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# The importance of seed dispersal in the Alexandria Coastal Dunefield, South Africa

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**Abstract.** The endozoochorous dispersal of seeds by mammals and birds between distinct vegetation communities was assessed to determine the importance of these processes in coastal dune field management. Isolated pockets of thicket vegetation (bush-pockets) within a large coastal dune field provided the opportunity to study vertebrate seed dispersal and its contribution to their origin and maintenance. Mammalian and avian faeces were collected for the quantification of seeds dispersed via endozoochory. Birds and mammals showed considerable overlap, dispersing intact seeds of 17 and 29 plant species, respectively, but mammals dispersed a greater diversity and size range than birds. Extrapolation of mammalian faecal data indicates an annual input of 23 million intact seeds to the dune field. Significantly more seeds are deposited by mammals and birds in the bush-pockets than on open sand, and birds deposited greater numbers of seeds nearer the seed source. Zoochory appears to be critical for the maintenance of the bush-pocket habitats through the dispersal of climax woody plant species into the dune field. Directional dispersal by birds and mammals to the bush-pockets is considered to be responsible for the maintenance and possible origin of these bush-pockets. The high number of exotic plant propagules dispersed by both avian and mammalian zoochory highlights the importance of management of the Alexandria Coastal Dunefield (ACD) beyond the reserve boundaries. In a dynamic system such as the ACD which is within a declared nature reserve, the continued existence of the bush-pockets may depend on the maintenance, beyond the reserve boundaries, of a reservoir of not only plant material but vertebrate dispersers as well.

**Key words:** Artificial perches; Bird; Conservation; Endozoochory; Mammal; Management.

**Nomenclature:** Arnold & De Wet (1993) for plants; Skinner & Smithers (1990) for mammals; Maclean (1993) for birds.

**Abbreviation:** ACD = Alexandria Coastal Dunefield.

## Introduction

Noss (1983) suggested that the primary goal in the conservation of natural areas is to ensure the perpetuation of ecosystem structure, function and integrity, while minimizing species loss. These sentiments were supported by Walker (1992). However, ecological processes are not generally confined to even large protected areas, and smaller areas may require active management in an effort to preserve these processes and systems. Future management of protected areas therefore requires that processes which operate on a landscape scale, frequently beyond the reserve boundaries, be identified.

Even though the current matrix of protected areas in South Africa potentially conserves examples of more than 90% of floral and faunal diversity (Siegfried 1992; Siegfried & Brown 1992), in just over 6% of the total area (Wynberg 1993), there is little evidence to show how well the current system maintains the ecological processes which operate in such areas, particularly small reserves. By virtue of the large distances covered by vertebrate seed dispersers, zoochory can be identified as one of these processes. Habitats which rely on such vertebrate dispersal vectors for the maintenance of vegetation communities may therefore be influenced by the land use practices in adjacent unprotected habitats.

Zoochorous dispersal could result in the establishment of new plant species in patchy or fragmented environments or could result in the propagation or establishment of vegetation communities. Avian zoochory has been well documented (van der Pijl 1972; Howe 1979; Snow 1981a, b; Howe & Smallwood 1982; Herrera 1984; Gautier-Hion et al. 1985; Wheelright & Janson 1985; Debussche & Isenmann 1989; Willson & Whelan 1990; French 1991), whereas the importance of mammalian zoochory has received relatively little attention. However, reviews by Herrera (1989), Debussche and Isenmann (1989), and Willson (1993) have recently highlighted the importance of mammals as seed dispersal agents. In environments such as coastal dune fields, where dispersal of fleshy-fruited plant species via wind, water and ballistic mechanisms are unlikely, the contribution of vertebrate dispersers to the propagation of fleshy-fruit species could be of paramount importance. Coupled to this is the fact that coastal dune fields often have highly fragmented vegetation communities and the relative roles of mammals and birds as dispersers among habitat islands or across habitat boundaries probably shifts according to the vegetation structure (Willson 1993), suggesting that management should take these effects into consideration (Kerley et al. 1996).

This study aims to investigate the importance of zoochory in the maintenance of a subtropical thicket vegetation community within an extensive coastal dune field and associated mosaic of adjacent agricultural land use. We investigated endozoochorous dispersal in the Alexandria Coastal Dunefield (ACD), the largest (120 km$^2$) active coastal dune system in South Africa (McLachlan et al. 1982; Tinley 1985). This dune field contains several distinct habitat types (McLachlan et al. 1982), including 277 isolated fragments of thicket (bushpockets) interspersed among the unvegetated sand dunes (McLachlan et al. 1982; Talbot & Bate 1991; Bate & Dobkins 1992). There are no large mammals and few birds resident in the pockets, these species venturing into the dune field from the adjacent, inland thicket (McLachlan et al. 1982; Brown 1990; Brown et al. 1995).

The ACD and its associated flora and fauna lend themselves to investigating seed dispersal ecology, and were used to further our understanding of the role of endozoochory in the maintenance of isolated plant communities in migrating dune fields. The dynamic nature of the dune field results in the continued extinction and establishment of new vegetation communities. Plant species succession within the dune field relies on the non-random dispersal of plant species by endozoochorous vertebrates for the introduction and establishment of climax fleshy fruit species within this fragmented ecosystem.

The aims of the study were focused around a series of questions regarding the dispersal of seeds into the ACD. We assumed that birds and mammals are successful agents of seed dispersal although limited information exists on the viability and germination capacity of dispersed seeds. We addressed the following: which mammalian and avian species are involved in seed dispersal? What is the importance of various faunal species and taxa in seed dispersal? How do mammalian and avian species compare with regard to their role in seed dispersal? and is seed dispersal random or directional? Finally, we discuss the broader implications of these findings.

