F. (1977) Bird activity and seed dispersal of a tropical wet forest tree. *Ecology*, **58**, 539-550.

Iponga, D.M. (2009) Invasive potential of the Peruvian pepper tree *Schinus molle* in South Africa. Ph.D. Thesis, University of Stellenbosch, South Africa.

Johnson, S.D. & Bond, W.J. (1992) Habitat dependent pollination success in a Cape Orchid. *Oecologia*, **91**, 455-456.

Jordaan, L.A., Johnson, S.D. & Downs, C.T. (2011) Digestion of fruit of invasive alien plants by three southern African avian frugivores. *Ibis*, **153**, 863-867.

Jordano, P. (2007) Frugivores, seeds and genes: analysing the key elements of seed shadows. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Jordano, P. & Schupp, E.W. (2000) Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs,* **70**, 591–615.

Jordano, P. (1987) Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology*, **68**, 1711-1723.

Jordano, P. (2000) Fruits and frugivory. *Seeds: the ecology of regeneration in natural plant communities.* (ed. Fenner, M.) pp. 125-166. CABI Publishers, Wallingford, UK.

Kemper, J., Cowling, R.M. & Richardson, D.M. (1999) Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. *Biological Conservation*, **90**, 103-111.

Knight, R.S. & Siegfried, W.R. (1983) Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia*, **56**, 405-412

Knight, R.S. (1986) A comparative analysis of fleshy fruit displays in alien and indigenous plants. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 171-178. Oxford University Press: Cape Town.

Knight, R.S. (1988) Aspects of plant dispersal in the south-western Cape with particular reference to the roles of birds as dispersal agents. Ph.D. Thesis, University of Cape Town, South Africa.

Kollmann, J. (2000) Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 29–51.

Krug, C.B. & Krug, R.M. (2007) Restoration of old fields in renosterveld: a case study in a Mediterranean-type shrubland of South Africa. *Old fields: dynamics and restoration of abandoned farmland.* (eds. Cramer, V.A. & Hobbs, R.J.) pp. 265-334. Society for Ecological Restoration International. Island Press.

Kruger, F.J., Richardson, D.M. & Van Wilgen, B.W. (1986) Processes of invasion by alien plants. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 145–155. Cape Town, Oxford University Press.

LaFleur, N.E., Rubega, M.A. & Elphick, C.S. (2007) Invasive fruits, novel foods, and choice: an investigation of European Starling and American Robin frugivory. *Wilson Journal of Ornithology,* **119**, 429–438.

Lambert, F.R. (1989) Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. *Ibis*, **131**,521-527.

Larson, B.M.H. & Barrett, S.H. (2000) A comparative analysis of pollen limitation in flowering plants. *Biological Journal of the Linnean Society*, **69**, 503-520.

le Maitre, D.C. & Midgley, J.J. (1992) Plant reproductive ecology. *The ecology of fynbos.* (Ed. Cowling, R.) pp. 135-174. Oxford University Press: Cape Town.

Levine, J.M. & Murrell, D. (2003) Community-level consequences of seed dispersal patterns. *Annual Reviews of Ecology and Systematics*, **34**, 549-574.

Manders, P.T. & Richardson, D.M. (1992) Colonization of Cape fynbos communities by forest species. *Forest Ecology and Management*, **48**, 277-293.

McNamara, J.M., Houston, A.I. & Lima, L.S. (1994) Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology,* **25**, 287-302.

Milton, J.S., Wilson, J.R.U., Richardson, M.D., Seymour, C.L., Dean, W.R.J., Iponga, D.M. & Proches, S. (2007) Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. *Journal of Ecology*, **95**, 648-661.

Mucina, L. & Rutherford, M.C. (eds) (2006) The Vegetation of South Africa, Lesotho and Swaziland. *Strelitzia* 19, South African National Biodiversity Institute, Pretoria.

Muller-Landau, H.C. & Hardesty, B.D. (2005) Seed dispersal of woody plants in tropical forests: concepts, examples, and future directions. *Biotic interactions in the tropics: their role in the maintenance of species diversity*. (eds. Burslem, D., Pinard, M. & Hartley, S.) pp. 267–309. Cambridge University Press, Cambridge, UK.

Musil, C.F., Milton, S.J. & Davis, G.W. (2005) The threat of alien grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies. *South African Journal of Science,* **101**, 337-344.

Nathan, R. & Muller-Landau H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution,* **15**, 278-285.

Nathan, R. (2007) Total dispersal kernels and the evaluation of diversity and similarity in complex dispersal systems. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Oatley, T.B. (1984) Exploitation of a new niche by the rameron pigeon *Columba arquatrix* in Natal. *Proceedings of the Fifth Pan-African Ornithological Congress* (ed. Ledger, J.A.), pp. 323-330, Southern African Ornithological Society.

Proches, S., Wilson, J.R.U., Richardson, D.M. & Chown, S.L. (2008) Herbivores, but not other insects, are scarce on alien plants*. Austral Ecology*, **33,** 691–700.

Quix, J.C. (2007) The role of alien plants in the composition of fruit-eating bird assemblages in Brazilian urban ecosystems. *Orsis*, **22**, 87-104.

Reichard, S.H., Chalker-Scott, L. & Buchaman, S. (2001) Interaction among non-native plants and birds. *Avian ecology and conservation in an urbanising world*. (eds. Marcluff, J.M., Bowman, R. & Donnelly, R.) pp. 179- 223. Kluwer Academic Publishers.

Richardson, D.M. & Fraser, M.W. (1995) Birds of Swartboskloof, Jonkershoek Valley, Stellenbosch: a mountain fynbos ecosystem. *Southern Birds,* **18**, 1–44.

Richardson, D.M., Allsopp, N., D'Antonio C.M., Milton, S.J. & Rejmánek, M. (2000) Plant invasions - the role of mutualism. *Biology Reviews,* **75**, 65-93.

Richardson, D.M., Macdonald, I.A.W., Holmes, P.M. & Cowling, R.M. (1992) Plant and animal invasions. *The ecology of fynbos: nutrients, fire and diversity* (ed. Cowling, R.M.) pp. 271–308. Oxford University Press, Cape Town.

Roura-Pascual, N., Richardson, D.M., Krug, R.M., Brown, A., Chapman, A.R., Forsyth, G.G., le Maitre, D.C., Robertson, M.P., Stafford, L., Van Wilgen, B.W., Wannenburgh A, & Wessels, N. (2009) Ecology and management of alien plant invasions in South African fynbos: accommodating key complexities in objective decision-making. *Biological Conservation*, **142**, 1595–1604.

Sallabanks, R. & Courtney, S.P. (1993) On fruit-frugivore relationships: variety is the spice of life. *OIKOS*, **68**, 567-570.

Sallabanks, R. (1993) Fruiting plant attractiveness to avian seed dispersers: native vs. invasive Crataegus in western Oregon. *Madrono*, **40**, 108–16.

Schaefer, H.M., Schmidt, V. & Bairlein, F. (2003) Discrimination abilities for nutrients: which difference matters for choosy birds and why? *Animal Behaviour*, **65**, 531–541.

Schupp, E.W. (1993) Quantity, quality and effectiveness of seed dispersal by animals. *Vegetatio*, **107/108**, 12-29.

Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A., Nathan N. (2009) Long-distance seed dispersal. *Annual Plant Reviews*, **38,** 204–237.

Simberloff, D. & Holle, V.B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Sinclair, I. & Ryan, P. (2003) *Birds of Africa south of the Sahara.* Struik Publishers, Cape Town.

Snow, B. & Snow, D. (1988) *Birds and berries*. T. and A.D. Poyser, Calton, UK.

Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, **10**, 718–728.

Steadman, D.W. (1997) The historic biogeography and community ecology of Polynesian pigeons and doves. *Journal of Biogeography*, **24**, 737-753.

Telleria, J.L., Ramirez, A. & Perez-Tris, J. (2005) Conservation of seed-dispersing migrant birds in Mediterranean habitats: shedding light on patterns to preserve processes. *Biological Conservation*, **124**, 493–502.

Terborgh, J. & Diamond, J. M. (1970) Niche overlap in feeding assemblages of New Guinea birds. *Wilson Bulletin,* **82**, 29–52.

Traveset, A., & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecology and Evolution*, **21**, 208–216.

Underhill, G.L. & Hofmeyr, H.J. (2007) Barn swallows *Hirundo rustica* disperse seeds of rooikrans *Acacia cyclops*, an invasive alien plant in the fynbos biome. *Ibis*, **149**, 468-471.

van Wyk, B. & van Wyk, P. (1997) *Field guide to trees of southern Africa*. Struik Publishers, Cape Town.

Vazquez, D.P. & Simberloff, P. (2002) Ecological specialization and susceptibility to disturbance: conjectures and refutations. *The American Naturalist,* **159**, 606-623.

Vazquez, D.P., Morris, W.F. & Jordano P. (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters*, **8**, 1088-1094.

Williams, P. (2006) The role of blackbirds *Turdus merula* in weed invasion in New Zealand. *New Zealand Journal of Ecology*, **30**, 285-291.

Williams, P.A. & Karl B.J. (1996) Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. *New Zealand Journal of Ecology*, **20**,127-145.

Willson, M.F. & Whelan, C.J. (1993) Variation of dispersal phenology in a bird-dispersed shrub *Cornus drummondii*. *Ecological Monographs*, **63**, 151-172.

Willson, M.F., Irvine, A.K. & Walsh, G.N. (1989) Vertebrate dispersal syndromes in some Australian and New Zealand Plant Communities, with geographic comparisons. *Biotropica*, **21**, 133-147.

Chapter 4

Do birds forage fruits of alien shrubs in greater numbers and for longer periods than fruits of indigenous shrubs?

4.1. Abstract

The hypothesis tested was that fruits of alien shrubs are foraged by larger numbers of birds and for longer periods that those of indigenous shrubs. This was achieved by measuring the numbers of different species of birds included in heavily and moderately frugivorous groups and the times they spent foraging on fruits of two alien shrubs (*Solanum mauritianum* and *Lantana camara)* and two indigenous shrubs (the indigenous *Chrysanthemoides monilifera* and *Olea europaea* subsp *africana)* which co-occurred at four different sites (Hout Bay, Paarl, Hermanus and Swellendam) in the Cape Floristic Region. Both the heavily and moderately frugivorous birds as a whole did not forage fruits of the two alien shrubs in greater numbers than fruits of the two indigenous shrubs. However, heavily frugivorous birds as a whole foraged fruits of the alien *L. camara* for longer periods than fruits of the two indigenous shrubs, though this was not evident in the alien *S. mauritianum.* At the individual species level, only 4 of the 11 heavily frugivorous bird species, but none of the 14 moderately frugivorous species, foraged fruits of the alien shrubs in either greater numbers or for longer periods than fruits of the indigenous shrubs. Noteworthy, was that only the heavily frugivorous *Columba arquatrix* foraged fruits of the alien *S. mauritianum* in significantly greater numbers and for significantly longer periods than fruits of the two indigenous shrubs. This finding is consistent with previous reports that *S. mauritianum* has altered the feeding ecology of the African olive-pigeon. Five bird species, namely *Columba arquatrix, Colius striatus, Sturnus vulgaris*, *Zosterops capensis* and *Columba guinea*, were all observed foraging fruits of the alien *L. camara* in equivalent numbers and for equivalent periods as *O. africana* whose typical alien features, such as high fruit production and extended fruiting period, may explain its equal preference by foraging birds. Noteworthy also was that these five bird species, with the exception of the *Columba guinea*, foraged fruits of the indigenous *C. monilifera* in smaller numbers and for shorter periods than fruits of either or both of the alien shrubs. The lower partiality of these bird species for *C. monilifera* fruits is attributed to this shrub's short fruit display period, rapid fruit spoiling due to insect infestation and rapid fruit desiccation which renders the fruit unsuitable for consumption by specialised frugivorous birds. These and other irregular findings provided only partial support for the study hypotheses.

Keywords: numbers of birds, bird species, foraging periods, frugivore groups, fleshy fruits, alien and indigenous shrubs.

4.2. Introduction

The more attractive and rewarding fruits of alien invasive plant species over their native counterparts (Kollmann 2000; Traveset & Richardson 2006; LaFleur et al. 2007; Pysek & Richardson 2008; Kueffer et al. 2009; Gosper & Vivian-Smith 2010; Jordaan et al. 2011) might attract larger numbers of foraging birds, and lead to prolonged foraging periods. Consequently, foraging of birds in large numbers and over longer periods on alien fruits might increase their fruit/seed removal to the detriment of the native species (Courtney & Sallabanks 1992; Schupp 1993; Jordano & Schupp 2000; Trakhtenbrot et al. 2005; Traveset & Richardson 2006). This is based on the assumption that numbers of birds and their foraging times influence numbers of seeds removed fruiting trees (Schupp et al. 1993; Jordano 2000; Schurr et al. 2009). According to Schupp (1993), the numbers of seeds determine the quantity component of the effectiveness of seed dispersal. Often seed removal by birds has been found to be proportional to the numbers of visiting birds (Chavez & Slack 1994; Jordano & Schupp 2000; Schupp et al. 2010), fruit abundance (Izhaki 2002). Whereas larger birds are expected to remove more seeds if the stay longer in the fruiting tree (Pratt & Stiles 1983), the numbers of seeds removed may differ depending on whether is pulp biter, swallower or masher, and the size of the fruit being processed (see Schupp 1993).

The production of substantially larger fruit crops by alien trees and shrubs than native species often attract a larger variety of dispersal agents (Sallabank 1993; Izhaki 2002; Gosper et al. 2005; Carlo et al. 2007). For example, the numerous fruits produced by *Sambucus nigra* in New Zealand and by *Juniperus ashei* in Texas attract larger flocks of European starlings *Sturnus vulgaris,* cedar waxwings *Bombycilla cedrorum* and American robins *Turdus migratorius* (Chavez & Slack 1994; Williams & Karl 1996) which may remove larger portions of the fruit crop than solitary bird species (Laska & Stiles 1994; Williams & Karl 1996). Also, foraging times are likely to vary with a pertinent bird species' degree of frugivory with heavily frugivorous birds expected to spend longer periods foraging fruits than partially frugivorous birds (Pratt & Stiles 1983; Wheelwright 1991), especially on shrubs and trees where fruits ripen asynchronously. However, Pratt & Stiles (1983) argued that longer foraging periods might retard efficiency of dispersal if the frugivorous birds regurgitate and defecate seeds under the maternal plant canopy. Furthermore, the foraging time of a bird is influenced by its metabolic requirements, predation level and patch characteristics (Sallabanks & Courtney 1993; McNamara et al. 1994). For example, American robin *Turdus migratorius* in Western Oregon forage continuously for longer periods when energy-stressed to maximise fruit intake, but foraging for shorter periods to minimize energy expenditure and predation risk when less energy-stressed (Sallabanks & Courtney 1993).

Seed dispersal through frugivory determines the spatial structure, dynamics and composition of native plant communities (Herrera 1995; Jordano 2000; Godinez-Alvarez et al. 2002; Levine et al. 2003; Godinez-Alvarez & Jordano 2007; Jordano 2007; Spiegel & Nathan 2007). While most birds rely on fruits for food, fleshy-fruited plants in turn depend on birds as

their standard seed dispersal vector in many parts of the world (Howe & Smallwood 1982; Janzen 1985; Stiles 2000; Jordano 2007). Globally, approximately 50% of fleshy-fruited plants rely on birds for dispersal of their seed (Binggeli 1996). Especially high percentages occur in tropical ecosystems where more than 90% of the native plants rely on vertebrates for seed dispersal (Howe & Smallwood 1982; Jordano 2000) with birds being the dominant vertebrate dispersers (Willson et al. 1989; Whelan et al. 2008). In southern Africa, at least 23% of the fleshy-fruited native trees and shrubs rely on birds for seed dispersal (Knight & Siegfried 1983; Knight 1988), this including 80% of the fleshy-fruited woody species in succulent karroid scrubland, dune thicket and afromontane forests, 3 to 28% of true fynbos shrubs and 26 to 46% of renosterveld shrubs (le Maitre & Midgley 1992). Consequently, Knight (1986) predicted that presence of fleshy-fruited alien trees and shrubs in the same habitat with indigenous species might pose competition for dispersal agents in the Cape Floristic Region because alien species are able to form novel mutualism with many native species (Richardson et al. 2000b; Traveset & Richardson 2006). However, specific investigations of plant-bird mutualisms and their implications for native species' seed dispersal in alien-infested areas are limited globally yet birds are important dispersers of alien propagules (Rejmanek & Richardson 1996; Gosper et al. 2005; Kueffer 2006).

In southern Africa, *Solanum mauritianum* has been blamed for changing the feeding ecology of the African olive-pigeon *Columba arquatrix,* and its ability to attract large numbers of local avian dispersers may deprive native species of avian seed dispersal agents (Oatley 1984; Geldenhuys et al. 1986). Knight (1986) compared fruit displays of alien and indigenous fleshy-fruited plants dispersed by birds in southern Africa, and found that alien shrub species had fruit displays that were both more conspicuous and attractive than those of indigenous species although these differences were not sufficient to account for the observed level of tree and shrub invasions in the south-western Cape. In contrast, Milton et al. (2007) reported that alien species could infiltrate ecological processes since they found that birds dispersed the fruits of alien shrubs into the Kalahari savanna where they are likely to become invasive. Since foraging by avian frugivores is associated with seed dispersal (Howe & Smallwood 1982; Janzen 1985; Jordano 1993; Jordano 2007), a comparison of the numbers of birds of different species and the times spent foraging fruits of alien and indigenous shrubs in the Cape Floristic Region could effectively elucidate whether seed dispersal process of indigenous species is disrupted through competition with alien species (Green 2007). Therefore, the hypothesis tested in this study was that fleshy fruits of alien shrubs are foraged by larger numbers of frugivorous birds and for longer periods than those of indigenous shrubs.

4.3. Methods and material

4.3.1. Experimental design, study sites and species

The experimental design comprised four study sites, each comprising mixed populations of alien and indigenous shrubs, located on Peninsula Granite Fynbos (Hout Bay site), Swartland Shale Renosterveld site (Paarl site), Overberg Sandstone Fynbos (Hermanus site) and Breede Shale Renosterveld site (Swellendam site). The fynbos and renosterveld vegetation classifications were according to Mucina and Rutherford (2006). Within each site, there were intermixed populations of four different shrub species with fleshy fruit displays, namely the indigenous shrubs *Chrysanthemoides monilifera* (*C. monilifera)* and *Olea europaea* subsp. *africana* (*O. africana*), and the alien shrubs *Lantana camara* and *Solanum mauritianum*. Since vegetation composition strongly influences fruit and seed removal by birds (Garcia et al. 2001; Carlo et al. 2007), all shrub species were selected based on their co-occurrence over a wide range of natural vegetation types, their overlapping fruiting times (Van Wyk & Van Wyk 1997) and consumption of their fruit by local frugivorous birds (Richardson & Fraser 1995). *Lantana camara, C. monilifera* and *O. africana* possess similar fruit architectures, namely single-seeded drupes that turn black when ripe, whereas *S. mauritianum* produces green multi-seeded berry turning yellowish when ripe.

4.3.2. Numbers of foraging birds and foraging periods

At each site, bird surveillances were conducted during the peak fruiting periods of the alien and indigenous shrub species and restricted to 6 h daily periods of peak bird activity, namely a 3 h period after sunrise and a 3 h period before sunset (Howe 1977; Snow & Snow 1988; McNamara et al. 1994; Bibby et al. 2000). Individual shrubs that are reproductively mature were randomly selected for bird surveillances, which were conducted at approximately 30m distance from each shrub during the peak fruiting periods namely, spring and autumn of 2008 and 2009 (Knight 1988). The bird surveillances were performed manually with binoculars (8 x 42 magnification) and simultaneously recorded with a digital camcorder (Kodak C813: 8.2 megapixel, ISO 1250, digital IS) for a permanent record (Spiegel & Nathan 2007). Five days of bird surveillances were conducted on each of the four shrub species at each of the four sites (80 day surveillance period overall). The numbers of birds of different species and the times in seconds that they were observed foraging on fruits of the alien and indigenous shrubs over each 6-hour surveillance period were recorded and summed up for the five-day observation periods at each site. Plots of the cumulative numbers of foraging birds of all species against surveillance days (Figure 4.1) showed that the 20 surveillance days (120 surveillance hours) on each shrub species provided adequate samples of total foraging numbers of birds. Bird species were identified with the aid of descriptions and keys presented in Sinclair and Ryan (2003) and Hockey et al. (2005). They were classified into two groups based on descriptions presented in Hockey et al. (2005), namely heavily frugivorous birds with fruits constituting their main diet and

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moderately frugivorous birds with fruits constituting their secondary or occasional diet (Hockey et al. 2005).

4.3.3. Fruit density

At each site, approximately 35 reproductively mature flowering shrubs of each alien and shrub species were randomly selected and tagged for measurements of fruit production. Two 0.25 m square quadrats were positioned on either side of the canopy of each fruiting shrub and the numbers of individual fruits present in the quadrats counted. Due to the high temporal and spatial variability in fruit production by the alien and indigenous shrubs (Knight 1988), measurements of fruit production were conducted several times during each shrub species peak fruiting times (i.e. spring and autumn) spanning a 2-year period (2008-2009). Fruit production was expressed as the numbers of fruits m^{-2} of plant canopy and as total fruit dry mass m^{-2} of plant canopy, this calculated from the product of the numbers of fruits m^{-2} of plant canopy and the mean fruit dry mass of each shrub species at each site.
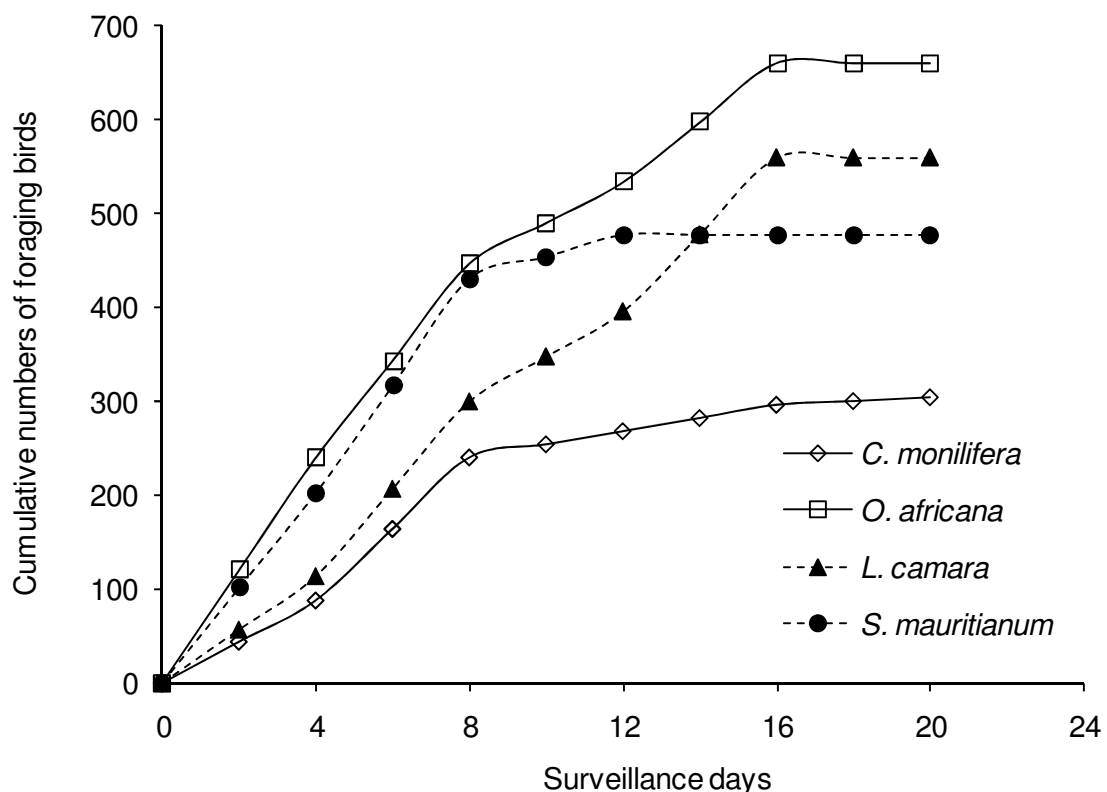
Figure 4.1. Plots of the cumulative numbers of recorded foraging birds against surveillance days for four shrub species (the indigenous *C. monilifera* and *O. africana,* and alien *L. camara* and *S. mauritianum*) at four diverse sites

4.4. Data synthesis and statistical analyses

4.4.1. Variance component analysis

All measurements were $\log_e$ transformed before statistical analysis to reduce the inequality of variance in the raw data so these more closely approximated normal distributions. The experimental design was unbalanced due to unequally replicated measurements on each bird species at each site. Consequently, a residual maximum likelihood (REML) variance component analysis (linear mixed model) was applied to test for differences in the numbers of birds of different species foraging on fruits of the alien and indigenous shrubs and their foraging periods. Three separate REML analyses were conducted using the Wald X^2 statistic generated by the REML (GENSTAT Discovery Edition 3, VSL Lty, UK). The first REML tested for differences in the total numbers of birds included in heavily and moderately frugivorous groups foraging on fruits of the alien and indigenous shrubs and their foraging periods. The second REML tested for differences in numbers of heavily frugivorous birds of different species foraging on fruits of the alien and indigenous shrubs and their foraging periods. The third REML tested for differences in the numbers of moderately frugivorous birds of different species foraging on fruits of the alien and indigenous shrubs and their foraging periods. In the first REML, bird frugivore group and shrub species variables were fitted in the fixed model and site, shrub and frugivore group factors in the random model. In the second and third REML, bird species and shrub species variables were fitted in the fixed model and site, shrub and bird species factors in the random model. Differences exceeding twice the mean standard error of differences were used to separate significantly different treatment means at P ≤ 0.05. This was based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is two.

Differences between alien and indigenous shrub species in measured fruit density and fruit mass were tested with Kruskal-Wallis H-test (UNISTAT ver. 5.5). Significantly different ranked means at P ≤ 0.05 were separated with Dunnet multiple range test.

4.4.2. Multiple correspondence analysis

Multiple correspondence analysis (MCA) was applied to determine associations between the numbers of fruit foraging frugivorous bird species, shrub species and sampling sites. It is an extension of correspondence analysis, which allows analysis of the pattern of relationships of several categorical dependent variables (Abdi & Valentin 2007). Its major premise is that strongly related categorical variables are closely associated (Hoffman & Leeuw 1992). In the application of MCA in this study, species exclusion criteria were applied by placing thresholds on recorded foraging numbers of birds and foraging bird times to exclude bird species with frequently low or absent values. The exclusion criteria applied were the omission of those bird species whose total foraging numbers were less than 50 individuals and whose total foraging times were less than 50 second. Computed standardized deviates and a correspondence map of the first two dimensions identified the degree of association between different species of

birds, alien and indigenous shrub species and sites. Large and positive values of standardized deviates indicated better than expected associations between bird species and shrub species or sites whereas the converse applies to large negative values of standardized deviates.

4.5. Results

4.5.1. Variance component analysis

The 400 field surveillance records yielded 11 species of heavily frugivorous and 14 species of moderately frugivorous bird species included in 32 genera and 17 families foraging on fruits of the alien and indigenous shrubs at the four study sites. There were no-significant (P ≥ 0.05) differences in the numbers of heavily frugivorous birds foraging on fruits of the alien and indigenous shrubs (Table 4.1, Figure 4.2A), and a similar pattern was observed in the moderately frugivorous birds. However, the heavily frugivorous birds foraged fruits of all four shrub species in significantly greater numbers than moderately frugivorous birds. With respect to foraging periods, there was a significant (P ≤ 0.05) interaction between shrub species and frugivore group (Table 4.1). Heavily frugivorous birds spent significantly (P ≤ 0.05) longer periods than moderately frugivorous birds foraging on fruits of the two alien species but not fruits of the two indigenous species (Figure 4.2B). Also, heavily frugivorous birds foraged fruits of the alien *L. camara* for significantly (P ≤ 0.05) longer periods than fruits of the two indigenous shrubs, though this was not evident in the alien *S. mauritianum* (Figure 4.2B).

Among the heavily frugivorous group of bird species, there were significant (P ≤ 0.001) interactions between shrub species and bird species for both numbers of foraging birds and foraging periods (Table 4.1). In this group, the large (>150 g) African olive-pigeon *Columba arquatrix* foraged fruits of the alien *S. mauritianum* in significantly (P ≤ 0.05) greater numbers and for significantly (P ≤ 0.05) longer periods than fruits of the two indigenous shrubs (Table 4.2). However, this bird species did not forage fruits of the other alien *L. camara* in significantly (P ≥ 0.05) greater numbers or for significantly (P ≥ 0.05) longer periods than fruits of the two indigenous shrubs (Table 4.2). Also, the medium size (50-150 g) speckled mousebird *Colius striatus* foraged fruits of both alien shrubs in significantly (P ≤ 0.05) greater numbers and for significantly (P ≤ 0.05) longer periods than fruits of the indigenous shrub *C. monilifera* but not fruits of indigenous shrub *O. africana* (Table 4.2).

Table 4.1. Wald χ² statistics derived from three separate REML'S (linear mixed models) which tested for differences in the $\log_e$-transformed average numbers of foraging birds (different groups and species) and their average foraging periods in seconds on fruits of indigenous (*C. monilifera* and *O. africana*) and alien (*L. camara* and *S. mauritianum*) shrubs. Significant at *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

MAIN EFFECTS AND INTERACTIONS	df	WALD X² STATISTIC	
		Numbers of foraging birds	Foraging periods
REML 1		Figure 4.2A	Figure 4.2B
Shrub species	3	2.34	1.09
Frugivore group	1	54.36***	43.56***
Shrub species x Frugivore group	3	4.88	8.95*
REML 2		Table 4.2	Table 4.2
Shrub species	3	2.92	5.29
Heavily frugivorous bird species	10	183.02***	147.96***
Shrub species x Heavily frugivorous bird species	30	73.27***	67.36***
REML 3		Table 4.3	Table 4.3
Shrub species	3	7.52	6.23
Moderately frugivorous bird species	13	66.43***	72.26***
Shrub species x Moderately frugivorous bird species	39	38.87	40.16

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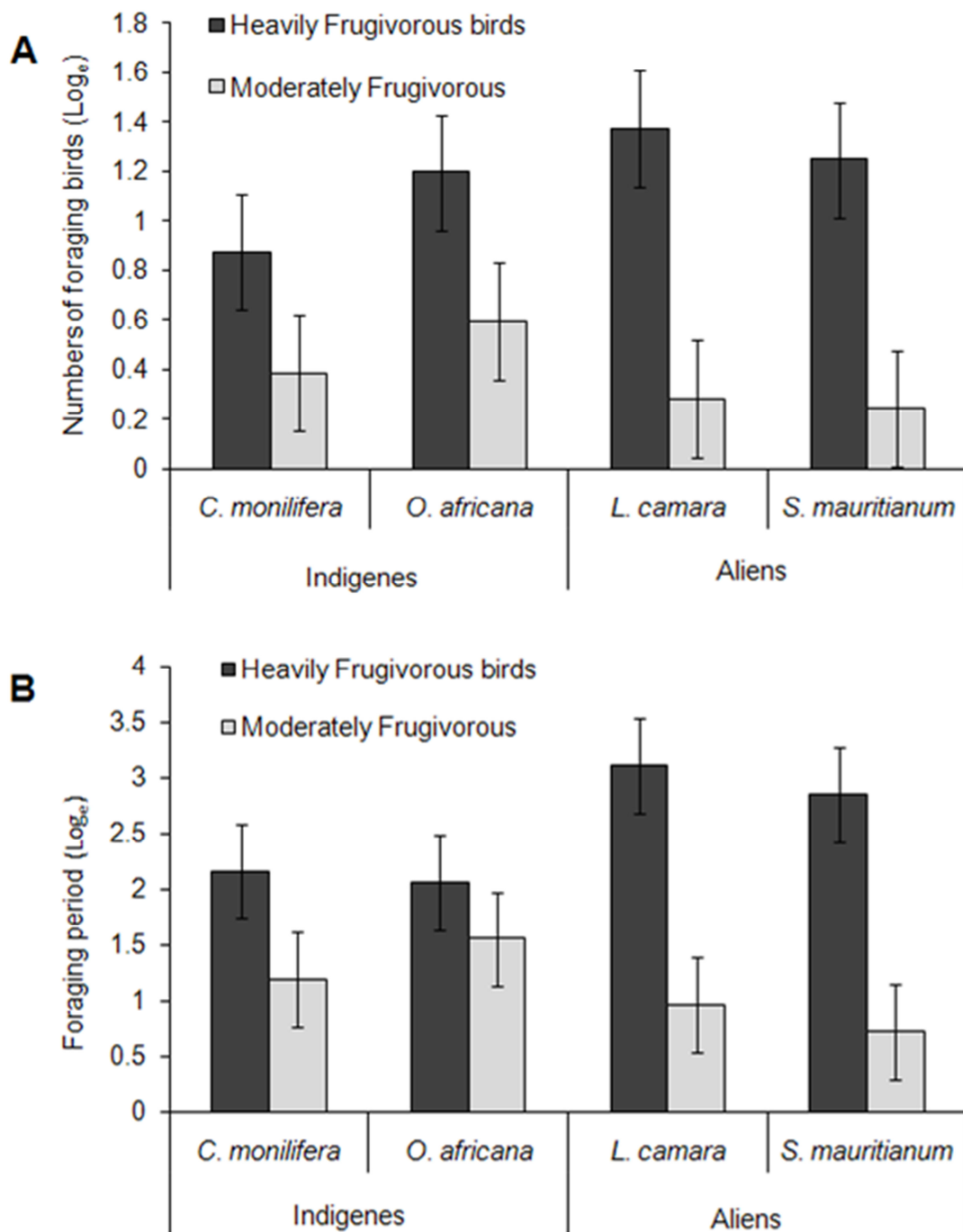
Figure 4.2. A. Numbers of heavily and moderately frugivorous birds and B. times spent foraging fruits of alien (*L. camara* and *S. mauritianum*) and indigenous (*C. monilifera* and *O. africana*) shrub species. Mean standard error of differences shown by bars

Similarly, the tiny (<30 g) Cape white-eye *Zosterops capensis* foraged fruits of both alien shrubs in significantly ($P \leq 0.05$) greater numbers, though not for significantly ($P \geq 0.05$) longer periods, than fruits of the indigenous shrub *C. monilifera* but not fruits of indigenous shrub *O. africana* (Table 4.2). Also, the small (30-50 g) Cape bulbul *Pycnonotus capensis* foraged fruits

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of both alien shrubs for significantly (P ≥ 0.05) longer periods, though not in significantly (P ≤ 0.05) greater numbers, than fruits of indigenous shrub *O. africana* but not fruits of the indigenous shrub *C. monilifera* (Table 4.2). In contrast, the medium size (50-150 g) red-winged starling *Onychognathus morio* foraged fruits of indigenous shrub *O. africana* in significantly (P ≤ 0.05) greater numbers than fruits of the other indigenous shrub *C. monilifera* but not fruits of the alien *L. camara* and avoided *S. mauritianum* fruits (Table 4.2). The medium size (50-150 g) red-faced mousebird *Urocolius indicus* foraged fruits of both alien shrubs and the other indigenous shrub for similar (P ≥ 0.05) periods but avoided fruits of indigenous shrub *O. africana* (Table 4.2).

Among the moderately frugivorous group of bird species, there were no significant (P ≥ 0.05) interactions between shrub species and bird species for both numbers of foraging birds and foraging periods (Table 4.3). The large (>150 g) speckled pigeon *Columba guinea* and the large (>150 g) Cape turtledove *Streptopelia capicola* foraged fruits of both indigenous shrubs and the alien *L. camara* in similar (P ≥ 0.05) numbers and for similar (P ≥ 0.05) periods but avoided fruits of alien *S. mauritianum* (Table 4.3). A notable exception was the southern masked-weaver *Ploceus velatus* which foraged fruits of indigenous shrub *O. africana* for significantly (P ≥ 0.05) longer periods than fruits of the other indigenous shrub and the two alien shrubs (Table 4.3).

4.5.2. Fruit density

The aliens *L. camara* and *S. mauritianum* displayed higher canopy fruit densities than the indigenous shrubs at all four study sites (Figure 4.3). However, *S. mauritianum* exhibited the highest canopy fruit mass over all, except the Cape Town, site with the indigenous *C. monilifera* displaying the lowest canopy fruit mass at all four study sites. Canopy fruit masses of *L. camara* and *O. africana* were probably equal when averaged over all sites with *O. africana* displaying a higher canopy fruit mass than *L. camara* at the Hermanus and Swellendam sites with the converse evident at the Cape Town and Paarl sites.

4.5.3. Multiple correspondence analysis

The multiple correspondence analysis maps and tables of standardized deviates indicated that positive associations between bird species and shrub species in terms of bird foraging numbers (Figure 4.4) and foraging times (Figure 4.5) were site specific. Four bird species were positively associated in terms of their numbers with the indigenous *O. africana*. These included the southern masked-weaver *P. velatus* and Cape canary *S. canicollis* association with *O. africana* at the Paarl site, the red-winged starling *O. morio* association with *O. africana* at the Cape Town site and the common starling *S. vulgaris* association with *O. africana* at the Swellendam site (Figure 4.4). In terms of foraging times, nine bird species were positively associated with *O. africana*. These included the common starling *S. vulgaris*, Cape bulbul *P. capensis* and southern boubou *L. ferrugineusis* association with *O. africana* at the

Swellendam site, the house sparrow *P. domesticus*, southern tchagra *T. tchagra*, Cape bunting *E. capensis* and Cape canary *S. canicollis* association with *O. africana* at the Hermanus site, the Cape turtledove *S. capicola* association with *O. africana* at the Cape Town site only (Figure 4.5).

Three bird species, in terms of their numbers, were associated with the alien *L. camara*. These included speckled mousebird *C. striatus* and the red-faced mousebird *U. indicus* association with *L. camara* at the Swellendam site and the Cape white-eye *Z. capensis* association with *L. camara* at the Paarl site only (Figure 4.4). In terms of foraging times, four bird species were positively associated with *L. camara*. These included the olive thrush *T. olivaceous*, Cape robin *C. caffra* and cape white-eye *Z. capensis* association with *L. camara* at the Paarl site and the red-faced mousebird *U. indicus* association with *L. camara* at the Hermanus site only (Figure 4.5).

One bird species in terms of foraging numbers was positively associated with the alien *S. mauritianum.* This included the African olive-pigeon *C. arquatrix* whose association with *S. mauritianum* was restricted to the Cape Town site (Figure 4.3). In terms of foraging times, three bird species were positively associated with *S. mauritianum.* These included the association between the African olive-pigeon *C. arquatrix* and the grey tit *P. afer* with *S. mauritianum* at the Cape Town site and the association between the southern mouse bird and *S. mauritianum* at the Paarl site only (Figure 4.4).

One bird species in terms of foraging numbers was positively associated with indigenous *C. monlifera.* This included the Cape bulbul *P. capensis* whose association with *C. monilifera* was restricted to the Swellendam site (Figure 4.4). In terms of foraging times, three bird species were positively associated with *C. monilifera*. These included red-winged starling *O. morio* and speckled pigeon *C. guinea* association with *C. monilifera* at the Cape Town site and the Cape weaver *P. capensis* association with *C. monilifera* at the Swellendam site only (Figure 4.5).
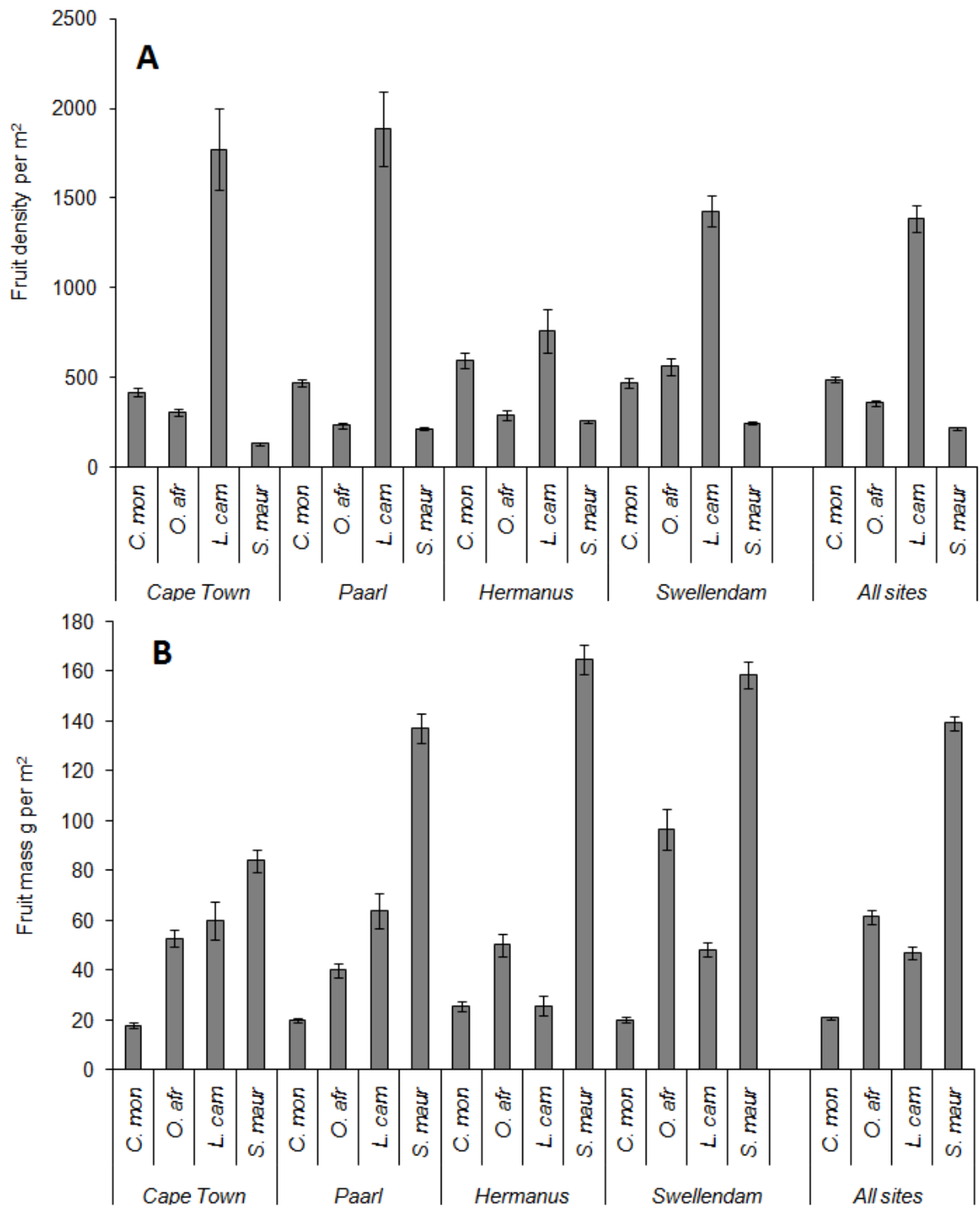
Figure 4.3. Mean fruit density per m^2 (A) and fruit dry mass per m^2 (B) ± standard errors of indigenous *C. monilifera* (*C. mon*) and *O. africana* (*O. afr*) and alien *L. camara* (*L.* cam) and *S. mauritianum* (*S. maur*) and trees shrubs in different sites – Cape Town, Paarl, Hermanus and Swellendam

Table 4.2. REML predicted mean numbers of heavily frugivorous bird species and their foraging periods (log$_e$) on fruits of indigenous (*C. monilifera* and *O. africana)* and alien (*L. camara* and *S. mauritianum*) shrubs. Significantly (P ≤ 0.05) different means with uncommon letters shown in bold; se is mean standard error of differences; * show alien birds

Common Name	Parameter	Indigenes		Aliens	
		C. monilifera	*O. africana*	*L. camara*	*S. mauritianum*
African olive-pigeon	Numbers of Birds	**1.478a**	**0.576a**	**0.922a**	**3.214b**
	Foraging Period	**3.251a**	**0.833a**	**2.947a**	**6.798b**
Speckled mousebird	Numbers of Birds	**0.599a**	**2.547b**	**2.708b**	**2.683b**
	Foraging Period	**1.269a**	**4.387b**	**5.272b**	**6.378b**
Red-winged starling	Numbers of Birds	**1.422a**	**2.844b**	**2.296ab**	**0.000c**
	Foraging Period	**3.039a**	**4.029a**	**4.519a**	**0.000b**
*Common starling	Numbers of Birds	0.000a	1.066a	0.000a	0.000a
	Foraging Period	0.000a	1.199a	0.000a	0.000a
Red-faced mousebird	Numbers of Birds	0.997a	0.000a	1.366a	0.708a
	Foraging Period	**2.272ab**	**0.000a**	**3.202b**	**1.515ab**
Olive thrush	Numbers of Birds	0.520a	0.448a	0.922a	0.520a
	Foraging Period	2.401a	1.562a	3.122a	2.0250a
Sombre greenbul	Numbers of Birds	0.000a	0.000a	0.173a	0.000a
	Foraging Period	0.000a	0.000a	0.641a	0.000a
Cape bulbul	Numbers of Birds	1.522a	**0**.858a	1.979a	2.147a
	Foraging Period	**4.167ab**	**1.764a**	**4.631b**	**5.490b**
*House sparrow	Numbers of Birds	0.000a	0.833a	0.000a	0.000a
	Foraging Period	0.000a	2.070a	0.000a	0.000a
Cape robin-chat	Numbers of Birds	0.896a	0.520a	0.795a	0.621a
	Foraging Period	2.961a	0.749a	3.323a	2.551a
Cape white-eye	Numbers of Birds	**2.177a**	**3.454ab**	**3.917ab**	**3.804b**
	Foraging Period	4.423a	6.049a	6.555a	6.647a
se of differences	Numbers of Birds	± 0.688			
	Foraging Period	± 1.386			

Table 4.3. REML predicted mean numbers of moderately frugivorous bird species and their foraging periods (Log$_e$) on fruits of indigenous (*C. monilifera* and *O. africana)* and alien (*L. camara* and *S. mauritianum*) shrubs. Significantly (P ≤ 0.05) different means with uncommon letters shown in bold; se is mean standard error of differences.