## Methods

### *Study area*

The ACD (Fig. 1) is an extensive sheet of coastal dunes on the southeast coast of South Africa, stretching 48 km from the Sundays River mouth (33° 44' S; 25° 51' E) to Cape Padrone (33° 47' S; 26° 28' E) (Illenberger 1986; McLachlan et al. 1987). The dune field averages 2.2 km in width, with dunes rising in height from the sea to a landward boundary at 100-150 m elevation, the latter being truncated in a sharp dropoff at the main

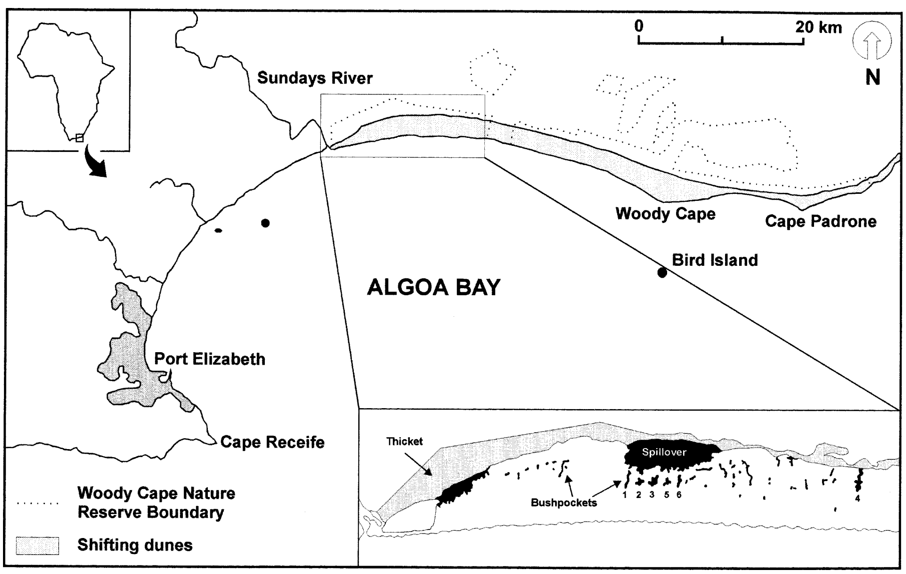


**Fig. 1.** Locality of the Woody Cape Nature Reserve, Algoa Bay, South Africa. Study bushpockets and thicket habitat are indicated within the Alexandria Coastal Dunefield which forms a large part of the reserve.

slipface or precipitation ridge (Brown 1990). The dominant southwesterly wind pattern in Algoa Bay is the driving force that creates the dune field, blowing sand from the adjacent beach into the dune field. On average about 170 000 $m^3$ of sand accumulates per year which results in the vertical accretion and landward movement of the dune field at a rate of 1 mm/yr and 0.25 m/yr respectively (Illenberger 1986). However, the wind regime varies seasonally and the dune characteristics are also influenced by the east-southeasterly wind which prevails during the summer (Nov-Mar) months. As a result the dominant dunes are of the reversing transverse type with dune ridges running along a N/S axis which form part of a greater aklé dune pattern covering almost the entire dune field (Illenberger 1986). Unvegetated, mobile dunes make up 81% of the dune field while coastal thicket characterized by evergreen broad-leaved sclerophyll vegetation grows inland of the main slipface. Bush-pockets which make up 3.2% of the dune field are usually associated with inter-dune hollows and may contain calcite outcrops (aeolianite), or may occur as knolls of vegetation (Bate & Dobkins 1992). These bush-pockets average 1.2 ha in area and are usually found within 1 km of the landward edge of the dune field. Pockets are inundated by advancing dunes from the west and migrate eastwards through the colonization of new habitat by plants at rates of 1-8 m/yr, depending on their size and shape, with a mean rate of about 4 m/yr (McLachlan et al. 1982). Inundation of bush-pockets by sand movement is a continuous process and the longevity of bush-pockets is determined by their size and shape as well as the vegetation structure and presence of aeolianite outcrops.

The climate of the dune field is warm temperate, although fairly variable and unpredictable. Precipitation increases eastwards, ranging from 392 mm/yr at the Sundays River mouth to about 700 mm/yr inland of Woody Cape and Cape Padrone. Rainfall is bimodal with peaks in winter (June) and spring (October) (McLachlan et al. 1982).

The evergreen broad-leaved sclerophyll thicket landward of the dune field is dominated by the trees *Sideroxylon inerme, Cassine aethiopica, Schotia afra, Euclea undulata, Pterocelastrus tricuspidatus, Colpoon compressum*, and shrubs *Azima tetracantha, Olea exasperata, Carissa bispinosa, Rhus longispina, Nylandtia spinosa* and *Lycium afrum*. The dominant plant species in the bush-pockets is *Myrica cordifolia* (waxberry), which is the primary colonizer responsible for establishing and advancing the pockets (Ascaray 1986; Young 1987). Other common bush-pocket species are the trees *Brachylaena discolor* and *C. compressum* and bushes *Stoebe plumosa, Metalasia muricata, Rhus crenata, Anthospermum littoreum, Passerina rigida, Chrysanthemoides monilifera, Helichrysum cymosum. Acacia cyclops* used in earlier stabilization practices is alien to the dune field and is an invasive species in the bush-pockets (Avis 1989).

Six bush-pockets (pockets 1-6) were chosen for the study ranging in size from 1.45-5.45 ha. Bush-pocket area was calculated from aerial photographs using a scanning digitizer. The bush-pockets were situated 7-15 km east of the Sundays River mouth (Fig. 1).

The resident dune field large mammal fauna is relatively poor with few species venturing beyond the vegetation of the main slipface. However, there are a number of species which make regular excursions into the dune field and bush-pockets and these include *Potamochoerus porcus* (bush-pig), *Tragelaphus scriptus* (bushbuck), *Raphicerus melanotis* (grysbok), *Cercopithecus aethiops* (vervet monkey), *Lepus capensis* (Cape hare), *Genetta tigrina* (small-spotted genet) and *Canis mesomelas* (black-backed jackal). Species which use the dune field and bush-pocket habitats infrequently, but are present in the thicket include, *Tragelaphus strepsiceros* (kudu), *Sylvicapra grimmia* (common duiker), *Philantomba monticola* (blue duiker) and *Felis caracal* (caracal) (McLachlan et al. 1982; McLachlan et al. 1987). As the majority of the antelope are browsers they could play an important role in the dispersal of seeds in these coastal habitats.

*Phenology*

Flowering and fruiting characteristics of plant species in bush-pockets 1-4 (28 species), and the thicket hinterland (38 species) were determined monthly from January to December 1991 (App. 1). Only dominant species identified as being zoochorous (presence of fleshy fruits) were monitored. Most grasses and forbs, particularly in the thicket vegetation, were excluded. Common species were considered to be in a particular phenophase if the majority (> 50%) of the plants inspected were in that phase, while determination of rare species' phenologies followed Hoffman (1989). In conjunction with the phenological studies, ripe fruits were collected to establish a seed reference collection.

*Faecal material collection*

*Mammals*

All mammal faeces were collected monthly from January to December 1991 from four bush-pockets (1-4) along 15 random strip transects, each 100 m × 2 m. Faeces were identified from published descriptions (Walker 1988), in addition to recognition of tracks in the dune field. Additional faecal samples were collected monthly from transects in the open dunes (18.2 ha) between the bush-pockets.