Common Name	Parameter	Indigenes		Aliens	
		C. monilifera	*O. africana*	*L. camara*	*S. mauritianum*
Speckled pigeon	Numbers of Birds	**0.708ab**	**0.916b**	**0.677ab**	**0.000a**
	Foraging Period	**1.683ab**	**2.215ab**	**2.839b**	**0.000a**
Cape turtledove	Numbers of Birds	1.171a	1.161a	0.693a	0.000a
	Foraging Period	**3.841bc**	**4.040c**	**1.709ab**	**0.000a**
Red-eyed dove	Numbers of Birds	0.000a	0.402a	0.000a	0.000a
	Foraging Period	0.000a	0.916a	0.000a	0.000a
Laughing dove	Numbers of Birds	0.000a	0.000a	0.000a	0.000a
	Foraging Period	0.000a	0.000a	0.000a	0.000a
Southern boubou	Numbers of Birds	0.621a	0.889a	0.347a	0.173a
	Foraging Period	2.592a	2.459a	1.364a	0.347a
Common fiscal	Numbers of Birds	0.000a	0.000a	0.000a	0.000a
	Foraging Period	0.000a	0.000a	0.000a	0.000a
Southern masked-weaver	Numbers of Birds	**0.519a**	**2.163b**	**0.576a**	**1.191a**
	Foraging Period	2.535a	4.003a	2.066a	2.166a
Cape weaver	Numbers of Birds	0.761a	0.173a	0.000a	0.173a
	Foraging Period	1.526a	0.347a	0.000a	1.089a
Southern tchagra	Numbers of Birds	0.173a	0.347a	0.000a	0.000a
	Foraging Period	0.486a	1.128a	0.000a	0.000a
Yellow canary	Numbers of Birds	0.487a	0.000a	0.000a	0.000a
	Foraging Period	0.922a	0.000a	0.000a	0.000a
Cape bunting	Numbers of Birds	0.000a	0.621a	0.519a	0.000a
	Foraging Period	0.000a	1.698a	1.615a	0.000a
Grey tit	Numbers of Birds	0.000a	0.000a	0.0000a	0.448a
	Foraging Period	0.000a	0.000a	0.0000a	1.803a
Cape canary	Numbers of Birds	0.489a	0.832a	0.649a	0.749a
	Foraging Period	1.312a	2.529a	1.697a	2.681a
Fiscal flycatcher	Numbers of Birds	0.000a	0.000a	0.000a	0.000a
	Foraging Period	0.000a	0.000a	0.000a	0.000a
se of differences	Numbers of Birds	**± 0.424**			
	Foraging Period	**± 1.113**			

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2D Plot of Column Coordinates; Dimension: 1 x 2
Input Table (Rows x Columns): 17 x 17 (Burt Table)
Include condition: "Forag_Nos(sum)">50

Heavily Frugivorous		
African Olive-Pigeon	A-O-Pige
Speckled Mousebird	S-Mous
Red-winged Starling	R-W-Sta
Common Starling	C-Star
Red-faced Mousebird	R-F-Mou
Olive Thrush	O-Thru
Cape Bulbul	C-Bul
House Sparrow	H-Spa
Cape Robin-Chat	C-Rob
Cape White-eye	C-Wh-ey

Moderately Frugivorous	
Speckled Pigeon	S-Pige
Laughing Dove	C-Turt
Southern Boubou	S-Bou
Southern Masked-Weaver	S-M-Wea
Cape Weaver	C-Weav
Southern Tchagra	S-Tchag
Cape Bunting	C-Bun
Grey Tit	G-Tit
Cape Canary	C-Cana

Cape Town	CTA
Paarl	PRA
Hermanus	HRA
Swellendam	SWA
C. monilifera	C. mon
O. africana	O. afr
L. camara	L. cam
S. mauritianum	S. maur

Standardized Deviates

	A-O-Pige	S-Mous	R-W-Sta	C-Star	R-F-Mou	C-Bul	C-Wh-ey	S-M-Wea	C-Cana
CTA	3.9387	0.0198	3.3190	-3.9611	-4.4915	-2.0971	-0.1576	-0.2292	-0.8922
PRA	-1.3152	0.1779	-5.6335	-2.7122	-3.0753	-0.4761	5.5194	1.6615	2.6552
HRA	-4.0484	-2.9012	0.8206	-4.2194	0.8591	-0.7479	4.6044	-0.2488	1.6909
SWA	0.9349	2.1634	-0.2464	7.5660	4.1687	2.3622	-6.2553	-0.4720	-2.0007
C. mon	4.6508	-4.2337	3.5453	-3.0323	0.3425	3.3247	-2.5350	-1.7441	0.7159
O. afr	-6.7703	1.1327	7.7090	9.7314	-5.4573	-2.0276	-4.1716	3.8178	0.7406
L. cam	-5.7580	2.1640	-2.5828	-4.4933	6.8776	-0.4529	4.1758	-3.4204	-1.1593
S. maur	10.6177	-0.5595	-8.6769	-4.1775	-1.3590	0.4098	2.1548	0.5465	-0.1260

Figure 4.4. Two-dimensional correspondence map and tabulated standardized deviates showing relationships between recorded numbers of foraging bird species, shrubs species and sites derived from a multiple correspondence analysis. Standardized deviates in bold indicating the most positive associations of individual bird species with shrub species and sites. Shaded bird species are those that display REML derived significant differences between shrub species (Tables 4.2 & 4.3)

Heavily Frugivorous		
African Olive-Pigeon	A-O-Pige
Speckled Mousebird	S-Mous
Red-winged Starling	R-W-Sta
Common Starling	C-Star
Red-faced Mousebird	R-F-Mou
Olive Thrush	O-Thru
Cape Bulbul	C-Bul
House Sparrow	H-Spa
Cape Robin-Chat	C-Rob
Cape White-eye	C-Wh-ey

Moderately Frugivorous		
Speckled Pigeon	S-Pige
Laughing Dove	C-Turt
Southern Boubou	S-Bou
Southern Masked-Weaver	S-M-Wea
Cape Weaver	C-Weav
Southern Tchagra	S-Tchag
Cape Bunting	C-Bun
Grey Tit	G-Tit
Cape Canary	C-Cana

Cape Town	CTA
Paarl	PRA
Hermanus	HRA
Swellendam	SWA
C. monilifera	C. mon
O. africana	O. afr
L. camara	L. cam
S. mauritianum	S. maur

Standardized Deviates

	A-O-Pige	S-Mous	R-W-Sta	C-Star	R-F-Mou	O-Thru	C-Bul	H-Spa	C-Rob	C-Wh-ey	S-Pige	C-Turt	S-Bou	S-M-Wea	C-Weav	S-Tchag	C-Bun	G-Tit	C-Cana
CTA	4.6455	-6.8548	31.2333	-6.3775	-29.0102	-2.1457	-22.0961	-6.5350	-12.8692	-10.743	30.4268	30.9678	-2.2892	-3.5102	0.9903	0.9799	-7.2482	5.9311	-10.2856
PRA	-4.3990	13.0615	-23.6133	-3.4834	-15.8452	8.8502	-7.8353	-3.5694	19.4503	28.070	-11.0112	-16.1079	-8.6083	7.1221	-3.7893	-3.9717	3.3663	-2.8442	10.8790
HRA	-8.7126	-15.4685	-19.0213	-4.3513	27.3941	-6.7388	12.8182	12.3619	4.0885	16.525	-16.4163	-14.8038	-7.9153	0.2848	-4.7334	13.1792	14.8712	-3.5528	26.4658
SWA	3.3984	9.4326	-4.9186	10.3271	17.4191	1.7531	16.1851	0.0461	-0.4994	-14.564	-12.1291	-11.0802	11.3760	-0.5271	3.9558	-7.1631	-4.3488	-1.7935	-12.5899
C. mon	0.7473	-31.1284	37.9085	-4.8813	-8.7384	-1.1805	3.1590	-5.0019	4.9713	-17.326	27.1426	7.5530	15.5087	-3.8722	6.3662	-4.4875	-5.5477	-3.9856	-6.8694
O. afr	-37.7618	6.7152	11.9259	18.0727	-23.4909	-6.4820	8.4193	18.5190	-12.2330	2.115	-5.6248	16.1526	19.3015	14.8144	-5.0836	9.3970	12.1913	-4.2165	12.6631
L. cam	-20.4851	2.4733	-1.7056	-5.8823	38.9070	6.5150	-12.4859	-6.0275	8.3164	6.423	4.7995	6.9893	-13.8984	-5.8081	-6.3988	2.2393	0.6442	-4.8028	-9.1635
S. maur	52.7875	17.3873	-40.0483	-5.9078	-10.9845	0.1547	2.4622	-6.0537	-1.6947	6.072	-22.2886	-27.3191	-15.8477	-3.9673	5.5548	-6.7360	-6.7144	11.7609	3.7305

Figure 4.5. Two-dimensional correspondence map and tabulated standardized deviates showing relationships between recorded foraging times of bird species, shrubs species and sites derived from a multiple correspondence analysis. Standardized deviates in bold indicating the most positive associations of individual bird species with shrub species and sites. Shaded bird species names are those that display REML derived significant differences between shrub species (Tables 4.2 & 4.3)

4.6. Discussion

Fruits constitute the primary diet for heavily frugivorous birds (Jordano 1987a; Hockey et al. 2005); this feature was clearly reflected in the proportionately greater numbers of heavily than moderately frugivorous birds as a whole observed foraging on fruits of both the alien and indigenous shrubs. Both the heavily and moderately frugivorous birds as a whole did not forage fruits of the two alien shrubs in greater numbers than fruits of the two indigenous shrubs. However, heavily frugivorous birds as a whole foraged fruits of the alien *L. camara* for longer periods than fruits of the two indigenous shrubs, though this was not evident in the alien *S. mauritianum.* At the individual species level, only four of the 11 heavily frugivorous bird species, but none of the 14 moderately frugivorous species, foraged fruits the alien shrubs in either greater numbers or for longer periods than fruits of the indigenous shrubs. These irregular findings provided only partial support for the hypotheses that fruits of alien shrubs are foraged by larger numbers of birds and for longer periods than those of indigenous shrubs. They concur with similar foraging activities reported for frugivorous birds on fruits of two invasive plants (*Rubus ulmifolius* and *Ligustrum lucidum)* and three native plants in a subtropical forest (Montaldo 2000), as well as on fruits of the invasive Oriental bittersweet *Celastrus orbiculatus* and native holly *Ilex opaca* in North American woodlands (Greenberg et al. 2001). However, a high preference by starlings and robins for fruits of the alien autumn olive (*Elaeagnus umbellata*) was reported in Connecticut. The findings of this study suggest relatively homogeneous exploitation of alien and indigenous fruits by birds in the Cape Floristic Region might be due to complementary effects of alien fruits on indigenous fruits in bird diet (Jordano 1988; Henderson 2007; Lafleur et al. 2007). High levels of alien tree and shrub invasion (Rouget et al. 2003), fruit desiccation and insect infestations (Scott 1996; Proches et al. 2008) that reduce fruit quality to birds (Traveset et al. 1995; Herrera 1998) may also partly account for these obscure patterns in fruit-bird interactions.

Knight (1986, 1988) reported that birds prefer large multi-seeded *S. mauritianum* fruits (berries) to small single seed fruits (drupes), which were also previously reported in Costa Rica where berry-producing flora is predominant (Bradford & Smith 1977). The preference by birds of larger fruits maximises their energy intake (see Figure 4.5B), since pulp mass ingested is proportional to energy taken (Johnson et al. 1985), the seeds swallowed with the pulp normally regurgitated (Hegde et al. 1991; Levey & Martinez del Rio 2001). The preference for large fruits of *S. mauritianum* by birds also concurs with reports on American robin *Turdus migratorius* in the western Oregon (Sallabanks 1993). However, in this study only one of the 25 heavily and moderately frugivorous bird species examined, namely the African olive-pigeon *C. arquatrix,* displayed a distinct preference for large multi-seeded *S. mauritianum* fruits which concurs with previous reports that *S. mauritianum* has altered the feeding ecology of the African olive-pigeon *C. arquatrix* (Oatley 1984; Geldenhuys et al. 1986). This observation discredits the crop size hypothesis, which asserts that fruit density is likely to predict numbers of birds because *S. mauritianum* had the lowest fruit density per square meter of the canopy. Thus, variation in

numbers of birds foraging on fleshy fruits of alien and indigenous shrubs may be partly explained by differences in fruit density for some bird species.

Nevertheless, three of the 25 bird species examined, namely the red-winged starling *Onychognathus morio*, speckled pigeon *Columba guinea*, and the Cape turtledove *Streptopelia capicola* avoided *S. mauritianum* fruits yet were observed foraging on small single seed fruits of the two indigenous shrubs and the alien *L. camara.* In fact, some birds might prefer small single seed fruits for maximising rate of energy intake since their relatively larger seeds are more rapidly excreted than the tiny seeds present in large multi-seeded fruits (Kollmann 2000; Levey and Martinez del Rio 2001). Consistently, *O. africana* fruits with are highly foraged by passerine birds with 58 to 90 birds per ha reported in Spain (Rey 1995; Herrera 1995; Rey 2010). In southern Africa, *O. africana's* prolonged fruiting period and wide distribution makes it a reliable source of food for bird species (Cowling & Richardson 1995; Carlo et al. 2003; Wilms & Kappelle 2006).

The similarity in fruit architecture between the alien *L. camara* and that of indigenous shrub species may have facilitated the integration of *L. camara* into native bird-fruit mutualisms and its consequent spread throughout the in southern Africa (Knight 1986; Richardson et al. 2000a; Traveset & Richardson 2006; Milton et al. 2007). This was assisted by *L. camara's* uninterrupted flowering and fruiting thereby providing continuous supplementary sources of energy such as nectar and insects for birds during periods of environmental stress and fruit scarcity. Previous study (Knight 1988) also found that use of fleshy fruits by birds was proportional to the availability (Figure 4.5A). Indeed, five bird species, namely the African olive-pigeon *Columba arquatrix,* speckled mousebird *Colius striatus,* red-winged starling *O. morio*, Cape white-eye *Zosterops capensis* and the speckled pigeon *Columba guinea*, were all observed foraging fruits of the alien *L. camara* and indigenous *O. africana* in equivalent numbers and for equivalent periods. This finding concurred with observations on frugivorous birds in Costa Rica where birds of different size and fruit-feeding modes foraged for approximately equal periods on different fruits (Wheelwright 1991). It is suggested that this foraging pattern is a consequence of a dietary insufficiency offered by one type of fruit (Jordano 1988; Wheelwright 1991). The keystone food-resource status of *O. africana* has been reported in wintering avian frugivores of the Mediterranean Basin (Rey 1995; Herrera 1995; Peres 2000; Rey 2010) and this may apply to the Cape Floristic Region. Surprisingly, species that possess the potential for being keystone food-resources are either aliens or share characteristics with typical aliens. *Olea africana* does seem to possess some typical alien features, such as high fruit production and extended fruiting period, which may explain the high preference of its fruits by birds. However, Cowling et al. (2005) maintains that *O. africana* is an ancestral component of southern Africa thicket vegetation, yet other authors assert that *O. africana* has its ancestry in the cultivated olives of southern Mediterranean-climate Europe, since it possesses similar chromosomal numbers to the cultivated olive, though both may be descendants of common ancestors through hybridisation (Angiolillo et al. 1999; Lumaret et al. 2004).

The larger complement of bird species, both in terms of foraging numbers and foraging times, which displayed positive associations (e.g. in the multiple correspondence analysis) with *O. africana* are a likely consequence of the attractiveness of this shrub's abundant fruit supply for overwintering birds in fynbos. In fact, it has been reported that birds are attracted by plant species with high fruit abundance as demonstrated in *Sambucus nigra* and *Juniperus ashei* in New Zealand and Texas respectively (Chavez & Slack 1994; Williams & Karl 1996). Similarly, the speckled and red-faced mousebirds close association with *L. camara* may be due to presence of abundant fruit resources and the dense thickets that this shrub forms which are particularly suitable for these birds' wary behaviour (Hockey et al. 2005).

Noteworthy also was that several bird species, namely the African olive-pigeon *Columba arquatrix, s*peckled mousebird *Colius striatus,* red-winged starling *O. morio* and the Cape white-eye *Z. capensis* foraged fruits of the indigenous *C. monilifera* in smaller numbers and for shorter period than fruits of either or both of the alien shrubs. This observation is consistent with the reported preference by European starling *S. vulgaris* for indigenous than alien fruits in Connecticut (LaFleur et al. 2007). The lower partiality of bird species in this study for *C. monilifera* fruits might be consequent to short fruit display period by this shrubs (Knight 1988), rapid fruit spoiling due to insect infestation and rapid fruit desiccation (Scott 1996) which renders the fruit unsuitable for consumption by specialised frugivorous birds (Traveset et al. 1995).

4.7. Reference list

Abdi, H. & Valentin, D. (2007) Multiple correspondence analysis. *Encyclopedia of Measurement and Statistics.* (ed. Salkind, N.) pp. 651-657. Thousand Oaks (CA): Sage.

Angiolillo, A., Mencuccini, M. & Baldoni, L. (1999) Olive genetic diversity assessed using amplified fragment length polymorphisms. *Theoretical and Applied Genetics*, **98**, 411-421.

Bibby, C.J., Burgess, N.D. Hill, D.A. & Mustoe, S. (2000) *Bird census techniques.* Academic Press, London.

Binggeli, P. (1996) A taxonomic, biogeographical and ecological overview of invasive woody plants. *Journal of Vegetation Science,* **7**, 121-124.

Blendinger, P.G., Loiselle, B.A. & Blake, J.G. (2008) Crop size, plant aggregation, and microhabitat type affect fruit removal by birds from individual melastome plants in the Upper Amazon. *Oecologia*, **158**, 273-283.

Blossey, B. & Notzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887-89.

Bradford, D.F. & Smith, C.C. (1977) Seed predation and seed number in Scheelea palm fruits. *Ecology*, **58**, 667-673.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hayes, D. (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology,* **16**, 630-640.

Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment,* **2**, 436-443.

Carlo, T.A., Aukema, A.G. & Morales, J.M. (2007) Plant-frugivore interactions as spatially explicit networks: integrating frugivore foraging with plant spatial patterns. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 369-390. Reading: Biddles Ltd.

Christian, C.E. (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature*, **413**, 635-639.

Cornell, H.V. & Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, **61**, 1-12.

Cowling, R.M. & Richardson, D.M. (1995) *Fynbos: South Africa's unique floral kingdom.* Fernwood Press, Cape Town.

Cowling, R.M., Proches, S. & Vlok, J.H.J. (2005) On the origin of southern African subtropical thicket vegetation. *South African Journal of Botany*, **71**, 1-23.

Eckhardt, R.C. (1979) The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. *Ecological Monographs*, **49**, 130-149.

Garcia, D., Zamora, R., Gomez, J.M. & Hodin, J.H. (2001) Frugivory in *Juniperus communis* depends more on population characteristics than on individual attributes. *Journal of Ecology*, **89**, 639–647.

Geldenhuys, C.J., le Roux, P.J. & Cooper, K.H. (1986) Alien invasions in indigenous evergreen forest. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 119-131. Oxford University Press, Cape Town.

Godinez-Alvarez, H. & Jordano, P. (2007) An empirical approach to analysing the demographic consequences of seed dispersal by frugivores. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 391-406. Reading: Biddles Ltd.

Goldblatt, P. & Manning, J.C. (2002) Plant diversity of the Cape Region of Southern Africa. *Annals of the Missouri Botanical Garden*, 89, 281–302. 200.

Gosper, C.R. (2004) Consequences of weed invasion and control on plant-bird interactions and bird communities. Ph.D. Thesis, Department of Biological Sciences, University of Wollongong, Wollongong.

Gosper, C.R., Stansbury, C.D. & Vivian-Smith, G. (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distributions*, **11**, 549-558.

Green, R.J. (2007) Refining the conservation management of seed-dispersing frugivores and their fruits: examples from Australia. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 579-598. Reading: Biddles Ltd.

Greenberg, C.H., Smith, L.M. & Levey, D.J. (2001) Fruit fate, seed germination, and growth of an invasive vine: an experimental test of 'sit and wait' strategy. *Biological Invasions*, **3**, 363–372.

Hegde, S.G., Ganeshaiah, K.N. & Shaanker, R.U. (1991) Fruit preference criteria by avian frugivores: their implications for the evolution of clutch size in *Solanum pubescens*. *OIKOS*, **60**, 20-26.

Herrera, C.M. (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs*, **68**, 511-538.

Herrera, C.M. (1995) Plant-vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics*, **26**, 705-727.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (eds) (2005) *Roberts' birds of Southern Africa*, 7th edn. John Voelcker Bird Book Fund: Cape Town.

Hoffman, D.L. & Leeuw, J. (1992) Interpreting multiple correspondence analysis as a multidimensional scaling method. *Marketing Letters,* **3,** 259-272.

Howe, H.F. (1977) Bird activity and seed dispersal of a tropical wet forest tree. *Ecology*, **58**, 539-550.

Howe, H.F. & Estabrook, G.F. (1979) On intraspecific competition for avian dispersers in tropical trees. *The American Naturalist,* **111**, 817-832.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review Ecological Systematics*, **13**, 201–228.

Hulme, P.E. (2002) Seed-eaters: see dispersal destruction and demography. *Seeds dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D. J., Silva, R. W. & Galleti, M.) pp. 161-175. Wallingford: CABI Publishing.

Izhaki, I. (2002) The role fruit traits in determining fruit removal in east Mediterranean ecosystems. *Seeds dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D.J., Silva, R.W. & Galleti, M.) pp. 161-175. Wallingford: CABI Publishing

Janzen, D. H. (1985) The natural history of mutualisms. *The biology of mutualism: ecology and evolution.* (ed. Boucher, D.H.) pp. 40-99. Croom Helm, London.

Johnson, R.A., Willson, M.F., Thompson, J.N. & Bertin, R.I. (1985) Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology*, **66**, 819-827.

Jordano, P. (1988) Diet, fruit choice and variation in body conditions for frugivorous Warblers in Mediterranean Schrubland. *Ardea*, **76**, 193-209.

Jordano, P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *The American Naturalist,* **129**, 657-677.

Jordano, P. (2000) Fruits and frugivory. *Seeds: the ecology of regeneration in natural plant communities*. (ed. Fenner, M.) pp. 125-166. CABI Publishers, Wallingford, UK.

Jordano, P. (2007) Frugivores, seeds and genes: analysing the key elements of seed shadows. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Jordano, P., Garcia, C., Godoy, J.A. & Garcia-Castano, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3278-3282.

Knight, R.S. & Siegfried, W.R. (1983) Inter-relationships between type, size and colour of fruits and dispersal in southern African Trees. *Oecologia*, **56**, 405-412.

Knight, R.S. (1986) A comparative analysis of fleshy fruit displays in alien and indigenous plants. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 171-178. Oxford University Press, Cape Town.

Knight, R.S. (1988) Aspects of plant dispersal in the south-western Cape with particular reference to the roles of birds as dispersal agents. Ph.D. Thesis, University of Cape Town, South Africa.

Kollmann, J. (2000) Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 29–51.

Kruger, F.J. Richardson, D.M. & van Wilgen, B.W. (1986) Processes of invasion by alien plants. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A. A.) pp. 145-155. Oxford University Press, Cape Town.

Kueffer, C. (2006) Impacts of woody invasive species on tropical forests of the Seychelles. Ph.D. Thesis, Swiss Federal Institute of Technology Zurich, Switzerland.

Kueffer, C., Kronauer, L. & Edwards, P.J. (2009) Wider spectrum of fruit traits in invasive than native floras may increase the vulnerability of oceanic islands to plant invasions. *OIKOS*, **118**, 1327-1334.

LaFleur, N.E., Rubega, M.A. & Elphick, C.S. (2007) Invasive fruits, novel foods, and choice: an investigation of European Starling and American Robin frugivory. *Wilson Journal of Ornithology*, **119**, 429–438.

Laska, M.S. & Stiles, E.W. (1994) Effects of fruit crop size on intensity of fruit removal in *Viburnum prunifolium* (Caprifoliaceae). *OIKOS*, **69**, 199-202.

Lavergne, C., Rameau J-C. & Figier, J. (1999) The invasive woody weed *Ligustrum robustum* subsp. *walkeri threatens* native forests on La Reunion. *Biological Invasions*, **1**, 377–392.

le Maitre, D.C. & Midgley, J.J. (1992) Plant reproductive ecology. *The ecology of fynbos.* (ed. Cowling, R.) pp. 135-174. Oxford University Press: Cape Town.

Levey, D.J. (1987) Sugar-tasting ability and fruit selection in tropical fruit-eating birds. *The Auk*, **104**, 173-179.

Levey, D.J. & Martinez del Rio, C. (2001) It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. *The Auk*, **118**, 819-831.

Levine, J.M., Vila M, D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceeding of Royal Society London Botany*, **270**, 775–781.

Lumaret, R., Ouazzani, N., Michaud, H., Vivier, G., Deguilloux, M.F., & Giusto, F.D. (2004) Allozyme variation of oleaster populations (wild olive tree) (*Olea europaea L.*) in the Mediterranean Basin. *Heredity*, **92**, 343-351.

Macdonald, I.A.W. & Richardson, D.M. (1986) Alien species in the terrestrial ecosystems of the fynbos biome. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 77-91. Oxford University Press, Cape Town.

Manders, P.T. & Richardson, D.M. (1992) Colonization of Cape fynbos communities by forest species. *Forest Ecology and Management*, **48,** 277-293.

Martínez del Rio, C., Baker, H. G. & Baker, I. (1992) Ecological and evolutionary implications of digestive processes: bird preferences and the sugar constituents of floral nectar and fruit pulp. *Cellular and Molecular Life Sciences*, **48**, 544-551.

McNamara, J.M., Houston, A.I. & Lima. S.L. (1994) Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology*, **25**, 287-302.

Milton, S.J., Wilson J.R.U., Richardson, D.M., Seymour, C.L., Dean, W.R.J., Iponga, D.M. & Proches, S. (2007) Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. *Journal of Ecology*, **95**, 648–661.

Moll, E.J. & Bossi, L. (1983) 1:250 000 scale map of the vegetation of 3322 Oudshoorn. Eco-lab, University of Cape Town.

Montaldo, N.H. (2000) Reproductive success of bird-dispersed plants in a subtropical forest relict in Argentina. *Revista Chilena de Historia Natur,* **73,** 511–524.

Mucina, L., Rutherford, M.C. & Powrie L.W. (2006) The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute: Pretoria.

Oatley, T. B. (1984) Exploitation of a new niche by the Rameron Pigeon *Columba arquatrix* in Natal. *Proceedings of the Fifth Pan-African Ornithological Congress* (Ed. Ledger, J.A.), pp. 323-330. Southern African Ornithological Society.

Peres, C. A. (2000) Identifying keystone plant resources in tropical forests: the case of gums from *Parkia* pods. *Journal of Tropical Ecology*, **16**, 287-317.

Pratt, K.T. & Stiles, W.E. (1983) How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. *The American Naturalist*, **122**, 797-805.

Proches, S., Wilson, J.R.U., Richardson, D.M. & Chown, S.L. (2008) Herbivores, but not other insects, are scarce on alien plants. *Austral Ecology,* **33**, 691-700.

Pysek, P. & Richardson, D.M. (2008) Invasive plants. Ecological Engineering Vol **3** of *Encyclopedia of Ecology* (eds. Jorgensen, S.E. & Fath, F.D.) pp. 2011-2020. Oxford: Elsevier.

Reichard, S.H., Chalker-Scott, L. & Buchaman, S. (2001) Interaction among non-native plants and birds. *Avian ecology and conservation in an urbanising world.* (eds. Marcluff, J. M., Bowman, R. & Donnelly, R.) pp. 179- 223. Kluwer Academic Publishers.

Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 165*5*–1660*.

Rejmanek, M. (1996) A theory of seed plant invasiveness: the first sketch. *Biological Conservation*, **78**, 171-181.

Rey, P.J. (2010) Preserving frugivorous birds in agro-ecosystems: lessons from Spanish olive orchards. *Journal of Applied Ecology,* **48**, 228-237.

Rey, P.J. (1995) Spatio-temporal variation in fruit and frugivorous bird abundance in Olive orchards. *Ecology*, **76**, 1625-1635.

Richardson, D.M. & Fraser, M.W. (1995) Birds of Swartboskloof, Jonkershoek Valley, Stellenbosch: a mountain fynbos ecosystem. *Southern Birds,* **18**, 1–44.

Richardson, D.M. & Pysek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invisibility. *Progress in Physical Geography*, **30**, 409–431.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmanek, M. (2000b) Plant invasions - the role of mutualism. *Biology Reviews*, **75**, 65-93.

Richardson, D.M., Cowling, R.M. & le Maitre, D.C. (1990) Assessing the risk of invasive success in Pinus and Banksia in South African mountain fynbos. *Journal of Vegetation Science*, **1**, 629-642.

Richardson, D.M., Pysek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D. & West, C.J. 2000a. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions,* **6**, 93-107.

Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation,* **112**, 63-85.

Sakai, A.K., Weller, S.G., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A, Baughman, S, Cabin, R.J, Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M. & Thompson, J.N. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–32.

Sallabanks, R. (1993) Fruiting plant attractiveness to avian seed dispersers: native vs. invasive *Crataegus* in western Oregon. *Madrono*, **40**, 108–16.

Sallabanks, R. & Courtney, S.P. (1992) Frugivory, seed predation, and insect-vertebrate interactions. *Annual Review Entomology,* **37**, 377–400.

Schupp, E.W. (1993) Quantity, quality and effectiveness of seed dispersal by animals. *Vegetatio*, **107**/**108**, 12-29.

Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A. & Nathan, N. (2009) Long-distance seed dispersal. *Annual Plant Reviews*, **38,** 204–237.

Scott, J.K. (1996) Population ecology of *Chrysanthemiodes monilifera* in South Africa: implications for its control in Australia. *Journal of Applied Ecology,* **33**, 1496-1508.

Sinclair, I. & Ryan, P. (2003) *Birds of Africa south of the Sahara*. Cape Town: Struik Publishers.

Snow, B. & Snow, D. (1988) *Birds and berries*. T. & A.D. Poyser, Calton, UK.

Snow, D.W. (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica*, **13**, 1-14.

Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, **10**, 718–728.

Steadman, D.W. (1997) The historic biogeography and community ecology of Polynesian pigeons and doves. *Journal of Biogeography*, **24**, 737-753.

Stiles, E.W. (2000) Animals as seed dispersers. *Seeds: the ecology of regeneration in plant communities*. (ed. Fenner, M.) pp. 111-124. CABI Publishing: Wallingford.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173–181

Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecology & Evolution*, **21**, 208–216.

Traveset, A., Willson, M.F. & Gaither, J.C. Jr. (1995) Avoidance by birds of insect-infested fruits of *Vaccinium ovalifolium*. *OIKOS*, **73**, 381-386.

van Wyk, B. & van Wyk, P. (1997) *Field guide to trees of southern Africa*. Struik Publishers: Cape Town.

Vila, M. & D'Antonio, C.M. (1998) Fruit choice and seed dispersal of invasive vs. noninvasive Carpobrotus (Aizoaceae) in coastal California. *Ecology*, **79**, 1053-1060.

Walther, G.-R., Roques, A., Hulme, P.E., Sykes, M. T., Pysek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarosík, V., Kenis, M. Klotz, S. Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K. & Settele, J. (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution*, **24**, 686-693.

Wheelwright, N.T. (1985) Fruit size, gape width, and diets of fruit-eating birds. *Ecology*, **66**, 808-818.

Wheelwright, N.T. (1991) How long do fruit-eating birds stay in the plants where they feed? *Biotropica*, **23**, 29-40.

Whelan, C.J., Wenny, D.G. & Marquis, R.J. (2008) Ecosystem services provided by birds. *Annals of the New York Academy of Sciences*, **1134**, 25–60.

Willson, M.F., Irvine, A.K. & Walsh, G.N. (1989) Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica*, **21**, 133-147.

Wilms, J.J.A.M. & Kappelle M. (2006) Frugivorous birds, habitat preference and seed dispersal in a fragmented Costa Rican Montane oak forest landscape. pp. 309-324. *Ecology and Conservation of Neotropical Montane Oak Forests*. Springer Berlin Heidelberg.

Chapter 5

Fruit consumption intensities and seed dispersal potential of birds foraging on alien and indigenous shrubs in the Cape Floristic Region

5.1. Abstract

This study tested the hypothesis that frugivorous birds consume fleshy fruits of alien shrubs at greater intensity and that alien seeds have a higher seed dispersal potential than those of indigenous shrubs. This was achieved by comparing fruit consumption intensities and seed dispersal potentials in different bird species included in heavily and moderately frugivorous bird groups foraging on two indigenous shrubs (*Chrysanthemoides monilifera* and *Olea europaea* subsp. *africana)* and two alien shrubs (*Lantana camara* and *Solanum mauritianum)* at four different study sites (Hout Bay, Paarl, Hermanus and Swellendam) in the Cape Floristic Region. Fruit consumption intensity was computed from the product of the numbers of foraging birds, their foraging time and visitation frequency. Seed dispersal potential was computed from the product of consumption intensity, reciprocal of seed size and maximum foraging distance derived from bird-ring recapture records. Results partly supported the study hypothesis in that heavily frugivorous birds, especially *Columba arquatrix*, *Colius striatus* and *Zosterops capensi*s consumed fruits of the alien *S. mauritianum* at greater intensity than fruits of the two indigenous species. Also, these bird species together with *Pycnonotus capensis* displayed a greater potential for dispersal of seeds of both the alien than the indigenous shrubs. Among the moderately frugivorous bird species, only *Ploceus velatus* consumed fruits of the alien *S. mauritianum* at greater intensity than fruits of *C. monilifera* but not fruits of *O. africana.* This bird species and *Serinus canicollis* also displayed greater dispersal potential for seed of the alien *S. mauritianum* than for seed of *C. monilifera* but not for seed of indigenous O*. africana*. Despite the preference of these bird species for *S. mauritianum* fruits, 4 of the 11 heavily frugivorous bird species and 6 of the 14 moderately frugivorous bird species avoided *S. mauritianum* fruits entirely, a possible consequence of high fruit concentrations of laxative glycoalkoids which disrupt nutrient assimilation in the guts of some bird species. Results highlights that birds choose fruits based on their physiological and morphological adaptation to fruit diet.

Keywords: fruit consumption intensity, frugivorous birds, seed dispersal potential, alien and indigenous plants, Cape Floristic Region

5.2. Introduction

The successful colonisation of new habitats and rapid range expansion by alien plants has been attributed to the high consumption intensities fruits by birds than those of native species and to the greater seed dispersal ability over long distances (Richardson et al. 2000; Cordeiro et al. 2004; Trakhtenbrot et al. 2005; Traveset et al. 2006; Vittoz & Engler 2007). This is attributed to the conspicuous fruits possessed by alien species that attract birds (Knight 1986; Richardson & Rejmanek 2011), their fruit availability in abundance when the native fruits are out of season (Sallabanks 1993; Buckley et al. 2006; Greenberg & Walter, 2010; Gleditsch & Carlo 2010; Richardson & Rejmanek 2011) and high fruit sugar content (Kueffer et al. 2009; Gosper & Vivian-Smith 2010). Furthermore, possession of small fruits and thus seeds, that are readily consumed by birds of different sizes allow alien plants to have greater chances of reaching the save sites (Fleming et al. 1993; Rejmanek & Richardson 1996; Rejmanek 2000; Gosper et al. 2005; Milton et al. 2007). The advantages for bird dispersed plant species include escape, colonisation, focused seed distribution as well as seed release from dormancy (Wenny 2001; Higgins & Richardson 1999; Robertson et al. 2006; Schurr et al. 2009). Birds are efficient seed dispersal agents due to their ability to retain seeds in their guts during long distant flights in habitat exploitation (Nathan & Muller-Landau 2000; Higgins et al. 2003; Telleria et al. 2005; Spiegel & Nathan 2007; Whelan et al. 2008; Schurr et al. 2009). Long distance seed dispersal offsets localised plant species extinctions by facilitating the transport of seeds to novel areas where they can form new self-sustaining populations (Neubert & Caswell 2000; Schurr et al. 2007; Schurr et al. 2009). Dispersal of seeds away from parents assists in seedling escape from competition by adults and local siblings, as well as from seed predators and parasites which focus their activities in close proximity to parents where resources are abundant (Willson & Traveset 2000; Godinez-Alvarez & Jordano 2007). Moreover, bird flights between diverse habitats provide essential genetic links between habitat fragments that are otherwise inaccessible and facilitate species coexistence (Opdam & Wascher 2004; Schupp et al. 2010). Studies of seed movement have focused on the dispersal by specific birds of seeds of individual plant species. However, there exist few comparisons of seed dispersal of fleshy-fruited alien and indigenous plant species by birds, which prevent formulation of effective management protocols (Gosper et al. 2005; Buckley et al. 2006; Tsoar et al. 2011). In addition, there is lack of data on movement patterns of birds that restricts understanding of potential dispersal ranges of different plant species (Higgins et al. 2003; Kay et al 2011).

Compared with other global Mediterranean ecosystems, there are few quantitative data on the dispersal of seeds of fleshy-fruited trees and shrubs by birds in the Cape Floristic Region (Herrera 2002). Previous studies merely identified which bird species dispersed seeds of alien trees and shrub (Glyphis et al. 1981; Oatley 1984; Geldenhuys et al. 1986; Knight 1986, 1988; Manders & Richardson 1992; Underhill & Hofmeyr 2007) as means of determining level of invasiveness such as the study for the Brazillian pepper tree *Shinus molle* (Iponga 2009). Indeed, dispersal of seeds over long distances in Mediterranean climate ecosystems is limited

due to the predominance of small and medium size fruit foraging birds and the transformed natural habitats that result in altered distribution of resources (Oatley 1984; Herrera 1995). Thus, behavioural patterns of birds and the subsequent seed dispersal process are pertinent to changes in resource distribution. Gosper et al. (2005) reported that availability of extra alien fruits changed migratory behaviour of blackcaps *Sylvia atricapilla* in Europe. However, it has been argued that only a small fraction of invasive plant species out-competes native plants for avian frugivore seed dispersal services (Williamson 1996; Byers et al. 2001; Daehler 2003; Gleditsch & Carlo 2010). Alternatively fleshy-fruited invasive plants may provide a supplementary sources of food that attract birds foraging on fruits of both native and alien plants, especially in areas cleared of natural forests (Buckley et al. 2006; Aslan & Rejmanek 2010; Gleditsch & Carlo 2010); thereby facilitating seed dispersal of the coexisting alien and indigenous species (Simberloff & Holle 1999; Gleditsch & Carlo 2010). In fact, a strong positive correlation has been reported between the quantities of fruits produced by the invasive alien *Lonicera* and the abundance of the native bird species *Turdus migratorius* and *Dumetella carolinensis* in central Pennsylvania, this associated with a corresponding 30% increase in fruit removal from indigenous trees (Gleditsch & Carlo 2010).

Knowledge of the distances that birds disperse seed of alien species may assist in predicting future distribution ranges and in selecting suitable management strategies to limit alien plant spread (Sakai et al. 2001). However, previous studies have been limited in their estimation of dispersal distances of bird ingested seed (Nathan 2001; Russo et al. 2006; Nathan 2007) owing to unpredictable bird movements (Schupp et al. 2002; Muller-Landau & Hardesty 2005; Russo et al. 2006). This is further complicated by distorted plant-animal mutualisms resulting from human induced habitat fragmentation and defaunation (Herrera 1995; Opdam & Waschar 2004; Muller-Landau & Hardesty 2005). Nevertheless, it has been established that seed dispersal distance is directly proportional to the body size of the disperser in flying vertebrates (Schurr et al. 2009; Tsoar et al. 2011), since large birds often disperse seeds to more distant microsites than smaller birds (Jordano 2000; Jenkins et al. 2007; Spiegel & Nathan 2007; Tsoar et al. 2011). Seeds of the fleshy-fruited shrub *Ochradenus baccatus,* for example, are dispersed to greater distances by large Tristram's grackles *Onychognathus tristramii* than by smaller bulbuls *Pycnonotus xanthopygos* in Israel (Spiegel & Nathan 2007). Nevertheless, smaller birds may also disperse seeds to distant sites in their movement between intermittently fruiting populations (e.g. fruit tracking) along geographical gradients (Saracco et al. 2004; Telleria et al. 2008). The territorial European robin *Erithacus rubecula,* for example, tracks spatially variable fruit availability in the Spanish Mediterranean scrubland, which overrides the constraints of body size on dispersal distances of ingested seeds (Telleria et al. 2008).