*Avifauna*

All bird faeces were collected monthly from January to December 1991 from aeolianite outcrops in bush-pockets 1- 4. These outcrops act as natural perch sites for birds where avian faeces may be readily collected. Bird faeces could not be identified to species level and individual stools could not be distinguished in most cases, precluding the calculation of avian faecal numbers per outcrop and the possible role of specific avian species. Therefore, birds identified from the bush-pockets (Brown 1990; this study) were grouped into feeding guilds to give some indication of those species important in seed dispersal. In addition, bird faeces were collected from a series of artificial perches erected within bush-pockets and adjacent open dunes.

*Artificial perches*

An array of faecal collection perches was erected in the dune field to test specific hypotheses regarding directional dispersal and the effects of distance from the seed source. Each perch consisted of a wooden pole 2.4 m long, sunk 0.5 m into the sand. Two 30-cm dowel rods inserted horizontally at right angles through the top of the pole acted as perches while a 55-cm diameter net bag (knitted polyester with a 0.45-mm mesh size) was suspended 35 cm below the perches. In order to test for the effects of distance from the seed source on avian seed dispersal, five rows of perches were set up extending from the main slipface into the dune field, with eight perches per row. These were set up at distances of – 50 m (in the thicket), and at 0, 20, 50, 100, 200, 400 and 800 m from the main slipface. Consecutive rows were at least 100 m apart and were erected as far as possible away from bush-pockets. Furthermore, in order to test whether seed deposition was concentrated in bush-pockets, perches were set up within five of the bush-pockets (pockets 1-3, 5, 6). We deployed five perches per pocket, and also set perches at 10, 25 and 50 m from each of these pockets in the four cardinal directions. We hypothesized that seed deposition would be greater within the bush-pockets than outside bush-pockets. Avian faeces were collected monthly from each perch for six months from March to August 1991 and analysed for seeds in the same manner as those collected from aeolianite outcrops.

*Analysis of faecal material*

*Mammals*

Faecal material was washed and strained through a 0.5 mm mesh sieve to remove soluble material and then oven dried overnight at 60 °C. Dehydrated faeces were softened by boiling them in water, which facilitated breakdown of the material. Due to the sheer volume of *Potamochoerus porcus* faeces recovered, 25% sub-samples were analysed. All intact and broken seeds were collected and identified after sieving and hand sorting samples with the aid of a dissection microscope. Mammalian faecal numbers were standardized to faecal stools per 0.08 ha (maximum transect area covered) for interpretation, while faecal weights were log transformed before performing analysis of variance (ANOVA; Zar 1984). We proposed that mammalian species contributed equally to seed deposition in the dune field and tested this variation in seed number using a one-way analysis of variance. The importance of the mammalian and avian taxa as dispersal agents was tested using one-way analysis of variance and Tukey's multiple range analysis (Zar 1984). To determine the relative importance of individual species as effective dispersal agents we employed an information theory approach and calculated the Shannon Wiener diversity index ($H'$) for each species as well as all mammal species combined.

*Avifauna*

Faecal material was washed through a 0.2-mm sieve. All intact and broken seed material was collected and identified with the aid of a dissection microscope. Avian seed numbers were log transformed before statistical analysis (Zar 1984). Differences in seed numbers recovered from artificial perch and aeolianite treatments were investigated using ANOVA and Student's *t*-test, at the 95% level of significance.

Seeds were identified using the seed reference collection established during plant phenology observations. For both bird and mammal samples, ratios of intact to broken seeds were determined to estimate loss of seed through digestive processes. Although the viability and germination potential of seeds recovered as well as site suitability were not investigated during the study, defecated seeds were regularly seen germinating from faecal stools within bush-pockets and on aeolianite outcrops.

## Results

*Phenology*

The most important phases for this study are the flowering and fruiting periods. Flowering differed slightly: two flowering peaks were seen in the pockets during late summer and winter while flowering in the thicket peaked during late winter/spring. The majority of flowering phenophases were short, preceding or coinciding with fruit production.

The majority of plants (*M. cordifolia, R. crenata, E. racemosa, Viscum obscurum, V. rotundifolium, S. inerme, Protoasparagus racemosus, P. tricuspidatus, Chironia baccifera, O. exasperata* and *A. tetracantha*) fruited in winter, with ripe fruits persistent for at least four months. *Colpoon compressum* and *Scutia myrtina* fruited for virtually the entire year (Table 1). *Colpoon compressum, C. monilifera* and *S. myrtina* had green fruits over most of the year, with fruits ripening slowly and apparently being consumed as they ripened. These species did not fruit prolifically, but rather had few fruits present at any specific time. *Acacia cyclops* and *N. spinosa* fruited in summer.

A greater proportion of plants with ripe fruits available to dispersers were found in the pockets earlier in the year (summer- autumn), shifting to greater numbers in the thicket later in the year (winter-spring). Fruiting peaks of individual plant species were slightly delayed in the thicket, generally being one month later than those in the pockets. Some species, such as *N. spinosa, P. racemosus, S. inerme*, and *Eugenia capensis* had a higher fruit yield in the thicket with few or no fruits available in the pockets. Plant species attractive to dispersers showed extended fruiting periods (Table 1).

**Table 1.** Fruiting phenology of zoochorous plant species recorded from the bush-pockets and thicket during 1991. Shaded areas show periods during which fruit was available either in green (g), green and ripe (g/r) or only ripe fruit (r).

| Plant species | Site | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Myrica cordifolia* | Pocket | g | g | g | g | r | r | r | r | r | | | |
| | Thicket | Not present in thicket | | | | | | | | | | | |
| *Scutia myrtina* | Pocket | | | g | g/r | g/r | g/r | g/r | g/r | g/r | g/r | g/r | |
| | Thicket | No fruiting recorded in thicket | | | | | | | | | | | |
| *Carpobrotus deliciosus* | Pocket | | | | | | | | | g | g | r | r |
| | Thicket | | | | | | | | | | g | r | |
| *Euclea racemosa* | Pocket | No fruiting recorded in pockets | | | | | | | | | | | |
| | Thicket | | | | | | | g/r | g/r | g/r | g/r | | |
| *Rhus crenata* | Pocket | | | | g | g/r | r | r | r | | | | |
| | Thicket | | | | | g | | | | | | | |
| *Olea exasperata* | Pocket | Not present in pockets | | | | | | | | | | | |
| | Thicket | | | | | g | g | g/r | g/r | g/r | g/r | g | |
| *Sideroxylon inerme* | Pocket | g | | | | | | | | g | g | g | |
| | Thicket | g/r | | | | g | g | g | g/r | | g | | |
| *Nylandtia spinosa* | Pocket | r | | | | | | | | g | g | g/r | r |
| | Thicket | r | | | | | | | | g | g | g/r | r |
| *Acacia cyclops* | Pocket | r | r | g/r | g/r | g | g | g | g | g | g | g/r | g/r |
| | Thicket | | g/r | g/r | g | g/r | g | g | g | g | g | g | g/r |
| *Viscum obscurum* | Pocket | g | g | g | g/r | r | g/r | r | r | r | | g | g |
| | Thicket | | g | g | g | g/r | r | r | r | r | | | g |
| *Colpoon compressum* | Pocket | g/r | g/r | g/r | g/r | g/r | g/r | g/r | g/r | g/r | g/r | g/r | g/r |
| | Thicket | g/r | g/r | g/r | g/r | g/r | g/r | g | g/r | g/r | g/r | g/r | g/r |
| *Chrysanthemoides monilifera* | Pocket | | | g | g | g | g | g | g/r | g | g | g | |
| | Thicket | | | | | | | | g/r | | g | | |
| *Pterocelastrus tricuspidatus* | Pocket | Not present in pockets | | | | | | | | | | | |
| | Thicket | g | g | g | g/r | g/r | r | r | r | | | | |
| *Rhus glauca* | Pocket | | | | | | | | g | g | g/r | | |
| | Thicket | | | | | | | | g | g | g | g/r | r |
| *Lycium afrum* | Pocket | Not present in pockets | | | | | | | | | | | |
| | Thicket | | | | | | | g | g | | | g | r |
| *Azima tetracantha* | Pocket | Not present in pockets | | | | | | | | | | | |
| | Thicket | | g | g | g | g | g | r | | | | | |
| *Eugenia capensis* | Pocket | | | | | | | | | g | | | |
| | Thicket | | | | | | | | | g | g/r | g/r | r |
| *Protoasparagus racemosus* | Pocket | | | | | | g | | | | | | |
| | Thicket | | | | g | g/r | g/r | g | | | | | |
| *Chironia baccifera* | Pocket | | g | g | g/r | g/r | r | r | | | | | |
| | Thicket | | g | g/r | r | g/r | r | | | | | | |
| *Viscum rotundifolium* | Pocket | Not present in pockets | | | | | | | | | | | |
| | Thicket | | | | | g | g/r | r | r | r | | | |
| SEASON | | summer | | | | | winter | | | | | summer | |

**Table 2.** Intact seed numbers of plant species seeds recovered from the faeces of large mammalian fauna and birds. Seed numbers are represented as seed #'s / species / year. - denotes absence of seeds in the faeces. Diversity values (*H'*) are shown as well as numbers of faecal samples.

| Plant species | Bush-pig | Bushbuck | Grysbok | Jackal | Genet | Monkey | Mammals | Birds |
|---|---|---|---|---|---|---|---|---|
| *n* (faeces) | 119 | 103 | 19 | 11 | 22 | 32 | 306 | ? |
| average seed # / faecal bolus | 133 | 6.5 | 0.05 | 1.7 | 14.7 | 211.8 | - | ? |
| *Myrica cordifolia* | 2044 | - | - | 1 | - | 1 | 2046 | 8858 |
| *Scutia myrtina* | 28 | - | - | - | 16 | 22 | 66 | 101 |
| *Carpobrotus deliciosus* | 8596 | 21 | - | - | - | 6342 | 14 959 | - |
| *Euclea racemosa* | - | - | - | - | 149 | - | 149 | 132 |
| *Rhus crenata* | - | 9 | - | - | - | - | 9 | 58 |
| *Olea exaperata* | - | - | - | 1 | 24 | 5 | 30 | 23 |
| *Sideroxylon inerme* | - | - | - | - | 4 | - | 4 | 21 |
| *Nylandtia spinosa* | - | - | - | - | 7 | - | 7 | 1 |
| *Acacia cyclops* | 8 | - | - | - | 20 | - | 28 | 2965 |
| *Viscum obscurum* | - | 1 | - | - | 3 | 34 | 38 | 343 |
| *Opuntia ficus indica* | 4924 | 1 | - | - | - | - | 4925 | - |
| *Colpoon compressum* | - | - | - | - | 14 | 1 | 15 | - |
| *Chrysanthemoides monilifera* | - | 103 | - | - | 3 | 1 | 107 | 2 |
| *Pterocelastrus tricuspidatus* | 4 | - | - | - | 2 | - | 6 | 236 |
| *Rhus glauca* | 24 | - | - | - | 5 | 93 | 122 | 6 |
| *Emex australis* | - | - | - | 14 | - | - | 14 | 71 |
| *Lycium afrum* | - | 26 | - | 1 | - | 41 | 68 | - |
| *Azima tetracantha* | - | - | - | - | 2 | 6 | 8 | - |
| *Eugenia capensis* | - | - | - | - | 42 | 132 | 174 | 4 |
| *Protoasparagus racemosus* | - | - | - | - | 3 | - | 3 | - |
| *Medicago agrestis* | - | - | - | 1 | - | - | 1 | 13 |
| *Chironia baccifera* | - | - | - | - | 26 | - | 26 | - |
| *Chenopodium* sp. | 12 | 419 | 1 | 1 | - | - | 432 | - |
| Poaceae | - | 26 | - | - | - | - | 26 | - |
| Unidentified 1 | - | 61 | - | - | - | - | 61 | - |
| Unidentified 2 | 156 | - | - | - | - | - | 156 | - |
| Unidentified 3 | - | 3 | - | - | - | - | 3 | - |
| Unidentified 4 | - | - | - | - | 5 | - | 5 | - |
| Total | 15796 | 670 | 1 | 19 | 325 | 6778 | 23 588 | 12 834 |
| Diversity (*H'*) | 0.450 | 0.548 | 0 | 0.434 | 0.837 | 0.182 | 0.526 | 0.406 |

*Faecal data*

*Mammals*

Large numbers of intact (Table 2) and broken seeds of several species were found in mammalian faeces. Of the 23 588 recovered intact seeds transported into the dune field by large mammals, the majority were dispersed by bush-pig. Vervet monkey were also important as seed dispersers whereas all other species dispersed relatively few seeds. Seeds dispersed were dominated by *Myrica cordifolia*, *Carpobrotus deliciosus*, and the exotic invader *Opuntia ficus-indica*. Both genet and jackal dispersed seeds, although the proportion that fruits made up in the total diet of these species in the current study is unknown.