Seed dispersal distance is dependent on length of time seeds are retained in the gut of a bird (Schupp 1993; Gosper et al. 2005; Schurr et al. 2009). However, measurements of gut retention time of seeds have mostly been estimated for birds in captivity (Kays et al. 2011) thereby reducing reliability of such data in the natural environment. Seed retention time in a

bird's gut may vary considerably with seed size, although there are no clear trends (Levey & Martinez del Rio 2001), as well as with other dietary components, such as laxative fruits that shorten gut retention time regardless of the seed size (Cipollini & Levey 1997). High lipid content in fleshy fruits also increases gut passage time due to slow processing of such fruits in bird guts (Fuentes, 1994). In addition, different bird feeding modes have also been associated with differences in gut passage rates with specialised frugivore species having rapid seed passage rates through their guts, whereas partial frugivores display slower gut passage time of seeds (Charalambidou et al. 2003 and authors therein). However, studies that have measured gut passage times as estimates of seed dispersal by individual bird species do tend to underestimate dispersal kernels of plant species and communities (Richardson et al. 2000; Dennis & Westcott 2007).

Traditional approaches of investigating seed dispersal have focused on seed attributes in determining seed dispersal mechanisms and dispersal distances (reviewed in Schurr et al. 2009). The major assumption was that seeds are dispersed by a standard vector inferred from the morphological features of the fruits and seeds (Higgins et al. 2003) but ignored the complex movements of the dispersal agents thereby limiting accurate estimates of seed dispersal distances (see Russo et al. 2006; Kays et al. 2011). Tsoar et al. (2011) found that fruit and seed characteristics interact with a set of frugivores attracted by the plant, which in turn may differ in their movement characteristics based on their body size and other environmental factors. Better understanding of such interactions could form an important basis for the comparison of seed dispersal processes between established alien and indigenous plants. Indeed, seed dispersal potential by birds maybe approximated from their body mass, flight distances (Schupp 1993; Nathan & Muller-Landau 2000; Russo et al. 2006) and seed size (Jenkins et al. 2007; Nathan 2007; Schurr et al. 2009). The seed size is particularly relevant since small seeds are ingested in larger quantities than large seed (Levey 1987; Martinez del Rio & Restrepo 1993; Rejmanek & Richardson 1996) which translates into a greater probability of dispersal (Schupp 1993; Jordano & Schupp 2000). Another approximation about long seed distance dispersal is that the smallest fraction of the seed load ingested by birds may reach the maximum distance travelled by birds (Nathan et al. 2008). Therefore, in this study, empirical data on fruit consumption and movement data of frugivorous birds was used to estimate the probability of long distance dispersal from maternal plants of seeds ingested by specific bird species (Nathan 2001; Levine & Murrell 2003; Levin et al. 2003; Westcott et al. 2005; Carlo & Morales 2008). The hypothesis tested was that frugivorous birds consume fleshy fruits of alien shrubs at greater intensity than those indigenous shrubs and that the seeds of alien shrubs have a greater dispersal potential than those of indigenous shrubs.

5.3. Methods and materials

5.3.1. Experimental design, study sites and species

The experimental design comprised four study sites each comprising mixed populations of alien and indigenous shrubs, located on Peninsula Granite Fynbos (Hout Bay site), Swartland Shale Renosterveld site (Paarl site), Overberg Sandstone Fynbos (Hermanus site) and Breede Shale Renosterveld site (Swellendam site). The fynbos and renosterveld vegetation classifications were according to Mucina and Rutherford (2006). Within each site, there were intermixed populations of four different shrub species with fleshy fruit displays, namely the indigenous shrub *Chrysanthemoides monilifera,* indigenous shrub *Olea europaea* subsp *africana* (*O. africana*) of southern European Mediterranean climate origin, and the alien shrubs *Lantana camara* and *Solanum mauritianum*. Since vegetation composition strongly influences fruit and seed removal by birds (Garcia et al. 2001; Carlo et al. 2007), all shrub species were selected based on their co-occurrence over a wide range of natural vegetation types, their overlapping fruiting times (Van Wyk & Van Wyk 1997) and consumption of their fruit by local frugivorous birds (Richardson & Fraser 1995). *Lantana camara, C. monilifera* and *O. africana* possess similar fruit architectures, namely single-seeded drupes that turn black when ripe, whereas *S. mauritianum* produces green multi-seeded berry turning yellowish when ripe.

5.3.2. Fruit consumption intensities and seed dispersal potential

At each site, bird surveillances were conducted during the peak fruiting periods of the alien and indigenous shrub species and restricted to 6 h daily periods of peak bird activity, namely a 3 h period after sunrise and a 3 h period before sunset (Howe 1977; Snow & Snow 1988; McNamara et al. 1994; Bibby et al. 2000). Individual shrubs that are reproductively mature were randomly selected for bird surveillances, which were conducted at approximately 30m distance from each shrub. The bird surveillances were performed manually with binoculars (8 x 42 magnification) and simultaneously recorded with a digital camcorder (Kodak C813: 8.2 megapixel, ISO 1250, digital IS) for a permanent record (Spiegel & Nathan 2007). Five days of bird surveillances were conducted on each of the four shrub species at each of the four sites (80 day surveillance period overall). The numbers of individuals of each bird species and the times in seconds that they spent consuming fruits of the alien and indigenous shrubs and their visitation frequencies over each 6-hour daily surveillance period were recorded. Each visitation comprised an arrival and departure of a foraging bird species. Bird species were identified with the aid of descriptions and keys presented in Sinclair and Ryan (2003) and Hockey et al. (2005). They were classified into two groups based on descriptions presented in Hockey et al. (2005), namely heavily frugivorous birds with fruits constituting their main and moderately frugivorous birds with fruits constituting their secondary or occasional diet (Hockey et al. 2005).

Consumption intensities were calculated for each bird species and foraging group from the product of the recorded daily numbers of foraging birds, foraging times (hrs) and visitation

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frequencies (Eckhardt 1979; McNamara et al. 1994; Schupp et al. 2010). Seed dispersal potential were computed for each bird species and bird foraging group from the product of the fruit consumption intensity, reciprocal of seed diameter and foraging distances derived from bird-ring records. It was assumed that consumption intensities were positively correlated with the numbers of seeds removed (Schupp & Jordano 2000; Vazquez et al. 2005; Schupp et al. 2010), that gut retention times of seeds were proportional to bird body mass and thus movement ability (Schurr et al. 2009; Tsoar et al. 2011), and that seed diameter was negatively correlated with dispersal distance. Bird-ring records provided a proxy of bird foraging distances (Nathan & Muller-Landau 2000). They were extracted from the South African Bird Atlas Project (SABAP 1 & 2) databases (Animal Demography Unit, University of Cape Town). About 5 880 recapture ring records from different locations within South Africa's borders were extracted for 34 of the 37 recorded species of birds from which foraging distances were derived from the initial ring location and subsequent recapture locations, these were calculated geo-spherically with foraging distance measures based on the earth's contour rather than on direct vectors. Only the heavily and moderately frugivorous bird species were considered in this study.

5.3.3. Data synthesis and statistical analyses
5.3.3.1. Regressions and correlations

From the bird foraging distance records, minimum, maximum, mean, median, lower and upper quartile foraging distances were computed and these tested for correspondence with bird body mass applying a Pearson correlation coefficient, multiple linear and stepwise regressions. A student's t-test tested the computed Pearson correlation coefficient and the slopes and intercepts of the linear regressions for significance. Maximum foraging distance displayed the best correspondence overall with bird body mass (Table 5.1) and from the regression function relating bird body mass to maximum foraging distance. Indeed, Bowman et al. (2002) reported that 50% variance in maximum dispersal distance of mammals can be explained by body size. Maximum foraging distances were also estimated for the three outstanding bird species, namely the African olive-pigeon *Columba arquatrix*, Cape canary *Serinus canicollis* and southern tchagra *Tchagra tchagra* for which no recapture ring records were available.

In addition, Pearson correlations tested for correspondence between measured fruit consumption intensities, seed dispersal potential, bird mass and seed size in heavily and moderately frugivorous bird groups. A student's t-test tested the computed Pearson correlation coefficient for significance.

5.3.3.2. Variance component analysis

A residual maximum likelihood (REML) variance component analysis (linear mixed model) was applied to test for differences in fruit consumption intensities and seed dispersal potential between the alien and indigenous shrubs by heavily and moderately frugivorous bird groups

and by individual bird species included in each frugivore bird group. The REML was applied as the experimental design was unbalanced due to unequally replicated measurements on each bird species at each site. All measurements were $\log_e$ transformed before statistical analysis to reduce the inequality of variance in the raw data so these more closely approximated normal distributions. Three separate REML analyses were conducted using the Wald X^2 statistic generated by the REML (GENSTAT Discovery Edition 3, VSL Lty, UK). The first REML tested for differences in fruit consumption intensities and seed dispersal potentials between the alien and indigenous shrubs by heavily and moderately frugivorous bird groups. The second REML tested for differences in fruit consumption intensities and seed dispersal potentials between the alien and indigenous shrubs by individual bird species included in the heavily frugivorous bird group. The third REML tested for differences in fruit consumption intensities and seed dispersal potentials between the alien and indigenous shrubs by individual bird species included in the moderately frugivorous bird species. In the first REML, bird frugivore group and shrub species variables were fitted in the fixed model and site, shrub and frugivore group factors in the random model. In the second and third REML, bird species and shrub species variables were fitted in the fixed model and site, shrub and bird species factors in the random model. Differences exceeding twice the mean standard error of differences were used to separate significantly different treatment means at $P \leq 0.05$. This was because for a normal distribution from REML estimates, the 5% two-sided critical value is two.

5.3.3.3. Multiple correspondence analysis

Multiple correspondence analysis (MCA) was applied to determine associations between frugivorous bird species, shrub species and sampling sites based on measured bird consumption intensities. It is an extension of correspondence analysis which allows analysis of the pattern of relationships of several categorical dependent variables (Abdi & Valentin 2007). Its major premise is that strongly related categorical variables are closely associated (Hoffman & Leeuw 1992). In the application of MCA in this study, species exclusion criteria were applied by placing thresholds on recorded consumption intensities to exclude bird species with frequently low or absent values. The exclusion criteria applied were the omission of those bird species whose consumption intensities were below a value of 1.0. Computed standardized deviates and a correspondence map of the first two dimensions identified the degree of association between different species of birds, alien and indigenous shrub species and sites. Large and positive values of standardized deviates indicated better than expected associations between bird species and shrub species or sites whereas the converse applies to large negative values of standardized deviates.

Table 5.1. Tests for correspondence between bird mass and minimum, maximum, mean,

median, lower and upper quartile foraging distances

Variable	Multiple linear regression				Pearson correlation	
	Coefficient	Standard error	$t_{1,34}$	Significance	$t_{1,32}$	Significance
Constant	117.068	63.118	1.855	0.075		
Lower Quartile	-4.056	20.497	-0.198	0.845	1.052	0.150
Maximum	0.018	0.008	2.119	0.044	3.116	0.002
Mean	0.194	0.392	0.496	0.624	0.449	0.328
Median	9.412	4.406	2.136	0.042	0.698	0.245
Minimum	-77.815	33.858	-2.298	0.029	-0.647	0.261
Upper Quartile	-0.301	0.219	1.373	0.181	-0.451	0.328

Step	Stepwise regression (forward selection)					
	In/Out	Variable	Multiple Correlation	r-squared	$F_{1,34}$	Significance
1	In	Maximum	0.483	0.233	9.709	0.004

5.4. Results

5.4.1. Variance components analysis

5.4.1.1. Fruit consumption intensities

There was a significant (P ≤ 0.05) interaction between shrub species and frugivore group for fruit consumption Intensity (Table 5.2) with only the heavily frugivorous bird group consuming fruits of the alien *S. mauritianum* at a significantly (P ≤ 0.05) greater quantities than fruits of the two indigenous species (Figure 5.1A). In addition, fruits of alien *L. camara* were consumed by the heavily frugivorous bird group at a significantly (P ≤ 0.05) greater quantities than fruits of *C. monilifera* but not fruits of *O. africana* (Figure 5.1A).

Within the heavily frugivorous bird group, there was a significant (P ≤ 0.001) interaction between shrub species and bird species for consumption quantities (Table 5.2). Among the 11 heavily frugivorous bird species, the African olive-pigeon *Columba arquatrix* consumed fruits of the alien *S. mauritianum* at a significantly (P ≤ 0.05) greater quantities than fruits of the two indigenous species as well as fruits of the other alien *L. camara*, whereas the speckled mousebird *Colius striatus* and the Cape white-eye *Zosterops capensis* consumed fruits of both alien shrubs at a significantly (P ≤ 0.05) greater intensity than fruits of *C. monilifera* but not fruits of *O. africana* (Table 5.3). Similarly among the 14 moderately frugivorous bird species, only the southern masked-weaver *Ploceus velatus* consumed fruits of *S. mauritianum* shrubs at a significantly (P ≤ 0.05) greater quantities than fruits of *C. monilifera* but not fruits of indigenous *O. africana* (Table 5.4).

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In both the heavily and moderately frugivorous bird groups consumption intensity was significantly (P ≤ 0.001) positively correlated with maximum foraging distance and in the moderately frugivorous bird group consumption intensity was also significantly (P ≤ 0.01) positively correlated with bird mass. Bird body mass in turn was significantly (P ≤ 0.001) positively correlated with maximum foraging distance in both frugivorous bird groups (Table 5.5).

5.4.1.2. Seed dispersal potential

There was a significant (P ≤ 0.05) interaction between shrub species and frugivore group (Table 5.2) for seed dispersal potential with only the heavily frugivorous bird group displaying a significantly (P ≤ 0.05) greater dispersal potential for seeds of both of the aliens *S. mauritianum* and *L. camara* than for seeds of the two indigenous species (Figure 5.1B).

Within the heavily frugivorous bird group, there was a significant (P ≤ 0.001) interaction between shrub species and bird species for seed dispersal potential (Table 5.1). Among the 11 heavily frugivorous bird species, the African olive-pigeon *Columba arquatrix*, the speckled mousebird *Colius striatus*, the Cape bulbul *Pycnonotus capensis* and the Cape white-eye *Zosterops capensis* all displayed a significantly (P ≤ 0.05) greater dispersal potential for seeds of the alien *S. mauritianum* than for seeds of the two indigenous species, the African olive-pigeon's dispersal potential for *S. mauritianum* seeds also significantly greater than for seeds of the other alien *L. camara* (Table 5.2). In addition, the red-faced mousebird *Urocolius indicus* displayed a significantly (P ≤ 0.05) greater dispersal potential for seeds of both alien shrubs than for seeds of indigenous O*. africana* but not *C. monilifera*. In contrast, the red-winged starling *Onychognathus morio* displayed a significantly (P ≤ 0.05) smaller dispersal potential for *S. mauritianum* seeds than for seeds of the two indigenous shrubs and the other alien *L. camara*. Within the 14 moderately frugivorous bird species, the southern masked-weaver *Ploceus velatus* displayed a significantly (P ≤ 0.05) greater dispersal potential for seeds of the alien *L. camara* than for seeds of the two indigenous shrubs whose seed dispersal potential did not differ significantly (P ≥ 0.05) from that of *S. mauritianum*. However, the Cape canary *Serinus canicollis* displayed a significantly (P ≤ 0.05) greater dispersal potential for seeds of the alien *S. mauritianum* than for seeds of *C. monilifera* but not for seeds of indigenous O*. africana* (Table 5.3). In contrast, the Cape turtledove *Streptopelia capicola* displayed a significantly (P ≤ 0.05) greater dispersal potential for seeds of the two indigenous shrubs than for seeds of the alien *S. mauritianum* but not the alien *L. camara* (Table 5.3).

In both the heavily and moderately frugivorous bird groups' seed dispersal potential was significantly (P ≤ 0.05) positively correlated with bird mass and in the heavily frugivorous bird group seed dispersal potential was significantly (P ≤ 0.001) negatively correlated with seed size (Table 5.5).

Table 5.1. Wald χ² statistics derived from three separate REML'S (linear mixed models) which tested for differences in fruit consumption intensities and seed dispersal potentials by different bird foraging groups and individual bird species on indigenous (*C. monilifera* and *O. africana)* and alien (*L. camara* and *S. mauritianum*) shrub species. Significant at *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

MAIN EFFECTS AND INTERACTIONS	df	WALD X^2 STATISTIC	
		Fruit consumption Intensity	Seed dispersal potential
REML 1		Figure 5.1A	Figure 5.1B
Shrub species	3	2.95	2.82
Frugivore group	1	52.43***	44.10***
Shrub species x Frugivore group	3	8.08*	10.63*
REML 2		Table 5.3	Table 5.3
Shrub species	3	5.62	10.04*
Heavily frugivorous bird species	10	182.70***	308.02***
Shrub species x Heavily frugivorous bird species	30	68.27***	94.90***
REML 3		Table 5.4	Table 5.4
Shrub species	3	2.44	4.92
Moderately frugivorous bird species	13	38.63***	114.03***
Shrub species x Moderately frugivorous bird species	39	29.02	46.85

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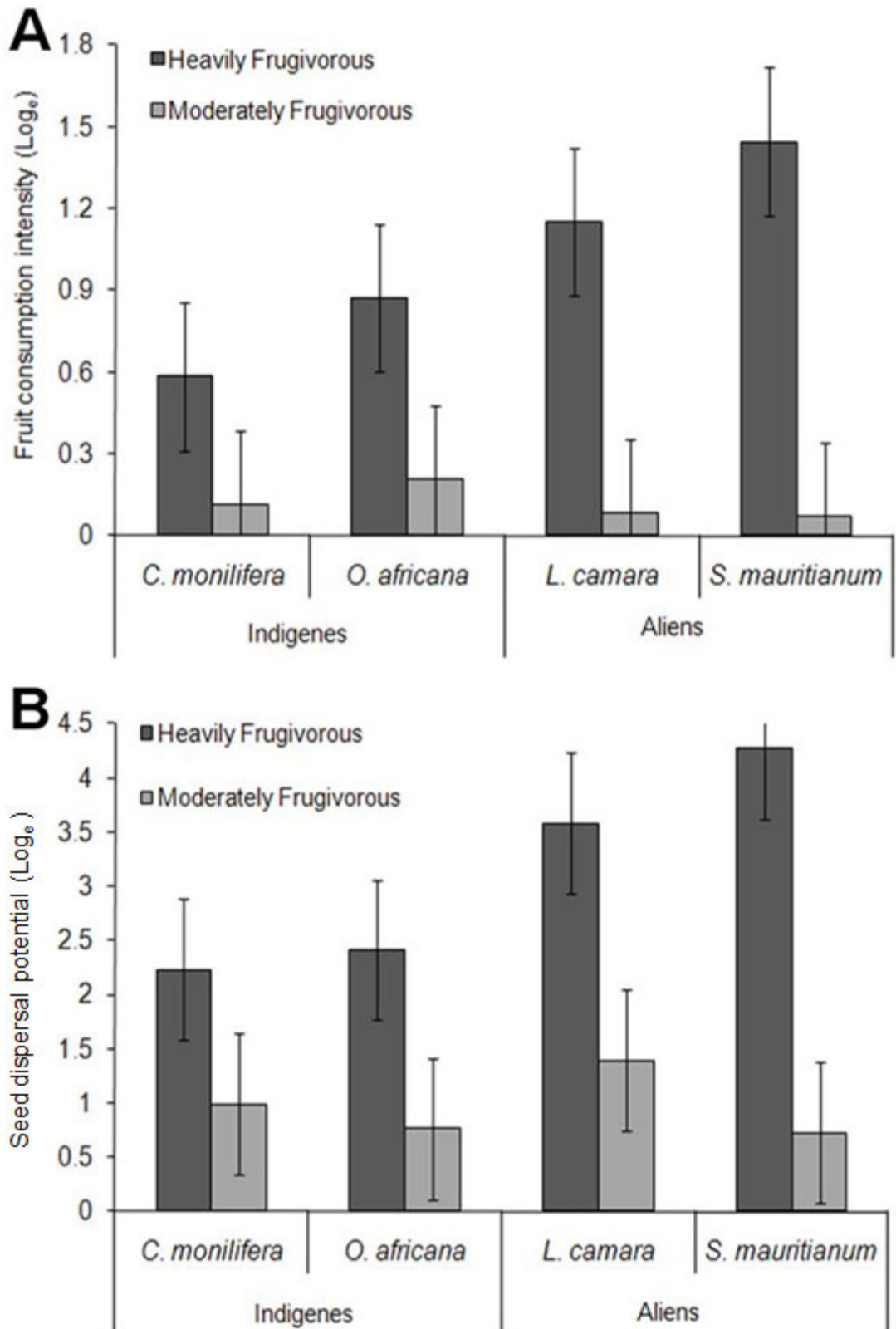
Figure 5.1. Fruit consumption intensities (A) and seed dispersal potentials (B) for heavily and moderately frugivorous bird groups foraging on fruits alien (*L. camara* and *S. mauritianum*) and indigenous (*C. monilifera* and *O. africana)* shrub species. Average standard error of differences shown by bars

Table 5.3. Consumption intensities and seed dispersal potentials of heavily frugivorous bird species foraging on fruits of indigenous (*C. monilifera* and *O. africana)* and alien (*L. camara* and *S. mauritianum*) shrubs. Means in each row with different letters significantly different at P ≤ 0.05; se is mean standard error of differences; * shows alien birds

Common Name	Parameter	Indigenes		Aliens	
		C. monilifera	*O. africana*	*L. camara*	*S. mauritianum*
African olive -pigeon	Consumption Intensity	**1.263a**	**0.032a**	**0.598a**	**4.383b**
	Seed dispersal potential	**4.831a**	**1.206a**	**3.734a**	**12.466b**
Speckled mousebird	Consumption Intensity	**0.211a**	**2.320b**	**2.404b**	**3.295b**
	Seed dispersal potential	**1.488a**	**6.105b**	**7.059bc**	**9.702c**
Red-winged starling	Consumption Intensity	1.345a	1.864a	1.518a	0.000a
	Seed dispersal potential	**2.599ab**	**3.646b**	**3.932b**	**0.000a**
*Common starling	Consumption Intensity	0.000a	0.520a	0.000a	0.000a
	Seed dispersal potential	0.000a	0.996a	0.000a	0.000a
Red-faced mousebird	Consumption Intensity	0.246a	0.000a	1.434a	0.538a
	Seed dispersal potential	**2.216ab**	**0.000a**	**3.718b**	**1.976ab**
Olive thrush	Consumption Intensity	0.008a	0.010a	0.162a	0.078a
	Seed dispersal potential	0.638a	0.510a	2.322a	1.650a
Sombre greenbul	Consumption Intensity	0.000a	0.000a	0.001a	0.000a
	Seed dispersal potential	0.000a	0.000a	0.007a	0.000a
Cape bulbul	Consumption Intensity	1.158a	1.317a	1.335a	2.042a
	Seed dispersal potential	**2.884ab**	**1.965a**	**3.492ab**	**5.554b**
*House sparrow	Consumption Intensity	0.000a	0.086a	0.000a	0.000a
	Seed dispersal potential	0.000a	1.807a	0.000a	0.000a
Cape robin-chat	Consumption Intensity	0.073a	0.003a	0.215a	0.063a
	Seed dispersal potential	2.530a	0.340a	2.885a	2.144a
Cape white-eye	Consumption Intensity	**2.116a**	**3.423ab**	**4.979bc**	**5.506c**
	Seed dispersal potential	**7.388a**	**9.957ab**	**12.231bc**	**13.459c**
se of differences	Consumption Intensity	**± 0.858**			
	Seed dispersal potential	**± 1.720**			

Table 5.4. Consumption intensities and seed dispersal potentials of moderately frugivorous bird species foraging on fruits of indigenous (*C. monilifera* and *O. africana)* and alien (*L. camara* and *S. mauritianum*) shrubs. Means in each row with different letters significantly different at P ≤ 0.05; se is mean standard error of differences

Common Name	Parameter	Indigenes		Aliens	
		C. monilifera	*O. africana*	*L. camara*	*S. mauritianum*
Speckled pigeon	Consumption Intensity	0.6918a	0.2440a	0.2574a	0.0000a
	Seed dispersal potential	2.4624a	2.4245a	3.3394a	0.0000a
Cape turtledove	Consumption Intensity	0.5376a	0.8614a	0.7008a	0.0000a
	Seed dispersal potential	**4.6021a**	**4.9368a**	**2.4906ab**	**0.0000b**
Red-eyed dove	Consumption Intensity	**0.0000a**	**0.0103a**	**0.0000a**	**0.0000a**
	Seed dispersal potential	**0.0000a**	**0.5548a**	**0.0000a**	**0.0000a**
Laughing dove	Consumption Intensity	0.000a	0.000a	0.000a	0.000a
	Seed dispersal potential	0.000a	0.000a	0.000a	0.000a
Southern boubou	Consumption Intensity	0.1747a	0.4369a	0.0091a	0.0002a
	Seed dispersal potential	1.7363a	1.7359a	0.3821a	0.0323a
Common fiscal	Consumption Intensity	0.000a	0.000a	0.000a	0.000a
	Seed dispersal potential	0.000a	0.000a	0.000a	0.000a
Southern masked-weaver	Consumption Intensity	**0.0349a**	**0.7431bc**	**0.0830ac**	**0.6442c**
	Seed dispersal potential	**1.9476a**	**5.4471a**	**2.3178b**	**4.4196ab**
Cape weaver	Consumption Intensity	0.0440a	0.0002a	0.0000a	0.0105a
	Seed dispersal potential	1.2238a	0.0293a	0.0000a	0.7971a
Southern tchagra	Consumption Intensity	0.0008a	0.0349a	0.0000a	0.0000a
	Seed dispersal potential	0.1740a	0.8381a	0.0000a	0.0000a
Yellow canary	Consumption Intensity	0.0578a	0.0000a	0.0000a	0.0000a
	Seed dispersal potential	0.2878a	0.0000a	0.0000a	0.0000a
Cape bunting	Consumption Intensity	0.0000a	0.1103a	0.0082a	0.0000a
	Seed dispersal potential	0.0000a	0.0758a	0.0096a	0.0000a
Grey tit	Consumption Intensity	0.0000a	0.0000a	0.0000a	0.0419a
	Seed dispersal potential	0.0000a	0.0000a	0.0000a	0.0422a
Cape canary	Consumption Intensity	0.0326a	0.4627a	0.1428a	0.2990a
	Seed dispersal potential	**1.4223a**	**3.4543ab**	**2.1513a**	**4.8774ba**
Fiscal clycatcher	Consumption Intensity	0.0000a	0.0000a	0.0000a	0.0000a
	Seed dispersal potential	0.0000a	0.0000a	0.0000a	0.0000a
se of differences	Consumption Intensity	**± 0.288**			
	Seed dispersal potential	**± 1.264**			

Table 5.5. t-statistics for Pearson correlations which tested for correspondence between measured fruit consumption intensities, seed dispersal potentials, bird mass and seed size in heavily and moderately frugivorous bird groups. Significant at *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

Correlated variables	Heavily Frugivorous	Moderately Frugivorous
Consumption Intensity x Bird Mass	$t_{1, 174} = 1.237$	**$t_{1, 222} = 2.682$****
Consumption Intensity x Maximum Foraging Distance	**$t_{1, 174} = 4.686$*****	**$t_{1, 222} = 3.533$*****
Consumption Intensity x Seed Size	$t_{1, 174} = -1.291$	$t_{1, 222} = 1.380$
Consumption Intensity x Seed Dispersal Potential	**$t_{1, 174} = 26.872$*****	**$t_{1, 222} = 41.588$*****
Bird Mass x Maximum Foraging Distance	**$t_{1, 174} = 9.384$*****	**$t_{1, 222} = 12.281$*****
Bird Mass x Seed Size	$t_{1, 174} = -0.000$	$t_{1, 222} = -0.000$
Bird Mass x Seed Dispersal Potential	**$t_{1, 174} = 2.253$***	**$t_{1, 222} = 2.829$****
Seed Size x Maximum Foraging Distance	$t_{1, 174} = -0.000$	$t_{1, 222} = -0.000$
Seed Size x Seed Dispersal Potential	**$t_{1, 174} = -2.123$***	$t_{1, 222} = 0.121$

5.4.2. Multiple correspondence analysis

The multiple correspondence analysis maps and tables of standardized deviates indicated that positive associations between bird species and shrub species in terms of bird consumption intensities (Figure 5.2) were site specific. Seven bird species were positively associated with the indigenous *O. africana.* These included the red-winged starling *O. morio*, cape bulbul *P. capensis* and southern boubou *L. ferrugineusis* association with *O. africana* at the Swellendam site, the speckled mousebird *C. striatus* and Cape turtle dove *S. capicola* association with *O. africana* at the Cape Town site, the southern masked-weaver *P. velatus* association with *O. africana* at the Paarl site and the Cape canary *S. canicollis* association with *O. africana* at the Swellendam site (Figure 5.2). Four bird species were positively associated with the alien *L. camara*. These included the red-faced mousebird *U. indicus* association with *L. camara* at the Swellendam site, the Cape white-eye *Z. capensis* association with *L. camara* at the Hermanus site, the Cape robin *C. caffra* association with *L. camara* at the Paarl site and the olive thrush *T. olivaceus* association with *L. camara* at the Cape Town site (Figure 5.2). Two bird species, namely the red-winged starling *O. morio* and the speckled pigeon *C. guinea*, were positively associated with the indigenous *C. monilifera* at the Cape Town site only and one bird species, namely the African olive-pigeon *C. arquatrix* was positively associated with the alien *S. mauritianum* at the Swellendam site only.

Figure 5.2. Two-dimensional correspondence map and tabulated standardized deviates showing relationships between recorded consumption intensities of foraging bird species, shrubs species and sites derived from a multiple correspondence analysis. Standardized deviates in bold indicating the most positive associations of individual bird species with shrub species and sites. Shaded bird species names are those that display REML derived significant differences between shrub species (Tables 5.3 & 5.4)

	A-O-Pige	S-Mous	R-W-Sta	C-Star	R-F-Mou	O-Thru	C-Bul	C-Rob	C-Wh-ey	S-Pige	C-Turt	S-Bou	S-M-Wea	C-Cana
CTA	-12.0478	8.6947	9.2075	-1.23779	-7.0853	0.45584	-7.5419	-0.49834	3.8371	6.46262	5.40603	-0.66205	-0.41227	-0.66536
PRA	-8.8519	-3.7262	-6.2265	-0.73496	-4.2071	-0.13698	-3.5772	2.83051	13.1231	-1.16635	-1.62335	-0.63056	1.48310	1.25246
HRA	-14.3134	-10.0613	-9.2391	-1.15066	-5.1932	-0.43589	-0.4497	-0.45170	20.9994	-1.84670	-2.50721	-0.89561	-1.20047	2.52848
SWA	19.9587	1.8720	2.0072	1.78910	9.3965	0.02002	6.5751	-0.49713	-20.3113	-2.64293	-1.37670	1.21868	0.42227	-1.58369
Shrub														
C. mon	-4.1708	-6.3827	28.1127	-0.64279	-3.2966	-0.15216	3.7765	0.60788	-7.1689	13.42672	2.60513	0.95421	-0.79404	-0.38967
O. afr	-16.3039	5.6961	20.1257	4.99378	-6.5315	-0.38390	16.7811	-0.57236	-4.5911	-0.94174	2.61244	3.41991	3.94522	2.59537
L. cam	-20.8402	4.6996	-10.0824	-1.48686	17.3803	0.63216	-7.0424	0.88264	14.1708	-1.76374	1.43556	-1.25395	-2.02139	-0.89553
S. maur	29.8126	-5.3524	-14.8539	-1.75331	-9.2799	-0.23047	-6.3332	-0.59889	-6.4013	-2.81389	-3.87263	-1.51207	-0.56218	-0.78673

5.5. Discussion

Only fruits of the alien *S. mauritianum* were consumed at greater intensity and displayed higher seed dispersal potential when consumed by the heavily frugivorous birds, such as the African olive-pigeon *C. arquatrix*, speckled mousebird *C. striatus*, Cape bulbul *P. capensis* and Cape white-eye *Z. capensis*, and to a lesser extent by moderately frugivorous bird, such as the southern masked-weaver *P. velatus* and Cape canary *S. canicollis* than those of the indigenous shrubs. These findings, which partly supported the study hypothesis, concurred with previously reported preference by birds for *S. mauritianum's* large nutritious berries over the smaller drupes produced by indigenous shrubs (Knight & Siegfried 1983; Johnson et al. 1985; Oatley 1984; Knight 1986; Gosper et al. 2005). A high ability of the heavily frugivorous bird species to extract nutrients from *S. mauritianum* fruits is a typical feature of highly specialised frugivores (Cipollini & Levey 1997b; Bosque & Pacheco 2000). The suggestion is supported by the observed increased acquisition of protein by yellow-vented bulbuls *Pycnonotus xanthopygos* foraging substantially on one type of fruit instead of mixed fruits in Israel (Izhaki 1992). Alternatively, high specialisation and adaptation to frugivory might entail low protein diet requirement as observed in the cedar waxwings *Bombycilla cedrorum* (Witmer 1998), since fruit pulp largely constitutes carbohydrates compounds (Witmer & Soest 1998). The greater consumption intensity on large nutritious berries of *S. mauritianum* by the heavily frugivorous African olive-pigeon *C. arquatrix* reflected the high nutritional demands of this nomadic bird's metabolic requirements (Rowan 1983; Martin 1984; McNamara et al. 1994) and concurred with previous local observations on this bird's foraging behaviour (Oatley 1984; Geldenhyus et al. 1986; Knight 1988). Also, the high consumption intensities displayed by small birds on *S. mauritianum's* nutritious fruits might be explained by limited dietary resource acquisition imposed by small body size (McNamara et al. 1994), since small birds such as the white-backed mousebird and malachite sunbirds tend generate endogenous heat to counteract increased heat loss during activity and cold nights (Downs & Brown 2002). Similarly, the greater consumption intensity of *S. mauritianum* fruits by the moderately frugivorous southern masked-weaver *P. velatus* possibly reflected an increased nutritional requirement for the multiple broods reared by females during this bird's colonial breeding period when (Hockey et al. 2005). This was evident from the numerous southern masked-weaver nests observed on large fruiting *S. mauritianum* shrubs whose high nectar production during flowering and nutritious fruits (Waring et al. 1993; Ghazoul 2004) attract many insects (Proches et al. 2008) that provide important supplementary sources of food for nestlings (Moermond & Denslow 1985). In addition, the greater consumption intensity and higher dispersal potential of *S. mauritianum* seeds by the territorial speckled mousebird *C. striatus,* Cape white-eye *Z. capensis* and Cape bulbul *P. capensis* were a likely consequence of their spatial fruit tracking behaviour (Hockey et al. 2005), a feature displayed by the European robin *Erithacus rubecula* in the Spanish Mediterranean scrubland (Hampe 2008; Telleria et al. 2008). The reliance of these heavily frugivorous birds on a fruit diet result in high fruit selectivity as reported in overwintering birds in the Mediterranean

climate regions (Herrera 1995) and consequent tracking of the spatially distributed fruits (Telleria et al. 2008; Holbrook 2010).

Nevertheless several heavily frugivorous bird species, namely the red-winged starling *O. morio*, common starling *S. vulgaris*, sombre bulbul *A. importanus* and house sparrow *P. domesticus* and several moderately frugivorous species, namely the speckled pigeon *C. guinea*, Cape turtledove *S. capicola,* red-eyed dove *S. semitorquata*, southern tchagara *T. tchagra*, yellow canary *C. flaviventris* and Cape Bunting *E. capensis* avoided *S. mauritianum* fruits entirely. Solanaceae fruits, such as those of *Witheringia solanacea,* contain high concentrations of laxative glycoalkaloids (Murray et al. 1994) which disrupt nutrient assimilation in bird guts and consequently, are less preferred by some bird species. In Florida, for example, it has been observed that the American robin *Turdus migratorius* consumes fruits of the invasive *Solanum carolinense* with high concentrations of glycoalkaloids at the lower intensity than those of the indigenous S*. americanum* with lower concentrations (Cipollini & Levey 1997a; Levey & Martinez del Rio 2001). Therefore, geophagy observed in the African olive-pigeon *C. arquatrix* and speckled mousebird *C. striatus* in South Africa have been associated with detoxification of secondary metabolites (Downs 2006). Since frugivorous birds differ in their ability to detoxify nitrogenous compounds (Moermond & Denslow 1985), retention of glycoalkaloids in ripe *S. mauritianum* fruits might represent a compromise between avoiding seed predators and attracting dispersers (Cipollini & Levey 1997a), though predators may also be important dispersers where obligate frugivores are scarce (Carlo et al. 2003).

Unlike *S. mauritianum,* fruits of the other alien *L. camara* were only consumed in greater intensity and had higher dispersal potential than those of the indigenous *C. monilifera* but not *O. africana.* This finding concurred with the proposition that not all invasive plant species out-compete native plants for avian frugivore seed dispersal services (Williamson 1996; Byers et al. 2002; Gosper et al. 2005; Buckley et al. 2006; Gleditsch & Carlo 2010). Similarly, there are reports that similar quantities of indigenous and alien fruits consumed by the blackbirds *Turdus merula* and song thrushes *Turdus philomelos* in New Zealand (Willams & Karl 1996) and Europe (Herrera 1984; Snow & Snow 1988). Irregularity of fruit production by indigenous shrubs in the Western Cape may have swayed the attention of frugivorous birds to the more frequently predictably available supplementary sources of food provided by alien plant fruits (Knight 1988). The occurrence of *C. monilifera* in open and disturbed habitats, which frugivorous birds tend to avoid (Manders & Richardson 1992; Wilms & Kappelle 2006; Gomes et al. 2008), and the relatively short life span its fruits due to their rapid desiccation (Knight 1988) may account for lower bird preference. In addition, fruit damage by insects (Scott 1996) may explain why birds consumed fruits of *C. monilifera* less than fruits of *O. africana*. Moreover, unlike *C. monilifera, O. africana* has prolonged fruiting period (Rey & Alcantara 2000).

It has been proposed that high fruit foraging intensities by birds are associated with high seed dispersal potentials (Carlo et al. 2003; Vazquez et al. 2005; Schupp et al. 2010). In this study, this proposal is supported by the significant positive correlation found between

consumption intensity and seed dispersal potential, and also between consumption intensity and maximum foraging distance in both heavily and moderately frugivorous bird groups. Consistently, the heavily frugivorous African olive-pigeon *C. arquatrix*, speckled mousebird *C. striatus* and Cape white-eye *Z. capensis* and moderately frugivorous southern masked-weaver *P. velatus* consumed fruits of alien *S. mauritianum* at greater intensity, and this was coupled with high seed dispersal potentials by these birds. These findings are possibly explained by the relatively large home ranges of the African olive-pigeon *C. arquatrix*, and speckled mousebird *C. striatus* (about 6 hectares; Tende 2005) and by fruit tracking between patches by the smaller Cape white-eye *Z. capensis* and southern masked-weaver *P. velatus* (Rowan 1983; Hockey et al. 2005). Consistently, Bowman et al. (2002) found that 74% variance in dispersal distance of mammals can be explained by home range size. Another factor that might account for the high seed dispersal potential is bird body mass, which is positively correlated with seed dispersal distance (Schurr et al. 2009; Tsoar et al. 2011). This assumption is supported by significant positive correlations found between bird mass and seed dispersal potentials, and between bird mass and maximum foraging distance in this study. The seeds consumed by the large grackles *Onychognathus tristramii* possess greater potential to be dispersed over long distances than smaller bulbuls *Pycnonotus xanthopygos* in Israel (Spiegel & Nathan 2007) due to the Tristram's grackles' long flights in groups from their roosting sites to daily hunting grounds while strictly territorial bulbuls having smaller home ranges (Spiegel & Nathan 2007). However, Izhaki et al. (1991) did not find any positive relationships between body mass of avian dispersers and dispersal potential of birds in eastern Mediterranean scrub. Furthermore, the reported correspondence between the intensity of fruit frugivory and bird body mass (Jordano 2000) was supported in this study by the significant positive correlation found between consumption intensity and bird mass, though this was apparent only in the moderately frugivorous bird group. Historically, large, heavily frugivorous birds are scarce in Mediterranean-climate regions (Herrera 1995) with the African olive-pigeon being the only large heavily frugivorous bird species recorded in the Cape Floristic Region, and thus, the statistically insignificant correlation observed between consumption intensity and bird mass in the heavily frugivorous bird group. Also, Carlo et al. (2003) demonstrated that partially frugivorous birds are more important dispersers than heavily frugivorous birds in Puerto Rico due to their greater abundance and regularity of visitations to fruiting shrubs.

It has been reported that small seeds are more easily ingested in large numbers by different size birds and thus, have greater probability of long distance dispersal (Moermond & Denslow 1985; Levey 1987; Martinez del Rio & Restrepo 1993; Rejmanek 2000; Charalambidou et al. 2003; Gosper et al. 2005). However, in this study no significant positive correlations were found between seed size, bird mass, consumption intensity and maximum foraging distance. This is because gape width limitations associated with bird body mass do not always apply as to the size of fruits and seeds that birds may process fruits. For example, species of Taucan's in Brazil have been observed swallowing whole fruits larger than their gape

width (Galletti et al. 2000) and in this study the tiny Cape white-eye was also observed swallowing entire fruit of *O. africana* which could be considered restrictive through gape width limitations (Wheelwright 1985). Lack of significant positive relationship between bird mass and maximum foraging distance is likely to be due to fruit tracking habits in small birds, which overrides the body size constraints to movement. This finding partly discredits estimation of dispersal distance from body mass in favour of foraging distances.

The observation that birds consumed *S. mauritianum* berries at greater intensity than black drupes produced by *L. camara* and indigenous shrubs, is consistent with the finding (Knight 1986, 1988) that frugivorous birds in southern Africa prefer black-coloured drupes with berries being especially favoured. The impact of fruit colour on fruit preference is further supported by the observed equivalent consumption intensities by heavily frugivorous birds of *L. camara* and *O. africana* fruits. Indeed, the MCA correspondence map and tabulated standardized deviates showed that the largest complement of bird species based on their measured consumption intensities were positively associated with *O. africana* (7 species) followed by *L. camara* (4 species), *C. monilifera* (2 species) and *S. mauritianum* (1 species). The smaller bird species complement consuming *C. monilifera* fruits probably due to the reported high insect infestations during flowering and fruiting stages (Scott 1996). It is thought that metabolic requirements and environmental factors such as predation determine differences in foraging behaviour between individual bird species. Bird species that possess high consumption intensities are likely to be nomadic since their local environments have scarce food resources, a feature typical of birds occupying fynbos in southern Africa (Hockey et al. 2005). Higher consumption intensities by birds on alien fruits may therefore result in a greater dispersal potential of seeds of alien than indigenous shrubs (Schupp 1993; Schupp et al. 2010) However, these dispersal potentials will be modified by bird foraging ranges (Bowman et al. 2002) and their physiological and morphological adaptations to fruit diets (Jordano 2000). This was evident from the observed higher consumption intensities by heavily frugivorous birds of fruits of alien plants with the moderately frugivorous birds displaying higher consumption intensities on fruits of indigenous plants due possibly to their smaller tolerance of defensive chemicals present in the alien fruits. Clearly, bird mediated seed dispersal of alien and indigenous species cannot be explained by fruit preference alone but also by vector foraging behaviour, which is affected by multiple environmental factors.

5.7. Reference list

Abdi, H. & Valentin, D. (2007) Multiple correspondence analysis. *Encyclopedia of Measurement and Statistics.* (ed. Salkind, N.) pp. 651-657. Thousand Oaks (CA): Sage.

Angiolillo, A., Mencuccini, M. & Baldoni, L. (1999) Olive genetic diversity assessed using amplified fragment length polymorphisms. *Theoretical and Applied Genetics*, **98**, 411-421.

Ankney, C.D. & Scott, D.M. (1980) Changes in nutrient reserves and diet of breeding Brown-Headed Cowbirds. *The Auk*, **97**, 684-696.

Bibby, C.J., Burgess, N.D. Hill, D.A. & Mustoe, S. (2000) Bird census techniques. Academic Press, London.

Blossey, B. & Notzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887-89.

Bosque, C. & Pacheco, A. M. (2000) Dietery nitrogen as a limiting nutrient in frugivorous birds. *Revista Chilena de Historia Natural*, **73**, 441-445.

Bowman, J., Jaeger, J.A.G. & Fahrig, L. (2002) Dispersal distance of mammals is proportional to home range size. *Ecology,* **83**, 2049–2055.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hayes, D. (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology*, **16**, 630-640.

Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, **2**, 436-443.

Carlo, T.A., Aukema, A.G. & Morales, J.M. (2007) Plant-frugivore interactions as spatially explicit networks: integrating frugivore foraging with plant spatial patterns. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 369-390. Reading: Biddles Ltd.

Carlo, T.A., Collazo, J.A. & Groom, M.J. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia*, **134**, 119-131.

Charalambidou, I., Santamaria, L. & Langevoord, O. (2003) Effect of ingestion by five avian dispersers on the retention time, retrieval and germination of *Ruppia maritima* seeds. *Functional Ecology*, **17**, 747-753.

Chen, C.C. & Chou, L.S. (2008) Differences in foraging ecology between generalized and specialized frugivorous birds in the Fushan experimental forest, northeastern Taiwan. *Taiwan Journal of Forest Science*, **23**, 233-42.

Cipollini, M.L. & Levey, D.J. (1997a) Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *The American Naturalist*, **150**, 346-372.

Cipollini, M.L. & Levey, D.J. (1997b) Antifungal activity of Solanum fruit glycoalkaloids: implications for frugivory and seed dispersal. *Ecology*, **78**, 799-809.

Cody, L.M. (1983) Bird diversity and density in South African forests. *Oecologia*, **59**, 201-215.

Cowling, R.M. & Holmes, P.M. (1992) Flora and vegetation. *The ecology of fynbos: nutrients, fire and diversity.* (ed. Cowling, R.M.) pp. 23– 61. Oxford University Press, Cape Town.

Cowling, R.M., Proches, S. & Vlok, J.H.J. (2005) On the origin of southern African subtropical thicket vegetation. *South African Journal of Botany*, **71**, 1-23.

Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien invasive plants: Implictions for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics,* **34**, 183-211.

Dennis, A.J. & Westcott, D.A. (2007) Estimating dispersal kernels produced by diverse community of vertebrates. *Seed dispersal: theory and its application in a changing world* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 201-228. Reading: Biddles Ltd.

Downs, C.T. (2006) Geophagy in the African Olive Pigeon *Columba arquatrix Ostrich-Journal of Ornithology,* **77**, 40-44.

Fleming, T.H., Venable, D.L. & Herrera, L.M.G.H. (1993) Opportunism vs. specialization: the volution of dispersal strategies in fleshy-fruited Plants. *Vegetatio,* **107**/**108,** 106-120.

Fuentes, M. (1994) Diets of fruit-eating birds: What are the causes of interspecific differences? *Oecologia,* **97**, 134-142.

Galetti, M., Laps, R. & Pizo, M.A. (2000) Frugivory by toucans (Ramphastidae) at two altitudes in the Atlantic forest of Brazil. *Biotropica,* **32**, 842-850.

Garcia, D. & Ortiz-Pulido, R. (2004) Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography*, **27**, 187-196.

Garcia, D., Zamora, R., Gomez, J.M. & Hodin, J.H. (2001) Frugivory in *Juniperus communis* depends more on population characteristics than on individual attributes. *Journal of Ecology*, **89**, 639–647.

Geldenhuys, C.J., le Roux, P.J. & Cooper, K.H. (1986) Alien invasions in indigenous evergreen forest. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 119-131. Oxford University Press, Cape Town.

Glyphis, P. J., Milton, J. S. & Siegfried, R. W. (1981) Dispersal of *Acacia cyclops* by birds. *Oecologia*, **48**, 138-141.

Godinez-Alvarez, H. & Jordano, P. (2007) An empirical approach to analysing the demographic consequences of seed dispersal by frugivores. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 391-406. Reading: Biddles Ltd.

Goldblatt, P. & Manning, J.C. (2002) Plant diversity of the Cape Region of Southern Africa. *Annals of the Missouri Botanical Garden*, **89**, 281–302. 200.

Gomes, L.G.L., Oostra, V. Nijman, V., Cleef, A.M. & Kappelle, M. (2008) Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. *Biological Conservation*, **141**, 860-871.

Gosper, C.R. (2004) Consequences of weed invasion and control on plant-bird interactions and bird communities. Ph.D. Thesis, Department of Biological Sciences, University of Wollongong, Wollongong.

Gosper, C.R., Stansbury, C.D. & Vivian-Smith, G. (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distributions*, **11**, 549-558.

Hampe, A. (2008) Fruit tracking, frugivore satiation, and their consequences for seed dispersal. *Oecologia*, **156**, 137-145.

Herrera, C.M. (1995) Plant-vertebrate seed dispersal systems in the Mediterranean: Ecological, Evolutionary, and Historical Determinants. *Annual Review of Ecology and Systematics,* **26**, 705-727.

Herrera, C.M. (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs*, **68**, 511-538.

Herrera, C.M. (2002) Seed dispersal by vertebrates. *Plant-animal interactions: an evolutionary approach*. (eds. Herrera, C.M. & Pellmyr, O.) pp. 185 210. Blackwell Science, Oxford, UK.

Higgins, S.I. & Cain, M.L. (2002) Spatially realistic metapopulation models and the colonization-competition tradeoff. *Journal of Ecology,* **90**, 616-26.

Higgins, S.I. & Richardson, D.M. (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *The American Naturalist,* **153**, 464-475.

Higgins, S.I., Nathan, R. & Cain, M.L. (2003). Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology*, **84**,1945-1956.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (eds) (2005) *Roberts' birds of Southern Africa,* 7th edn. John Voelcker Bird Book Fund: Cape Town.

Hoffman, D.L. & Leeuw, J. (1992) Interpreting multiple correspondence analysis as a multidimensional scaling method. *Marketing Letters,* **3,** 259-272.

Holbrook, K.M. (2010) Home range and movement patterns of toucans: implications for seed dispersal. *Biotropica,* **43**, 265–392.

Holmes, P.M., Richardson, D.M., Esler, K.J., Witkowski, E.T.F. & Fourie, S. (2005) Identifying strategic interventions for restoring alien-invaded riparian zones in South Africa. *South African Journal of Science*, **101**, 553–564.

Howe, H.F. & Estabrook, G.F. (1979) On intraspecific competition for avian dispersers in tropical trees. *The American Naturalist,* **111**, 817-832.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review Ecological Systematics*, **13**, 201–228.

Howe, H.F. (1977) Bird activity and seed dispersal of a tropical wet forest tree. *Ecology*, **58**, 539-550.

Hulme, P.E. (2002) Seed-eaters: see dispersal destruction and demography. *Seeds dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D.J., Silva, R.W. & Galleti, M.) pp. 161-175. Wallingford: CABI Publishing.

Izhaki, I. & Safriel, U.N. (1989) Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *OIKOS*, **54**, 23-32.

Izhaki, I. (1992) A comparative analysis of nutritional quality of mixed and exclusive fruit diets for yellow-vented bulbuls. *Condor*, **94**, 912-923.

Izhaki, I., Walton, P.B. & Safriel, U.N. (1991) Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *Journal of Ecology*, **79**, 575-590.

Jordano, P. & Schupp, E.W. (2000) Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, **70**, 591–615.

Jordano, P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *The American Naturalist,* **129**, 657-677.

Jordano, P. (1988) Diet, fruit choice and variation in body condition of frugivorous warblers in the Mediterranean scrubland. *Ardea*, **76**, 193-209.

Jordano, P. (2000) Fruits and frugivory. *Seeds: the ecology of regeneration in natural plant communities*. (ed. Fenner, M.) pp. 125-166. CABI Publishers, Wallingford, UK.

Jordano, P. (2007) Frugivores, seeds and genes: analysing the key elements of seed shadows. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Jordano, P., Garcia, C., Godoy, J. A. & Garcia-Castano, J. L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3278-3282.

Kays, R., Jansen, P.A., Knecht, E.M.H., Vohwinkel, R. & Wikelski, M. (2011) The effect of feeding time on dispersal of Virola seeds by toucans determined from GPS tracking and accelerometers. *Acta Oecologica*, **37**, 625-631.

Kemper, J., Cowling, R.M. & Richardson, D.M. (1999) Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. *Biological Conservation*, **90**, 103-111.

Knight, R.S. & Siegfried, W.R. (1983) Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia*, **56**, 405-412.

Knight, R.S. (1986) A comparative analysis of fleshy fruit displays in alien and indigenous plants. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 171-178. Oxford University Press, Cape Town.

Knight, R.S. (1988) Aspects of plant dispersal in the south-western Cape with particular reference to the roles of birds as dispersal agents. Ph.D. Thesis, University of Cape Town, South Africa.

Krug, C.B. & Krug, R.M. (2007) Restoration of old fields in renosterveld: a case study in a Mediterranean-type shrubland of South Africa. *Old fields: dynamics and restoration of abandoned farmland*. (eds. Cramer, V.A. & Hobbs, R.J.) pp. 265-334. Society for Ecological Restoration International. Island Press.

Kueffer, C. (2006) Impacts of woody invasive species on tropical forests of the Seychelles. Ph.D. Thesis, Swiss Federal Institute of Technology Zurich, Switzerland.

le Maitre, D.C. & Midgley, J.J. (1992) Plant reproductive ecology. *The ecology of fynbos.* (ed. Cowling, R.) pp. 135-174. Oxford University Press: Cape Town.

Levey, D.J. & Martinez del Rio, C. (2001) It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. *The Auk*, **118**, 819-831.

Levey, D.J. (1987) Sugar-tasting ability and fruit selection in tropical fruit-eating birds. T*he Auk,* **104**,173-179.

Levin, S. A., Muller-Landau, H. C., Nathan, R. & Chave, J. (2003) The ecology and evolution of seed dispersal: a theoritical perspective. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 575-604.

Levine, J.M. & Murrell, D.J. (2003) The community-level consequences of seed dispersal patterns. *Annual Review of Ecology and Systematics*, **34**, 549 - 574.

Lumaret, R., Ouazzani, N., Michaud, H., Vivier, G., Deguilloux, M.F. & Giusto, F. (2004) Allozyme variation of oleaster populations (wild olive tree) (*Olea europaea* L.) in the Mediterranean Basin. *Heredity*, **92**, 343-351.

Malcarney, H.L., Martínez del Rio, C. & Apanius, V. (1994) Sucrose intolerance in birds: simple nonlethal diagnostic methods and consequences for assimilation of complex carbohydrates. *The Auk,* **111**,170-177.

Manders, P.T. & Richardson, D.M. (1992) Colonization of Cape fynbos communities by forest species. *Forest Ecology and Management,* **48,** 277-293.

Mandon-Dalger, I., Clergeau, P., Tassin, J., Riviere, J.-N. & Gatti, S. (2004) Relationships between alien plants and an alien bird species on Reunion Island. *Journal of Tropical Ecology*, **20**,635-642.

Martinez del Rio, C. & Restrepo, C. (1993) Ecological and behavioral consequences of digestion in frugivorous animals. *Plant Ecology*, **107-108**, 205-216.

Martinez del Rio, C., Baker, H.G. & Baker, I. (1992) Ecological and evolutionary implications of digestive processes: bird preferences and the sugar constituents of floral nectar and fruit pulp. *Cellular and Molecular Life Sciences*, **48**, 544-551.

McNamara, J.M., Houston, A.I. & Lima, S.L. (1994) Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology*, **25**, 287-302.

Moermond, T.C. & Denslow, J.S. (1985) Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs*, **36**, 865-897.

Moll, E.J. & Bossi, L. (1983) 1:250 000 scale map of the vegetation of 3322 Oudshoorn. Eco-lab, University of Cape Town.

Montaldo, N.H. (2000) Reproductive success of bird-dispersed plants in a subtropical forest relict in Argentina. *Revista Chilena de Historia Natur*, **73,** 511–524

Mucina, L., Rutherford, M.C. & Powrie L.W. (2006) The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute: Pretoria.

Muller-Landau, H.C. & Hardesty, B.D. (2005) Seed dispersal of woody plants in tropical forests: Concepts, examples, and future directions. *Biotic interactions in the tropics: their role in the maintenance of species diversity*, (eds. Burslem, D., Pinard, M. & Hartley, S.) pp. 267–309. Cambridge University Press, Cambridge, UK.

Myers, J.H., Simberloff, D., Kuris, A.M. & Carey, J.R. (2000) Eradication revisited dealing with exotic species. *Trends in Ecology & Evolution*, **15**, 8316-320.

Nathan, R. (2001) The challenges of studying dispersal. *Trends in Ecology & Evolution*, **16**, 481-483.

Nathan, R. (2007) Total dispersal kernels and the evaluation of diversity and similarity in complex dispersal systems. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. (2008) Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, **23**, 638 – 647.

Oatley, T.B. (1984) Exploitation of a new niche by the rameron pigeon *Columba arquatrix* in Natal. *Proceedings of the Fifth Pan-African Ornithological Congress* (ed. Ledger, J.A.) pp. 323-330, Southern African Ornithological Society.

Olckers, T. (1999) Biological control of *Solanum mauritianum* Scopoli (Solanaceae) in South Africa: a review of candidate agents, progress and future prospects. *African Entomology Memoir,* **1**, 65–73.

Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285-297.

Pratt, K.T. & Stiles, W.E. (1983) How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. *The American Naturalist,* **122**, 797-805.

Proches, S., Wilson, J.R.U., Richardson, D.M. & Chown, S.L. (2008) Herbivores, but not other insects, are scarce on alien plants. *Austral Ecology*, **33**, 691-700.

Pysek, P. & Richardson, D.M. (2008) Invasive plants. Ecological Engineering Vol **3** of *Encyclopedia of Ecology* (eds. Jorgensen, S.E. & Fath, F.D.) pp. 2011-2020. Oxford: Elsevier.

Reichard, S.H., Chalker-Scott, L. & Buchaman, S. (2001) Interaction among non-native plants and birds. *Avian ecology and conservation in an urbanising world*. (eds. Marcluff, J.M., Bowman, R. & Donnelly, R.) pp. 179- 223. Kluwer Academic Publishers.

Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology,* **77**, 165*5*–1660.

Rejmanek, M. (2000) Invasive plants: approaches and predictions. *Austral Ecology*, **25**, 497-506.

Richardson, D.M. & Fraser, M.W. (1995) Birds of Swartboskloof, Jonkershoek Valley, Stellenbosch: a mountain fynbos ecosystem. *Southern Birds,* **18**, 1–44.

Richardson, D.M. & Pysek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invisibility. *Progress in Physical Geography*, **30**, 409–431.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmanek, M. (2000b) Plant invasions - the role of mutualism. *Biology Reviews*, **75**, 65-93.

Richardson, D.M., Pysek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000a). Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93-107.

Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation,* **112**, 63-85.

Rowan, M. K. (1983) *The doves, parrots, louries, and cuckoos of southern Africa.* John Voelcker bird book fund, Claremont.

Russo, S.E., Portnoy, S. & Augspurger, C.K. (2006) Incorperating animal behavior into seed dispersal models: implications for seed shadows. *Ecology*, **87**, 3160-3174.

Sakai, A.K., Weller, S.G., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A, Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M. & Thompson, J.N. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–32.

Sallabanks, R. (1993) Fruiting plant attractiveness to avian seed dispersers: native vs. invasive Crataegus in western Oregon. *Madrono*, **40**, 108–16.

Saracco, J.F., Collazo, J.M. & Groom, M.J. (2004) How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia*, **139**, 235-245.

Schupp, E.W. (1993) Quantity, quality and effectiveness of seed dispersal by animals. *Vegetatio*, **107**/**108**, 12-29.

Schupp, E.W., Jordano, P. & Gómez, J.M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, **188**, 333-353.

Schupp, E.W., Milleron, T. & Russo, S.E. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. *Seed dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D.J., Silva W.R. & Galetti, M.) pp. 19-33. Wallingford, UK: CAB International.

Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar A. & Nathan, N. (2009) Long-distance seed dispersal. *Annual Plant Reviews*, **38,** 204–237.

Scott, J.K. (1996) Population ecology of *Chrysanthemiodes monilifera* in South Africa: implications for its control in Australia. *Journal of Applied Ecology*, **33**, 1496-1508.

Shilton, L.A., Altringham, J.D., Compton, S.G. & Whittaker, R.J. (1999) Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. Proceedings of the Royal Society of London. Series B: *Biological Sciences*, **266**, 219-223.

Sinclair, I. & Ryan, P. (2003) *Birds of Africa south of the Sahara*. Cape Town: Struik Publishers.

Snow, B. & Snow, D. (1988) *Birds and berries*. T. & A.D. Poyser, Calton, UK.

Snow, D.W. (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica*, **13**, 1-14.

Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, **10**, 718–728.

Steadman, D.W. (1997) The historic biogeography and community ecology of Polynesian pigeons and doves. *Journal of Biogeography,* **24**, 737-753.

Telleria, J.L., Ramirez, A. & Perez-Tris, J. (2005) Conservation of seed-dispersing migrant birds in Mediterranean habitats: shedding light on patterns to preserve processes. *Biological Conservation*, **124**, 493–502.

Telleria, L.J., Ramirez, A. & Pérez-Tris, J. (2008) Fruit tracking between sites and years by birds in Mediterranean wintering grounds. *Ecography*, **31**, 381-388.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173–181.

Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecology & Evolution,* 21, 208–216.

Tsoar, A., Shohami, D. & Nathan, R. (2011) A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats. *Fifty years of invasion ecology. The legacy of Charles Elton* (ed. Richardson, D.M.) pp. 103-119, Wiley-Blackwell, Oxford.

van Wyk, B. & van Wyk, P. (1997) *Field guide to trees of southern Africa*. Struik Publishers: Cape Town.

Vitousek, P.M., D'Antonio, C., Loope, L.L., Rejmanek, M. & Westbrook, R. (1997) Introduced species: a significant component of human-caused global. *New Zealand Journal of Ecology*, **21***,* 1-16.

Wang, B.C. & Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology & Evolution*, **17**,379-386.

Westcott, D. A., Bentrupperbaumer, J., Bradford, M. G. & McKeown, A. (2005) Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, **146**, 57–67

Wheelwright, N.T. (1985) Fruit-size, gape width, and the diets of fruit-eating birds. *Ecology*, **66**, 808-818.

Whelan, C.J., Wenny, D.G. & Marquis, R.J. (2008) Ecosystem services provided by birds. *Annals of the New York Academy of Sciences*, **1134**, 25–60.

Wilms, J.J.A.M. & Kappelle, M. (2006) Frugivorous birds and seed dispersal in disturbed and old growth montane oak forests in Costa Rica. *Ecology and Conservation of Neotropical Montane Oak Forests*, (ed. Kappelle, M.) pp. 309–324. Ecological Studies Series 185. Springer-Verlag, New York/Berlin/Heidelberg.

Witmer, M.C. & Van Soest, P.J. (1998) Contrasting digestive strategies of fruit-eating birds. *Functional Ecology*, **12**, 728–741.

Witmer, M.C. (1998) Ecological and evolutionary implications of energy and protein requirements of avian frugivores eating sugary diets. *Physiological Zoology*, **71**, 599-610.

Chapter 6

Do frugivorous birds remove larger amounts of fruits and seeds from especially alien plants with high fruit production and nutritional contents?

6.1. Abstract

This study tested the hypothesis that frugivorous birds remove larger amounts of fruits and associated seeds from especially alien plants with high fruit production and nutritional contents, and that the germination of the bird-ingested seeds is enhanced. This was achieved by measuring fruit production and nutritional contents in two indigenous (*Chrysanthemoides monilifera* and *Olea europaea* subsp *africana*) and two alien (*Lantana camara* and *Solanum mauritianum)* shrubs at four different study sites (Hout Bay, Paarl, Hermanus and Swellendam) in the Cape Floristic Region and monitoring the amounts of fruits and coupled seeds removed by birds and the ingested seeds that germinated. In compliance with study hypothesis, canopy seed production, fruit mass and monosaccharide content were all positively correlated with the total numbers of seeds removed by birds and viable seeds excreted by birds. The 14 frugivorous bird species examined as a whole removed greater numbers of seeds and excreted larger numbers of viable seeds of *S. mauritianum* than those from other shrub species. However, there were subtle differences in the amounts of seeds removed by individual bird species from fruits of the four study species, and this was attributed to a combination of fruit nutritional content, bird body mass and seed size. Only defecated seeds of the indigenous *C. monilifera* and alien *L. camara* displayed enhanced germination following their ingestion by birds, which only partly complied with the study hypothesis. All these findings are discussed with reference to those previously reported and explanations for discrepancies advanced.

Keywords: Seed production, frugivorous birds, germination, ingested seeds, seed size, alien and indigenous shrubs.

6.2. Introduction

High reproductive output, and therefore propagule pressure, is generally associated with increased fitness in natural plant populations (Kelly & Sork 2002) and invasiveness in alien plant species (Richardson & Rejmanek 1996; Levine et al. 2003; Colautti et al. 2006). Alien plant species with relatively high fruit abundance are likely to attract more birds (Izhaki 2002; Laska & Stiles 1994) because frugivorous birds concentrate their activities where resources are most abundant (Willson & Traveset 2000; Hulme 2002; Saracco et al. 2005; Blendinger et al. 2008). In addition, different studies support that fruit abundance (e.g. large crop size) attracts foraging birds. Saracco et al. (2005) reported a positive correlation between the crop size of the dwarf umbrella tree *Schefflera morototoni* and avian visitation rate in central Puerto Rico. Gosper (2004) found that the presence of multiple large fruit crops throughout the year rendered the invasive bitou bush *Chrysanthemoides monelifera* more preferential to vertebrate dispersers than the co-existing indigenous species in New South Wales, Australia. Contrastingly, in the southwestern Cape Region of South Africa, Knight (1988) found that *C. monilifera* has a larger fruit crop size than some alien shrubs yet not locally invasive due to high fruit spoilage by insect infestation observed by Scott (1996). Therefore, attractive and large fruit displays of alien species (Knight 1986; Richardson et al. 2000b; Gosper et al. 2005; Kueffer et al. 2009) may swing a birds' attention away from fruits of native species (LaFleur et al. 2007; Kueffer et al. 2009).

In addition, birds prefer the high nutritional quality of the pulp especially high concentrations of soluble monosaccharides such as glucose and fructose (Martinez del Rio & Restrepo 1993; Jordano 2000; Izhaki 2002; Kueffer et al. 2009; Gosper & Vivian-Smith 2010). Gosper and Vivian-Smith (2010) found that fleshy-fruited alien species dispersed by birds in common possess high pulp simple sugars in south-eatern Queensland, Australia. It has been shown several monophyletic bird lineages, including starlings, mimids, and thrushes, display sucrose-intolerance as their low intestinal maltase activity is correlated with a lack of sucrase activity (Malcarney et al. 1994). Gray catbirds (*Dumetella carolinensis*, Mimidae) and purple-headed glossy-starlings (*Lamprotornis purpureiceps*, Sturnidae), for example, exhibit depressed ingestion and increased faecal sugar contents when shifted from solutions of glucose and fructose to sucrose. Also, these species show no increases in plasma glucose after ingestion of sucrose, but an increase in plasma glucose after ingestion of equicaloric doses of a mixture of glucose and fructose. Furthermore, in vitro measurements of intestinal disaccharidase activities in *D. carolinensis* have revealed insignificant sucrase activity, and low levels of maltase activities (Malcarney et al. 1994). Therefore, birds tend choose fruits with high water content and high concentration of simple sugars that are readily assimilated in the gut (Jordano 2000), thereby suggesting that alien fruits may be more preferential to birds than indigenous fruits (Gosper & Viavian-Smith 2010; Jordaan et al 2011). Consistently, Gosper (2004a) found that nutritional quality in terms of sugar content of invasive *C. monilifera* was significantly greater than   that of native species in southeastern Australia, which together with its consistent fruit

supply, rendered *C. monilifera* preferential to local frugivores. However, this finding was partly refuted by comparisons showing high variation between the nutritional quality of fleshy fruits of alien and native species in Seychelles (Kueffer et al. 2009); for example, certain fruit nutritional traits of some invasive species had higher values than any native species whereas others had relatively low values. Consequently, both the large fruit crop size and high nutritional quality of the alien fruits may potentially decrease the quantity (e.g. numbers of seeds removed per visit) aspect of seed dispersal effectiveness (Schupp 1993) of indigenous species coexisting with fleshy-fruited alien plants.

The quantity of different size seeds dispersed by birds are influenced by number of factors including bird body mass, bird numbers and foraging times and bird gape sizes (Wheelwright 1985; Schupp 1993; Jordano 2000; Schupp et al. 2010). However, following principles generally apply. That flocking bird species tend to remove larger portions of the fruit crop than solitary bird species (Snow & Snow 1988). That large birds ingest greater numbers of seeds than small birds, since the numbers of fruits and seeds removed are positively correlated to bird body mass (Jordano 2000; Schurr et al. 2009) with small seeds ingested in greater numbers than large seeds (Moermond & Denslow 1985; Levey 1987; Schupp 1993; Levey & Martinez del Rio 2001. The small and medium size birds are mostly inefficient in seed transport as they tend to regurgitate seeds under maternal plants (Pratt & Stiles 1983).

Although birds often prefer fleshy fruits of alien species (Greenberg & Walter 2010), it is unclear which factors drive foraging activity and seed removal by birds since many fruit characteristics tested fail to apply universally (e.g. Foster 1990; Laska & Stiles 1994; Levey & Martinez del Rio 2001; Gosper et al. 2005). Moreover, the processes of seed dispersal by birds within Mediterranean-climate ecosystems and in temperate areas and tropics differ substantially may be due difference in pertinent flora and fauna (e.g. Snow & Snow 1988; Herrera 1995; Clark et al. 1999). Only a few studies have compared bird fruit preferences between alien invasive and native plants (reviewed in Daehler 2003; Levine et al. 2003; Gosper et el. 2005; Buckley et al. 2006; Kueffer et al. 2009) with several producing conflicting results. Comparison of the consumption rates of fruits by caged birds in Australia have shown that fruits of the invasive European hawthorn *Crataegus monogyna* are more attractive to American robins *T. migratorius* than fruits of indigenous American hawthorn *C. douglasii* (Sallabanks 1993). This is apparent also in Reunion and Mauritius where fruits of the invasive alien *Ligustrum robustum* are preferred, and removed faster by birds than fruits of indigenous species (Lavergne et al. 1999). Conversely, there were no differences in the removal rates of fruits of two alien species (*Rubus ulmifolius* and *Ligustrum lucidum)* and three native species by birds as observed in a subtropical forest (Montaldo 2000). Similarly, bird-mediated fruit removal in the alien *Celastrus orbiculatus* and the native *Ilex opaca* in a North American forest, the birds tending to prefer the fruits of the native species (Greenberg et al. 2001). Despite these discrepancies, fleshy-fruited alien species do attract a greater variety of dispersal agents (Gosper 2004b; Kueffer 2006; LaFleur et al. 2007; Greenberg & Walter 2010) which tend to shift from one tree species to

another for purposes of diet variation and nutritional supplementation (Izhaki & Safriel 1989; Whelan & Willson 1994).

The concept of seed dispersal effectiveness also relates seed treatment in the gut of the disperser to seed dispersal quality (Schupp 1993; Schupp et al. 2010). Birds may alter the dormancy of ingested seeds (Schupp 1993; Samuels & Levey 2005; Traveset et al. 2001; Robertson et al. 2006) through physical and chemical effects on seed coat permeability (Wenny 2001; Traveset et al. 2001; Traveset et al. 2008). This in turn is influenced by how birds consume fruits, the length of their digestive tracts, gizzard and gut retention times and the corrosiveness of their digestive fluids (Traveset et al. 2001; Nogales et al. 2005; Traveset et al. 2008). Frugivorous birds are classified into swallowers, mashers and biters depending on how they consume fruits (Jordano 2000; Luck & Daily 2003). Swallowers generally ingest the whole fruit including the seeds (Jordano 2000) and then extract the fruit pulp in the gizzard or gut (Traveset et al. 2001). Mashers chew fruits and ingest both the fruit pulp and seeds whereas biters remove portions of the fruit pulp by biting or pecking (Levey 1987; Jordano 2000; Luck & Daily 2003). Scarification of the seed coat through physical damage during fruit and seed consumption and through chemical damage by digestive fluids during seed ingestion often promotes seed germination (Barnea et al. 1990; Traveset & Wilson 1997; Traveset et al. 2001; Robertson et al. 2006). The magnitude of bird-mediated effects on germination of ingested seeds does differ with bird and plant species. Consistently, Traveset et al. (2001), for example, showed that *Rubus* and *Rubia* seeds ingested by *Turdus merula* displayed different germination rates to those ingested by *Sylvia melanocephala* in the western Mediterranean of which was attributed to different gut-treatment regime in different birds. Alternatively, there is a report of germination inhibition in bird-ingested seeds of *Lonicera maackii* in the United States (Bartuszevige & Gorchov 2006).

In view of all these conflicting findings, this study tested the hypotheses that frugivorous birds remove larger amounts of fruits and seeds from especially alien plants with high fruit production and nutritional contents, and that the germination of the seeds ingested by the birds is enhanced.

6.3. Methods and materials

6.3.1. Experimental design, study sites and species

The experimental design comprised four study sites, each comprising mixed populations of alien and indigenous shrubs, located on different vegetation units described in Mucina and Rutherford (2006), namely: Peninsula Granite Fynbos (Hout Bay site), Swartland Shale Renosterveld (Paarl site), Overberg Sandstone Fynbos (Hermanus site) and Breede Shale Renosterveld (Swellendam site). Each site contained populations of two indigenous (*Chrysanthemoides monilifera* and Olea *europaea* subsp *africana*) shrubs intermixed with two alien (*Lantana camara* and *Solanum mauritianum)* shrubs all producing fleshy fruits. Since

vegetation composition strongly influences fruit and seed removal by birds (Garcia et al. 2001; Carlo et al. 2007), all shrub species were selected based on their co-occurrence over a wide range of natural vegetation types, their overlapping fruiting times (Van Wyk & Van Wyk 1997) and consumption of their fruit by local frugivorous birds (Richardson & Fraser 1995). *Lantana camara, C. monilifera* and *O. africana* possess similar fruit architectures, namely single-seeded drupes that turn black when ripe, whereas *S. mauritianum* produces green multi-seeded berry turning yellowish when ripe.

6.3.2. Fruit and seed production

At each site, approximately 35 reproductively mature flowering shrubs of each alien and native shrub species were randomly selected and tagged for measurements of fruit production. Two 0.25 m square quadrats were positioned on either side of the canopy of each fruiting shrub and the numbers of individual fruits present in the quadrats counted. Simultaneously, 3 to 5 ripe fruits were sampled from each quadrat and stored in sealed specimen bottles for measurement of fruit dry mass and nutritional content. Due to the high temporal and spatial variability in fruit production by the alien and indigenous shrubs (Knight 1988), measurements of fruit production were conducted several times during each shrub species fruiting stage spanning a 2-year period. Fruit production was expressed as the numbers of fruits m^{-2} of plant canopy and as total fruit dry mass m^{-2} of plant canopy, this calculated from the product of the numbers of fruits m^{-2} of plant canopy and the mean fruit mass of each shrub species at each site. All shrub species, except *S. mauritianum*, produced single-seeded fruits and consequently measured fruit production equalled seed production. In *S. mauritianum,* seed production was computed from the product of the measured numbers of fruits m^{-2} of plant canopy and the average numbers of seeds produced per fruit determined from sub-samples of 50 multi-seeded fruits sampled at random from shrubs at each study site.

6.3.3. Fruit nutritional content

Soluble monosaccharides (glucose and fructose) were extracted from 50 mg oven dried and milled fruit samples of each shrub species at each site which were suspended in two, 10 ml volumes of 80% ethanol (80:20, v:v, ethanol:water) for 72h. After centrifuging, the supernatants were adjusted to 25 ml in volumetric flasks for spectrophotometric (Beckman DU-640) determination at 490 nm of glucose and fructose concentrations at phenol concentrations of 23% and 33% respectively after addition of 5 cm^3 of concentrated sulphuric acid (Buysse & Merckx 1993). Standard curves in the concentration ranges of 20 to 80 $\mu g\ cm^{-3}$ were prepared for glucose and fructose in 80% ethanol. The relative proportions of glucose and fructose were calculated from their different absorbance at the two phenol concentrations (Buysse & Merckx 1993). Total soluble monosaccharide (glucose plus fructose) concentrations were expressed as $\mu g\ g^{-1}$ fruit dry mass and these multiplied by the numbers of fruits m^{-2} of plant canopy; and the

mean fruit dry mass measured for each shrub species at each site to obtain the masses of soluble monosaccharide per m^2 of plant canopy.

6.3.4. Collection of bird ingested seed

Ingested seeds defecated by birds were collected in three faecal traps (Izhaki et al. 1991) placed beneath the canopies of each alien and indigenous shrub at each study site (12 traps per site). Each trap comprised a collecting tray constructed from white plastic sheeting supported by metal fencing standards whose basal dimensions approximated the canopy areas of each shrub and whose sides were 0.25 cm high (Appendix 6.1 A). The tops of the traps were covered with 1 cm diameter wire mesh to minimise seed predation by rodents (Bond & Breytenbach 1985; Scott 1996; Hulme 1998). Seed bearing faecal samples were removed from the collecting trays weekly, and also collected from the lower foliage of the indigenous and alien shrubs as described by Twigg et al. (2009) (Appendix 6. 1 B & C). The collected faecal samples were dried at 30°C in a forced draft oven and sealed in labelled paper packets. Recognisable undamaged seed of the four study shrub species were manually extracted from the dry faecal samples under an illuminated magnifying glass (PRCB0090). The extracted seeds represented a wide variety of bird species that normally visit such shrubs (Williams & Karl 1996; Stansbury & Vivian-Smith 2003; Denis & Westcott 2007).

6.3.5. Germination of bird ingested seed

Between 140 and 340 bird ingested seeds of each shrub species were extracted from the faecal traps at the four study sites. Also, 480 non-ingested seeds of each shrub species were extracted from ripe fruits at the 4 study sites. The ingested and non-ingested seeds were sown separately into 31 cm long x 28 mm wide x 11 cm deep germination trays each containing a mixture of sand, loam and organic material at a ratio of 3:1:1. Each tray contained 20 either ingested or 20 non-ingested seeds of each shrub species sown into five rows of four seeds each. The 136 germination trays in total were randomised within a passively ventilated greenhouse, the randomisation process repeated at 2-weekly intervals. Air temperatures monitored in the greenhouse with a radiation-shielded thermocouple interfaced with a miniature Watchdog Model 450 data logger (Spectrum Technologies Inc., Plainfield, Illinois, USA) closely approximated those outdoors. The germination trays were irrigated at 2 daily intervals with equivalent volumes of water supplied by an automated irrigation system. Irrigation commenced at the beginning of winter (June) and terminated in early spring (September), the natural germination period for seeds in Mediterranean climate ecosystems (Bond 2005). The numbers of seedlings that emerged from each germination tray were recorded at weekly intervals over the 16-week monitoring period and expressed as percentages of the numbers of seeds initially sown. The identities of the seedlings that emerged from each germination tray were validated by comparison with herbarium specimens.

6.3.6. Fruit and seed removal and excretion by birds

A digital camcorder (Kodak C813: 8.2 megapixel, ISO 1250, digital IS) provided permanent photographic records of the numbers of whole or partial fruits of the alien and indigenous shrubs consumed by different species of birds over specific time intervals. Camcorder surveillances were conducted during early morning (3 h period after sunrise) and late afternoon (3 h period before sunset) periods of peak bird activity over a 5-day monitoring period when the alien and indigenous shrub species were in full fruit (Howe 1977; Snow & Snow 1988; McNamara et al. 1994; Bibby et al. 2000). From the photographic records, the total foraging periods in seconds spent by each bird species on each shrub per day were documented. In addition, the numbers of seeds in fractions of fruits swallowed by each bird species from each shrub species over the recorded foraging time intervals in seconds were determined. For the small single seed fruits of *C. monilifera, O. africana* and *L. camara*, all bird species consumed the entire fruit, *i.e.* one seed per mouthful. For the large multi-seed fruits of *S. mauritianum*, the fraction of the whole fruit removed by each bird species in one mouthful was estimated from its gape size. From the fractions of whole *S. mauritianum* fruits consumed, the numbers of seeds removed in one mouthful of fruit were determined from the average numbers of seeds present in each fruit. The latter derived from sub-samples of 50 multi-seeded fruits sampled at random from *S. mauritianum* shrubs at each study site. The total numbers of seeds removed by each bird species from each shrub per day (6-h observation period) were calculated from the product of the average numbers of seeds removed per second and the average foraging periods in seconds per day. These values were multiplied by the measured germination percentages of excreted seed to obtain estimates of the numbers of viable seeds of each shrub species excreted per day (see Godinez-Alvarez & Jordano 2007) on the assumption that all seeds consumed by birds were defecated (Johnson et al. 1985; Snow & Snow 1988; Murray et al. 1993; Jordano 2000).

6.4. Statistical analyses

Differences between alien and indigenous shrub species in measured fruit and seed production, fruit mass and monosaccharide content, numbers of seeds removed by birds, the fractions of bird ingested seed that germinated, and the numbers of viable seeds ingested by birds were tested with Kruskal-Wallis H-test (UNISTAT ver. 5.5). Significantly different ranked means at $P \leq 0.05$ were separated with Dunnet multiple range test. Correspondence between the numbers of seeds removed and excreted by birds and measured fruit and seed production, fruit mass and monosaccharide content were tested with Pearson Product Moment, Spearman Rank and Kendall Rank Correlations.

6.5. Results

6.5.1. Fruit and seed production and nutritional content

The alien *S. mauritianum* had the lowest canopy fruit production of the four shrubs, but the highest canopy fruit mass and canopy seed production. Its fruit monosaccharide concentration and canopy monosaccharide content was significantly ($P \leq 0.05$) higher than that of the other alien *L. camara* but not significantly ($P \geq 0.05$) higher than that of the two indigenous shrubs (Table 6.1). In contrast, the alien *L. camara* had the highest canopy fruit production of all three shrubs but the lowest canopy fruit mass, fruit monosaccharide concentration and canopy monosaccharide content (Table 6.1). This species' seed production was significantly ($P \leq 0.05$) lower than that of S*. mauritianum*, significantly ($P \leq 0.05$) higher than that of the indigenous *C. monilifera* but not significantly ($P \geq 0.05$) different from that of the other indigenous *O. africana* (Table 6.1). Canopy fruit and seed production and fruit mass, fruit monosaccharide concentration and canopy monosaccharide content of the indigenous *O. africana* were in between those of the two alien shrubs and so were those of *C. monilifera,* with the exception of its canopy fruit mass which was significantly ($P \leq 0.05$) lower than those of the other three shrubs (Table 6.1).