Significantly fewer seeds were dispersed by all other large mammals when compared to bush-pig ($F = 26.71$; $df = 6{,}52$; $p < 0.0001$). Bush-pig showed the highest levels of seed destruction, 85.6% of all recovered seeds being damaged. Vervet monkeys showed lowest levels of seed destruction, with only 7.2% of recovered seeds being damaged. Bush-pig and bushbuck defaecated a greater proportion of broken than intact seeds, while all other mammals defaecated higher proportions of intact seeds. Bush-pig transported significantly greater numbers of broken seeds than all other species, with vervet monkey and bushbuck transporting more than genet, jackal and grysbok ($F = 32.39$; $df = 5, 41$; $p < 0.0001$).

There was no significant monthly variation in the total number of mammalian faeces deposited in the dune field by all species ($F = 0.54$; $df = 10, 36$; $p = 0.85$), although numbers for the different mammals differed over the year ($F = 7.63$; $df = 4, 50$; $p < 0.0005$) with bush-pig and bushbuck defaecating significantly more than all other species. Extrapolation of mammalian faecal data from bush-pocket and dune field transect areas to cover the entire dune field indicate that a total of 291 265 faecal boli were potentially brought into the dune field during the study year, with significantly more (251 771 or 86.4%) being transported directly to the bush-pockets and the remainder (39 494 or 13.6%) deposited on bare sand ($\chi^2 = 6.38 \times 10^6$; $df = 1$; $p < 0.0001$). These faeces could contain 23 million intact seeds (17.7 million in bush-pockets, 5.3 million on bare sand) which are potentially viable and could germinate. Faecal material in excess of 10 000 kg is estimated to be deposited into the dune field annually, providing an important nutrient input in these poor sands (McLachlan 1991).

**Table 3.** Species list of birds recorded in bush-pockets. Feeding guilds from Maclean (1993).

| Common name | Species | Feeding guild |
|---|---|---|
| Helmeted guineafowl | *Numida meleagris* | Omnivore |
| Cape turtle dove | *Streptopelia capicola* | Granivore/omnivore |
| Redeyed dove | *Streptopelia semitorquata* | Granivore/omnivore |
| Cinnamon dove | *Alpopelia larvata* | Granivore/omnivore |
| Rameron pigeon | *Columba arquatrix* | Frugivore |
| Spotted eagle Owl | *Bubo africanus* | Carnivore |
| European swallow | *Hirundo rustica* | Insectivore |
| Speckled mousebird | *Colius striatus* | Frugivore/folivore/florivore |
| Redfronted tinker barbet | *Pogoniulus pusillus* | Frugivore/omnivore |
| Cape wagtail | *Motacilla capensis* | Insectivore |
| Forktailed drongo | *Dicrurus adsimilis* | Omnivore |
| Sombre bulbul | *Andropadus importunus* | Frugivore/omnivore |
| Blackeyed bulbul | *Pycnonotus barbatus* | Frugivore/omnivore |
| Cape bulbul | *Pycnonotus capensis* | Frugivore/omnivore |
| Familiar chat | *Cercomela familiarus* | Insectivore |
| Cape robin | *Cossypha caffra* | Insectivore |
| Barthroated apalis | *Apalis thoracica* | Insectivore |
| Neddicky | *Cisticola fulvicapilla* | Insectivore |
| Spotted prinia | *Prinia maculosa* | Insectivore |
| Fiscal flycatcher | *Sigelus silens* | Insectivore |
| Paradise flycatcher | *Tersiphone viridis* | Insectivore |
| Dusky flycatcher | *Muscicapa adusta* | Insectivore |
| Fiscal shrike | *Lanius collaris* | Insectivore |
| Southern boubou shrike | *Laniarus ferrugineus* | Insectivore/frugivore |
| Redwinged starling | *Onychognathus morio* | Frugivore/insectivore |
| Pied starling | *Spreo bicolor* | Frugivore/insectivore |
| Cape glossy starling | *Lamprotornis nitens* | Frugivore/insectivore |
| Malachite sunbird | *Nectarina famosa* | Nectarivore/insectivore |
| Greater double-collared sunbird | *Nectarina afra* | Nectarivore/insectivore |
| Cape white-eye | *Zosterops pallidus* | Insectivore/frugivore |
| Yellowthroated sparrow | *Petronia superciliaris* | Insectivore |
| Yellow canary | *Serinus flaviventris* | Granivore |
| Streakyheaded canary | *Serinus gularis* | Granivore/insectivore |

*Avifauna*

The major frugivorous birds found in the pockets (Table 3) were *Streptopelia capicola, S. semitorquata* (doves), *Pycnonotus barbatus* (blackeyed bulbuls), *Onychognathus morio, Spreo bicolor* and *Lamprotornis nitens* (starlings), *Colius striatus* and *C. indicus* (mousebirds), *Numida meleagris* (helmeted guineafowl), *(Columba arquatrix* (rameron pigeons) and *Cossypha caffra* (cape robins). Mousebirds were rarely seen in the bush-pockets although they are numerous in the thicket throughout the year. Rameron pigeons were abundant in the bush-pockets for only three months of the year (July to September), presumably attracted by ripe fruit.

Nearly all seeds (96.7%) recovered from avian faeces were intact. Birds dispersed large numbers of *M. cordifolia* ($n$ = 8858) and *A. cyclops* ($n$ = 2965) seeds. The bulk of seeds recovered from avian faeces were deposited on outcrops during winter (Fig. 2), coinciding with elevated fruit availability, but showed no significant monthly variation ($F$ = 1.87; $df$ = 11,36; $p$ = 0.077) for the four study pockets.

*Artificial perches*

Although many avian faeces were recovered from the artificial perches, few contained seeds (Table 4). *Myrica cordifolia, A. cyclops* and *C. monilifera* were the dominant species recorded. Seeds were found on perches within the thicket and up to 50 m from the thicket vegetation, while perches 100 m and further from the thicket contained no seeds. Due to low numbers of seeds recovered from transect perches, there was no significant difference in seed numbers to account for increasing distance from the seed source ($F$ = 1.113, $df$ = 7; 32; $p$ = 0.379). The relationship between seed deposition and distance from the thicket were best described by a negative power curve ($y = 57.48x^{-0.61}$; $r$ = 0.87; $df$ = 6; $p < 0.01$; Fig. 3), after transformation to remove zero and negative values (Zar 1984). Significantly more seeds were found on perches within bush-pockets than on those outside pockets ($F$ = 22.99; $df$ = 1, 83; $p < 0.0001$).