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Table 6.1. Kruskal Wallis tests for differences between the indigenous (*C. monilifera* & *O. africana)* and alien (*L. camara* & *S. mauritianum*) shrubs in fruit and seed production, fruit mass and fruit monosaccharide (glucose and fructose) contents. Means and ranked means in parenthesis in each column with different superscript letters significantly different at P ≤ 0.05

Shrub type	Shrub species	Fruit production Numbers m^{-2} plant canopy	Fruit mass g m^{-2} plant canopy	Fruit monosaccharide µg g^{-1} fruit dry mass	Fruit monosaccharide mg m^{-2} plant canopy	Seed production Numbers m^{-2} plant canopy
		Mean (rank mean)	Mean (rank mean)	Mean (rank mean)	Mean (rank mean	Mean (rank mean)
Indigenous	*C. monilifera*	489.8 (1591.6)^a	20.9 (796.6)^a	5180.9 (97.0)^a	110.4 (821.3)^a	489.8 (686.8)^b
	O. africana	357.3 (1161.7)^b	61.4 (1206.8)^b	5791.3 (112.2)^a	351.1 (1248.4)^b	357.3 (943.2)^a
Alien	*L. camara*	1386.4 (1462.8)^c	47.0 (892.1)^a	3850.2 (53.5)^b	180.8 (783.8)^a	1386.4 (936.7)^b
	S. mauritianun	216.7 (891.5)^d	139.2 (1875.2)^c	6435.7 (123.3)^a	876.0 (1943.1)^c	14425.5 (2071.6)^c
H-statistic		368.9	960.6	43.7	1210.1	1551.5
Degrees freedom		3	3	3	3	3
Number samples		2492	2492	192	2492	2492
Probability		P ≤ 0.001	P ≤ 0.001	P ≤ 0.001	P ≤ 0.001	P ≤ 0.001

Table 6.2. Kruskal Wallis tests for differences in germination between non-ingested and bird ingested seeds of the indigenous (*C. monilifera* and *O. africana*) and alien (*L. camara* and *S. mauritianum*) shrubs. Means and ranked means in parenthesis in each column with different superscript letters significantly different at P ≤ 0.05

Statistical Analysis	Seed type	*C. monilifera* Mean (rank mean)	*O. africana* Mean (rank mean)	*L. camara* Mean (rank mean)	*S. mauritianum* Mean (rank mean)
	Ingested	**61.4 (28)[a]**	39.4 (23.1)[a]	**40.0 (24.3)[a]**	31.0 (14.3)[a]
	Non-Ingested	**0.0 (12.5)[b]**	32.7 (19.5)[a]	**16.2 (13.9)[b]**	40.7 (17.3)[a]
H-statistic		**29.4**	0.9	**7.5**	0.6
Degrees freedom		**1**	1	**1**	1
Number samples		**31**	41	**32**	32
Probability		**P ≤ 0.001**	P ≥ 0.05	**P ≤ 0.01**	P ≥ 0.05

Table 6.3. Kruskal Wallis tests for differences in numbers of seeds removed and excreted per day by all 14 frugivorous bird species and the 3 most common heavily frugivorous bird species between the indigenous (*C. monilifera* and *O. africana*) and alien (*L. camara* and *S. mauritianum*) shrubs. Means and ranked means in parentheses in each column with different superscript letters significantly different at P ≤ 0.05

Shrub Type	Shrub species	Numbers of seeds removed day^{-1}				Numbers of viable seed excreted day^{-1}
		All bird species Mean (rank mean)	Speckled mousebird Mean (rank mean)	Cape bulbul Mean (rank mean)	Cape white-eye Mean (rank mean)	All bird species Mean (rank mean)
Indigenous	*C. monilifera*	73.4 (71.8)^{a}	115.2 (8.0)^{ab}	20.1 (4.0)^{a}	249.8 (27.3)^{a}	45.0 (83.7)^{a}
	O. africana	89.8 (70.6)^{a}	17.1 (1.0)^{a}	51.0 (7.0)^{ab}	169.8 (17.7)^{a}	35.5 (66.2)^{a}
Alien	*L. camara*	68.5 (81.6)^{a}	26.7 (3.5)^{a}	60.6 (5.5)^{a}	121.8 (19.7)^{a}	27.4 (76.3)^{a}
	S. mauritianum	620.0 (133.7)^{b}	589.3 (14.0)^{b}	462.3 (16.0)^{b}	1191.7 (45.9)^{b}	192.2 (128.2)^{b}
H-statistic		47.8	14.4	15.4	27.9	36.0
Degrees freedom		3	3	3	3	3
Number samples		188	17	21	54	188
Probability		P ≤ 0.001	P ≤ 0.01	P ≤ 0.01	P ≤ 0.001	P ≤ 0.001

Table 6.4. Pearson Product Moment, Spearman Rank and Kendall Rank Correlations between the total numbers of seeds removed and excreted by birds and measured canopy fruit and seed production, fruit mass and monosaccharide contents of the indigenous (*C. monilifera* and *O. africana*) and alien (*L. camara* and *S. mauritianum*) shrubs

Parameter		Total seeds removed shrub^{-1} site^{-1} day^{-1}			Viable seeds excreted shrub^{-1} site^{-1} day^{-1}		
		Correlation	n	Probability	Correlation	n	Probability
Fruit production m^{-2} canopy	Pearson	-0.4494	16	0.0404	-0.4633	16	0.0343
	Spearman	-0.5147	16	0.0207	-0.5000	16	0.0243
	Kendall	-0.4167	16	0.0122	-0.3833	16	0.0192
Seed production m^{-2} canopy	Pearson	0.8415	16	0.0000	0.8196	16	0.0001
	Spearman	0.5382	16	0.0157	0.5529	16	0.0132
	Kendall	0.3500	16	0.0293	0.3833	16	0.0192
Fruit mass g m^{-2} canopy	Pearson	0.7655	16	0.0003	0.7319	16	0.0001
	Spearman	0.6059	16	0.0064	0.5265	16	0.0127
	Kendall	0.4333	16	0.0096	0.3667	16	0.0153
Monosaccharide mg m^{-2} canopy	Pearson	0.8343	16	0.0000	0.8058	16	0.0001
	Spearman	0.6235	16	0.0049	0.5559	16	0.0127
	Kendall	0.4667	16	0.0058	0.4000	16	0.0153

6.5.2. Germination of bird-ingested seeds

Seeds of the indigenous *C. monilifera* and the alien *L. camara* ingested by birds displayed significantly (P ≤ 0.001) higher germination percentages than those not ingested by birds. However, the other two shrub species displayed insignificantly (P ≥ 0.05) different germination percentages between bird ingested and non-ingested seeds (Table 6.2).

6.5.3. Seed removal by birds and its correspondence with fruit production

The recorded 14 frugivorous bird species as whole removed significantly (P ≤ 0.05) greater numbers of seeds of the alien *S. mauritianum* and excreted significantly (P ≤ 0.05) greater number of viable *S. mauritianum* seeds than those from the other shrub species (Table 6.3). This pattern of differences in seed removal of seeds was also apparent among individual bird species. The Cape white-eye *Zosterops capensis* also removed significantly (P ≤ 0.05) greater numbers of seeds of the alien *S. mauritianum* than seeds of the other shrub species (Table 6.3). However, the speckled mousebird *Colius striatus* only removed significantly (P ≤ 0.05) greater numbers of *S. mauritianum* seeds than *L. camara* and *O. africana* seeds but not *C. monilifera* seeds (Table 6.3). Similarly, the Cape bulbul *Pycnonotus capensis* removed significantly (P ≤ 0.05) greater numbers of S. *mauritianum* seeds than *L. camara* or *C. monilifera* seeds but not *O. africana* seeds (Table 6.3).

Canopy seed production, fruit mass and monosaccharide content were all significantly (P ≤ 0.05) positively correlated with the total numbers of seeds removed by birds and viable seeds excreted by birds from each shrub at each site (Table 6.4). In contrast, canopy fruit production was significantly (P ≤ 0.05) negatively correlated with numbers of seeds removed by birds and the numbers of viable seeds excreted by birds (Table 6.4).

6.6. Discussion

The negative correlation found between the total numbers of seeds removed and viable seeds excreted by birds and canopy fruit production, expressed as numbers of fruits per square meter of canopy area, did not concur with the proposal that plants with high fruit abundance are likely to attract more birds (Sallabanks 1993; Izhaki 2002; Blendinger et al. 2008). This proposal supported by observations on American robins *Turdus migratorius* foraging on *Crataegus monogyna* fruits in western Oregon, and other comparative studies on alien and indigenous fruit removal by birds (Sallabanks 1993; Gosper et al. 2005; Kueffer et al. 2009). However, Laska and Stiles (1994) did report the absence of a correlation between *Viburnum prunifolium* fruit production and removal by birds in New Jersey, though trees bearing larger fruit crops did experience greater fruit removal by birds. Laska and Stiles (1994) attributed their conflicting findings to different foraging behaviours among avian dispersers in their choice of fruit crops. Flocking American robins

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T. migratorius, for example, choose large fruit crops matching their numbers whereas solitary bird species are less affected in their choice by fruit crop size (Sallabanks 1992; Schupp et al. 2010).

The positive correlations found between the total numbers of seeds removed and viable seeds excreted by birds and canopy fruit mass and monosaccharide content and canopy seed production supported the report that frugivorous birds concentrate their activities where resources are most abundant (Willson & Traveset 2000; Hulme 2002; Saracco et al. 2005; Blendinger et al. 2008); and preferentially consume fruits that possess a high nutritional content (Gosper et al. 2005; Kueffer et al. 2009; Gosper & Vivian-Smith 2010). In fact, Herrera et al. (1994) found that the fruit crop size was the best predictor of efficiency of fruit removal in *Phillyrea latifolia* trees growing in scrubland, whereas Sallabanks (1993) reported that fruit mass is an important determinant of fruit choice for the American robin *T. migratorius*. Birds might consume large fruits probably due to a correspondence between amount pulp swallowed and energy gained (Johnson et al. 1985). The observed birds' preference for the large nutritious berries of *S. mauritianum* over the small drupes of the other alien *L. camara* has been previously reported in southern Africa (Knight & Siegfried 1983; Oatley 1984; Knight 1988; Jordaan et al. 2011), and this is supported by possession of significantly higher fruit monosaccharide concentration in this study. Frugivorous birds tend to select fruits with high monosaccharide concentrations as they lack the sucrase enzyme, which cleaves sucrose into readily assimilated glucose and fructose fractions in the gut (Malcarney et al. 1994; Martinez del Rio & Restrepo 1993; Jordano 2000; Gosper &Vivian-Smith 2010). Fruits with high sucrose content are avoided as they cause osmotic diarrhoea that disrupts overall assimilation of nutrients in the guts of birds (Martinez del Rio et al. 1992; Levey & Martinez del Rio 2001). The higher fruit monosaccharide content of indigenous *C. monilifera* and *O. africana'*s than that of the alien *L. camara* might serve as a foraging cue for frugivorous birds (Foster 1990; Gosper et al. 2010). The relatively low nutritional quality of globally invasive *L. camara* fruits has been reported by previous avian frugivore diet studies (e.g. Gosper &Vivian-Smith 2010; Jordaan et al. 2011) and suggests that the success of its seed dispersal might rely on periods of native fruit-scarcity (Snow & Snow 1988). Despite this finding, the seed removal rates by the Cape white-eye *Z. capensis,* the speckled mousebird *C. striatus* and the Cape bulbul *P. capensis* did not differ significantly between indigenous *C. monilifera* and *O. africana,* and alien *L. camara.* This finding concurs with reports of *Turdus merula* and *T. philomelos* consuming similar proportions of indigenous and alien fruits consumed in New Zealand (Williams & Karl 1996) and Europe (Herrera 1984; Snow & Snow 1988).

It has been suggested that bird body mass of vector, fruit nutritional content and seed size have direct influence on quantities of seed ingested by birds (Jordano 2000; Gosper et al. 2005). For instance, a larger body mass in birds is associated with a larger gape width allowing birds to swallow a wider range of fruit/seeds of different sizes (Wheelwright 1985; Jordano 2000). This was evident from a strong positive correlation found between bird body mass and average number of

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Prunus mahaleb seeds ingested by birds in the southeastern Spanish Mediterranean (Jordano & Schupp 2000). However, the converse was observed in this study where greater numbers of both small *S. mauritianum* seeds and larger *C. monilifera, O. africana* and *L. camara* seeds were removed daily by the Cape white-eye *Z. capensis* with a substantially smaller body mass (10.9 g) than that of the speckled mousebird *C. striatus* (55 g) and the Cape bulbul *P. capensis* (38.6 g). This finding supports the reports that high feeding frequency improves the dispersal effectiveness of bird (Carlo et al. 2003; Vazquez et al. 2005; Schupp et al. 2010) since the Cape white-eye *Z. capensis* displayed highest foraging visitation frequency to the study plants (see Chapter 3). In fact the bird species included in this study, with the African olive-pigeon *C. arquatrix* excluded, have body masses below 140 g, and there was a negative correlation between bird body mass and average numbers of seeds removed daily from the four shrub species by each bird species, though statistically insignificant.

Only seeds of the indigenous *C. monilifera* and alien *L. camara* displayed enhanced germination following their ingestion by birds, which partly supported the study hypothesis. These findings concurred with the improved germination previously reported in bird-ingested seeds of these shrub species elsewhere (Gosper 2004b; Day et al. 2003; Mandon-Dalger et al. 2004; Sharma et al. 2005) and those of other fleshy-fruited shrubs such as *Myrtus communis* (Traveset et al. 2001; Robertson et al. 2006; Traveset et al. 2007, 2008). The enhanced germination was attributed to the release of seed dormancy enforced by water impermeable seed endocarps through seed scarification and chemical treatment during passage through the bird gut (Weiss 1983; Traveset et al. 2001; Day et al. 2003; Gosper 2004b; Turner & Downey 2008). Indeed, *C. monilifera's* invasiveness in Australia has been blamed on the dispersal and improved germination of its seeds ingested by fruit-eating vertebrates (Gosper 2004b). The unaltered germination observed in bird-ingested *O. africana* seeds was possibly due to their thick, impervious seed endocarps because Cuneo and Leishman (2006) noted high seed viability (e.g. 88%) when the woody endocarps were removed. Furthermore, limited retention times of large seeds in bird guts (Charalambidou et al. 2003) might in turn limit seed treatment as Traveset et al. (2008) also reported in *Phillyrea angustifolia*. Moreover, *O. africana* seeds do also exhibit morphophysiological dormancy (Baskin & Baskin 1998; Cuneo & Leishman 2006) which entails embryo maturation and its release from physiological inhibitors and pericarp breakage over a period of up to 20 months (Alacantara & Rey 2003; Cuneo & Leishman 2006). In fact, only a portion of *O. africana* seeds ingested by birds in Ethiopia germinate immediately after dispersal, which was partly facilitated by removal of the fruit pulp in vertebrate guts while the remaining seeds remain dormant and only germinate after the dry season (Aerts et al. 2006). The unaltered germination observed in the smaller *S. mauritianum* seeds ingested by birds might be attributed to their imperviousness to damage during their passage through the bird gut, this feature was also reported in *Solanum*

nigrum seeds ingested by bulbuls *Pycnonotus xanthopygos* and blackbirds *T. merula* in Israel (Barnea et al. 1990). Also, Solanaceae fruits possess a laxative effect that promotes rapid seed passage through the gut of the disperser (Murray et al. 1994; Wahaj et al. 1998) which thereby limits gut treatment times for release of enforced seed dormancy (Baskin & Baskin 2004; Hoyle et al. 2008).

In conclusion, this study's findings supported the study hypothesis that frugivorous birds remove larger amounts of fruits and seeds from especially alien plants with high fruit production and nutritional contents, since canopy seed production, fruit mass and monosaccharide content were all positively correlated with the total numbers of seeds removed by birds and viable seeds excreted by birds. Indeed, the 14 frugivorous birds as a whole removed the greatest numbers of seeds of the alien *S. mauritianum,* which was attributed to the small seed size, large seed density per fruit and high fruit monosaccharide content of fruits of *S. mauritianum* (Rejmanek & Richardson 1996). The smaller numbers of seeds of the indigenous *C. monilifera* removed by the 14 frugivorous birds as a whole was a likely consequence of poor fruit quality due to insect infestation (Scott 1996), though this was partly offset by the considerably improved germination of the ingested seeds following passage through bird guts.

6.7. Reference list

Aerts, R., Maes, W., November, E., Negussie, A., Hermy, M. & Muys, B. (2006) Restoring dry Afromontane forest using bird and nurse plant effects: direct sowing of *Olea europaea* ssp. *cuspidata* seeds. *Forest Ecology and Management*, **230**, 23-31.

Alcantara, J.M. & Rey, P.J. (2003) Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea. Journal of Evolutionary Biology*, **16**, 1168-1176.

Barnea, A., Yom-Tov, Y. & Friedman, J. (1990) Differential germination of two closely related species of Solanum in response to bird ingestion. *OIKOS*, **57**, 222-228.

Bartuszevige, A.M. & Gorchov, D.L. (2006) Avian dispersal of an invasive shrub. *Biological Invasions*, **5**, 1013-1022.

Baskin, C.C. & Baskin, J.M. (1998) *Seeds- Ecology, biogeography and evolution of dormancy and germination.* Academic Press, San Diego.

Baskin, J.M. & Baskin, C.C. (2004) A classification system for seed dormancy. *Seed Science Research*, **14**, 1-16.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. (2000) *Bird census techniques.* Academic Press, London.

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Bond, W.J. & Breytenbach, G.J. (1985) Ants, rodents and seed predation in Proteaceae. *South African Journal of Zoology*, **20,** 150-154.

Bond, W.J. (2005) Functional types for predicting biodiversity changes: a case in Cape fynbos. *Plant functional type: their relevance to ecosystem properties and global change.* (eds. Smith, T.M., Shugart, H.H. & Woodward, F.I.) pp. 174-192. Cambridge University Press, New York.

Buysse, J.A.N. & Merckx, R. (1993) An improved colorimetric method to quantify sugar content of plant tissue. *Journal of Experimental Botany*, **44**, 1627-1629.

Carlo, T.A., Aukema, A.G. & Morales, J.M. (2007) Plant-frugivore interactions as spatially explicit networks: integrating frugivore foraging with plant spatial patterns. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 369-390. Reading: Biddles Ltd.

Carlo, T.A., Collazo, J.A. & Groom, M.J. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia*, **134**, 119-131.

Charalambidou, I., Santamaria, L. & Langevoord, O. (2003) Effect of ingestion by five avian dispersers on the retention time, retrieval and germination of *Ruppia maritima* seeds. *Functional Ecology*, **17**, 747-753.

Clark, J.S., Silman, M., Kern, R., Macklin, E. & HilleRisLambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475-1494.

Colautti, R.I., Bailey, S.A., van Overdijk, C.D.A., Amundsen, K. & MacIsaac, H.J. (2006) Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions*, **8**, 45 - 59.

Cuneo, P. & Leishman, M.R. (2006) African Olive (*Olea europaea* subsp*. cuspidata*) as an environmental weed in eastern Australia: a review. *Cunninghamia*, **9**, 545-557.

Day, M., Wiley, C.J., Playford, J. & Zalucki, M.P. (2003) *Lantana: current management status and future prospect*s. ACIAR, Canberra, ACT, Australia.

Dennis, A.J. & Westcott, D.A. (2007) Estimating dispersal kernels produced by diverse community of vertebrates. *Seed dispersal: theory and its application in a changing world* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 201-228. Reading: Biddles Ltd.

Foster, M.S. (1990) Factors influencing bird foraging preferences among conspecific fruit trees. *The Condor*, **92**, 844-854.

Garcia, D., Zamora, R., Gómez, J.M. & Hodin, J.H. (2001) Frugivory in *Juniperus communis* depends more on population characteristics than on individual attributes. *Journal of Ecology*, **89**, 639–647.

Geldenhuys, C.J., le Roux, P.J. & Cooper, K.H. (1986) Alien invasions in indigenous evergreen forest. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 119–131. Cape Town, Oxford University Press.

Godinez-Alvarez, H. & Jordano, P. (2007) An empirical approach to analysing the demographic consequences of seed dispersal by frugivores. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 391-406. Reading: Biddles Ltd.

Gosper, C. & Vivian-Smith, G. (2010) Fruit traits of vertebrate-dispersed alien plants: smaller seeds and more pulp sugar than indigenous species. *Biological Invasions,* **12**, 2153-2163.

Gosper, C.R. (2004b) Consequences of weed invasion and control on plant-bird interactions and bird communities. Ph.D. Thesis, Department of Biological Sciences, University of Wollongong, Wollongong.

Gosper, C.R. (2004a) Fruit characteristics of invasive bitou bush, *Chrysanthemoides monilifera* (Asteraceae), and a comparison with co-occurring native plant species. *Australian Journal of Botany*, **52**, 223–230.

Gosper, C.R., Stansbury, C.D. & Vivian-Smith, G. (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distributions,* **11**, 549-558.

Greenberg, C., Smith, L. & Levey, D. (2001) Fruit fate, seed germination and growth of an invasive vine – an experimental test of 'sit and wait' strategy. *Biological Invasions*, **3**, 363-372.

Greenberg, C.H. & Walter, S.T. (2010) Fleshy fruit removal and nutritional composition of winter-fruiting plants: a comparison of non-native invasive and native species. *Natural Areas Journal*, **30**, 312-321.

Herrera, C.M. (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs*, **54**, 2-23.

Herrera, C.M. (1995) Plant-vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics*, **26**, 705-727.

Herrera, C.M., Jordano, P. Lopez-Soria, L. & Amat, J.A. (1994) Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs*, **64**, 315-344.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (eds) (2005) *Roberts' birds of Southern Africa*, 7th edn. John Voelcker Bird Book Fund: Cape Town.

Howe, H.F. (1977) Bird activity and seed dispersal of a tropical wet forest tree. *Ecology*, **58**, 539-550.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201-228.

Hoyle, G.L., Steadman, K.J., Daws, M. I. & Adkins, S. W. (2008) Physiological dormancy in forbs native to south-west Queensland: Diagnosis and classification. *South African Journal of Botany*, **74**, 208-213.

Hulme, P. E. (1998) Post-dispersal seed predation and seed bank persistence. *Seed Science Research*, **8**, 513-519.

Hulme, P.E. (2002) Seed-eaters: see dispersal destruction and demography. *Seeds dispersal and frugivory: ecology, evolution and conservation* (eds. Levey, D. J., Silva, R. W. & Galleti, M.) pp. 161-175. Wallingford: CABI Publishing.

Izhaki, I. (2002) The role fruit traits in determining fruit removal in east Mediterranean ecosystems. *Seeds dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D. J., Silva, R.W. & Galleti, M.) pp. 161-175. Wallingford: CABI Publishing.

Izhaki, I. & Safriel, U.N. (1989) Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *OIKOS*, **54**, 23-32.

Izhaki, I., Walton, P.B. & Safriel, U.N. (1991) Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *Journal of Ecology*, **79**, 575-590.

Jordaan, L.A., Johnson, S.D. & Downs, C.T. (2011) Digestion of fruit of invasive alien plants by three southern African avian frugivores. *Ibis*, **153**, 863-867.

Jordano, P. (2000) Fruits and frugivory. *Seeds: the ecology of regeneration in natural plant communities.* (ed. Fenner, M.) pp. 125-166. CABI Publishers, Wallingford, UK.

Kelly, D. & Sork, V.L. (2002) Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics,* **33**, 427-447.

Knight, R.S. (1986) A comparative analysis of fleshy fruit displays in alien and indigenous plants. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 171-178. Oxford University Press, Cape Town.

Knight, R.S. (1988) Aspects of plant dispersal in the south-western Cape with particular reference to the roles of birds as dispersal agents. Ph.D. Thesis, University of Cape Town, South Africa.

Knight, R.S. & Siegfried, W.R. (1983) Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia*, **56**, 405-412.

Kueffer, C., Kronauer, L. & Edwards, P.J. (2009) Wider spectrum of fruit traits in invasive than native floras may increase the vulnerability of oceanic islands to plant invasions. *OIKOS*, **118**, 1327-1334.

LaFleur, N.E., Rubega, M.A. & Elphick, C.S. (2007) Invasive fruits, novel food, and choice: an invesitagtion of European starling and American robins frugivory. *The Wilson Journal of Ornithology*, **119**, 429-438.

Latimer, A.M., Silander, J.A., Gelfand, A.E., Rebelo, A.G. & Richardson, D.M. (2004) A method for quantifying the magnitude of threat to plant biodiversity from alien plant invasions and other anthropogenic factors – a case study in the CFR, South Africa. *South African Journal of Science,* **100**, 81–86.

le Maitre, D.C. & Midgley, J.J. (1992) Plant reproductive ecology. *The ecology of fynbos.* (ed. Cowling, R.) pp. 135-174. Oxford University Press: Cape Town.

Levey, D.J. & Martinez del Rio, C. (2001) It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. *The Auk,* **118**, 819-831.

Levey, D.J. (1987) Seed size and fruit-handling techniques of avian frugivores. *The American Naturalist,* **129**, 471-485.

Levine, J.M., Vila, M., D'Antonio, C.M. Dukes, J.S. Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London*, **270**, 775 - 781.

Luck, G.W. & G.C. Daily. (2003) Tropical countryside bird assemblages: richness, composition, foraging differ by landscape context. *Ecological Applications*, **13**, 235-247.

Malcarney, H.L., Martínez del Rio, C. & Apanius, V. (1994) Sucrose intolerance in birds: simpel nonlethal diagnostic methods and consequences for assimilation of complex carbohydrates. *The Auk*, **111**, 170-177.

Manders, P.T. & Richardson, D.M. (1992) Colonization of Cape fynbos communities by forest species. *Forest Ecology and Management*, **48**, 277-293.

Mandon-Dalger, I., Clergeau, P., Tassin, J., Rivière, J.N. & Gatti, S. (2004) Relationships between alien plants and an alien bird species on Reunion Island. *Journal of Tropical Ecology*, **20**, 635–642.

Martinez del Rio, C. & Restrepo, C. (1993) Ecological and behavioral consequences of digestion in frugivorous animals. *Plant Ecology*, **107-108**, 205-216.

Martinez del Rio, C., Baker, H.G. & Baker, I. (1992) Ecological and evolutionary implications of digestive processes: bird preferences and the sugar constituents of floral nectar and fruit pulp. *Cellular and Molecular Life Sciences*, **48**, 544-551.

McNamara, J.M., Houston, A.I. & Lima, S.L. (1994) Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology*, **25**, 287-302.

Milton, S.J., Wilson, J.R.U., Richardson, D.M., Seymour, C.L., Dean, W.R.J. & Iponga, D.M. (2007) Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. *Journal of Ecology*, **95**, 648-661.

Moermond, T. C. & Denslow, J. S. (1985) Neotropical avian frugivores: patterns of behaviour, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs, 36*, 865-897.

Mucina, L. & Rutherford, M.C. (eds) (2006) *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19, South African National Biodiversity Institute, Pretoria.

Murray, K.G., Russell, S., Picone, C.M., Winnett-Murray, K., Sherwood, W. & Kuhlmann, M.L. (1994) Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. *Ecology,* **75,** 989-994.

Murray, K.G., Winnett-Murray, K., Cromie, E.A., Minor, M. & Meyers, E. (1993) The Influence of seed packaging and fruit color on feeding preferences of American Robins. *Vegetatio,* **107/108,** 217-226.

Nogales, M., Nieves, C., Illera, J.C., Padilla, D.P. & Traveset, A. (2005) Effect of native and alien vertebrate frugivores on seed viability and germination patterns of *Rubia fruticosa* (Rubiaceae) in the eastern Canary Islands. *Functional Ecology*, **19**, 429-436.

Oatley, T.B. (1984) Exploitation of a new niche by the rameron pigeon *Columba arquatrix* in Natal. *Proceedings of the Fifth Pan-African Ornithological Congress* (ed. Ledger, J.A.), pp. 323-330, Southern African Ornithological Society.

Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655-1661.

Richardson, D.M. & Fraser, M.W. (1995) Birds of Swartboskloof, Jonkershoek Valley, Stellenbosch: a mountain fynbos ecosystem. *Southern Birds*, **18**, 1–44.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmanek, M. (2000) Plant invasions: the role of mutualisms. *Biological Reviews,* **75**, 65-93.

Robertson, A.W., Trass, A, Ladley, J.J. & Kelly, D. (2006) Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Functional Ecology*, **20**, 58–66.

Sallabanks, R. (1993) Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology*, **74**, 1326-1336.

Samuels, I.A. & Levey, D.J. (2005) Effects of gut passage on seed germination: do experiments answer the questions they ask? *Functional Ecology*, **19**, 365-368.

Schupp, E.W. (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, **107/108**, 15-29.

Schupp, E.W., Jordano, P. & Gómez, J.M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, **188**, 333-353.

Scott, J.K. (1996) Population ecology of *Chrysanthemiodes monilifera* in South Africa: implications for its control in Australia. *Journal of Applied Ecology*, **33**, 1496-1508.

Sharma, G.P., Singh, J.S. & Raghubanshi, A.S. (2005) Plant invasions: emerging trends and future implications. *Current Science*, **88**, 726 - 734.

Sinclair, I. & Ryan, P. (2003) *Birds of Africa south of the Sahara*. Cape Town: Struik Publishers.

Snow, B. & Snow, D. (1988) *Birds and berries.* T. & A.D. Poyser ltd, Calton, UK.

Stansbury, C.D. & Vivian-Smith, S.G. (2003) Interactions between frugivorous birds and weeds in Queensland as determined from a survey of birders. *Plant Protection Quarterly*, **18**, 157-165.

Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution,* **21**, 208-216.

Traveset, A., Riera, N. & Mas, R.E. (2001) Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology*, **15**, 669-675.

Traveset, A., Robertson, A.W. & Rodriguez-Perez, J. (2007) A review of the role of endozoochory in seed germination. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 78-103. Reading: Biddles Ltd.

Turner, P.J. & Downey P.O. (2008) The role of native birds in weed invasion, species decline, revegetation, and reinvasion: consequences for lantana management. *Proceedings of 16th Australian Weeds Conference* (eds. van Klinken, R.D., Osten, V.A., Panetta, F.D. & Scanlan, J.C.) pp. 30–32. Queensland Weeds Society, Brisbane, Australia.

Twigg, L.E., Lowe, T.J., Taylor, C.M., Calver, M.C., Martin, G.R., Stevenson, C. & How, R.I.C. (2009) The potential of seed-eating birds to spread viable seeds of weeds and other undesirable plants. *Austral Ecology,* **34,** 805-820.

van Wyk, B. & van Wyk, P. (1997) *Field guide to trees of southern Africa.* Struik Publishers: Cape Town.

Vazquez, D. P., Morris, W. F. & Jordano P. (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters*, **8**, 1088-1094.

Vila, M. & D'Antonio, C.M. (1998) Fruit choice and seed dispersal of invasive vs. noninvasive Carpobrotus (Aizoaceae) in coastal California. *Ecology*, **79**, 1053-1060.

Wahaj, S.A., Levey, D.J., Sanders, A.K. & Cipollini, M.L. (1998) Control of gut retention time by secondary metabolites in ripe Solanum fruits. *Ecology*, **79**, 2309-2319.

Weiss, P.W. (1983) Invasion of coastal Acacia communities by Chrysanthemoides. Ph.D. Thesis, Australian National University.

Wenny, D.G. (2000) Seed dispersal of a high quality fruit by specialized frugivores: high quality dispersal? *Biotropica*, **32**, 327-337.

Whelan, C.J., Wenny, D.G. & Marquis, R.J. (2008) Ecosystem services provided by birds. *Annals of the New York Academy of Sciences*, **1134**, 25-60.

Williams, P.A. & Karl, B.J. (1996) Fleshy fruits of indigenous and adventives plants in the diet of birds in forest remnants, Nelson, New Zealand. *New Zealand Journal of Ecology*, **20**, 127-145.

Willson, M. & Traveset, A. (2000) The ecology of seed dispersal. *The ecology of regeneration in plant communities*. (ed. Fenner, M.) pp. 85-110. CAB International, Wallingford, UK.

Willson, M.F. & Whelan, C.J. (1993) Variation of dispersal phenology in a bird-dispersed shrub, *Cornus drummondii. Ecological Monographs*, **63**, 151-172.

Appendix 6.1 Faecal collecting tray constructed from white plastic sheeting supported by metal fencing standards placed beneath S*. mauritianum* (A), the tray covered by wire mesh to minimise seed predation by rodents (B) and a faecal sample deposited on a leaf bearing *L. camara* seeds (C)

Chapter 7

A comparison of seed removal rates by birds from alien and indigenous shrubs using experimental and photographic approaches and an assessment of seed dispersal distances

7.1. Abstract

Seed removal rates by birds from indigenous (*Chrysanthemoides monilifera* and *Olea europaea* subsp *africana)* and alien (*Lantana camara* and *Solanum mauritianum)* shrubs at 4 different study sites (Hout Bay, Paarl, Hermanus and Swellendam) in the Cape Floristic Region were measured using experimental and photographic approaches. The experimental approach involved counting the numbers of fruits and associated seeds removed monthly by birds, excluding those naturally abscised, from the alien and indigenous shrubs. The photographic approach involved visual counts from images captured by a digital camcorder of the numbers of whole or partial indigenous and alien fruits and associated seeds consumed by different species of birds over specific time intervals. Daily seed removal rates measured by the photographic and experimental approaches were similar with no significant interactions evident between measuring approaches, site and shrub species. Both the experimental and photographic approaches displayed higher seed removal rates by frugivorous birds as a whole from the alien shrub *S. mauritianum* than the other shrub species, this was also evident among individual bird species. Foraging distances for each bird species were derived from their initial capture location and recapture ring location extracted from the South African Bird Atlas Project database and the fractions of bird-ring recapture records present in different distance categories plotted. Seed dispersal distance limits were estimated for birds of different body masses from the product of seed gut retention time and bird flight speeds obtained from published records. The dispersal curves separated bird species into potential short and long distance seed dispersal vectors, which appeared partly related to the home range size of the bird species. Whereas the relatively short seed dispersal distance limits of between 0.41 and 0.81 km estimated for a subset of 19 heavily and moderately frugivorous bird species suggest that fleshy-fruited alien plants are dispersed into natural habitats from adjacent propagule sources, the dispersal distance curves indicate the possibility for long distance dispersal.

Keywords: fleshy fruits, frugivorous birds, seed dispersal distance, alien and indigenous plants, Cape Floristic Kingdom, scientific methods

7.2. Introduction

A better understanding of the effectiveness of bird-mediated seed dispersal of fleshy-fruited plants could elucidate plant population dynamics of natural plant communities invaded by alien shrubs and trees such as those in the South African Cape Floristic Region (Schupp 1993; Bullock et al. 2006; Jordano 2007; Green 2007; Tsoar et al. 2011). Several studies have examined the effectiveness of different empirical approaches for collecting data on seed removal by birds (Nathan & Muller-Landau 2000; Nathan 2001b; Bullock et al. 2006). However, the lack of consistency among different approaches used to measure the quantities of seeds removed by birds and their potential dispersal distances preclude generalisations. In fact, similar approaches have yielded different results for comparable environmental conditions, plant and bird species (Nathan & Muller-Landau 2000; Nathan 2001b; Bullock et al. 2003, 2006). This was due partly to diffuse interactions between birds and plant species (Carlo et al. 2007; Dennis & Westcott 2007; Nathan 2007). Nevertheless, direct observations in measuring seed dispersal by birds (Nathan 2001b) coupled with other methods can be useful in establishing the reliability of different approaches (Bullock et al. 2006). Experimental approaches in determining seed removal rates by birds have been applied in several studies (Sallabanks 1993; Korine et al. 2000; Bache & Kelly 2004), these entailing direct counts of the numbers of fruits consumed by birds over specific time intervals coupled with placement of fruit traps underneath the plant canopies to measure fruit loss by abscission. The difference between the total numbers of fruits present in the canopy at the commencement of the study minus those present in the fruit traps plus those remaining in the plant canopy at the end of the study represents bird removal (Sallabanks 1993). Conversely, photographic approaches have entailed the use of digital camcorders to photograph birds consuming fruits (Spiegel & Nathan 2007). Photographic approaches have several advantages in that they provide permanent visual and time-lapse records for the individual foraging bird species allowing greater measurement precision and interpretation of fruit removal behaviour by birds.

Dispersal of seeds away from parents assists in seedling escape from competition by adults and local siblings, as well as from seed predators and parasites which focus their activities in close proximity to parents where resources are abundant (Willson & Traveset 2000; Godinez-Alvarez & Jordano 2007). Moreover, bird movement between diverse habitats provide essential genetic links between habitat fragments that are otherwise inaccessible (Opdam & Wascher 2004; Schupp et al. 2010). Seed dispersal offsets localised plant species extinctions by facilitating the transport of seeds to novel areas where they can form new self-sustaining populations (Neubert & Caswell 2000; Schurr et al. 2007; Schurr et al. 2009). Although fleshy-fruited plant species dispersed by birds are successful in colonising new habitats and expanding their range rapidly (Richardson et al. 2000; Cordeiro et al. 2004; Trakhtenbrot et al. 2005; Traveset et al. 2006; Quix 2007), there are a few empirical data on dispersal distances of seed consumed by birds. The knowledge of the

distances to which birds disperse seed of alien species may assist in predicting future distribution ranges and in selecting suitable management strategies to limit alien spread (Sakai et al. 2001; Tsoar et al. 2011).

In most plant species, the majority of seeds are dispersed over relatively short distances by birds, the distances rarely exceeding a few dozen meters from original seed sources (Willson 1993). The bulk of locally dispersed seeds generate a spatial template that often moulds the local dynamics of plant populations and communities (Howe & Smallwood 1982; Levin et al. 2003). It has been suggested that although long-distance dispersal (LDD) events are typically rare, they play a major role in determining large-scale processes such as population spread, the flow of individuals between populations, the colonization of unoccupied habitats and the assembly of local communities from the metacommunity (Levine & Murrell 2003). In addition, LDD rather than local dispersal determines the spread of invasive plants, range shifts following climate change and the persistence of species in fragmented landscapes (Trakhtenbrot et al. 2005; Schurr et al. 2007; Nathan et al. 2008). Consequently, despite immense difficulty in measurement and prediction seed dispersal distances (Cain et al. 2000; Nathan et al. 2003), LDD research is currently experiencing an upsurge of general interest especially in plant ecology and management of invasive alien plants dispersed by birds (Levin et al. 2003; Nathan 2005; Schurr et al. 2009; Tsoar et al. 2011).

Historically, reliable estimates of dispersal distances of seed ingested by birds are restricted by erratic bird flight patterns (Nathan 2001a; Schupp et al. 2002; Muller-Landau & Hardesty 2005; Russo et al. 2006), and distorted plant-animal mutualisms induced by habitat fragmentation and defaunation (Herrera 1995; Opdam & Waschar 2004; Muller-Landau & Hardesty 2005). Some studies have applied various analytical models (mechanistic and phenomenological) to predict seed dispersal distances. However, these models do not fully incorporate all the complexities of long-distance seed dispersal (Nathan & Muller-Landau 2000; Russo et al. 2006) such as bird behavioural dynamics such as fruit tracking (Schupp et al. 2002; Sarraco et al. 2004; Telleria et al. 2005), and changes in bird flight patterns due to habitat disturbance and fruit preferences (Gosper et al. 2005; Wilms & Kappelle 2006; Gomes et al. 2008). An alternate vector-based approach has been proposed, based on the assumption that seed dispersal distance is directly proportional to the body size of the disperser in flying vertebrates (Schurr et al. 2009; Tsoar et al. 2011). Large birds often disperse seeds to more distant microsites than smaller birds during habitat exploitation (Jordano 2000; Bowman et al. 2002; Jenkins et al. 2007; Tsoar et al. 2011). Examples include the observed greater dispersal distance of seeds of the fleshy-fruited shrub *Ochradenus baccatus* by large Tristram's grackles *Onychognathus tristramii* than by smaller bulbuls *Pycnonotus xanthopygos* in Israel (Spiegel & Nathan 2007). However, smaller birds may also disperse seeds to distant sites in their movement between intermittently fruiting populations along geographical gradients (fruit tracking), and occasionally through extended seed gut retention times (Shilton et al.

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1999; Saracco et al. 2004; Telleria et al. 2008). The territorial European robin *Erithacus rubecula,* for example, tracks spatially variable fruit availability in the Spanish Mediterranean scrubland (Telleria et al. 2008), which overrides the constraints of body size on dispersal distances of seeds ingested by mammals (Bowman et al. 2002).

Previous studies have computed seed dispersal distance as a function of seed retention time in the gut of a bird and flight speed (Fukui 1996; Holbrook & Smith 2000; Higgins et al. 2003; Westcott & Graham 2000; Schurr et al. 2009; Tsoar et al. 2011). McConkey et al. (2004), for example, determined the dispersal distances of *Myristica hypagyria* seeds ingested by the fruit pigeon *Ducula pacifica* in Tonga, Western Polynesia from the product of this bird's gut retention time of seeds and its flight speed. Retention times of seed in bird guts are positively correlated with bird body mass (Schurr et al. 2009; Tsoar et al. 2011), and the tendency for large birds to fly more rapidly over larger distances may potentially greater dispersal distances than small birds (Schurr et al. 2009; Tsoar et al. 2011). However, gut retention time of seeds is influenced by seed size with large seeds consumed by bigger birds expelled more rapidly than small seeds (Whittaker & Jones 1994; Martinez del Rio 2001; Charalambidou et al. 2003). In addition, high concentrations of sucrose and glycoalkaloids in some fruit types have a laxative effect causing seeds also to be expelled more rapidly (Murray et al. 1994; Malcarney et al. 1994; Wahaj et al. 1998). That measurement of gut retention time of seeds have mostly been estimated for birds in captivity (Kays et al. 2011), may also reduce reliability of such data in the natural environment. Also, the mechanistic models have not incorporated spatially explicit data on the directionality of movements in such a way that allows prediction of the spatial pattern of seed deposition (Russo et al. 2006). Therefore, mechanistic approaches are likely to either overestimate or underestimate the dispersal distances (Russo et al. 2006; Muller-Landau & Hardesty 2005) and thus require empirical data on movement of frugivorous birds to provide estimates of seed dispersal distances from maternal plants (Nathan 2001b; Westcott et al. 2005; Russo et al. 2006; Holbrook 2010). Moreover, short and long-distance dispersal are associated with different dispersal mechanisms hence the overall distribution of dispersal distances may be best represented by mixing several dispersal kernels (Schupp et al. 2002; Levin et al. 2003). Consequently, some studies have combined gut retention times with reliable distance measurements from mobile GPS loggers tagged on birds. For instance, the gut passage time of seeds and measurements of foraging ranges of the *Ceratogymna* hornbills and trumpeter hornbills *Bycanistes bucinator* were used to estimate potential dispersal distances of ingested seeds in Cameroon and South African forests respectively (Holbrook & Smith 2000; Lenz et al. 2010). Therefore, in this study, potential dispersal distances of seed were estimated from bird foraging distances derived from bird-ring recapture data (Nathan & Muller-Landau 2000; Schupp et al. 2002), and published bird gut retention times as functions of their body mass and flight speeds (Schurr et al. 2009; Tsoar et al. 2011). The aims of this study were to compare the efficacy of

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experimental and photographic methods for determining seed removal rates by birds from fleshy-fruited alien and indigenous shrubs and to evaluate foraging distances for different groups and species of birds and seed dispersal distance limits.

7.3. Methods and materials

7.3.1. Study sites and shrub species

The experimental design comprised 4 study sites , each comprising mixed populations of alien and indigenous shrubs, located on different vegetation units described in Mucina and Rutherford (2006), namely: Peninsula Granite Fynbos (Hout Bay site), Swartland Shale Renosterveld (Paarl site), Overberg Sandstone Fynbos (Hermanus site) and Breede Shale Renosterveld (Swellendam site). Each site contained populations of two indigenous (*Chrysanthemoides monilifera* and *Olea europaea* subsp *africana*) shrubs intermixed with two alien (*Lantana camara* and *Solanum mauritianum)* shrubs all producing fleshy fruits. Since vegetation composition strongly influences fruit and seed removal by birds (Garcia et al. 2001; Carlo et al. 2007), all shrub species were selected based on their co-occurrence over a wide range of natural vegetation types, their overlapping fruiting times (Van Wyk & Van Wyk 1997) and consumption of their fruit by local frugivorous birds (Richardson & Fraser 1995). *Lantana camara, C. monilifera* and *O. africana* possess similar fruit architectures, namely single-seeded drupes that turn black when ripe, whereas *S. mauritianum* produces green multi-seeded berry turning yellowish when ripe.