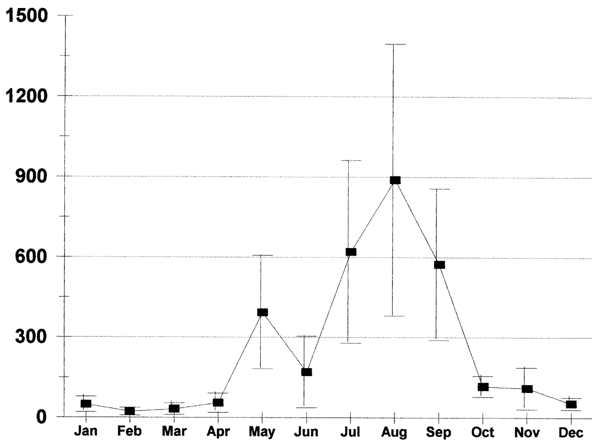


**Fig. 2.** Average number of seeds recovered each month from avian faeces found on bush-pocket aeolianite outcrops.

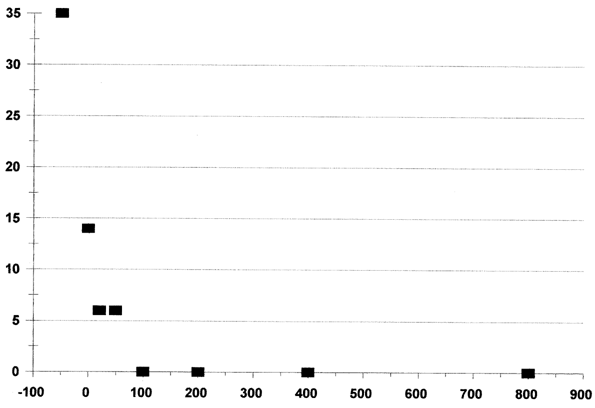


**Fig. 3.** Power curve showing the number of seeds found at various distances from the thicket in faecal collection perches erected in unvegetated dunes.

### *Comparison between birds and mammals*

A comparison of the Shannon Wiener diversity indices for seeds dispersed by birds and mammals indicates that genet disperse the greatest diversity of plant species ($H' = 0.837$) while all mammals together ($H' = 0.526$) disperse a greater diversity of plant species compared to birds ($H' = 0.408$). Considerable overlap is exhibited between plant species dispersed by birds and mammals ($F = 0.03$; $df = 1{,}20$; $p = 0.87$), although mammals disperse a wider range of plant species than birds and include all species dispersed by birds. Birds, bush-pig and vervet monkey transported significantly greater numbers of intact seeds than remaining mammals while bushbuck and genet transport significantly greater numbers of intact seeds than jackal and grysbok ($F = 26.71$; $df = 6{,}52$; $p < 0.0001$). After the exclusion of grysbok from the analyses as they dispersed few seeds, birds, bush-pig and monkey retained their dominance as seed dispersers, with bushbuck and genet dispersing significantly more seeds than jackal ($F = 20.78$; $df = 5{,}47$; $p < 0.0001$).

**Table 4.** Seed numbers of plant species found recovered from avian faeces on 125 artificial perches and 100 random aeolianite outcrops during a six month study period (perches) and once off sample (aeolianite) (Bruton 1992) in the Alexandria Coastal Dunefield.

| Plant species | Perches | Aeolianite |
|---|---|---|
| *Myrica cordifolia* | 375 | 594 |
| *Rhus glauca* | - | 77 |
| *Acacia cyclops* | 71 | 53 |
| *Chrysanthemoides monilifera* | 50 | 23 |
| *Viscum obscurum* | 7 | 21 |
| *Rhus crenata* | 9 | 4 |
| *Scutia myrtina* | 6 | 14 |
| *Pterocelastrus tricuspidatus* | 6 | - |
| *Olea exasperata* | - | 8 |
| *Eugenia capensis* | - | 5 |
| *Nylandtia spinosa* | - | 4 |
| *Colpoon compressum* | - | 2 |
| *Euclea racemosa* | - | 1 |
| *Chironia baccifera* | - | 1 |

## Discussion

### *Mammalian zoochory*

The large mammals of the ACD are important seed dispersers, estimated to transport over 23 million seeds into and within the dune field annually. Different species show distinct variation in their dispersal of intact seeds. Bush-pig are nocturnal omnivores (Skinner & Smithers 1990), feeding on a number of fruit species and their importance in the dispersal of plant species has previously been reported by Phillips (1926) and Breytenbach & Skinner (1981). Although seed destruction by bush-pig is high (Phillips 1926; this study), the seeds that remain are not only viable but show enhanced germination after passage through the gut (Phillips 1926). However, the germination potential of seeds from faeces deposited within the bush-pockets by large mammals has yet to be tested. In addition, bush-pig could provide improved local seed banks (Phillips 1926) and establish germination microclimates through patch disturbance (Huenneke & Vitousek 1990) as a result of rooting activities. Bush-pig are recognized as dispersers of precursor coastal forest species to neighbouring grassland areas (Breytenbach & Skinner 1981) and, as shown here, play a similar role in the dispersal of climax woody species from the sclerophyllous thicket behind the main slipface into the bush-pockets of the ACD.

Primates are major seed dispersers in tropical areas (Howe 1980; Chapman 1989) and transport large quantities of seeds that pass through the gut in viable condition (Middlemiss 1963; Chapman 1989). Vervet monkeys have been shown to act as dispersers in other coastal dune environments where seeds were transported between established and rehabilitated dune areas (Foord et al. 1994). However, primates could cause seed and seedling mortality as they readily drop seeds under canopies or leave them in faecal clumps (Howe 1980), thereby exposing them to poor germination environments and seedling competition following germination. Although vervet monkeys were only active in the dune field for three months, they transported an average of 2226 intact seeds (recovered from the sampled faeces) per month within the transects – greater numbers than all other dispersers including bush-pig during this period.

Although the majority of seed dispersal studies emphasize the importance of birds (Debussche & Isenmann 1989), carnivores have been recorded as effective seed dispersers in many regions (Herrera 1989; Willson 1993). Herrera (1989) showed that carnivores can be important as dispersers since not only are a large proportion of the fleshy fruits they consume dispersed, but seed destruction is low. The majority of seeds dispersed by carnivores are also dispersed by other means and are thus not totally dependent on carnivores for dispersal (Herrera 1989). As with North American studies (see Willson 1993) the carnivorous mammals in the present study showed varied frugivory and seed dispersal. Jackal were transient and spent little time in the bush-pockets, with most faeces being voided on the bare dunes. Jackal have previously been recorded as potential seed dispersers as grasses, wild fruits and seeds dominate plant items in their diet although only making up a small proportion of the total diet (Bothma 1971; Hiscocks & Perrin 1987). Jackals could also possibly contribute to secondary dispersal as a result of their scatophagous habit (Rowe-Rowe 1983). Genets play a selective role in dispersal in that they had latrine areas which were concentrated on aeolianite outcrops. Proportions of intact seeds in their faeces were higher than those in faeces of large herbivores. Genets may be important as dispersers because of their omnivorous habit (Skinner & Smithers 1990).

Grysboks are insignificant as dispersers, with only a single seed being recorded in grysbok faeces *(n* = 19) over the entire year, most seeds probably being destroyed through mastication. The grysbok is, however, a frequent visitor and possible resident, and could provide an important source of nutrients in latrine areas which create habitat patches for seedlings. Faecal masses may enhance germination potential (Hamilton & May 1977; Janzen 1984), but seedlings germinating from faeces may be subject to strong competitive pressure, not only from other seedlings, but also from already established species that show extensive vegetative growth (e.g. *M. cordifolia*).

Clumping of seeds is prevalent in this study as manifested in the average numbers of seeds per faecal bolus for the mammalian species (Table 2). Greatest numbers/bolus are found from monkey faeces while lowest numbers/bolus are found from grysbok faeces. No data are available for average seed numbers per avian faecal bolus although in most cases avian faeces/regurgitations would contain fewer seeds than mammalian faeces (R. Knight pers. comm.). Although clumped seed banks could negatively influence post-dispersal seed germination and seedling establishment (Howe 1980), weathering and seed removal by birds and rodents could spread out the remaining seeds (Willson 1993) thereby enhancing seed survival. Seed removal rates by rodents from experimental seed baits, particularly nocturnal rodents, were significantly higher within bush-pockets than thicket habitats (Castley et al. 2001).

*Avian zoochory*

There is evidence to suggest that the directional dispersal of seeds by birds to the bush-pockets does occur. Seeds of *O. exasperata* and *A. tetracantha* were found in bird faeces in the bush-pockets while these species grew only in the thicket. Furthermore, seeds of *E. racemosa* were recovered from bird faeces in the bush-pockets although this species only fruited in the thicket. The rameron pigeon is considered an important disperser of many plant species, and was found by Phillips (1927) to disperse *O. exasperata*, *P. tricuspidatus, S. inerme, Scutia commersonii, Rhus laevigata*, and *Euclea lanceolata* among others in the Knysna forest, South Africa. Unfortunately no species specific data could be extracted from the present data set.

*Myrica cordifolia* was dispersed in large numbers by birds, comprising 69% of the total intact seed numbers. As birds are relatively dependent on stable resources (Mares & Rosenzweig 1978) they may be attracted to *M. cordifolia* since it fruits for nearly nine months of the year. The exotic *Acacia cyclops* is eaten by a wide variety of birds (Middlemiss 1963; Winterbottom 1970) as they are attracted to the bright red arils encircling the seeds (Gill 1985; Glyphis et al. 1981; Knight & Macdonald 1991). The fact that *A. cyclops* is eaten by many bird species probably contributes to its success as an invader, since the dispersal of a seed depends partly on the habits and ranging behaviour of the various bird species dispersing it. The high avian dispersal of this exotic invader has important management implications, as it is not possible to exclude birds by fencing, suggesting continuous reintroduction of this alien species in areas which have been cleared of aliens by management.

Seeds of *S. myrtina* and *C. monilifera* were found in the faeces throughout the year. These species bore few fruit over much of the year and the fruit seemed to be consumed as it ripened. With only a few fruits ripening at a time, a plant may gain a wide dispersal of its seeds because the frugivore does not remain at the plant for long periods and would thus be unlikely to disgorge or defaecate seeds near the parent plant (Stiles 1982).

*Viscum obscurum* seeds were also found over virtually the entire year from avian faeces. Birds are the primary dispersers of *Viscum* in general (Sutton 1951; van der Pijl 1972; McKey 1975; Walsberg 1975; Snow 1981a, b), and tinker barbets are the main dispersers of *Viscum* in Africa (Frost 1980; Snow 1981a, b; Maclean 1993). Redfronted tinker barbets were present in the bush-pockets, and it is likely that they are largely responsible for the dispersal of *V. obscurum* in the dune field. Few mammals in the bush-pockets were found to eat *V. obscurum,* the exception being monkeys (Table 2).

### *Comparison of birds and mammals*

Birds and mammals showed extensive overlap in the plant species that were dispersed, which is similar to situations elsewhere (Janson 1983; Knight & Siegfried 1983; Gautier- Hion et al. 1985). However, mammals as a whole dispersed seeds of a greater diversity of plant species than did birds. Although the importance of birds in the functioning of the dune field appears redundant given that mammals disperse all seeds dispersed by birds but not *vice vers*a, birds could disperse seeds to different germination sites. Birds also appear to disperse a different suite of seeds to mammals. Seeds of *E. capensis, C. baccifera, L. afrum, Chenopodium* spp. and *Emex australis*, as well as large numbers of *Carpobrotus deliciosus* and *Opuntia ficus indica* seeds were dispersed exclusively by mammals, while birds dispersed markedly more seeds of *R. crenata, A cyclops, M. cordifolia, C. monilifera* and *V. obscurum*.

The efficacy of dispersal could vary considerably among birds and mammals. As mentioned previously birds disperse the majority of seeds intact whereas mammals disperse higher proportions of broken seeds. However, this could be influenced by the size ranges of seeds consumed by both birds and mammals. The assessment of the relative importance of mammals and birds as dispersal agents is complicated as Willson (1993) has shown, due to the lack of quantitative data describing seed shadows (patterns of seed dispersal away from the parent plant) created by terrestrial mammals. Seed retention times could significantly alter dispersal quality with seeds often being retained for longer periods in the gut of mammals than in birds. Establishment success too could be enhanced from bird faeces, as there are fewer seeds per faecal bolus, ultimately reducing potential competition between seedlings. Although undocumented, it is possible that mammals and birds produce different patterns of seed distribution and seedling recruitment (Willson 1993). Undoubtedly however, both birds and mammals are crucial to the seed dispersal dynamics within this fragmented ecosystem.