7.3.2. Fruit and seed removal rates by birds

The experimental and photographic approaches were applied in determining rates of fruit and seed removal from the alien and indigenous shrubs during their periods of peak fruit production. In the experimental approach, labelled tags were affixed to four fruiting branches on 15 individuals of each shrub species at each site. Horizontal and vertical canopy dimensions of the shrubs to which the labelled tags were affixed were measured and their fruiting canopy areas calculated. The entire canopies of *C. monilifera, L. camara* and *O. africana* were occupied in fruit production whereas in *S. mauritianum* where fruits were confined to terminal branched corymbs, only about 20% of the total canopy area was involved in fruit production. The 0.25 m² quadrats were placed at the positions marked by the labelled tags on the fruiting branches of each shrub and the numbers of whole fruits present within each quadrat recorded at the commencement and again at the termination of the 30-day monitoring period. In *S. mauritianum,* the numbers of partly (25%, 50%, 75%) consumed fruits remaining in the corymbs after the 30-day monitoring interval were also recorded. Abscised fruits lost from the tagged branches of each shrub over the 30-day monitoring

interval were collected in 0.29 m^2 traps placed beneath the tagged fruiting branches (Appendix 7.1). Each trap comprised a 0.64 m long x 0.45 m wide x 0.18 m high collecting box whose open apices were clad with 1 cm diameter wire mesh to allow fruit passage but prevent fruit predation by rodents (Bond & Breytenbach 1985; Scott 1996; Hulme 1998). It was assumed that fruits lost from the tagged branches over the 30-day monitoring interval either were consumed by birds or abscised (Sallabanks 1993; Bach & Kelly 2004). Daily seed removal rates (DSR) per shrub were computed from the following formula:

$$\text{DSR} = \{[(F_{t1} - (F_{t2} + AF) \times 4]/30\} \times SF \times FCA \dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots(1)$$

where: F_{t1} = numbers of whole fruits at commencement of monitoring

F_{t2} = numbers of whole and partial fruits at termination of monitoring

AF = numbers of abscised fruits

4 = conversion factor to m^2

30 = monitoring interval in days

SF = average numbers of seeds per whole or partial fruit

FCA = fruiting canopy area m^2

Chrysanthemoides monilifera, O. africana and *L. camara* fruits contained single seeds whereas those of *S. mauritianum* contained an average of 66 ± 3 seeds per fruit. This was derived from sub-samples of 50 fruits sampled at random from *S. mauritianum* shrubs at each study site

In the photographic approach, a digital camcorder (Kodak C813: 8.2 megapixel, ISO 1250, digital IS) provided permanent photographic records of the numbers of whole or partial fruits consumed by different species of birds over specific time intervals. Camcorder surveillances were conducted approximately 30 m distance from randomly selected individual reproductively mature alien and indigenous fruiting shrubs at each site. Surveillances were conducted during early morning (3 h period after sunrise) and late afternoon (3 h period before sunset) periods of peak bird activity over a 5-day monitoring period when the alien and indigenous shrub species were in full fruit (Howe 1977; Snow & Snow 1988; McNamara et al. 1994; Bibby et al. 2000). From the photographic records, the total foraging periods in seconds spent by individual birds per day on each shrub species were documented. Also, the numbers of mouthfuls of fruits taken by each bird species from each shrub species over the recorded foraging time intervals in seconds were determined. For the small single seed fruits of *C. monilifera, O. africana* and *L. camara*, all bird species consumed the entire fruit*, i.e.* one seed per mouthful. For the large multi-seed fruits of *S. mauritianum*, the fraction of the whole fruit removed by each bird species in one mouthful was estimated from its gape size. From the fractions of whole *S. mauritianum* fruits consumed, the

numbers of seeds removed in one mouthful of fruit were determined from the average numbers of seeds present in each fruit. The latter derived from sub-samples of 50 multi-seeded fruits sampled at random from *S. mauritianum* shrubs at each study site. The total numbers of seeds removed by each bird species from each shrub per day (6-h observation period) were calculated from the product of the average numbers of seeds removed per second and the average foraging periods in seconds per day.

7.3.3. Bird foraging distances and seed dispersal distance limits

Bird-ring recapture records provided spatial patterns of bird foraging distances (Nathan & Muller-Landau 2000; Russo et al. 2006). These records were extracted from the South African Bird Atlas Project (SABAP 1 & 2) databases (Animal Demography Unit, University of Cape Town). From 5 880 recapture ring records (i.e. within South Africa's borders) of 33 out of 37 bird species but only records for 9 heavily frugivorous (red-winged starling *Onychognathus morio,* common starling *Sturnus vulgaris,* speckled mousebird *Colius striatus,* red-faced mousebird *Urocolius indicus,* olive thrush *Turdus olivaceus,* Cape bulbul *Pycnonotus capensis* house sparrow *Passer domesticus*, Cape Robin *Cossypha caffra* and Cape white-eye *Z. capensis*) and 10 moderately frugivorous bird species (Speckled pigeon *Columba guinea,* laughing dove *Streptopelia senegalensis,* Cape turtledove *Streptopelia capicola,* red-eyed dove *Streptopelia semitorquata,* southern boubou *Laniarius ferrugeneus,* fiscal flycatcher *Segelus silens,* yellow canary *Crithagra flaviventris,* common fiscal *Lanius collaris,* southern masked-weaver *Ploceus velatus* and Cape canary *Ploceus capensis*) were examined. Only bird species having at least 50 or more recapture ring records were selected. From the bird-ring recapture records, foraging distances were derived from the initial ring location and subsequent recapture locations, these calculated geo-spherically with foraging distance measures based on the earth's contour rather than on direct vectors. Foraging distances derived for the heavily and moderately frugivorous birds species from the bird ring recapture records were classified into 10 different distance categories, namely >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 and > 400 km. The fractions (percentages) of bird-ring recapture records present in each distance category for each frugivorous bird species were calculated.

To determine the seed dispersal limits, published data on bird body mass (g) and times (min) for which they retain seeds of fleshy fruits in their guts, and flight speeds (m/s) were used (Table 7.1). Least squares regressions quantified relationships between bird body mass, gut retention times of consumed seed and flight speeds. These regression functions were used to predict gut retention times and flight speeds of 19 heavily and moderately frugivorous bird species based on their body masses provided in Hockey et al. (2005). The product of the predicted gut retention times and flight speeds provided estimates of seed dispersal distance limits for each bird

species, i.e. the flight distances covered by the respective bird species over the duration of their gut retention times of consumed seed (Schurr et al. 2009; Tsoar et al. 2005).

7.4. Statistical analyses

All measurements were $\log_e$ transformed before statistical analysis to reduce the inequality of variance in the raw data so these more closely approximated normal distributions. The experimental design was unbalanced due to unequally replicated measurements. Consequently, a residual maximum likelihood (REML) variance component analysis (linear mixed model) was applied to test for differences between the experimentally and photographically derived bird seed removal rates from the indigenous and alien shrub species at the different sites and their interactions using the Wald X^2 statistic generated by the REML (GENSTAT Discovery Edition 3, VSL Lty, UK). Experimental and photographic method, site and shrub species variables were fitted in the fixed model and method, site and shrub species factors in the random model. Differences exceeding twice the mean standard error of differences were used to separate significantly different treatment means at P ≤ 0.05. This was based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is two.

A student's t-test tested the slopes and the intercepts of least squares regressions for significance at P ≤ 0.05.

Table 7.1. Body masses, gut retention times of ingested seeds and flight speeds reported in previous studies for different frugivorous bird species

Bird species	Body mass (g)	Gut retention-time (mins)	Flight speed (m sec⁻¹)	Source
Sturnellu magna	120		10.19	Evans & Drickamer 1994
Agelaius phoeniceus	36		10.66	Evans & Drickamer 1994
Mimus polyglottos	46.5		9.75	Evans & Drickamer 1994
Progne subis	52.5		9.77	Evans & Drickamer 1994
Turdus migrotrius	77		8.79	Evans & Drickamer 1994
Sturnus vulgaris	85		11.35	Evans & Drickamer 1994
Passer domesticus	35		11.26	Evans & Drickamer 1994
Zenaidu macrouru	150		10.93	Evans & Drickamer 1994
Hirundo pyrrhonotu	22.7		9.29	Evans & Drickamer 1994
Tuchycinetu bicolor	19		9.62	Evans & Drickamer 1994
Manacus vitellinus	17.4	18		Bucher & Worthington 1982
Pipra mentalis	13.4	18		Bucher & Worthington 1982
Columba sp	50		10.72	Burtt & Giltz 1974
Hemiphaga novaeseelandiae	800	181		Burtt & Giltz 1974
Agelaius phoeniceus	64		20.11	Burtt & Giltz 1974
Anas sp	2500	360		Charalambidou et al. 2003
Bombycilla cedrorum	64.9	32.9		Corllet 1989
Carollia perspicillata	15	18		Fleming & Heithaus 1981
Procnias tricarunculata	210	45		Fleming & Heithaus 1981
Steatornis caripensi	445	50		Fleming & Heithaus 1981
Andropadus latirostris	27	20		Graham et al. 1995
Erithacus rubecula	17.3	36		Herrera 1984
Sylvia atricapilla	20.5	36		Herrera 1984
Chalcophaps indica	135		8.33	Lambert 1989
Pipra mentalis & *Manacus candei*	12.3	7.5		Levey 1987
Ducula pacifica	333	145		McConkey et al. 2004
Turdus merula	120.4	40		Schleucher 1999
Turdus merula	100	45		Sorensen et al. 1984
Onychognathus tristrami	140	135.1		Spiegel & Nathan 2007
Pycnonotus xanthopygos	46	37.9		Spiegel & Nathan 2007
Pycnonotus sp	35	22		Weir & Corlett 2007
Pycnonotus sinensis	35	19		Weir & Corlett 2007
Pycnonotus jocosus	42	36		Weir & Corlett 2007
Hwamei garrulax canorus	75	15		Weir & Corlett 2007
Zosterops japonica	9.5		12.78	Weir & Corlett 2007
Pycnonotus sp	35	30		Whittaker & Jones 1994
Treron & *Ptilinopus* sp	198	150		Whittaker & Jones 1994
Bombycilla cedrorum	32	75		Witmer & Soest 1998
Sturnus vulgaris	77	30	15.64	Worthington 1989

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7.5. Results

7.5.1. Photographic versus experimentally derived seed removal rates

There were no significant (P ≥ 0.05) differences in seed removal rates measured by the photographic and experimental approaches between sites and shrub species with no significant (P ≥ 0.05) 2-way and 3-way interactions apparent between measuring approach, site and shrub species (Table 7.2). However, both the experimental and photographic methods measured significantly (P ≤ 0.001) higher removal rates of seed by birds from the alien shrub *S. mauritianum* than the other alien and indigenous shrub species (Table 7.2, Figure 7.1).

7.5.2. Bird foraging distances and seed dispersal limits

Different distributions of foraging distance were observed between both the heavily and moderately frugivorous bird species (Figures 7.2). For example, the dispersal curves of the heavily bird species (red-winged starling *O. morio,* speckled mousebird *C. striatus,* olive thrush *T. olivaceus,* Cape bulbul *P. capensis* and Cape white-eye *Z. capensis*) displayed typical multimodal fat-tailed curves with the Cape Robin *C. caffra* being exception without several distance frequency peaks (Figures 7.2 A). All dispersal curves were fat-tailed and multimodal in the moderately frugivorous bird species (southern boubou *L. ferrugeneus,* fiscal flycatcher *S. silens,* yellow canary *C. flaviventris,* common fiscal *L. collaris,* southern masked-weaver *P. velatus* and Cape canary *P. capensis*). The highest peak foraging distances frequency for the above groups of birds was less than 1 km (Figures 7.2 A & C). However, the heavily frugivorous common starling *S. vulgaris,* red-faced mousebird *U. indicus* and house sparrow *P. domesticus* did not display typical fat-tailed curves although they were multimodal with the highest peak of foraging distance frequency greater than 5 km (Figure 7.2. B). A similar pattern was apparent in the moderately frugivorous Speckled pigeon *C. guinea,* red-eyed dove *S. senegalensis,* Cape turtledove *S. capicola* and laughing dove *S. semitorquata* and the highest peak foraging distance frequency was greater to 10 km (Figures 7.2 D).

The least squares regression of bird body mass against gut retention time of consumed seed had a significant (P ≤ 0.001) slope and intercept (Figure 7.3). In contrast, the regression of bird body mass against flight speed had a significant (P ≤ 0.001) intercept but an insignificant (P ≥ 0.05) slope (Figure 7.4) pointing to relatively uniform flight speeds for birds in the 20 g to 160 g mass range. Consequently, the flight speeds predicted from the regression function had only a minor influence on the computed seed dispersal distance limits, which ranged between 0.41 and 0.81 km.

Table 7.2. Wald χ² statistics derived from REML which tested for differences between experimentally and photographically measured seed removal rates by birds from alien (*L. camara* and *S. mauritianum*) and indigenous (*C. monilifera* and *O. africana*) shrub species at different sites and their interactions

Fixed term	Wald χ^2 statistic	df	Probability
Method	0.08	1	0.783
Site	0.05	3	0.997
Shrub species	22.14	3	0.001
Method x Site	0.31	3	0.958
Method x Shrub species	0.44	3	0.932
Site x Shrub species	1.67	9	0.996
Method x Site x Shrub species	4.18	8	0.841
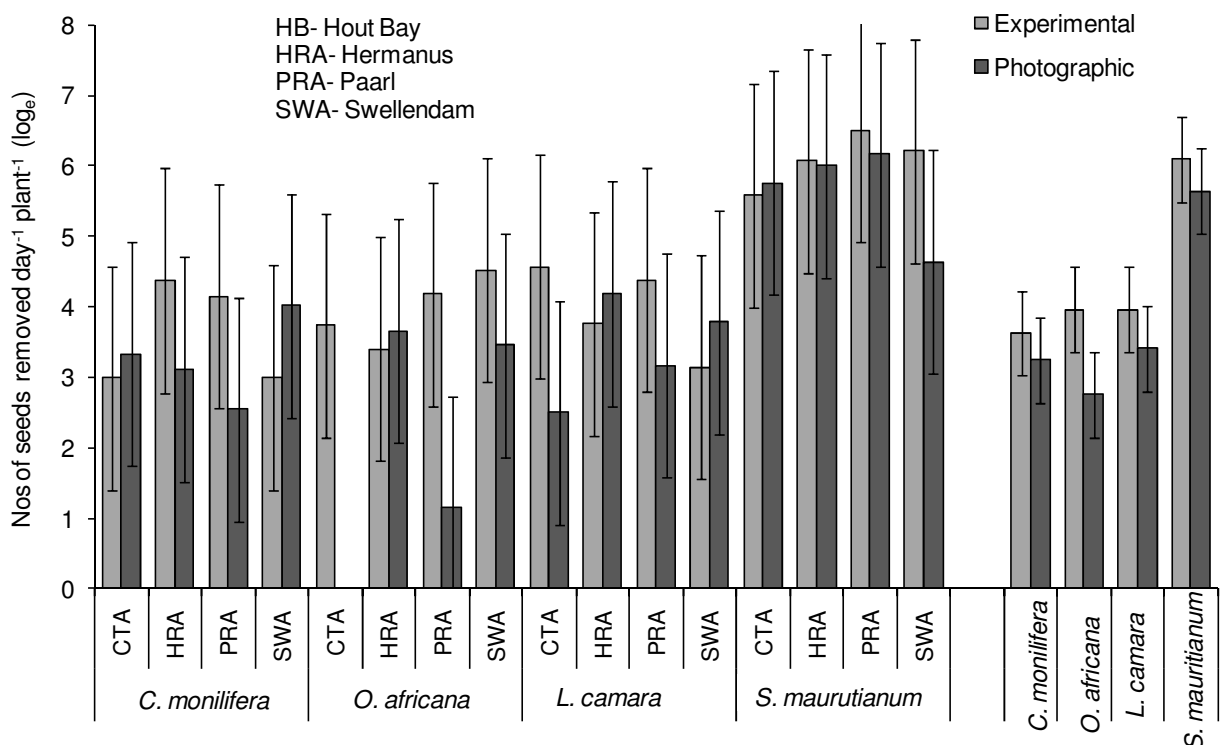
Figure 7.1. Average numbers of seeds removed per day by birds from the indigenous (*C. monilifera* and *O. africana)* and alien (*L. camara* and *S. mauritianum*) shrubs at different sites derived from experimental and photographic monitoring approaches. Average standard error of differences shown by bars
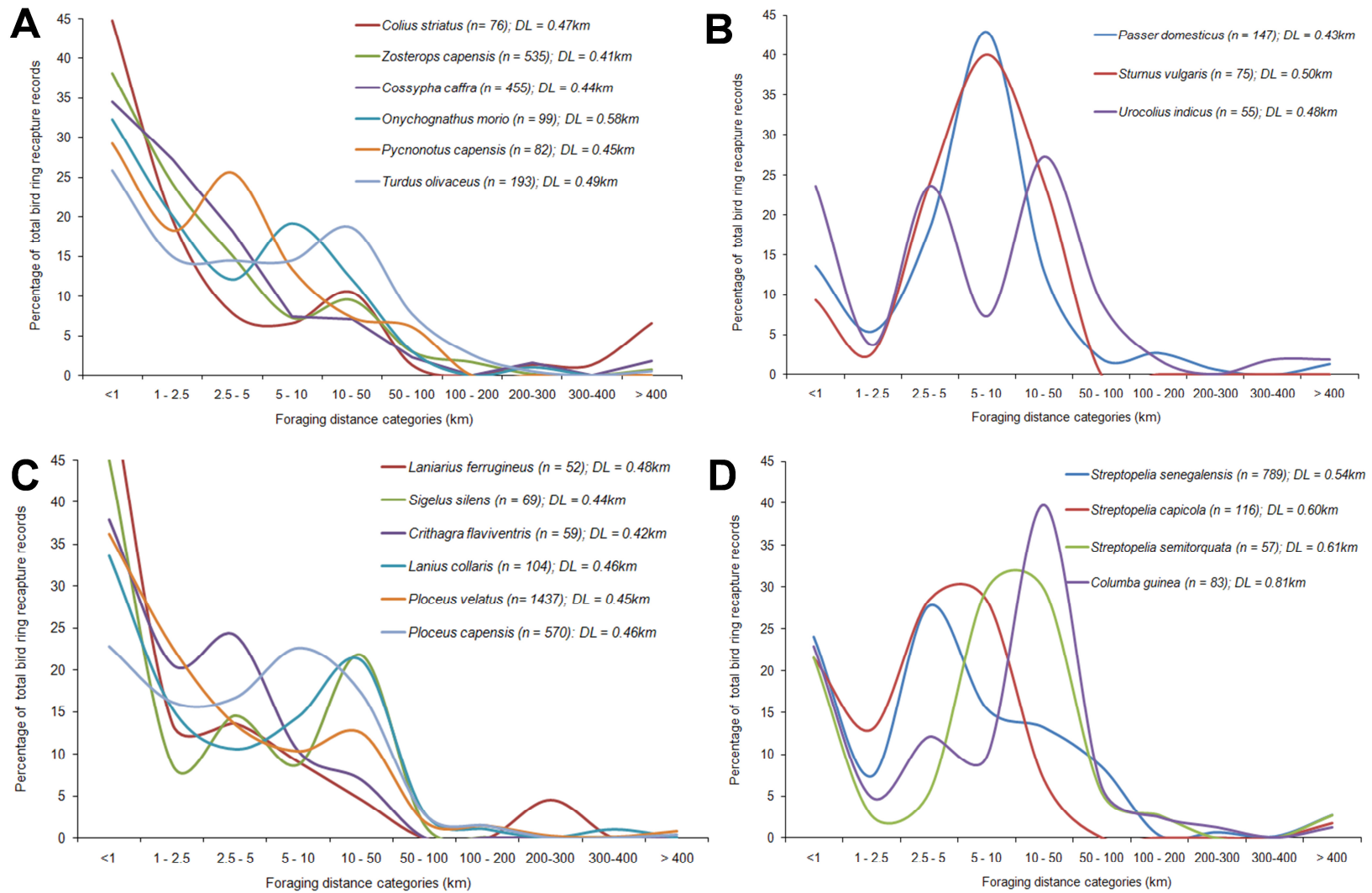
Figure 7.2. The fractions (percentages) of bird ring recapture records present in each foraging distance category for A, B heavily frugivorous and C, D moderately frugivorous bird species displaying different distribution patterns. The numbers of bird ring recapture records presented in parenthesis and computed seed dispersal distance limits (DL) for each bird species also shown
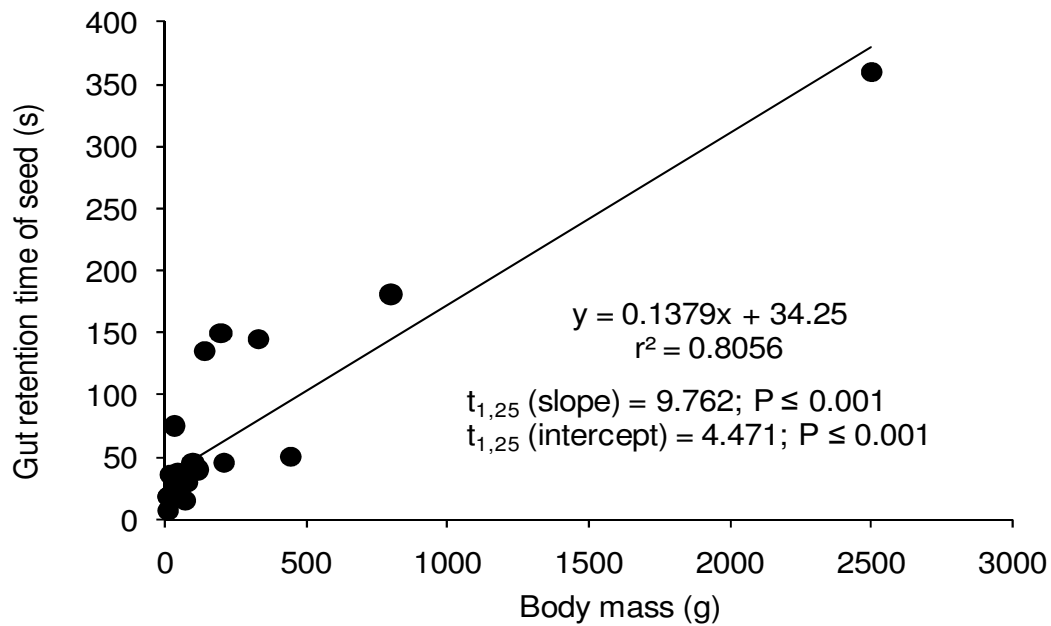
Figure 7.3. Relationship between reported gut retention times (seconds) of seeds and bird body masses of different bird species
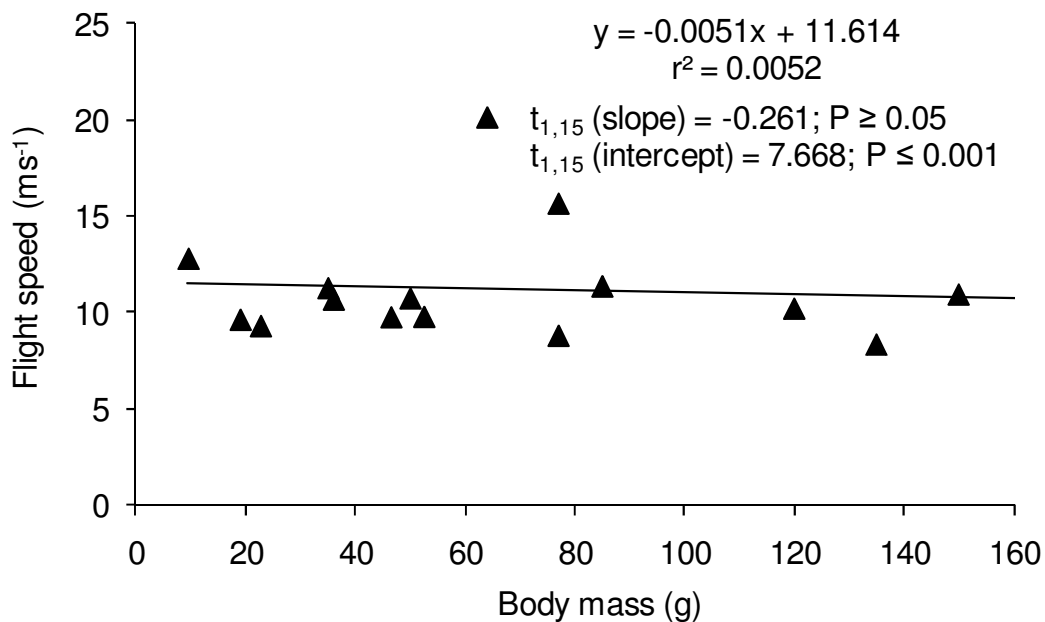
Figure 7.4. Relationship between reported avian flight speed of birds (m s^{-1}) and their body masses of different bird species

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7.6. Discussion

The insignificantly different seed removal rates measured by the short term photographic approach spanning a one day measuring interval and the longer term experimental approach spanning a 30-day measuring interval at each site pointed to relatively uniform daily fruit foraging intensities by the frugivorous birds over the peak fruiting periods of the alien and indigenous shrubs. However, there were several deficiencies associated with the experimental approach that could potentially affect fruit removal measurements. These included the inability of this approach to discriminate between asynchronous fruit production and fruit ripening (Knight 1988; Caceres & Mauro 2003) and individual foraging bird species as well as fruit consumption by other fruit foraging vertebrates, specifically rodents and baboons, both from the plant canopy and from the fruit traps (Bond & Breytenbach 1985). Indeed, in a subsequent study of seed removal by rodents and other dispersal vectors from open fruit traps revealed daily seed removal rates of 250.2 ± 52.7 seeds of *S. mauritianum,* 3.4 ± 0.8 seeds of *C. monilifera* and 11.3 ± 1.4 seeds of *O. africana* which comprised 40.4%, 4.6% and 12.6% respectively of the daily seed removal rates by foraging birds. Advantages associated with the photographic approach are that it provided a detailed permanent photographic record of individual foraging bird species, their numbers and precise times they spent actively foraging either the whole or partial fruits consumed by each bird species over specific time intervals, as well as other behavioural foraging traits (Spiegel & Nathan 2007) that could potentially be incorporated into analytical models (Nathan 2001; Bullock et al. 2006; Russo et al. 2006).

Nathan et al. (2008) reasoned that seed dispersal distance kernels portray the per-seed probability of dispersal by a vector to different distances, which is a product of the retention time by a dispersal vector and the vector displacement velocity. Two seed dispersal distribution patterns are distinguished, namely fat-tailed dispersal curves characterized by long tails and thin-tailed dispersal curves discriminated by short tails. Both curves reflect a multimodal complex pattern shaped by animal behaviour (Schupp et al., 2002) and dependent on seed load and gut retention time (Nathan et al. 2003, 2008; Hardy 2009).

For fat-tailed dispersal curves displayed by the heavily and moderately frugivorous bird species (Figure 7.2 A & C)*,* the per-seed probability of LDD is high with the expected number of LDD events (Nathan et al. 2008). This is because the retention time by a dispersal vector or the vector displacement velocity or both are at least occasionally high and consequently contribute considerably to LDD even if the seed load is relatively small (Nathan et al. 2008). Fat-tailed dispersal kernels allow higher propagule diversity movement from distant plant communities than thin-tailed kernels (Klein et al. 2006) and consequently are important for maintenance of metapopulations (Cain et al. 2000; Higgins & Cain 2002; Nathan et al. 2008). In addition, fat-tailed dispersal agents may account for large-scale changes in natural plant communities, spread of invasive plants, plant range shifts following climate change and persistence of species in

fragmented landscapes (Levin et al. 2003; Bohler et al. 2005; Schurr et al. 2007; Nathan et al. 2008; Lenz et al. 2010). The high per-seed probability of LDD displayed by the heavily and the moderately frugivorous (Figure 7.2 A & C) with fat-tailed dispersal curves, may also be associated with their relatively larger home range (Bowman et al. 2002; Hockey et al. 2005) despite their small to medium body masses which restrict long distance flights (Makarieva et al. 2005; Spiegel & Nathan 2007; Schurr et al. 2009). Moreover, some foraging behavioural strategies such as fruit tracking could lead to extended movements beyond these birds' normal home range (Nathan et al. 2008). Fruit tracking has been observed in the territorial European robin *Erithacus rubecula* in the Spanish Mediterranean scrubland (Telleria et al. 2005; 2008) and in flocks of wintering frugivorous thrushes *Turdus torquatus* and *T. viscivorus* in southeastern Spain, which fly between isolated populations of the common Juniper *Juniperus communis* their main source of fruits (Garcia & Ortiz-Pulido 2004). Such wide-ranging bird foraging movements have important implications for seed dispersal distances of especially fleshy-fruited alien plants in the Cape Floristic Region (le Maitre & Midgely 1992).

Although, the dispersal curves displayed by the heavily and moderately frugivorous bird species were fat-tailed (Figure 7.2 A & C), they are expected to have thin-tailed dispersal curves due to territoriality of these bird species in the fynbos (Manders & Richardson 1992; Hockey et al. 2005). The observed multimodality of the dispersal curves advocates Schupp et al. (2002)'s assertion that seed distribution is likely to display complex patterns owing multifaceted animal movement associated with seed disposition. The territorial bird species have a small per-seed probability of long distance dispersal (LDD) although it is expected that number of LDD events increase with seed load (Levin et al. 2003; Nathan et al. 2008; Schurr et al. 2009). This suggests that some birds with fat-tailed dispersal curves may also contribute very little to LDD even if their seed loads are large (Nathan et al. 2008; Schurr et al. 2009). In fact, *Zosterops* and *Colius* bird species display localised dispersal of seeds of many fleshy-fruited alien and indigenous species (Duncan & Chapman 1999; Simberloff & Holle 1999; Stansbury 2001; Williams 2006) which may be associated with their restricted home range and patchy fruit resource distribution in the fynbos (Hockey et al. 2005; Carlo et al. 2007). Short seed dispersal distances are common among frugivorous birds (Levin et al. 2003). For example, Wenny (2000) also reported seed dispersal distances by frugivorous birds of only 0.01 to 0.02 km in Costa Rica, and in Spain, Jordano et al. (2007) reported dispersal of seeds of *Prunus mahaleb* seeds to a distance 0.05 km by small passerine birds and to a distance of 0.11 km by medium sized birds. Also, short seed dispersal distances may be modified by changes in habitat preferences of individual birds. Wenny (2000) reported bimodal seed distribution peaks for the neotropical tree *Ocotea endresiana* where seeds were dispersed both near maternal trees and also at preferential perching sites for male bellbirds *Procnias tricarunculata* located at the edges of canopy gaps. A similar bias in distribution patterns

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was reported for *Acacia cyclops* seeds in South Africa (Glyphis et al. 1981). Also, a recent study on trumpeter hornbills *Bicanistes bucinator* in eastern South African forests (Oribi Gorge Nature Reserve) reported seed distributional patterns associated with habitat differences (Lenz et al. 2010). For instance, there was a unimodal pattern peaking at 0.086 km evident where foraging movements were restricted within the forest and a bimodal pattern peaking at 0.018 km and 0.512 km evident where these birds foraged in fragmented landscapes (Lenz et al. 2010).

The extremely large foraging distances peaking at 2.5 km and greater (up to 50 km) in the heavily and moderately frugivorous (Figure 7.2 B & D) may be associated with behavioural attributes such as large home range (Bowman et al. 2002; Hockey et al. 2005; Makarieva et al. 2005; Jenkins et al. 2007) and foraging strategies such as fruit tracking (Telleria et al 2008). Indeed, long distance seed dispersal have been associated with large home range birds (Bowman et al. 2002) such as the Tristram grackle *Onychognathus tristramii* with a foraging range of 142 to 283 ha in Israel (Spiegel & Nathan 2007). Similarly, *Ceratogymna* hornbills in West Africa, and trumpeter hornbills *Bicanistes bucinator* in eastern South Africa forests have been reported to fly distances of up to 14.5 km during their foraging bouts (Holbrook & Smith 2000; Holbrook 2010; Lenz et al. 2010).

Bird gut retention times, although inconsistent, determine how far seeds may be dispersed regardless of the bird's home range (Whittaker & Jones 1994; Fukui 1996; Holbrook & Smith 2000; Higgins et al. 2003; McConkey et al. 2004). However, gut retention times are influenced by whether seeds are regurgitated or defecated, with smaller defecated seeds having longer gut retention times than larger regurgitated seeds and consequently longer distance dispersal potentials (Whittaker & Jones 1994). Particularly, frugivorous birds that maximise energy acquisition through ingesting more pulp (Johnson et al. 1985; Meormond & Denslow 1985) are likely to regurgitate seeds in the foraging tree (Pratt & Stiles 1983). This phenomenon has been reported in obligate frugivores that possess short digestive systems whereas partial frugivores may keep fruits longer owing to poor adaptation of their gut systems to fruit diet (Meormond & Denslow 1985; Jordano 2000). The positive correspondence evident between seed gut retention time and bird body mass (McConkey et al. 2004; Spiegel & Nathan 2007) indicated that larger birds which retain seeds for longer periods in their guts (Jordano et al. 2007; Schurr et al. 2009; Tsoar et al. 2011) should disperse seeds over greater distances than smaller birds (Jetz et al. 2004; Makarieva et al. 2005). For the subset of 19 heavily and moderately frugivorous bird species in this study, the estimated seed dispersal distance limits ranged between 0.41 and 0.81 km, which suggest that these frugivorous birds disperse alien seeds mainly into natural habitat from adjacent propagule pool. However, much greater seed dispersal distances of up to 12 km have been reported for the small silvereye *Zosterops lateralis* in south-western Australia based on its flight speed and gut retention time (Stansbury 2001). In addition, trumpeter hornbills *Bicanistes bucinator* in eastern South Africa

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forests have been reported to fly distances of up to 14.5 km with the 2.5 h gut retention of indigestible seeds, though the distances differed considerably due to landscape types such as patchy forests on an agricultural landscape and in a continuous natural forests (Lenz et al. 2010). Noteworthy in this regard is that birds do display diverse flight speeds dependent on their activity whether they are foraging or migrating (Pratt & Stiles 1983; Evans & Drickamer 1994; Jenkins 1995). During migration, birds show relatively fast and directed movements with relatively higher flight speeds and increased gut retention times of ingested seeds (Nathan et al. 2008; Schurr et al. 2009) which could lead to extended seed dispersal distances. Extended gut retention of seeds has been found to be relevant for long distance dispersal of seeds of *Ficus* species by Old World fruit bats *Cynopterus sphinx* in Neotropic forests (Shilton et al. 1999) and the Egyptian fruit bat *Rousettus aegyptiacus* feeding on fleshy fruits of alien naturalised and invasive trees in central Israel (Tsoar et al. 2011). Also, the African olive-pigeon *C. arquatrix* which engages in extremely long flights to locate fruits, a characteristic nomadic behavioural trait of fruit pigeons in different parts of the world (Crome 1975; McConkey et al. 2004), may also result in the dispersal of ingested seeds to relatively longer distance than estimated (Rowan 1983; Jordano 1987).

Alternatively, the non-standard secondary vectors may contribute to increased long distance seed dispersal (Dean & Milton 1988; Higgins et al. 2003; Nathan et al. 2008; Schurr et al. 2009). For example, secondary dispersal of ingested seeds through predation of a legitimate disperser might account for extensive dispersal of seeds based on movement patterns of a predator (Dean & Milton 1988; Nogales et al. 1998; Galetti & Guimaraes 2004). Specifically, seeds of fleshy-fruited *Lycium intricatum* and *Rubia fruticosa* are likely to experience long distance dispersal by shrikes *Lanius excubitor* and Eurasian kestrel *Falco tinnunculus* preying on frugivorous lizards (*Gallotia atlantica*) on the Canary Islands (Valido & Nogales 1994; Nogales et al. 1998; Padilla & Nogales 2009). Consequently, *Lycium intricatum* and *Rubia fruticosa* might spread to distant sites beyond range of the lizards by shrikes and kestrels, a phenomenon that was also reported for raptors in the South African Karoo (Dean & Milton 1988; Galetti & Guimaraes 2004).

7.7. Reference list

Bach, C.E. & Kelly, D. (2004) Effects of forest edges, fruit display size, and fruit colour on bird seed dispersal in a New Zealand mistletoe, *Alepis flavida*. *New Zealand Journal of Ecology*, **28**, 93-103.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. (2000) *Bird census techniques*. Academic Press, London.

Bohrer, G.I.L., Nathan, R. & Volis, S. (2005) Effects of long-distance dispersal for metapopulation survival and genetic structure at ecological time and spatial scales. *Journal of Ecology,* **93**, 1029-1040.

Bond, W.J. & Breytenbach, G.J. (1985) Ants, rodents and seed predation in Proteaceae. *South African Journal of Zoolog*y, **20,** 150-154.

Bowman, J., Jaeger, J.A.G. & Fahrig, L. (2002) Dispersal distance of mammals is proportional to home range size. *Ecology,* **83**, 2049–2055.

Bucher, T.L. & Worthington, A. (1982) Nocturnal hypothermia and oxygen consumption in Manakins*. The Condor*, **84**, 327-331.

Bullock, J., Shea, K. & Skarpaas, O. (2006) Measuring plant dispersal: an introduction to field methods and experimental design. *Plant Ecology*, **186**, 217-234.

Bullock, J.M., Ibby L.M., Coulson, S.J. & Clarke, R.T. (2003) Habitat-specific dispersal: Environmental effects on the mechanisms and patterns of seed movement in a grassland herb *Rhinanthus minor. Ecography*, **26**, 692-704.

Burtt, H.E. & Giltz. M.L. (1974) Behavior of some Icterids and Starlings when released after banding. *Bird-Banding,* **45**, 33-45.

Caceres, N.C. & Moura, M.O. (2003) Fruit removal of a wild tomato, *Solanum granulosoleprosum* Dunal (Solanaceae), by birds, bats and non-flying mammals in an urban Brazilian environment. *Revista Brasileira de Zoologia*, **20**, 519–522.

Cain, M.L., Milligan, B.G. & Strand, A.E. (2000) Long-distance seed dispersal in plant populations. *American Journal Botany*, **87**, 1217–1227.

Carlo, T.A. (2005) Interspecific behaviour change seed dispersal pattern of an avian-dispersed plant. *Ecology*, **86**, 2440-2449.

Carlo, T.A., Aukema, A.G. & Morales, J.M. (2007) Plant-frugivore interactions as spatially explicit networks: integrating frugivore foraging with plant spatial patterns. Seed dispersal: theory and its application in a changing world. (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 369-390. Reading: Biddles Ltd.

Carlo, T.A., Collazo, J.A. & Groom, M.J. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia*, **134**, 119-131.

Charalambidou, I., Santamaria, L. & Langevoord, O. (2003) Effect of ingestion by five avian dispersers on the retention time, retrieval and germination of *Ruppia maritima* seeds. *Functional Ecology,* **17**, 747-753.

Cody, L.M. (1983) Bird diversity and density in South African forests. *Oecologia*, **59**, 201-215.

Cordeiro, N.J., Patrick, D.A.G., Munisi, B., & Gupta, V. (2004) Role of dispersal in the invasion of an exotic tree in an East African submontane forest. *Journal of Tropical Ecology*, **20**, 449-457.

Crome, F.H.J. (1975) The ecology of fruit pigeons in tropical Northern Queensland. *Australian Wildlife Research*, **2**, 155-185.

Dean, W.R.J. & Milton, S.J. (1988) Dispersal of seeds by raptors. *Africa Journal Ecology,* **26**, 173-176.

Duncan, R.S. & Chapman, C.A. (1999) Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications* **9**, 998-1008.

Evans, T.R. & Drickamer, L.C. (1994) Flight speeds of birds determined using doppler radar. *The Wilson Bulletin*, **106**, 154-156.

Fleming, T.H. & Heithaus, E.R. (1981) Frugivorous bats, seed shadows, and the structure of Tropical forests. *Biotropica*, **13**, 45-53.

Galetti, M. & Guimaraes Jr.P.R. (2004) Seed dispersal of *Attalea phalerata* (Palmae) by Crested caracaras (*Caracara plancus*) in the Pantanal and a review of frugivory by raptors. *Ararajuba*, **12,** 133-135*.*

Garcia, D. & Ortiz-Pulido, R. (2004) Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography*, **27**, 187 -196.

Garcia, D., Zamora, R., Gomez, J.M. & Hodin, J.H. (2001) Frugivory in *Juniperus communis* depends more on population characteristics than on individual attributes. *Journal of Ecology***, 89**, 639–647.

Geldenhuys, C.J., le Roux, P.J. & Cooper, K.H. (1986) Alien invasions in indigenous evergreen forest. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 119-131. Oxford University Press, Cape Town.

Gleadow, R.M. (1982) Invasion by *Pittosporum undulatum* of the forests of central Victoria. II. Dispersal, germination and establishment. *Australian Journal of Botany*, **30**, 185-198.

Gleditsch, J.M. & Carlo, T.A. (2010) Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. *Diversity and Distributions,* **17**, 244–253.

Glyphis, P.J., Milton, J.S. & Siegfried, R.W. (1981) Dispersal of *Acacia* c*yclops* by birds. *Oecologia*, **48**, 138-141.

Godinez-Alvarez, H. & Jordano, P. (2007) An empirical approach to analysing the demographic consequences of seed dispersal by frugivores. *Seed dispersal: theory and its application in a changing world* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.) pp. 391-406. Reading: Biddles Ltd.

Gomes, L.G.L., Oostra, V., Nijman, V., Cleef, A.M. & Kappelle, M. (2008) Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. *Biological Conservation*, **141**, 860-871.

Gosper, C.R., Stansbury, C.D. & Vivian-Smith, G. (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distributions,* **11**, 549-558.

Green, R.J. (2007) Refining the conservation management of seed-dispersing frugivores and their fruits: examples from Australia. *Seed dispersal: theory and its application in a changing world*. (eds. Dennis, A.J., Schupp, E.W., Green ,R.J., & Westcott, D.A.) pp. 579-598. Reading: Biddles Ltd.

Hardy, O. J. (2009) Direct monitoring of long-distance pollen and seed dispersals. How fat is the tail? *Heredity*, **103,** 437–438.

Herrera, C.M. (1984) Adaptation to frugivory of Mediterranean avian seed dispersers. *Ecology*, **65**, 609-617.

Herrera, C.M. (1995) Plant-vertebrate seed dispersal systems in the Mediterranean: Ecological, Evolutionary, and Historical Determinants. *Annual Review of Ecology and Systematics,* **26**, 705-727.

Higgins, S.I., Nathan, R. & Cain, M.L. (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology*, **84**, 1945–1956.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (eds) (2005) *Roberts' birds of Southern Africa*, 7th edn. John Voelcker Bird Book Fund: Cape Town.

Holbrook, K.M. & Smith, T.B. (2000) Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia*, **125**, 249-257.

Holbrook, K.M. (2010) Home range and movement patterns of toucans: implications for seed dispersal. *Biotropica,* **43**, 265–392.

Holmes, P.M., Richardson, D.M., Esler, K.J., Witkowski, E.T.F. & Fourie, S. (2005) Identifying strategic interventions for restoring alien-invaded riparian zones in South Africa. *South African Journal of Science*, **101**, 553–564.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review Ecological Systematics*, **13**, 201–228.

Howe, H.F. (1977) Bird activity and seed dispersal of a tropical wet forest tree. *Ecology*, **58**, 539-550.

Jenkins, R.A. (1995) Morphometrics and flight performance of southern African peregrine and Lanner Falcons. *Journal of Avian Biology,* **26**, 49-58.

Jordano, P. (2000) Fruits and frugivory. *Seeds: the ecology of regeneration in natural plant communities*. (ed. Fenner, M.) pp. 125-166. CABI Publishers, Wallingford, UK.

Jordano, P. (2007) Frugivores, seeds and genes: analysing the key elements of seed shadows. *Seed dispersal: theory and its application in a changing world* (eds Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Jordano, P., Garcia, C., Godoy, J.A. & Garcia-Castano, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3278-3282.

Kays, R., Jansen, P.A., Knecht, E.M.H., Vohwinkel, R. & Wikelski, M. (2011) The effect of feeding time on dispersal of *Virola* seeds by toucans determined from GPS tracking and accelerometers. *Acta Oecologica*, **37**, 625-631.

Klein, E.T., Lavigne, C. & Gouyon, H. (2006) Mixing of propagules from discrete sources at long distance: comparing a dispersal tail to an exponential. BMC *Ecology* (doi:10.1186/1472-6785-6-3).

Knight, R.S. (1986) A comparative analysis of fleshy fruit displays in alien and indigenous plants. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 171-178. Oxford University Press, Cape Town.

Knight, R.S. (1988) Aspects of plant dispersal in the south-western Cape with particular reference to the roles of birds as dispersal agents. Ph.D. Thesis, University of Cape Town, South Africa.

Lambert, F. (1989) Fig-eating by birds in a Malaysian lowland rain forest. *Journal of Tropical Ecology*, **5**, 401-412.

Le Maitre, D.C. & Midgley, J.J. (1992) Plant reproductive ecology. *The ecology of fynbos.* (ed. Cowling, R.) pp. 135-174. Oxford University Press: Cape Town.

Lenz, J., Fiedler, W., Caprano, T., Friedrichs, W., Gaese, B. H., Wikelski, M. & Bohning-Gaese, K. (2010) Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes. Proceedings of the Royal Society B: Biological Sciences (doi:10.1098/rspb.2010.2383).

Levey, D.J. & Martinez del Rio, C. (2001) It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. *The Auk,* **118**, 819-831.

Levey, D.J. (1987) Seed size and fruit-handling techniques of avian frugivores. *The American Naturalist,* **129**, 471-485.

Levin, S.A., Muller-Landau, H.C., Nathan, R. & Chave, J. (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 575–604.

Levine, J.M. & Murrell, D.J. (2003) The community-level consequences of seed dispersal patterns. *Annual Review of Ecology and Systematics*, **34**, 549 – 574.

Makarieva, A.M., Gorshkov, V.G. & Li, B.L. (2005) Why do population density and inverse home range scale differently with body size? Implications for ecosystem stability. *Ecological Complexity*, **2**, 259–271.

Malcarney, H.L., Martinez del Rio, C. & Apanius, V. (1994) Sucrose intolerance in birds: simple nonlethal diagnostic methods and consequences for assimilation of complex carbohydrates. *The Auk*, **111**, 170-177.

Manders, P.T. & Richardson, D.M. (1992) Colonization of Cape fynbos communities by forest species. *Forest Ecology and Management*, **48,** 277-293.

McConkey, K.R., Meehan M.H. & Drake, D.R. (2004) Seed dispersal Pacific Pigeon *Ducula pacifica* in Tonga, western Polynesia. *Emus*, **104,** 369-376.

McMahon, L. & Fraser, M. (1988) *A fynbos year*. David Philip, Cape Town.

McNamara, J.M., Houston, A.I. & Lima, S.L. (1994) Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology*, **25**, 287-302.

Meehan, H.J., McConkey, R.K. & Drake, R.D. (2002) Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. *Journal of Biogeography,* **29**, 695-712.

Muller-Landau, H.C. & Hardesty, B.D. (2005) Seed dispersal of woody plants in tropical forests: Concepts, examples, and future directions. *Biotic interactions in the tropics: their role in the maintenance of species diversity*, (eds. Burslem, D., Pinard, M. & Hartley, S.) pp. 267–309. Cambridge University Press, Cambridge, UK.

Munoz, J., Felicísimo, A.M., Cabezas, F., Burgaz, A.R. & Martínez, I. (2004) Wind as a long-distance dispersal vehicle in the Southern Hemisphere. *Science*, **304**, 1144–1147.

Murray, K.G., Russell, S., Picone, C.M., Winnett-Murray, K., Sherwood, W. & Kuhlmann, M.L. (1994) Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. *Ecology*, **75**, 989-994.

Nathan, R. (2001a) Dispersal biogeography. *Biodiversity Encyclopaedia*, **2**, 127-152.

Nathan, R. (2001b) The challenges of studying dispersal. *Trends in Ecology & Evolution*, **16**, 481-483.

Nathan, R. (2005) Long-distance dispersal research: building a network of yellow brick roads. *Diversity and Distribution*, **11**, 125–130.

Nathan, R. (2007) Total dispersal kernels and the evaluation of diversity and similarity in complex dispersal systems. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Nathan, R., Perry, G., Cronin, J.T., Strand, A.E. & Cain, M.L. (2003) Methods for estimating long-distance dispersal. *OIKOS*, **103**, 261 – 273.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. (2008) Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, **23**, 638 – 647.

Nogales, M., Delgado, J.D. & Medina, F.M. (1998) Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canary Islands). *Journal of Ecology*, **86**, 866-871.

Oatley, T.B. (1984) Exploitation of a new niche by the Rameron Pigeon *Columba arquatrix* in Natal. *Proceedings of the Fifth Pan-African Ornithological Congress* (ed. Ledger, J.A.), pp. 323-330, Southern African Ornithological Society.

Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285-297.

Quix, J.C. (2007) The role of alien plants in the composition of fruit-eating bird assemblages in Brazilian urban ecosystems. *Orsis*, **22**, 87-104.

Reichard, S.H., Chalker-Scott, L. & Buchaman, S. (2001) Interaction among non-native plants and birds. *Avian ecology and conservation in an urbanising world*. (eds. Marcluff, J.M., Bowman, R. & Donnelly, R.) pp. 179- 223. Kluwer Academic Publishers.

Rejmanek, M. (2000) Invasive plants: approaches and predictions. *Austral Ecology*, **25**, 497-506.

Richardson, D.M. & Fraser, M.W. (1995) Birds of Swartboskloof, Jonkershoek Valley, Stellenbosch: a mountain fynbos ecosystem. *Southern Birds*, **18**, 1–44.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmanek, M. (2000) Plant invasions – the role of mutualism. *Biology Reviews*, **75**, 65-93.

Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation,* **112**, 63-85.

Russo, S.E., Portnoy, S. & Augspurger, C.K. (2006) Incorperating animal behaviour into seed dispersal models: implications for seed shadows. *Ecology*, **87**, 3160-3174.

Sakai, A.K., Weller, S.G., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A, Baughman, S, Cabin, R.J, Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M. & Thompson, J.N. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–32.

Sallabanks, R. (1993) Fruiting plant attractiveness to avian seed dispersers: native vs. Invasive Crataegus in western Oregon. *Madrono*, **40**, 108–16.

Saracco, J.F., Collazo, J.M. & Groom, M.J. (2004) How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia*, **139,** 235-245.

Schleucher, E. (1999) Energy metabolism in an obligate frugivore, the superb fruit-dove (*Ptilinopus superbus*). *Australian Journal of Zoology*, **47**, 169–179.

Schupp, E.W, Milleron, T. & Russo, S.E. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. *Seed dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D.J., Silva W.R. & Galetti, M.) pp. 19-33. Wallingford, UK: CAB International.

Schupp, E.W. (1993) Quantity, quality and effectiveness of seed dispersal by animals. *Vegetatio*, **107/108**, 12-29.

Schupp, E.W., Milleron, T. & Russo, S.E. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. *Seeds dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D.J., Silva, R.W. & Galleti, M.) pp. 19-33. Wallingford: CABI Publishing.

Schurr, F.M., Midgley, G.F., Rebelo, A.G., Reeves, G., Poschlod, P. & Higgins, S.I. (2007) Colonization and persistence ability explain the extent to which plant species fill their potential range. *Global Ecology and Biogeography,* **16**, 449–459.

Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A. & Nathan, N. (2009) Long-distance seed dispersal. *Annual Plant Reviews*, **38,** 204–237.

Shilton, L.A., Altringham, J.D., Compton, S.G. & Whittaker, R.J. (1999) Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. Proceedings of the Royal Society of London. Series B: *Biological Sciences*, **266**, 219-223.

Simberloff, D. & Holle, V.B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Sinclair, I. & Ryan, P. (2003) *Birds of Africa south of the Sahara.* Cape Town: Struik Publishers.

Snow, B. & Snow, D. (1988) *Birds and berries.* T. & A.D. Poyser, Calton, UK.

Sorensen, A.E. (1984) Nutrition, energy and passage time: experiments with fruit preference in European Blackbirds (*Turdus merula*). *Journal of Animal Ecology*, **53**, 545-557.

Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, **10**, 718–728.

Stansbury, C.D. (2001)Dispersal of the environmental weed Bridal Creeper, Asparagus asparagoides, by Silvereyes, *Zosterops lateralis*, in southwestern Australia. *Emu*, **101**, 39–45.

Sun, C., Ives, A.R., Kraeuter, H.J. & Moermond, T.C. (1997) Effectiveness of three Turacos as seed dispersers in a Tropical Montane Forest. *Oecologia*, **112**, 94-103.

Telleria, L.J., Ramirez, A. & Pérez-Tris, J. (2008) Fruit tracking between sites and years by birds in Mediterranean wintering grounds. *Ecography*, **31**, 381-388.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173–181

Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecology & Evolution*, **21**, 208–216.

Tsoar, A., Shohami, D. & Nathan, R. (2011) A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats. *Fifty years of invasion ecology. The legacy of Charles Elton* (ed. Richardson, D.M.) pp. 103-119, Wiley-Blackwell, Oxford.

Valido, A. & Nogales, M. (1994) Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *OIKOS*, **70**, 403-411.

Van Wyk, B. & van Wyk, P. (1997) *Field guide to trees of southern Africa*. Struik Publishers: Cape Town.

Wahaj, S.A., Levey, D.J., Sanders, A.K. & Cipollini, M.L. (1998) Control of gut retention time by secondary metabolites in ripe Solanum fruits. *Ecology*, **79**, 2309-2319.

Wang, B.C. & Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology & Evolution,* **17**, 379-386.

Weir, J.E.S. & Corlett, R.T. (2007) How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? *Landscape Ecology*, **22**, 131-140.

Wenny, D.G. & Levey, D.J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 6204-6207.

Westcott, D.A., Bentrupperbaumer, J., Bradford, M.G. & McKeown, A. (2005) Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, **146**, 57–67

Whittaker, R.J. & Jones, S.H. (1994) The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography*, **21**, 245-258.

Williams, P. (2006) The role of blackbirds (*Turdus merula*) in weed invasion in New Zealand. *New Zealand Journal of Ecology,* **30**, 285-291.

Willson, M.F. (1993) Dispersal mode, seed shadows, and colonization patterns. *Vegetatio*, **107**/**108**, 261–280.

Wilms, J.J.A.M. & Kappelle, M. (2006) Frugivorous birds and seed dispersal in disturbed and old growth montane oak forests in Costa Rica. *Ecology and Conservation of Neotropical Montane Oak Forests*, (ed. Kappelle, M.) pp. 309–324. Ecological Studies Series 185. Springer-Verlag, New York/Berlin/Heidelberg.

Witmer, M.C. & Soest, P.J.V. (1998) Contrasting digestive strategies of fruit-eating birds. *Functional Ecology*, **12**, 728-741.

Worthington, A.H. (1989) Adaptations for avian frugivory: assimilation efficiency and gut transit time of *Manacus vitellinus* and *Pipra mentalis*. *Oecologia*, **80,** 382-389.

Appendix 7.1. An example of the the type of traps used in this study: Each trap was lined with white plastic sheeting (A) and cladded with wire mesh to prevent fruit removal by rodents and other vertebrate predators (B), this was apparent from the presence of a spine left in one of the traps by a porcupine attempting to remove the seed (C); and collection of abscised fruits of indigenous and alien shrubs (D)

Chapter 8

A comparison of bird foraging frequencies on the fleshy fruits of established and emergent alien shrubs in the Cape Floristic Region

8.1. Abstract

The hypothesis that fruits of established alien shrubs are foraged more frequently than those of emergent aliens was tested by comparing visitation frequencies of individual foraging bird species included in heavily and moderately frugivorous groups on two established aliens (*Lantana camara* and *Solanum mauritianum)* and two emergent aliens (*Myoporum tenuifolium* and *Pittosporum undulatum)* at six sites in the south-western Cape. Frugivorous birds as a whole displayed significantly higher visitation frequencies on fruits of the emergent than established alien shrubs. However, there was a significant interaction between frugivore group and shrub species on bird visitation frequency with the moderately frugivorous bird group only displaying significantly higher visitation frequencies on the emergent than established alien shrubs. Also, there were significant interactions between both heavily and moderately frugivorous bird species and alien shrub type on bird visitation frequency with the heavily frugivorous *Sturnus vulgaris* and house sparrow *Passer domesticus*, and the moderately frugivorous *Streptopelia senegalensis* displaying significantly higher visitation frequencies on fruits of the emergent than established alien shrubs. Diverse visitation frequencies were displayed by the other heavily and moderately frugivorous bird species on the different alien shrub types. The heavily frugivorous *Columba arquatrix*, *Colius striatus*, *Pycnonotus capensis* and *Zosterops capensis* all displayed significantly higher visitation frequencies on fruits of only the established alien *S. mauritianum* than the two emergent aliens. In contrast, *Columba guinea* exhibited a significantly lower visitation frequency on fruits of the established alien *S. mauritianum* than the two emergent aliens. Similarly, the *Streptopelia capicola* displayed a significantly lower visitation frequency on fruits of both established alien shrubs than the emergent alien *M. tenuifolium.* The observed preference of the generally more abundant moderately frugivorous bird species with less specialized fruit diets for fruits of emergent than established aliens suggest that control measures should be focused on eradicating these and other emergent alien species with fleshy fruits from especially urban environments to prevent their transport by birds into adjacent natural areas.

Keywords: frugivorous birds, emergent alien species, foraging frequency, Cape Floristic Kingdom

8.2. Introduction

Alien plant species bearing fleshy fruit displays might be a major threat to persistence of native plant species through disruption of their seed dispersal mutualisms with birds (Knight 1986; Traveset & Richardson 2006). Although a small proportion of alien plant species tend to have negative impacts on native ecological process in the invaded habitats (Williamson & Fitter 1996; Byers et al. 2002), southern African natural communities, especially fynbos, are exceptionally threatened by bird dispersed alien woody alien plants (Richardson et al. 2000; Rouget et al. 2003; Latimer et al. 2004).

Frugivorous birds have facilitated the spread of fleshy-fruited alien plants into natural ecosystems throughout the world (Sallabanks 1993; Williams & Karl 1996; Richardson et al. 2000b). They are efficient dispersal agents due to their ability to retain seeds in their guts during distant flights in habitat exploitation (Rejmanek 2000; Richardson et al. 2000b; Higgins et al. 2003; Whelan et al. 2008; Richardson & Rejmanek 2011). Long distance dispersal of seeds from maternal plants assists formation of new self-sustaining alien satellite populations and thus rapid range expansion (Richardson et al. 2000; Sakai et al. 2001; Trakhtenbrot et al. 2005). It has been suggested that the success of some invasive alien plants is partly due to their disproportionate appeal to seed dispersers, which provide alien plants with more rapid range expansion rates than native plants (Rejmanek & Richardson 1996; Richardson et al. 2000b; Richardson & Rejmanek 2011). Alien plants often attract native and alien dispersers, taking advantage of the generalist or diffuse nature of seed dispersal networks (Iwao & Rausher 1997; Traveset & Richardson 2006), because tight coevolution between plant and disperser are extremely rare (Richardson et al. 2000; Dennis & Westcott 2007). Even if generalizations are difficult (Richardson et al. 2000), plants with large fruit displays and small seeds seem to have generally faster invasive behaviour due to a higher dispersal capacity (e.g. Rejmanek & Richardson 1996; Gosper et al. 2005; Richardson & Rejmanek 2011).

Fleshy-fruited alien plants may be classified into established and emergent groups (Henderson 2001; Nel et al. 2004). The established alien plants comprise of widely distributed populations of high density that has reached the invasion stage (Richardson et al. 2000a) while the emergent group comprise partly of recently introduced isolated populations of low density (Nel et al. 2001), and restricted distribution while some species are undergoing naturalisation in the novel environment (Richarsdon et al. 2000a). The greater number of perches for foraging birds provided by established alien populations and their consequentially higher fruit abundance are likely to attract more birds than populations of emergent aliens with relatively smaller fruit abundance (Knight 1988; Manders & Richardson 1992; Izhaki 2002; Buckley et al. 2006). This complies with the fruit crop hypothesis, which asserts that predators concentrate their activities where resources are most abundant (Hulme 2002; Saracco et al. 2005; Blendinger et al. 2008). This assertion was

supported by Foster (1990) who examined the impact of 27 fruit characteristics on *Allophylus edulis* fruit removal in Paraguay and found that only the fruit crop size, percentage water and mineral ash were positively correlated to bird foraging visits. However, a disadvantage of large fruit crops is that they attract insects that spoil fruits (Jordano 1987; Scott 1996) thereby deterring avian seed dispersal agents through low quality fruits. Although fruit nutritional traits are emphasised as determinants of alien fruit choice by birds (Kueffer et al. 2009; Gosper & Vivian-Smith 2010), fruit removal by birds is also influenced by neighbouring trees in the habitat and vegetation structure (Foster 1990; Garcia et al. 2001; Saracco et al. 2005; Carlo et al. 2007). Bird foraging of *Juniperus communis* fruits, for example, increased significantly with the density of other neighbouring fruiting trees (Garcia et al. 2001). This was supported by experimental manipulations of monospecific *Solanum americanus* populations in Puerto Rico, which demonstrated that the presence of neighbouring *Cestrum diurnum* plants increased fruit removal due to more bird visitations to a mixed population. Knowledge of foraging preferences of birds as effective disperser of fleshy-fruited alien plants may facilitate managerial interventions for curbing further spread, for instance, use of biological control agent that reduce attractiveness of fruits (Buckley et al. 2006). In view of these findings, this study tested the hypothesis that frugivorous birds display higher visitation frequencies on fruits of established than emergent aliens in mixed indigenous-alien fynbos communities.

8.3. Methods and materials

8.3.1. Experimental design, study sites and species

The experimental design comprised seven study sites. The first four primary sites comprised mixed populations of the established aliens *Lantana camara* and *Solanum mauritianum*, located on Peninsula Granite Fynbos at Hout Bay, Swartland Shale Renosterveld near Paarl Overberg Sandstone Fynbos near Hermanus located and Breede Shale Renosterveld near Swellendam. The three other secondary study sites comprised mixed populations of the emergent aliens *Myoporum tenuifolium* and *Pittisporum undulatum* located on Peninsula Sandstone Fynbos near Simonstown and Boland Granite Fynbos at Franshhoek and Jonkershoek near Stellenbosch. The fynbos and renosterveld vegetation classifications according to Mucina and Rutherford (2006). Both the emergent and established aliens shared common fruit characteristics, namely single-seeded fruits that turn black or maroon when ripe produced by *L. camara* and *M. tenuifolium* and multi-seeded yellow or orange berries produced by *S. mauritianum* and *P. undulatum*.

8.3.2. Foraging bird frequency

At each site, bird surveillances were conducted during the peak fruiting periods of the emergent and established alien shrubs and restricted to 6 h daily periods of peak bird activity,

namely a 3 h period after sunrise and a 3 h period before sunset (Howe 1977; Snow & Snow 1988; McNamara et al. 1994; Bibby et al. 2000). Individual emergent and established reproductively mature alien shrubs were randomly selected for bird surveillances, which were conducted at approximately 30 m distance from each shrub. The bird surveillances were performed manually with binoculars (8 x 42 magnification) and simultaneously recorded with a digital camcorder (Kodak C813: 8.2 megapixel, ISO 1250, digital IS) for a permanent record (Spiegel & Nathan 2007). Five days of bird surveillances were conducted on each of the alien shrub species at each site (120 surveillance hours on each shrub species). Only those bird species that were observed either directly consuming the fruits of the established and emergent alien shrubs were recorded. Each visitation comprised an arrival and departure of a foraging bird species which were summed for the 5-day observation periods at each site (70-day observation period overall). Bird species were identified with the aid of descriptions and keys presented in Sinclair and Ryan (2003) and Hockey et al. (2005).

8.4. Statistical analysis

Bird species were classified into heavily and moderately frugivorous groups following description presented by Hockey et al. (2005). These included heavily frugivorous birds with fruits constituting their main diet and moderately frugivorous birds with fruits constituting their secondary or occasional diet. Tests for differences in bird visitation frequencies on fruits of established and alien shrubs were conducted on identical complements of bird species, namely 15 bird species in total, which comprised nine heavily, and six moderately frugivorous species. All measurements were $\log_e$ transformed before statistical analysis to reduce the inequality of variance in the raw data so that these more closely approximated normal distributions. The experimental design was unbalanced due to unequally replicated frequency measurements on each bird species at each site. Consequently, a residual maximum likelihood (REML) variance component analysis (linear mixed model) was applied to test for differences in visitation frequencies of birds foraging on fruits of the emergent and established alien shrubs. Three separate REML analyses were conducted using the Wald X^2 statistic generated by the REML (GENSTAT Discovery Edition 3, VSL Lty, UK). The first REML tested for differences in visitation frequencies of birds included in the heavily and moderately frugivorous groups foraging on fruits of the emergent and established alien shrubs. The second REML tested for differences in visitation frequencies of bird species included in the heavily frugivorous group foraging on fruits of the emergent and established alien shrubs. The third REML tested for differences in visitation frequencies of bird species included in the moderately frugivorous group foraging on fruits of the emergent and established alien shrubs. In the first REML, bird frugivore group and shrub species variables were fitted in the fixed model and site, shrub and frugivore group factors in the random model. In the second and third REML, bird species and shrub

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species variables were fitted in the fixed model and site, shrub and bird species factors in the random model. Differences exceeding twice the mean standard error of differences were used to separate significantly different treatment means at P ≤ 0.05. This was based on the fact that for a normal distribution from REML estimates, the 5% two-sided critical value is two.

8.5. Results

Frugivorous birds as a whole displayed significantly (P ≤ 0.001) higher visitation frequencies on fruits of the emergent than established alien shrubs (Table 8.1). However, there was a significant (P ≤ 0.001) interaction between frugivore group and shrub species on bird visitation frequency (Table 8.1) with the moderately frugivorous bird group only displaying significantly higher visitation frequencies on the emergent than established alien shrubs (Figure 8.2). Also, there was a significant interaction (P ≤ 0.01) between heavily frugivorous bird species and alien shrub species and between moderately frugivorous bird species and alien shrub species as well on bird visitation frequency (Table 8.1).

Among the nine heavily frugivorous bird species, the common starling *Sturnus vulgaris* and house sparrow *P. domesticus* displayed a significantly (P ≤ 0.05) higher visitation frequencies on fruits of the emergent than established aliens. Four bird species namely, the African olive-pigeon *C. arquatrix*, the speckled mousebird *Colius striatus*, the Cape bulbul *Pycnonotus capensis* and the Cape white-eye *Zosterops capensis* displayed significantly (P ≤ 0.05) visitation frequencies on fruits of the established alien *S. mauritianum* than the two emergent alien shrubs (Table 8.2). The remaining four bird species exhibited no significant (P ≥ 0.05) differences in visitation frequencies between the emergent and established alien shrubs (Table 8.2).

Among the six moderately frugivorous bird species only the laughing dove *Streptopelia senegalensis* displayed significantly (P ≤ 0.05) higher visitation frequencies on fruits of the emergent than established alien shrubs. The speckled pigeon *Columba guinea* exhibited a significantly (P ≤ 0.05) higher visitation frequency on fruits of the two emergent alien shrubs than fruits of the established alien *S. mauritianum* but not the established alien *L. camara*. Similarly, the Cape turtledove *Streptopelia capicola* displayed a significantly (P ≤ 0.05) higher visitation frequency on fruits of only the emergent alien *M. tenuifolium* than on fruits of the two established alien shrubs. Differences in visitation frequencies displayed by the other three moderately frugivorous bird species between the emergent and established alien shrubs were indistinct.

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Table 8.1. Wald χ² statistics derived from three separate REML'S (linear mixed models) which tested for differences in visitation frequencies by birds (different frugivorous groups and species) on fruits of emergent (*M. tenuifolium and P. undulatum*) and established (*L. camara and S. mauritianum*) alien shrubs. Significant at *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

MAIN EFFECTS AND INTERACTIONS	df	WALD X^2 STATISTIC Foraging frequency
REML 1		Figure 8.1
Shrub species	3	17.08***
Frugivore group	1	12.51***
Shrub species x Frugivore group	3	17.12***
REML 2		Table 8.2
Shrub species	3	3.55
Heavily frugivorous bird species	8	55.06***
Shrub species x Heavily frugivorous bird species	21	220.29***
REML 3		Table 8.2
Shrub species	3	37.4***
Moderately frugivorous bird species	5	9.95
Shrub species x Heavily frugivorous bird species	12	28.51**

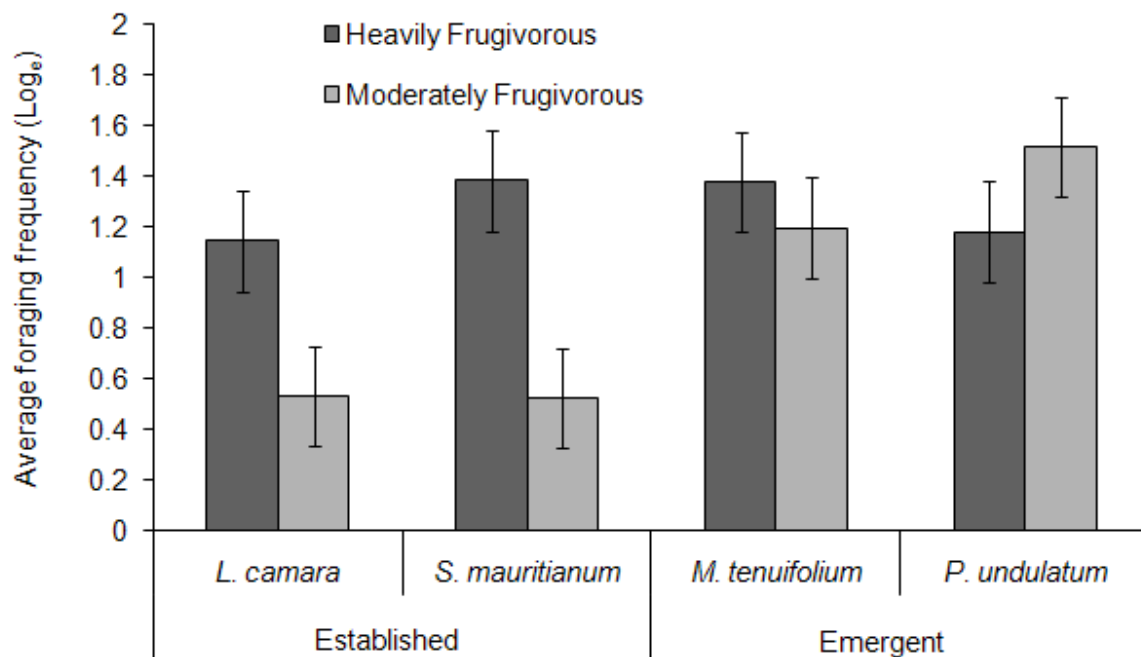

Figure 8.1. Average foraging frequency (log$_e$) of the heavily and moderately frugivorous bird groups on fruits of emergent (*M. tenuifolium and P. undulatum*) and established (*L. camara and S. mauritianum*) alien shrubs. Average standard error of differences shown by bars

Table 8.2. Average foraging frequencies (log$_e$) of heavily and moderately frugivorous bird species on fruits of emergent (*M. tenuifolium and P. undulatum*) and established (*L. camara* and *S. mauritianum*) alien shrubs. Values in bold with different letters significantly different at P ≤ 0.05; se is mean standard error of differences; * show alien birds

Common Name	Established aliens		Emergent aliens	
	L. camara	*S. mauritianum*	*M. tenuifolium*	*P. undulatum*
Overall effects	**0.837a**	**0.952a**	**1.287b**	**1.348b**
	se differences ± 0.142			
Heavily Frugivorous				
African olive-pigeon	**0.576a**	**2.662c**	**1.702b**	**0.000a**
Speckled mousebird	**1.848b**	**2.532b**	**1.312a**	**0.693a**
Red-winged starling	0.952a	0.000a	1.720a	1.410a
*Common starling	**0.000a**	**0.000a**	**1.754b**	**1.290b**
Olive thrush	1.069a	0.693a	1.411a	1.075a
Cape bulbul	**2.037b**	**2.456c**	**1.326ab**	**1.097a**
*House sparrow	**0.000a**	**0.000a**	**0.000a**	**1.298b**
Cape robin-chat	**1.024b**	**0.795b**	**1.140b**	**0.000a**
Cape white-eye	**2.777b**	**3.302b**	**1.312a**	**1.322a**
	Average se differences ± 0.382			
Moderately Frugivorous				
Speckled pigeon	**0.621ab**	**0.000a**	**1.257b**	**2.485c**
Cape turtledove	**0.402a**	**0.000a**	**1.692b**	**0.000a**
Laughing dove	**0.000a**	**0.000a**	**1.151b**	**1.615b**
Southern boubou	**0.621ab**	**0.173a**	**0.876ac**	**1.455bc**
Southern masked-weaver	**0.621ab**	**1.314b**	**0.913ab**	**0.000a**
Cape canary	**0.922ab**	**1.645b**	**0.000a**	**1.253b**
	Average se differences ± 0.481			

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8.6. Discussion

Only the moderately frugivorous birds displayed higher visitation frequencies on fruits of emergent than established alien shrubs, which contrasted with the study hypothesis. The observed preference by the moderately frugivorous birds for fruits of the emergent aliens was attributed to structural and compositional differences in the emergent and established alien populations, which is consistent with findings by Carlo et al. (2007) that density of vegetation affects the bird foraging activity on fruits and subsequent dispersal. Previous studies have shown that frugivorous birds do prefer foraging at the margins of forest gaps where emergent alien species tend to establish (Levey 1988; Carlo et al. 2007). The edges of forest gaps are characterised by an abundant and diverse fruit resources, which are targeted by a diverse array of bird species during breeding seasons (Levey 1988; Restrepo et al. 1999) and consequently fruiting plants established in these habitats experience frequent visitations. Although, fruiting alien and indigenous trees often coexist due to limited perch structures in fynbos (Manders & Richardson 1992), thick stands of established alien trees are less diverse in plant species and fruit resources, which limit bird species richness. This was evident from the reported unchanged numbers of frugivorous and granivorous birds with increased density of *Acacia cyclops* in tall mixed fynbos (Fraser & Crowe 1990; Armstrong et al. 1994; Carlo et al. 2007). In addition, the opportunistic foraging behaviour of especially partially frugivorous birds on fruits of novel alien plants in the habitat (Mandon-Dalger et al. 2004; LaFleur et al. 2007; Kueffer et al. 2009), may also explain the observed higher visitation frequencies of these birds on fruits of the emergent than established alien plants. Many foraging birds tend to prefer new fruits which are often more attractive than their customary fruits (e.g. Knight 1986; Richardson et al. 2000; Traveset & Richardson 2006) as they provide a means of maximizing energy acquisition (Pyke et al. 1977; Moermond & Denslow 1983; Sallabanks 1993). Consistently, LaFleur et al. (2007) found that European starlings *Sturnus vulgaris* and American robins *Turdus migortorius* tend to readily feed on novel fruits in the absence familiar fruit with the American robins *T. migratorius* however showing this behaviour all the time. The local frugivorous birds might also show higher preference of alien fruits where large scale habitat modification has lead limited variety of indigenous fruits. Therefore, the close association of birds with human settlements which are rich in emergent alien fruit resources (Reichard et al. 2001; Cowling & Richardson 1995; Quix 2007), may explain their seeming preference for their fruits since several of the secondary study sites containing the emergent aliens were in relatively closer proximity to urban areas than the primary study sites containing the established aliens.

The observed higher visitation frequencies by the heavily frugivorous common starling *S. vulgaris* on fruits of the emergent aliens were possibly associated with the massive fruit production by *M. tenuifolium* and the prolonged fruit availability in *P. undulatum* (Knight 1986). This suggestion

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was supported by the observed attraction of large flocks of European starlings *Sturnus vulgaris,* cedar waxwings *Bombycilla cedrorum* and American robins *Turdus migratorius* by the highly fruiting *Sambucus nigra* and *Juniperusa shei* in New Zealand and Texas respectively (Chavez & Slack 1994; Williams & Karl 1996). Also, the alien common starling *S. vulgaris* is highly selective in its fruit diet due to lack of sucrase in the digestive system (Martinez del Rio et al. 1988) and consequently its preference for emergent alien fruits may be related to the emergent alien's fruit nutritional composition, especially the relative amounts of amino acids and monosaccharides as they are effectively assimilated more than sucrose-rich diet by these birds gut systems (Espaillat & Mason 1990; Williams & Karl 1996). This contrasts with the preference by the heavily frugivorous African olive-pigeon *C. arquatrix*, speckled mousebird *C. striatus*, Cape bulbul *P. capensis* and Cape white-eye *Z. capensis* for fruits of the established alien *S. mauritianum* with its relatively high monosaccharide content (see Chapter 6) which such specialised frugivorous birds tend to prioritise (Jordano 2000; Kueffer et al. 2009; Gosper & Vivian-Smith 2010). Indeed, small to medium size passerine birds species belonging to the genera *Colidae, Pycnonotus* and *Zosterops* frequently forage such fruits of which may render them effective seed dispersers (Duncan & Chapman 1999; Simberloff & Holle 1999; Mandon-Dalger et al. 2004; Spiegel & Nathan 2007; Jordaan et al. 2011) in a variety of global habitats especially those in Mediterranean-climate ecosystems (Herrera 1995; Vazquez et al. 2005; Schupp et al. 2010). The observed preference by the moderately frugivorous laughing dove *S. senegalensis* and speckled pigeon *C. guinea* for fruits of the emergent alien *P. undulatum* may be explained by the preferences of these predominantly granivorous birds for the dry and tiny seeds of *P. undulatum* as observed (e.g. Lambert 1989; Hulme & Benkman 2002) in other dove species elsewhere. Although the alien house sparrow is classified as heavily frugivorous because of proportion of fruit diet in this study (Hockey et al. 2005), it is granivorous of which might explain why this species preferred foraging on *P. undulatum* more than the relatively more fleshy fruits of established alien plants and *M. tenuifolium*. It has been shown that birds tend to prioritise their diet based on availability (Moermond & Denslow 1985; LaFleur et al. 2007). Also birds display seasonal diet shift elicited by the scarcity of these birds primary diet (Zwickle et al. 1974; Herrera 1984; Williams 2006; Kearny & Porter 2009) and thus granivorous birds may feed on dry fruits and seeds more than fleshy fruits. In this regard, it has been reported that American robins *Turdus migratorius* exhibit a seasonal shift in fruit diet based on their activity and fruit availability with breeding frugivorous birds preferring an insect diet for high protein content (Herrera 1984; Meormond & Denslow 1985; Wheelwright 1988). Also, gut systems of partial frugivores are not well-adapted to processing fruit diets (Meormond & Denslow 1983; Herrera 1984; Jordano 1992, 2000) and the possibly higher concentration of laxative glycoalkaloids in fruits of the established than emergent aliens, which disrupt nutrient assimilation in the gut through osmotic diarrhoea, may

explain why these birds preferred the fruits of the emergent aliens (Cipollini & Levey 1997; Levey & Martinez de Rio 2001).

The generally insignificantly different in visitation frequencies displayed by the two heavily frugivorous birds (e.g. red-winged starling *O. morio* and olive thrush *T. olivaceous*) and shrub species specific differences exhibited by the three moderately frugivorous bird species (e.g. speckled pigeon *C. guinea,* Cape turtle-dove *S. capicola* and laughing dove *S. senegalensis*) on fruits of the established and emergent aliens may be explained by the heavy reliance of these wintering birds on broad-based fruit diets as reported in other Mediterranean climate ecosystems (Jordano 1987; Herrera 1995; LaFleur et al. 2007). In fact, the prolonged fruiting periods of alien plants provide sustenance to local frugivores during periods of environmental stress (White & Stiles 1992; Williams & Karl 1996; Buckley et al. 2006) and the similar visitation frequencies displayed by these birds on fruits of established and emergent alien shrubs may be elicited by a need for dietary supplementation where monospecific fruits are nutritionally inadequate (Jordano 1988; Williams & Karl 1996; Kueffer et al. 2009). This situation was observed in Europe, New Zealand and Australia where such bird species forage and disperse seeds of several fleshy-fruited plants (Snow & Snow 1988; Williams & Karl 1996; Williams 2006). Also, birds that defend fruiting trees often show frequent visits (Pratt 1984) with reports of interspecific bird aggression, agonistic displays and displacements among birds competing for similar fruit resource (Howe 1977; Pratt 1984; Greenberg et al. 1993; Daily & Ehrlich 1994). Reliance by birds on the similar fruit resources leads to interference competition between foraging bird species (Pratt & Stiles 1983) which tend to equalise their visitation frequencies ar least among those that possess similar attributes such as body mass.

The observed preference of the generally more abundant moderately frugivorous bird species with less specialized adaptation for fruits of emergent than established aliens suggest that control measures should be focused on eradicating these and other emergent alien species with fleshy fruits in especially urban environments to prevent their transport by birds into adjacent natural areas. In addition, significant preference of fruits of emergent alien trees and shrubs by the alien common starling *S. vulgaris* and house sparrow *P. domesticus* support the reports that invasion of some fleshy-fruited plants is accelerated by presence of other alien mutualist partners (see Simberloff & Holle 1999; Richardson et al. 2000). In addition, use of biological control method that spoils fruits to reduce their attractiveness to birds could be recommended to suppress spread of seeds over long distances.

8.7. References list

Armstrong, A.J. & van Hensbergen, H.J. (1994) Comparison of avifaunas in *Pinus radiata* habitats and indigenous riparian habitat at Jonkershoek, Stellenbosch. *South African Journal of Wildlife Research*, **24**, 48-55.

Beater, M.M.T., Garner, R.D. & Witkowski, E.T.F. (2008) Impacts of clearing invasive alien plants from 1995 to 2005 on vegetation structure, invasion intensity and ground cover in a temperate to subtropical riparian ecosystem. *South African Journal of Botany,* **74**, 495-507.

Bibby, C.J., Burgess, N.D. Hill, D.A. & Mustoe, S. (2000) *Bird census techniques*. Academic Press, London.

Blossey, B. & Notzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887-89.

Bosque, C. & Pacheco, A.M. (2000) Dietary nitrogen as a limiting nutrient in frugivorous birds. *Revista Chilena de Historia Natural*, **73**, 441-445.

Buckley, Y.M., Anderson. S., Catterall, C.P., Corlett, R.T., Engel, T., Gosper, C.R., Nathan, R., Richardson, D.M., Setter, M., Spiegel, O., Vivian-Smith, G., Voigt, F. A., Weir, J.E.S. & Westcott, D.A. (2006) Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology*, **43**, 848–857.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A. E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hayes, D. (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology*, **16**, 630-640.

Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment,* **2**, 436-443.

Carlo, T. A., Aukema, A. G. & Morales, J. M. (2007) Plant-frugivore interactions as spatially explicit networks: integrating frugivore foraging with plant spatial patterns. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A. J., Schupp, E. W., Green, R. J. & Westcott, D. A.) pp. 369-390. Reading: Biddles Ltd.

Carlo, T. A., Collazo, J. A. & Groom, M. J. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia*, **134**, 119-131.

Charalambidou, I., Santamaria, L. & Langevoord, O. (2003) Effect of ingestion by five avian dispersers on the retention time, retrieval and germination of *Ruppia maritima* seeds. *Functional Ecology*, **17**, 747-753.

Chen, C.C. & Chou, L. S. (2008) Differences in foraging ecology between generalized and specialized frugivorous birds in the Fushan experimental forest, northeastern Taiwan. *Taiwan Journal of Forest Science*, **23**, 233-42.

Cipollini, M.L. & Levey, D.J. (1997a). Antifungal activity of Solanum fruit glycoalkaloids: implications for frugivory and seed dispersal. *Ecology*, **78**, 799-809.

Cipollini, M.L. & Levey, D.J. (1997b). Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *The American Naturalist,* **150**, 346-372.

Cody, L.M. (1983) Bird diversity and density in South African forests. *Oecologia*, **59**, 201-215.

Cowling, R. M., Proches, S. & Vlok, J. H. J. (2005) On the origin of southern African subtropical thicket vegetation. *South African Journal of Botany*, **71**, 1-23.

Cowling, R.M., Kirkwood, D., Midgley, J.J. & Pierce, S.M. (1997) Invasion and persistence of bird-dispersed, subtropical thicket and forest species in fire-prone coastal fynbos. *Journal of Vegetation Science*, **8**, 475-488.

Daily, G.C. & Ehrlich, P.R. (1994) Influence of social status on individual foraging and community structure in a bird guild. *Oecologia*, **100**, 153–165.

Dennis, A.J. & Westcott, D.A. (2007) Estimating dispersal kernels produced by diverse community of vertebrates. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 201 – 228. Reading: Biddles Ltd.

Duncan, R.S. & Chapman, C.A. (1999) Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications*, **9**, 998-1008.

Espaillat, J. E. & Mason, J. R. (1990) Differences in taste preference between Red-winged Blackbird and European Starlings. *Wilson Bulletin*, **102**, 292-299.

Galetti, M., Laps, R. & Pizo, M.A. (2000) Frugivory by Toucans (Ramphastidae) at two altitudes in the Atlantic Forest of Brazil. *Biotropica*, **32**, 842-850.

Garcia, D. & Ortiz-Pulido, R. (2004) Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography*, **27**, 187-196.

Garcia, D., Zamora, R., Gomez, J.M. & Hodin, J.H. (2001) Frugivory in *Juniperus communis* depends more on population characteristics than on individual attributes. *Journal of Ecology*, **89**, 639–647.

Geldenhuys, C.J., le Roux, P.J. & Cooper, K.H. (1986) Alien invasions in indigenous evergreen forest. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 119-131. Oxford University Press, Cape Town.

Glyphis, P.J., Milton, J.S. & Siegfried, R.W. (1981) Dispersal of *Acacia cyclops* by birds. *Oecologia*, **48**, 138-141.

Godinez-Alvarez, H. & Jordano, P. (2007) An empirical approach to analysing the demographic consequences of seed dispersal by frugivores. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 391-406. Reading: Biddles Ltd.

Goldblatt, P. & Manning, J.C. (2002) Plant diversity of the Cape Region of Southern Africa. *Annals of the Missouri Botanical Garden*, **89**, 281–302. 200.

Gomes, L.G.L., Oostra, V. Nijman, V., Cleef, A.M. & Kappelle, M. (2008) Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. *Biological Conservation*, **141**, 860-871.

Gosper, C. & Vivian-Smith, G. (2010) Fruit traits of vertebrate-dispersed alien plants: smaller seeds and more pulp sugar than indigenous species. *Biological Invasions,* **12**, 2153-2163.