### *Dispersal and phenology*

Disperser populations may respond to the presence and availability of fruits (D'Antonio 1990). In the present study those species of plants consumed by mammals and birds showed extended fruiting seasons, thereby allowing for maximal removal and dispersal. Staggered fruit production by both bush-pocket and thicket species allows fruit to be presented to potential dispersers throughout the year while reducing competition with other plant species for dispersers (McKey 1975; Thompson 1981). Dispersal efficacy could be related to the production potential of the zoochorous plant species from the thicket. Liversidge (1972) recorded considerable monthly and yearly variation in fruit production (quantitative and qualitative) of coastal thicket species which could be correlated with prevailing climatic conditions. Although no data are available for fruit production from the sclerophyllous thicket behind the dune field, this could influence the seed dispersal dynamics of the area considerably. The availability of fruit has previously been shown to dictate the overall use of fleshy fruits by birds (Knight 1988).

Changes in the vegetation structure and composition are coupled to increases in bush-pocket size. *Myrica cordifolia* and *S. plumosa* dominated smaller pockets, while *M. muricata, R. crenata, P. rigida* and *C. monilifera,* became more dominant in the western half of the larger bush-pockets representing an older successional vegetation stage (Brown 1990). A larger number of climax woody thicket species *(E. racemosa, S. myrtina, S. inerme* and *Acokanthera oblongifolia*) were found as pocket size increased. Bush-pocket origin could therefore be a result of the colonization of dune hollows by wind dispersed plants, which then attract dispersers to the area, resulting in greater plant species richness and successional development.

If dispersers are indeed being attracted to the bush-pockets, this would imply that dispersal is directional. This hypothesis is supported by our findings. Markedly higher numbers of bird dispersed seeds were found within bush-pockets than outside pockets. This is to be expected, as birds characteristic of the thicket are more likely to frequent the bush-pockets than the open dunes, particularly frugivorous birds. Recruitment foci serve as the centre of establishment and subsequent growth of bird-dispersed species into areas, and these foci eventually form patches or clumps of vegetation that are unique (in both structure and composition) from the surrounding matrix of vegetation (McDonnell & Stiles 1983). Bird activity was concentrated both on flight lines between the thicket and the pockets as well as directly between pockets (Brown 1990) and has been shown to be responsible for directional patterns of seed dispersal (Howe & Primack 1975). This directional dispersal hypothesis is further supported by the mammal data. Even though bush-pockets make up only 3.2% of the total surface area of the dune field (McLachlan et al. 1982), 86% of the faeces were deposited in the bush-pockets.

## Conclusion

The large mammal fauna and birds of the Alexandria Coastal Dunefield appear to be critical for the maintenance of the bush-pocket vegetation communities. With over 23 million apparently viable seeds being transported into and within the dune field each year, together with over 10 tons of organic nutrients, it would appear that seeds dispersed in this way would have a distinct advantage over those transported by other means. The establishment of climax woody plant species *(E. racemosa, A. oblongifolia, S. inerme, S. myrtina, C. compressum, P. tricuspidatus, A. cyclops, R. glauca*) depends on whether the seeds are deposited in favourable sites for germination. The bush-pockets and aeolianite outcrops associated with these serve as foci for vertebrate dispersal agents and seeds voided in faeces in these areas could have a greater germination potential. Dispersal by mammals and birds to these focal areas lends support to the hypothesis that dispersal of climax plant species could be responsible for the maintenance and possible origin of the bush-pockets.

The Alexandria Coastal Dunefield, and other structurally similar coastal dune fields, therefore act as interlinked ecosystems with the associated subtropical thicket vegetation to the landward side. The adjacent thicket forms an integral component in the continued existence of the bush-pocket environment in that it provides both a sustainable seed source as well as suitable habitat for a variety of mammalian and avian zoochores. In order to effectively ensure the continued functioning of ecological processes (zoochory) with ongoing deterioration of the surrounding natural areas through habitat loss and local species extinction it is imperative that management of private properties adjacent to the dunefield allow for the maintenance of the plants and their dispersers. Protected area management plans for small or isolated reserves should incorporate collaborative conservation action beyond the reserve boundaries to enhance regional biodiversity.

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*For App. 1, see next page*.

**App. 1.** Plant species for which fruiting and flowering phenology were recorded from the bush-pockets and thicket. + denotes presence in either habitat type and whether seeds were recovered from avian and mammalian faeces.

| Species | Pocket | Thicket | Recovered from faeces |
|---|---|---|---|
| *Senecio littorosus* | + | | |
| *Myrica cordifolia* | + | | + |
| *Helichrysum cymosum* | + | | |
| *Asclepias physocarpa* | + | | |
| *Anthospermun littoreum* | + | | |
| *Stoebe plumosa* | + | | |
| *Cynanchium natalitium* | + | | |
| *Zalusianskya maritima* | + | | |
| *Passerina rigida* | + | + | |
| *Nylandtia spinosa* | + | + | + |
| *Rhus crenata* | + | + | + |
| *Helichrysum sordescens* | + | + | |
| *Metalasia muricata* | + | + | |
| *Carpobrotus deliciosus* | + | + | + |
| *Viscum obscurum* | + | + | + |
| *Acacia cyclops* | + | + | + |
| *Brachylaena discolor* | + | + | |
| *Colpoon compressum* | + | + | + |
| *Chironia baccifera* | + | + | + |
| *Rhynchosia carribaea* | + | + | |
| *Chrysnathemoides monilifera* | + | + | + |
| *Eugenia capensis* | + | + | + |
| *Felicia echinata* | + | + | |
| *Protoasparagus racemosus* | + | + | + |
| *Sideroxylon inerme* | + | + | + |
| *Rhus glauca* | + | + | + |
| *Acokanthera oblongifolia* | + | + | |
| *Euclea racemosa* | + | + | + |
| *Scutia myrtina* | + | + | + |
| *Agathosma apiculata* | | + | |
| *Agathosma ovata* | | + | |
| *Polygala fruticosa* | | + | |
| *Pterocelastrus tricuspidatus* | | + | + |
| *Rapanea gilliana* | | + | |
| *Olea exasperata* | | + | + |
| *Muraltia squarosa* | | + | |
| *Erica choroloma* | | + | |
| *Protoasparagua suavolens* | | + | |
| *Scotia afra afra* | | + | |
| *Azima tetracantha* | | + | + |
| *Cotyledon sp.* | | + | |
| *Zygophyllum morgsana* | | + | |
| *Rhus longispina* | | + | |
| *Carissa bispinosa* | | + | |
| *Viscum rotundifolium* | | + | |
| *Lycium afrum* | | + | + |