Gosper, C.R., Stansbury, C.D. & Vivian-Smith, G. (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distributions*, **11**, 549-558.

Green, R.J. (2007) Refining the conservation management of seed-dispersing frugivores and their fruits: examples from Australia. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 579-598. Reading: Biddles Ltd.

Greenberg, R., Niven, D.K., Hopp, S. & Boone, C. (1993) Frugivory and coexistence in a resident and a migratory vireo on the Yucatan peninsula. *Condor*, **95**, 990–999.

Guevara, S. & Laborde, J. (1993) Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. *Vegetatio*, **107**/**108**, 319-338.

Herrera, C.M. (1995) Plant-vertebrate seed dispersal systems in the Mediterranean: Ecological, Evolutionary, and Historical Determinants. *Annual Review of Ecology and Systematics*, **26**, 705-727.

Herrera, C.M. (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs*, **68**, 511-538.

Herrera, C.M. (2002) Seed dispersal by vertebrates. *Plant-animal interactions: an evolutionary approach*. (eds. Herrera, C.M. & Pellmyr, O.) pp. 185 210. Blackwell Science, Oxford, UK.

Higgins, S. I., Nathan, R. & Cain, M. L. (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology*, **84**, 1945-1956.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (eds) (2005) *Roberts' birds of southern Africa*, 7th edn. John Voelcker Bird Book Fund: Cape Town.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecological and Systematics*, **13**, 201–228.

Howe, H.F. (1977) Bird activity and seed dispersal of a tropical wet forest tree. *Ecology*, **58**, 539-550.

Hulme, P.E. & Benkman, C.W. (2002) Granivory. *Plant animal interactions: an evolutionary approach*. (eds. Herrera, C.M. & Pellmyr, O.) pp. 185-208. Blackwell Science, Oxford, UK.

Iwao, K. & Rausher, M.D. (1997) Evolution of plant resistance to multiple herbivores: quantifying diffuse coevolution. *American Naturalist,* **149**, 316-335.

Jordaan, L.A., Johnson, S.D. & Downs, C.T. (2011) Digestion of fruit of invasive alien plants by three southern African avian frugivores. *Ibis*, **153**, 863-867.

Jordano, P. (1988) Diet, fruit choice and variation in body conditions for frugivorous Warblers in Mediterranean Schrubland. *Ardea*, **76**, 193-209.

Jordano, P. (2007) Frugivores, seeds and genes: analysing the key elements of seed shadows. *Seed dispersal: theory and its application in a changing world.* (eds. Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.A.) pp. 252–276. Reading: Biddles Ltd.

Jordano, P. & Schupp, E.W. (2000) Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, **70**, 591–615.

Jordano, P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *The American Naturalist*, **129**, 657-677.

Jordano, P. (2000) Fruits and frugivory. *Seeds: the ecology of regeneration in natural plant communities.* (ed. Fenner, M.) pp. 125-166. CABI Publishers, Wallingford, UK.

Jordano, P., Garcia, C., Godoy, J.A. & Garcia-Castano, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3278-3282.

Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334-350.

Knight, R.S. (1986) A comparative analysis of fleshy fruit displays in alien and indigenous plants. *The ecology and management of biological invasions in Southern Africa.* (eds. Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A.) pp. 171-178. Oxford University Press, Cape Town.

Knight, R.S. (1988) Aspects of plant dispersal in the south-western Cape with particular reference to the roles of birds as dispersal agents. Ph.D. Thesis, University of Cape Town, South Africa.

Krug, C.B. & Krug, R.M. (2007) Restoration of Old Fields in Renosterveld: a case study in a Mediterranean-type shrubland of South Africa. *Old fields: dynamics and restoration of abandoned farmland.* (eds. Cramer, V.A. and Hobbs, R.J.) pp. 265-334. Society for Ecological Restoration International. Island Press.

Kueffer, C., Kronauer, L. & Edwards, P.J. (2009) Wider spectrum of fruit traits in invasive than native floras may increase the vulnerability of oceanic islands to plant invasions. *OIKOS*, **118**, 1327-1334.

Levey, D.J. & Martinez del Rio, C. (2001) It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. *The Auk*, **118**, 819-831.

Malcarney, H.L., Martínez del Rio, C. & Apanius, V. (1994) Sucrose intolerance in birds: simple nonlethal diagnostic methods and consequences for assimilation of complex carbohydrates. *The Auk*, **111**, 170-177

Mandon-Dalger, I., Clergeau, P., Tassin, J., Riviere, J.-N. & Gatti, S. (2004) Relationships between alien plants and an alien bird species on Reunion Island. *Journal of Tropical Ecology*, **20**, 635-642.

Martinez del Rio, C., Baker, H.G. & Baker, I. (1992) Ecological and evolutionary implications of digestive processes: Bird preferences and the sugar constituents of floral nectar and fruit pulp. *Cellular and Molecular Life Sciences*, **48**, 544-551.

Martinez del Rio, C., Stevens, B.R., Daneke, D.E. & Andreadis, P.T. (1988) Physiological correlates of preference and aversion for sugars in three species of birds. *Physiological Zoology*, **61**, 222-229.

McNamara, J.M., Houston, A.I. & Lima, S.L. (1994) Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology*, **25**, 287-302.

Meehan, H.J., McConkey, K.R. & Drake, R.D. (2002) Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. *Journal of Biogeography*, **29**, 695–712.

Moermond, T. C. & Denslow, J. S. (1985) Neotropical avian frugivores: patterns of behaviour, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs,* **36**, 865-897.

Moermond, T.C. & Denslow, J.S. (1983) Fruit choice in Neotropical birds: effects of fruit type and accessibility on selectivity. *Journal of Animal Ecology*, **52**, 407-420.

Moll, E.J. & Bossi, L. (1983) 1:250 000 scale map of the vegetation of 3322 Oudshoorn. Eco-lab, University of Cape Town.

Montaldo, N.H. (2000) Reproductive success of bird-dispersed plants in a subtropical forest relict in Argentina. *Revista Chilena de Historia Natur*, **73,** 511–524

Mucina, L., Rutherford, M.C. & Powrie L.W. (2006) *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. South African National Biodiversity Institute: Pretoria.

Murray, K.G., Russell, S., Picone, C.M., Winnett-Murray, K., Sherwood, W. & Kuhlmann, M.L. (1994) Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. *Ecology*, **75**, 989-994.

Nel, J.L., Richardson , D.M., Rouget, M., Mgidi, T.N., Mdzeke, N., le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L. & Neser, S. (2004) A proposed classification of invasive alien plant species in South Africa: towards prioritizing species and areas for management action. *South African Journal of Science*, **100**, 53-64.

Oatley, T.B. (1984) Exploitation of a new niche by the Rameron Pigeon *Columba arquatrix* in Natal. *Proceedings of the Fifth Pan-African Ornithological Congress* (ed. Ledger, J.A.) pp. 323-330, Southern African Ornithological Society.

Olckers, T. (1999) Biological control of *Solanum mauritianum* Scopoli (Solanaceae) in South Africa: a review of candidate agents, progress and future prospects. *African Entomology Memoir,* **1**, 65–73.

Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation,* **117**, 285-297.

Pratt, K.T. & Stiles, W.E. (1983) How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. *The American Naturalist*, **122**, 797-805.

Pratt, T.K. (1984) Examples of Tropical frugivores defending fruit-bearing plants. *The Condor*, **86**, 123-129.

Proches, S., Wilson, J.R.U., Richardson, D.M. & Chown, S.L. (2008) Herbivores, but not other insects, are scarce on alien plants. *Austral Ecology*, **33**, 691-700.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology*, **52**, 137-154.

Pysek, P. & Richardson, D.M. (2008) Invasive plants. Ecological Engineering Vol **3** of *Encyclopedia of Ecology* (eds. Jorgensen, S.E. & Fath, F.D.) pp. 2011-2020. Oxford: Elsevier.

Reichard, S.H., Chalker-Scott, L. & Buchaman, S. (2001) Interaction among non-native plants and birds. *Avian ecology and conservation in an urbanising world*. (eds. Marcluff, J. M., Bowman, R. & Donnelly, R.) pp. 179- 223. Kluwer Academic Publishers.

Rejmanek, M. (2000) Invasive plants: approaches and predictions. Austral Ecology, **25**, 497-506.

Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more inv`asive? *Ecology*, **77**, 165*5–1660.*

Restrepo, C., Gomez, N. & Heredia, S. (1999) Anthropogenic edges, treefall gaps, and fruit-frugivore interactions in a Neotropical montane forest. *Ecology*, **80**, 668-685.

Richardson, D.M. & Brink, M.P. (1985) Notes on *Pittosporum undulatum* in the south western Cape. *Veld and Flora,* **71**, 75-77.

Richardson, D.M. & Brink, M.P. (1985) Notes on *Pittosporum undulatum* in southwestern Cape. *Veld and Flora*, **71**, 75-77.

Richardson, D.M. & Fraser, M.W. (1995) Birds of Swartboskloof, Jonkershoek Valley, Stellenbosch: a mountain fynbos ecosystem. *Southern Birds*, **18**, 1–44.

Richardson, D.M. & Pysek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invisibility. Progress in Physical Geography, **30**, 409–431.

Richardson, D.M. & Rejmánek, M. (2011) Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions*, **17**, 788-809.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmanek, M. (2000b) Plant invasions – the role of mutualism. *Biology Reviews*, **75**, 65-93.

Richardson, D.M., Cowling, R.M. & le Maitre, D.C. (1990) Assessing the risk of invasive success in Pinus and Banksia in South African mountain fynbos. *Journal of Vegetation Science*, **1**, 629-642.

Richardson, D.M., Pysek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000a) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93-107.

Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation,* **112**, 63-85.

Roura-Pascual, N., Richardson, D.M., Krug, R.M., Brown, A., Chapman, A.R., Forsyth G.G., le Maitre, D.C., Robertson, M.P., Stafford, L., Van Wilgen, B.W., Wannenburgh, A. & Wessels, N. (2009) Ecology and management of alien plant invasions in South African fynbos: Accommodating key complexities in objective decision making. *Biological Conservation*, **142**, 1595–1604.

Rowan, M.K. (1983) The doves, parrots, louries, and cuckoos of southern Africa. John Voelcker bird book fund, Claremont.

Russo, S.E., Portnoy, S. & Augspurger, C.K. (2006) Incorperating animal behaviour into seed dispersal models: implications for seed shadows. *Ecology*, **87**, 3160-3174.

Sakai, A.K., Weller, S.G., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A, Baughman, S., Cabin, R.J., Cohen, J. E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M. & Thompson, J.N. (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–32.

Sallabanks, R. (1993) Fruiting plant attractiveness to avian seed dispersers: native vs. Invasive Crataegus in western Oregon. *Madrono*, **40**, 108–16.

Saracco, F.J., Collazo, J.A., Groom, M.J. & Carlo, T.A. (2005) Crop size and fruit neighbourhood effects on bird visitations to fruiting *Schefflera mototoni* trees in Puerto Rico. *Biotropica*, **37**, 81-87.

Saracco, J.F., Collazo, J.M. & Groom, M.J. (2004) How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia*, **139**, 235-245.

Schupp, E.W, Milleron, T. & Russo, S.E. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. *Seed dispersal and frugivory: ecology, evolution and conservation.* (eds. Levey, D.J., Silva, W.R. & Galetti, M.) pp. 19-33. Wallingford, UK: CAB International.

Scott, J.K. (1996) Population ecology of *Chrysanthemiodes monilifera* in South Africa: implications for its control in Australia. *Journal of Applied Ecology,* **33**, 1496-1508.

Simberloff, D. & Holle, V.B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions,* **1**, 21–32.

Sinclair, I. & Ryan, P. (2003) Birds of Africa south of the Sahara. Cape Town: Struik Publishers.

Snow, B. & Snow, D. (1988) *Birds and berries*. T. & A.D. Poyser, Calton, UK.

Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, **10**, 718–728.

Steadman, D.W. (1997) The historic biogeography and community ecology of Polynesian pigeons and doves. *Journal of Biogeography,* **24**, 737-753.

Telleria, J.L., Ramirez, A. & Perez-Tris, J. (2005) Conservation of seed-dispersing migrant birds in Mediterranean habitats: shedding light on patterns to preserve processes. *Biological Conservation*, **124**, 493–502.

Telleria, L. J., Ramirez, A. & Pérez-Tris, J. (2008) Fruit tracking between sites and years by birds in Mediterranean wintering grounds. *Ecography*, **31**, 381-388.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173–181

Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecology & Evolution*, **21**, 208–216.

Van Wyk, B. & van Wyk, P. (1997) *Field guide to trees of southern Africa*. Struik Publishers: Cape Town.

Vazquez, D. P., Morris, W. F. & Jordano P. (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters*, **8**, 1088-1094.

Vitousek, P.M., D'Antonio, C., Loope, L.L., Rejmanek, M. & Westbrook, R. (1997) Introduced species: a significant component of human-caused global. *New Zealand Journal of Ecology*, **21***,* 1-16.

Wang, B.C. & Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology & Evolution* **17**, 379-386.

Waring, G.H. Loope, L.L. & Medeiros, A.C. (1993) Study on use of alien versus native plants by nectarivorous forest birds on Maui, Hawaii. *The Auk*, **110**, 917-920.

Wheelwright, N.T. (1988) Seasonal changes in food preferences of American Robins in captivity. *The Auk,* **105**, 374- 37.

Whelan, C.J., Wenny, D.G. & Marquis, R.J. (2008) Ecosystem services provided by birds. *Annals of the New York Academy of Sciences*, **1134**, 25–60.

White, D.W. & Stiles, E.W. (1992) Bird dispersal of fruits of species introduced into eastern North America. *Canadian Journal of Botany*, **70**, 1689-1696.

Williams, P. (2006) The role of blackbirds (*Turdus merula*) in weed invasion in New Zealand. *New Zealand Journal of Ecology*, **30**, 285-291.

Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **77**, 1661–1666.

Wilms, J.J.A.M. & Kappelle, M. (2006) Frugivorous birds and seed dispersal in disturbed and old growth montane oak forests in Costa Rica. (ed. Kappelle, M.) pp. 309–324. *Ecology and*

conservation of neotropical montane Oak Forests, Ecological Studies Series 185. Springer-Verlag, New York/Berlin/Heidelberg.

Zwickel, F.C., Boag, D.A. & Brigham, J.H. (1974) The autumn diet of Spruce Grouse: a regional comparison. *The Condor*, **76**, 212-214.

Chapter 9
General discussion and conclusions

This study's primary aim was to determine whether the presence of fleshy-fruited alien shrubs and trees which share similar avian dispersal assemblages with fleshy-fruited indigenous trees and shrubs sway avian dispersers' attention from native to alien fruits thereby altering seed dispersal of native species. This was achieved by comparing the numbers of foraging bird species, the total numbers of foraging birds, their visitation frequencies and their foraging periods on fruits of two indigenous and two alien shrubs co-occurring at four different sites in the Cape Floristic Region. In addition, various multiples of foraging bird numbers, foraging times and visitation frequencies were applied as determinants of fruit consumption intensities and in combination with measures of seed size in determining proxies of potential dispersal capacities of indigenous and alien seeds ingested by birds.

A variance components analysis indicated no statistically significant differences in the average numbers of bird species foraging on alien and indigenous fruits over all sites. However, slightly fewer numbers of bird species in total were found visiting fruits of the alien shrubs (15 species on *S. mauritianum* and 17 species on *L. camara*) than the indigenous shrubs *(*20 species on *O. africana* and 21 species on *C. monilifera*)*. This contrasted with the higher recorded total visitations by 21 species overall of foraging birds on fruits of the alien shrubs (374 visitations on *S. mauritianum* fruits and 204 visitations on *L. camara* fruits) than the indigenous shrubs (176 visitations on *O. africana* fruits and 132 visitations on *C. monilifera* fruits). However, heavily frugivorous birds as a group did display statistically significantly higher average foraging frequencies on fruits of alien than indigenous shrubs over all sites but this was not apparent in the moderately frugivorous bird group. At the individual species level, only four heavily frugivorous bird species namely the African olive-pigeon *Columba arquatrix*, the speckled mousebird *Colius striatus*, the Cape bulbul *Pycnonotus capensis* and the Cape white-eye *Zosterops capensis* displayed significantly higher visitation frequencies on the alien *S. mauritianum* than the two indigenous shrubs. A multiple correspondence analyses map and tabulated standardized deviates of bird species' visitation frequencies on the alien and indigenous shrub species also indicated strong positive associations between the alien *S. mauritianum* and the African olive-pigeon *C. arquatrix* and the speckled mousebird *C. striatus* but these were site specific. However, there were exceptions with respect to the other bird species. For example, the variance components analysis found no significantly different visitation frequencies by the red-faced mousebird *Urocolius indicus* and the olive thrush *Turdus olivaceous* on *L. camara.* This contrasted with the MCA map and computed standardized deviates, which indicated a strong positive association with the alien *L. camara* and these two bird species but only at the Swellendam site.

With respect to bird foraging numbers and their foraging periods, the variance components analysis found no statistically significant differences in the numbers of heavily and moderately frugivorous birds as a group foraging on fruits of the alien shrubs. However, the heavily frugivorous birds as a group did forage fruits of only the alien *L. camara* for significantly longer periods than fruits of the two indigenous shrubs. At the individual species level, only 4 of the 11 heavily frugivorous bird species, but none of the 14 moderately frugivorous species, foraged fruits of the alien shrubs in either greater numbers or for longer periods than fruits of the indigenous shrubs. However, five bird species, (African olive-pigeon *C. arquatrix,* speckled mousebird *C. striatus,* common starling *Sturnus vulgaris*, Cape white-eye *Z. capensis,* speckled pigeon *Columba guinea*)*,* were observed foraging fruits of the alien *L. camara* in equivalent numbers and for the same periods as the indigenous *O. africana* which possess typical alien features, such as high fruit production and extended fruiting period. However, this was not apparent in the multiple correspondence analyses map and tabulated standardized deviates, which indicated strong positive but site-specific associations in terms of foraging bird numbers and foraging period only between *O. africana and* the common starling *S. vulgaris*.

The effectiveness of various derived multiples of visitation frequency, foraging bird numbers and foraging periods, in discriminating between bird foraging activities on fruits of alien and native plants was also explored. The variance components analysis found statistically significantly higher fruit consumption intensities and seed dispersal potentials by heavily frugivorous birds, especially the African olive-pigeon *C. arquatrix*, the speckled mousebird *C. striatus* and the Cape white-eye *Z. capensi*s, of the alien *S. mauritianum* than of the indigenous shrubs. However, the multiple correspondence analysis map and table of standardized deviates indicated a strong positive association between the alien *S. mauritianum* and the African olive-pigeon *C. arquatrix* only, this restricted to the Swellendam site. The dissimilarities found between the outputs from the variance components analysis (REML) and the multiple correspondence analysis (MCA) were primarily a consequence of the smaller data set analysed by the MCA. The MCA unlike the REML was unable to deal with zero values in the unbalanced data set and as consequence exclusion criteria had to be applied by placing thresholds on frequently low or absent values, which reduced the total information analysed. An additional limitation of the MCA was that it merely provided the degree of association, either positive or negative, between bird species, shrub species and sites but not their statistical significance.

Overall the simplest quantitative measure, namely that of bird visitation frequency, identified foraging preferences of individual bird species for fruits of alien and indigenous shrubs as well as the more complex measures foraging bird numbers and foraging times as well as products of these in the computed fruit consumption intensity and seed dispersal potential. This was evident from the significant ($P \leq 0.05$) correspondence between visitation frequency and the other more complex quantitative measures of foraging behaviour in all bird species with one exception (Table 9.1). Jordano and Schupp (2000) also found that bird species that were effective dispersers (e.g. dispersing large quantities of seeds) are characterised by their high visitation

frequencies, feeding rates and high probabilities of dispersing seeds. Consequently, visitation frequency should provide the most efficient and practical quantitative measure of bird foraging preferences in future surveys involving large complements of indigenous, emergent, and established alien shrub species. This recommendation complies with the proposal that the frequency of interaction between fruiting plants and vectors dependably indicate the net effect on seed dispersal (Jordano & Schupp 2000; Vazquez et al. 2005; Schupp et al. 2010).

To further understand seed removal dynamics by birds, fruit characteristics (Jordano 2000; Kueffer et al. 2009; Gosper & Vivian-Smith 2010) that influence choice and consumption of indigenous and alien fruits by birds were related to quantities of seeds removed. It was asked whether frugivorous birds remove larger amounts of fruits and associated seeds from especially alien plants with high fruit production and nutritional contents, and whether germination of the bird-ingested seeds is enhanced (Chapter 6). The results demonstrated that canopy seed production, fruit abundance and monosaccharide content were positively correlated with the total numbers of seeds removed by birds and viable seeds excreted by birds. The 14 frugivorous bird species examined as a whole removed greater numbers of seeds and excreted larger numbers of viable seeds of *S. mauritianum* than those from other shrub species, which shows that at least barriers to reproduction are overcome (see Figure 9.1). However, there were subtle differences in the amounts of seeds removed by individual bird species from fruits of the four study species, and this was attributed to a combination of fruit nutritional content, bird body mass and seed size. The observation that birds removed greater numbers of *S. mauritianum* than *L. camara* fruits and seeds supports other studies on invasive fleshy-fruited alien plants (Kueffer et al. 2009; Gosper & Vivian-Smith 2010). Since nutritional quality of fruits is critical for birds in environments with limited fleshy fruits resources such as the South African fynbos, indigenous species with similar fruit traits could replace eradicated fleshy-fruited alien plants in management protocols.

Table 9.1. A comparison of different quantitative measures of bird foraging preferences (log$_e$) for those heavily and moderately frugivorous bird species that displayed significant differences (values in bold type with different letters) between alien (*L. camara* and *S. mauritianum*) and indigenous (*C. monilifera* and *O. africana*) shrub species. * = P ≤ 0.05

		C. monilifera	*O. africana*	*L. camara*	*S. mauritianum*	Correlation with visitation frequency t-statistic
HEAVILY FRUGIVOROUS BIRDS						
African olive-pigeon	Visitation Frequency	**1.75a**	**0.50a**	**1.25a**	**15.00b**	**-**
	Bird Numbers	**1.478a**	**0.576a**	**0.922a**	**3.214b**	**5.50***
	Foraging Period	**3.251a**	**0.833a**	**2.947a**	**6.798b**	**3.55***
	Consumption Intensity	**1.263a**	**0.032a**	**0.598a**	**4.383b**	**7.39****
	Seed Dispersal Potential	**4.831a**	**1.206a**	**3.734a**	**12.466b**	**5.66***
Speckled mousebird	Visitation Frequency	**0.75a**	**5.50a**	**6.75a**	**12.25b**	**-**
	Bird Numbers	**0.599a**	**2.547b**	**2.708b**	**2.683b**	1.92
	Foraging Period	**1.269a**	**4.387b**	**5.272b**	**6.378b**	**4.27***
	Consumption Intensity	**0.211a**	**2.320b**	**2.404b**	**3.295b**	**4.16***
	Seed Dispersal Potential	**1.488a**	**6.105b**	**7.059bc**	**9.702c**	**6.53***
Red-winged starling	Visitation Frequency	1.75a	2.75a	2.00a	0.00a	-
	Bird Numbers	**1.422a**	**2.844b**	**2.296ab**	**0.000c**	**6.73***
	Foraging Period	**3.039a**	**4.029a**	**4.519a**	**0.000b**	**3.69***
	Consumption Intensity	1.345a	1.864a	1.518a	0.000a	**12.79****
	Seed Dispersal Potential	**2.599ab**	**3.646b**	**3.932b**	**0.000a**	**4.05***
Red-faced mousebird	Visitation Frequency	1.75a	0.00a	2.75a	1.00a	-
	Bird Numbers	0.997a	0.000a	1.366a	0.708a	**7.99****
	Foraging Period	**2.272ab**	**0.000a**	**3.202b**	**1.515ab**	**10.85****
	Consumption Intensity	0.246a	0.000a	1.434a	0.538a	2.30
	Seed Dispersal Potential	**2.216ab**	**0.000a**	**3.718b**	**1.976ab**	**6.31***
Cape bulbul	Visitation Frequency	**4.25a**	**5.00a**	**7.25ab**	**11.50b**	**-**
	Bird Numbers	1.522a	0.858a	1.979a	2.147a	1.63
	Foraging Period	**4.167ab**	**1.764a**	**4.631b**	**5.490b**	1.37
	Consumption Intensity	1.158a	1.317a	1.335a	2.042a	**4.93***
	Seed Dispersal Potential	**2.884ab**	**1.965a**	**3.492ab**	**5.554b**	**3.93***
Cape white-eye	Visitation Frequency	**7.00a**	**9.25a**	**17.00b**	**26.75c**	**-**
	Bird Numbers	**2.177a**	**3.454ab**	**3.917ab**	**3.804b**	1.44
	Foraging Period	4.423a	6.049a	6.555a	6.647a	1.66
	Consumption Intensity	**2.116a**	**3.423ab**	**4.979bc**	**5.506c**	**3.39***
	Seed Dispersal Potential	**7.388a**	**9.957ab**	**12.231bc**	**13.459c**	**3.44***
MODERATELY FRUGIVOROUS BIRDS						
Speckled pigeon	Visitation Frequency	1.00a	0.75a	1.25a	0.00a	-
	Bird Numbers	**0.708ab**	**0.916b**	**0.677ab**	**0.000a**	1.88
	Foraging Period	**1.683ab**	**2.215ab**	**2.839b**	**0.000a**	**3.65***
	Consumption Intensity	0.6918a	0.2440a	0.2574a	0.0000a	1.20
	Seed Dispersal Potential	2.4624a	2.4245a	3.3394a	0.0000a	**7.60****
Cape turtledove	Visitation Frequency	**2.00ab**	**3.75b**	**1.00a**	**0.00a**	**-**
	Bird Numbers	1.171a	1.161a	0.693a	0.000a	2.42
	Foraging Period	**3.841bc**	**4.040c**	**1.709ab**	**0.000a**	**3.10***
	Consumption Intensity	0.5376a	0.8614a	0.7008a	0.0000a	1.99
	Seed Dispersal Potential	**4.6021a**	**4.9368a**	**2.4906ab**	**0.0000b**	**3.03***
Southern masked-weaver	Visitation Frequency	**1.50c**	**4.00b**	**1.50c**	**6.50a**	**-**
	Bird Numbers	**0.519a**	**2.163b**	**0.576a**	**1.191a**	0.93
	Foraging Period	2.535a	4.003a	2.066a	2.166a	0.14
	Consumption Intensity	**0.0349a**	**0.7431bc**	**0.0830ac**	**0.6442c**	2.29
	Seed Dispersal Potential	**1.9476a**	**5.4471a**	**2.3178b**	**4.4196ab**	1.68
Cape canary	Visitation Frequency	**0.75b**	**2.75ab**	**2.00b**	**4.50a**	**-**
	Bird Numbers	0.489a	0.832a	0.649a	0.749a	1.64
	Foraging Period	1.312a	2.529a	1.697a	2.681a	**3.36***
	Consumption Intensity	0.0326a	0.4627a	0.1428a	0.2990a	1.26
	Seed Dispersal Potential	**1.4223a**	**3.4543ab**	**2.1513a**	**4.8774ba**	**8.39****

Both experimental and more intricate photographic methods were also applied to obtain reliable estimates of quantities of seeds removed by birds from alien and indigenous shrubs. Although the two methods yielded similar results, the photographic method had several advantages over the experimental approach and recommended for future studies. Knowledge of bird movement patterns is vital for predicting alien plant distributions and in guiding management protocols (Tsoar et al. 2011). Using empirical bird ring-recapture data combined with mechanistic data (gut retention time of seeds and flight speed), movement patterns of bird species consuming fleshy fruits of alien and indigenous plants were explored (Chapter 7). Foraging distances for each bird species were derived from their initial capture location and recapture ring location extracted from the South African Bird Atlas Project database and the fractions of bird-ring recapture records present in different distance categories plotted. The dispersal curves separated bird species into potentially short and long distance seed dispersal vectors, demonstrating that local birds do not only disperse alien seeds over short distance (e.g. 0.41 and 0.81 km), but can also help invaders to cross geographic barriers (e.g. ≥100km Figure 9.1; Nathan et al. 2008). The high alien propagule pressure in the Cape Floristic Region resulting from the combined effects of human-mediated introduction of alien plants and native birds from neighbouring biomes suggests that management protocols should also consider manipulating bird movements to minimise seed dispersal of the alien plants.
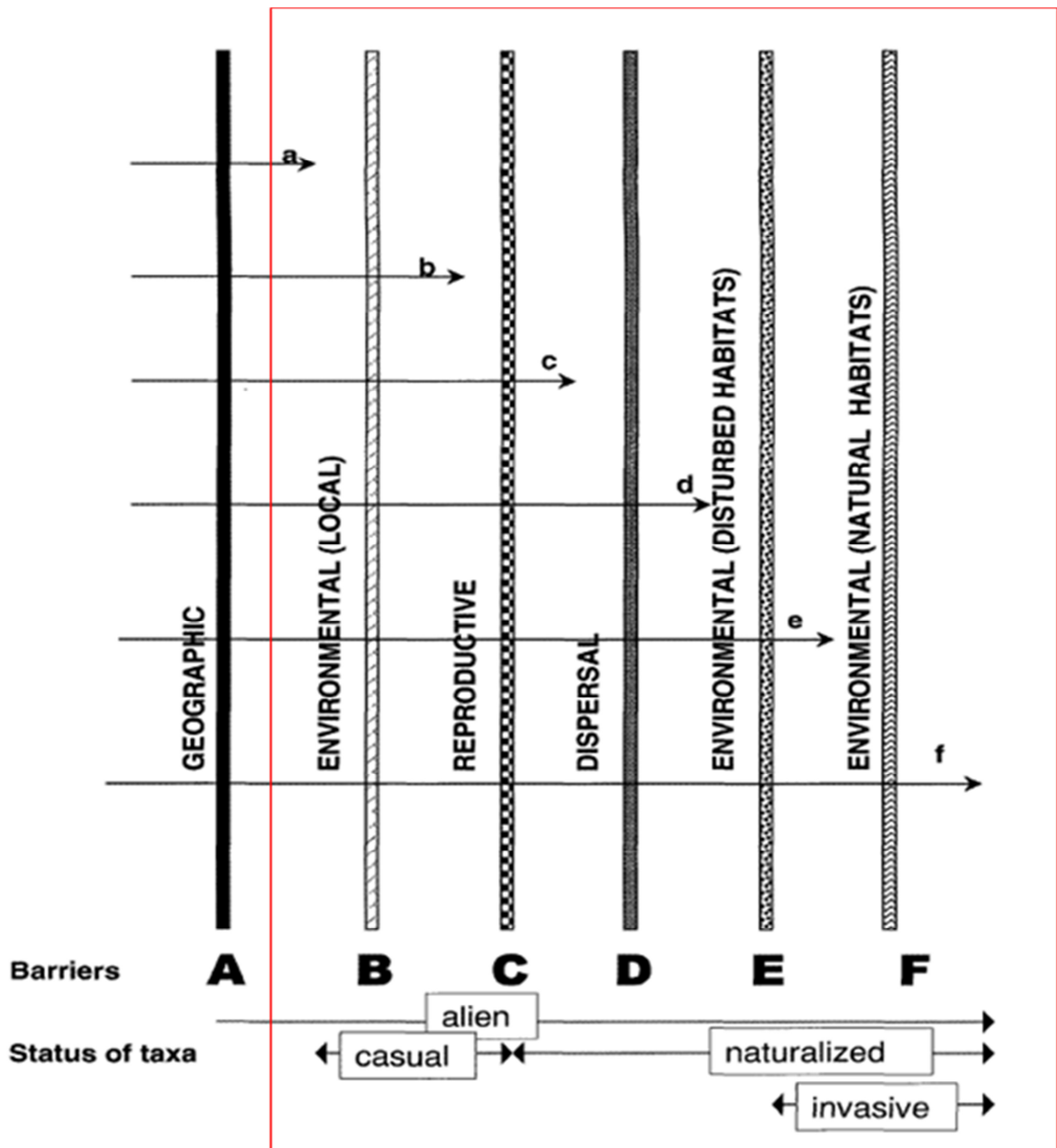
Figure 9.1. A schematic representation of major barriers that must be overcome for successful invasion of introduced plants; modified from Richardson et al. (2000). Once a fleshy-fruited plant has been introduced (e.g. crossed geographic barrier from its native range), bird-mediated seed dispersal assist to overcome local barriers (B – F in bold) thereby accelerating naturalisation and invasion of a species

There were several logistic, financial and time constraints (110-day sampling period overall) to this study, the major limitation being the small numbers of indigenous, established and emergent alien shrubs tested which comprised only a small fraction of the total numbers of indigenous and alien shrubs with fleshy fruits foraged by birds in the Cape Floristic Region. Clearly, future surveys of bird foraging preferences should include a much larger complement of fleshy-fruited alien and indigenous shrubs to establish the extent to which alien shrubs may be

disrupting seed dispersal of indigenous shrubs. Such surveys should also include large complements of both emergent and established alien shrubs to determine whether the observed preference by especially moderately frugivorous birds for fruits of emergent than established aliens (e.g. Chapter 8) is a consistent trend, since moderately frugivorous birds have a more variable diet than specialised frugivores (Carlo et al. 2003; Buckley et al. 2006). Such information would also assist in early detection and rapid response as well as eradication programs by prioritising those emergent alien species whose fruits are especially preferred by avian frugivores. Furthermore, records of bird visitation frequency should be accompanied by measurements of the nutritional composition of alien and indigenous fruits. Such measurements should include fruit concentrations of monosaccharide, disaccharides, proteins, lipids and laxative glycoalkaloids, since frugivorous birds differ in their ability to assimilate disaccharides and detoxify nitrogenous compounds (Moermond & Denslow 1985).

In conclusion, there exists an enigma in conservation measures involving removal of fleshy-fruited aliens as these may compromise available food source for indigenous birds leading to a decline in avian abundance and diversity (Buckley et al. 2006). Consequently, removal of aliens would need to be accompanied by the propagation of indigenous species with similar growth form and reproductive attributes as the alien species as a replacement perching, nesting and food source for frugivorous birds (Gosper & Vivian-Smith 2006; Marco et al. 2010). In this regard, the indigene *O. africana* could provide a good replacement for eradicated aliens in the restoration of natural habitats (Gosper & Vivian-Smith 2006; 2010). *O. africana* possess several features typical of alien plants, namely high fruit production and extended fruiting period, with its fruits were as heavily foraged by frugivorous birds as the alien *L. camara.* Such information provided in this study presents an initial guide for bird management protocols in the Cape Floristic Region, which previously were based on general consensus rather than empirical data (van Wilgen et al. 2011).

The suggestion that alien plants, unlike native plants, are likely to thrive under warmer conditions accompanying climate change (Walther et al. 2009) highlights their potential role for sustaining avian populations with a decline in native plant biodiversity accompanying climate change and. Also, alien plant species could assist in re-establishing collapsed mutualisms between birds and native plants (Kawakami et al. 2009), since the ability of certain alien fruits to attract large numbers of frugivorous birds have complementary effects on seed dispersal of neighbouring native species (Aslan & Rejmanek 2010; Gleditsch & Carlo 2010).

The observed low preference for *C. monilifera* fruits by frugivorous birds supports the findings of Scott (1996) who showed that *C. monilifera* does not produce large populations in its native range due to disruption of its sexual reproduction by insect infestation and indicates that local avian frugivores also are susceptible to fruit quality. In this regard, Buckley et al. (2006) suggested that the application of biological control agents that spoil fruits might reduce bird-mediated seed dispersal. Therefore, biological control agents that spoil fruits could be considered for suppressing spread of fleshy-fruited alien shrubs in the Cape Floristic Region.

Several authors have recommended holistic managerial approaches in limiting dispersal of seeds of alien plants by birds by targeting groups of alien plants that display either similar invasion characteristics or similar impacts (Gosper et al. 2005; Gosper & Vivian-Smith, 2009; Roura-Pascual et al. 2009; Downey et al. 2010; van Wilgen et al. 2011). The observed preference by moderately frugivorous bird species for fruits of emergent alien shrubs whose impacts on native species are likely less severe during early stages of invasion (Nel et al. 2004; Buckley et al. 2006) indicates that eradication of emergent aliens should be a priority. In this regard, quantification of impact thresholds of alien plants on native ecological processes such as seed dispersal (Myers et al. 2000; Gooden et al. 2009) should assist in the containment of current invasions and thus restrict further invasions.

9.4. Reference list

Aslan, C.E. & Rejmanek, M. (2010) Avian use of introduced plants: ornithologist records illuminate interspecific associations and research needs. *Ecological Applications*, **20**, 1005-20.

Buckley, Y.M., Anderson. S., Catterall, C.P., Corlett, R.T., Engel, T., Gosper, C.R., Nathan, R., Richardson, D.M., Setter, M., Spiegel, O., Vivian-Smith, G., Voigt, F.A., Weir, J.E.S. & Westcott, D.A. (2006) Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology*, **43**, 848–857.

Bullock, J., Shea, K. & Skarpaas, O. (2006) Measuring plant dispersal: an introduction to field methods and experimental design. *Plant Ecology*, **186**, 217-234.

Carlo, T.A., Collazo, J.A. & Groom, M.J. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia,* **134,** 119-131.

Charalambidou, I., Santamaria, L. & Langevoord, O. (2003) Effect of ingestion by five avian dispersers on the retention time, retrieval and germination of *Ruppia maritima* seeds. *Functional Ecology*, **17**, 747-753.

Cipollini, M.L. & Levey, D.J. (1997) Why are some fruits toxic? Glycoalkaloids in *Solanum* and fruit choice by vertebrates. *Ecology* 78:782–798

Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien invasive plants: Implictions for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics,* **34**, 183-211.

Gleditsch, J.M. & Carlo, T.A. (2010) Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. *Diversity and Distributions*, **17**, 244–253.

Gooden, B., French, K., Turner, P.J. & Downey, P.O. (2009) Impact threshold for an alien plant invader, Lantana camara L., on native plant communities. *Biological Conservation*, **142**, 2631-2641.

Gosper, C. & Vivian-Smith, G. (2010) Fruit traits of vertebrate-dispersed alien plants: smaller seeds and more pulp sugar than indigenous species. *Biological Invasions,* **12**, 2153-2163.

Gosper, C.R. & Vivian-Smith, G. (2006) Selecting replacements for invasive plants to support frugivores in highly modified sites: a case study focusing on *Lantana camara*. *Ecological Management & Restoration*, **7**, 197-203.

Gosper, C.R., Stansbury, C.D. & Vivian-Smith, G. (2005) Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. *Diversity and Distributions*, **11**, 549-558.

Herrera, C.M. (1984) Adaptation to frugivory of Mediterranean avian seed dispersers. *Ecology*, **65**, 609-617.

Kawakami, K., Mizusawa, L. & Higuchi, H. (2009) Re-established mutualism in a seed-dispersal system consisting of native and introduced birds and plants on the Bonin Islands, Japan. *Ecological Research,* **24,** 741-748.

Latimer, A.M., Silander, J.A., Gelfand, A.E., Rebelo, A.G. & Richardson, D.M. (2004) A method for quantifying the magnitude of threat to plant biodiversity from alien plant invasions and other anthropogenic factors – a case study in the CFR, South Africa. *South African Journal of Science*, **100**, 81–86.

Marco, A., Lavergne, S., Dutoit, T. & Bertaudiere-Montes, V. (2010) From the backyard to the backcountry: how ecological and biological traits explain the escape of garden plants into Mediterranean old fields. *Biological Invasions,* **12,** 761-779.

Moermond, T. C. & Denslow, J. S. (1985) Neotropical avian frugivores: patterns of behaviour, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs,* **36**, 865-897.

Myers, J.H., Simberloff, D., Kuris, A.M. & Carey, J.R. (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution*, **15**, 316-320.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. (2008) Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution*, **23**, 638-647.

Nel, J.L., Richardson, D.M., Rouget, M., Mgidi, T.N., Mdzeke, N., le Maitre, D.C., Wilgen, B.W.V., Schonegevel, L., Henderson, L. & Neser, S. (2004) A proposed classification of invasive alien plant species in South Africa: towards prioritizing species and areas for management action. *South African Journal of Science,* **100,** 53 - 64.

Richardson, D.M. & Rejmánek, M. (2011) Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions*, **17**, 788-809.

Roura-Pascual, N., Richardson, D.M., Krug, R.M., Brown, A., Chapman, A.R., Forsyth G.G., le Maitre, D.C., Robertson, M.P., Stafford, L., Van Wilgen, B.W., Wannenburgh, A. & Wessels, N. (2009) Ecology and management of alien plant invasions in South African fynbos: Accommodating key complexities in objective decision making. *Biological Conservation*, **142**, 1595–1604.

Russo, S.E., Portnoy, S. & Augspurger, C.K. (2006) Incorperating animal behavior into seed dispersal models: implications for seed shadows. *Ecology,* **87**, 3160-3174.

Schupp, E.W., Jordano, P. & Gómez, J.M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist,* **188,** 333-353.

Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar A. & Nathan, N. (2009) Long-distance seed dispersal. *Annual Plant Reviews*, **38,** 204–237.

Snow, D.W. (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica*, **13**, 1-14.

Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters,* **10,** 718-728.

Traveset, A, Robertson, A.W. & Rodriguez-Perez, J. (2007) A review of the role of endozoochory in seed germination. *Seed dispersal: theory and its application in a changing world*. (eds. Dennis, A.J., Green, R.J., Schupp, E.W. & Westcott, D.A.) pp. 78-103. Reading: Biddles Ltd.

Tsoar, A., Shohami, D. & Nathan, R. (2011) A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats. *Fifty years of invasion ecology. The legacy of Charles Elton* (ed. Richardson, D.M.) pp. 103-119, Wiley-Blackwell, Oxford.

Turner, P.J. & Downey, P.O. (2008) The role of birds in weed invasion, species decline, revegetation and reinvasion: consequences of *Lantana camara*. Proceedings of the 16th Australian Weeds Conference, Cairns Convention Centre, North Queensland, Australia, 18-22 May, 2008; Queensland: Queensland Weed Society, 30-32.

van Wilgen, B.W., Dye, C., Hoffmann, J.H., Philip Ivey, P., le Maitre, D.C., Moore, J., Richardson, D.M., Rouget, M., Wannenburgh, A. & Wilson, J.R.U. (2011) National-scale strategic approaches for managing introduced plants: insights from Australian acacias in South Africa. *Diversity and Distributions*, **17**, 1060–1075.

Vazquez, D.P., Morris, W.F. & Jordano, P. (2005) Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters,* **8,** 1088-1094.

Verdu, M. & Traveset, A. (2005) Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. *Ecology,* **86,** 1385-1394.

Vittoz, P. & Engler, R. (2007) Seed dispersal distances: a typology based on dispersal modes and plant traits. *Botanica Helvetica*, **117**, 109-124.

Walther, G.-R., Roques, A., Hulme, P.E., Sykes, M.T., Pysek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarosík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K. & Settele, J. (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution,* **24,** 686 - 693.