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Nest-site partitioning in a strandveld shrubland bird community

Dianah Nalwanga[1], Penn Lloyd[1,2]*, Morné A du Plessis[1] and Thomas E Martin[2]
[1] Percy FitzPatrick Institute of African Ornithology (DST/NRF Centre of Excellence), University of Cape Town, Rondebosch 7701, South Africa
[2] Montana Co-operative Wildlife Research Unit, University of Montana, Missoula, MT59812, United States of America
* Corresponding author, e-mail: plloyd@botzoo.uct.ac.za

Nest-site selection may vary adaptively among co-existing species as a result of competitive interactions among the species or in response to density-dependent nest predation. We examined nest-site characteristics and degree of partitioning among 14 co-existing bird species breeding in dwarf strandveld shrubland at Koeberg Nature Reserve, South Africa. Habitat characteristics of nest sites differed significantly among species, indicating strong nest-site partitioning. The principal variables distinguishing nest-site characteristics among species (substrate height, cover at 1m, cover at 2m) were features that distinguish tall-shrub species which are strongly associated with patches of Dune Thicket from shorter-shrub species which are strongly associated with more open Sand Plain Fynbos. Two groups of species which differ primarily in their selection of habitat patch type within the patchy nesting landscape were identified. One group nested predominantly in low shrubs associated with open Sand Plain Fynbos. A second group nested at a variety of heights within tall-shrub species associated with Dune Thicket. Species within each of these groups differed from each other in their relative nest height (ratio of nest height to substrate height), distance of nest from foliage edge, nest concealment and choice of particular substrate plant species. On average, stepwise discriminant function analysis classified 52.6% of the nest sites correctly as belonging to one of the 14 species, considerably better than the expected random classification of 11.8%. Individual species' classifications were 2–12 times better than a random classification. We suggest that high levels of nest predation may have selected for strong nest-site partitioning in this community.

Introduction

The structuring of bird species assemblages has been explained by competition for food (Wiens 1989, Martin 1995), by the partitioning of nest sites among co-occurring species in response to density-dependent nest predation (Connell 1975, Reitsma and Whelan 1999), or by abiotic influences on the differing physiological tolerances of co-existing species (James *et al*. 1984, Wiens 1989, Martin 2001). These ideas remain both influential and attractive in trying to understand the factors that may have led to the observed patterns of resource partitioning among co-existing species.

Nest sites are a resource that has important fitness consequences for birds. Nest-site selection may be influenced by a variety of factors, including nest predation risk, physiological tolerances to abiotic factors (Martin 2001) and inter-specific competition (MacArthur 1972, Diamond 1978, Martin and Martin 2001). The responses of different species to these selective agents will likely differ due to differences in morphology, physiology and behaviour among species. Nest predation is the major cause of reproductive loss in most land birds (Martin 1988a, 1988b), especially in southern Africa (Lloyd *et al*. 2000, Muchai 2002). It is therefore considered the strongest selective force in nest-site selection. Nest predation may be avoided or minimised in at least two ways: (1) by individual birds selecting cryptic or safer nest sites, and (2) by scattering nests in space or time to reduce potential density-dependent predation (Reitsma and Whelan 1999). Species are expected to diverge in their nest placement to avoid density-dependent predation as a result of the development by predators of clearly-defined search images (Ford 1999, Barber *et al.* 2001). This latter mechanism, generated by the effects of shared predators among co-occurring species, has been referred to as the concept of 'competition for enemy-free space' (Jeffries and Lawton 1984). Although this concept implies direct interspecific competition, it need not be so. This is because density-dependent predation in a multi-dimensional nesting niche space may independently select for nest-site partitioning among co-existing species over evolutionary time in the absence of costs associated with direct inter-specific competition (James *et al.* 1984).

The intensity of predation may influence the relative abundance of co-existing species, the degree of overlap and the intensity of competition between competing species (Holt 1984). For this reason, most birds select nest sites that reduce the probability of clutch predation. In this study, we examine nest-site selection and whether there is nest-site partitioning among 14 ground- and shrub-nesting species in a breeding-bird community.

Study area and methods

Study area

The study was conducted within a 1.7km^2 area in the 3 000ha Koeberg Nature Reserve (33°41'S, 18°27'E), Western Cape Province, South Africa. It has a Mediterranean climate with hot, dry summers (October–April) and cool, wet winters (May–September). The vegetation is dwarf shrubland (up to 3m tall), comprising a diffuse mosaic of Dune Thicket and Sand Plain Fynbos vegetation types (Low and Rebelo 1996) on a low-lying coastal plain. The vegetation is in a mature state, having not been burned for at least 20 years. Taller shrubs, often aggregated into thicket patches, especially on dune slopes (Dune Thicket), are dispersed within a more open, shorter shrubland (Sand Plain Fynbos). Plant species primarily associated with Dune Thicket included *Olea exasperata, Euclea racemosa, Rhus glauca, R. lucida*, *Putterlickia pyracantha, Euphorbia mauritanica, Pterocelastris tricuspidatus*, *Zygophyllum morgsana*, and tall restios (Restionaceae). Because of their strong association with thicket proper, we label even isolated individual plants of the above-mentioned species as constituting 'patches' of Dune Thicket. Plant species primarily associated with Sand Plain Fynbos included *Chrysanthemoides incana, Helichrysum revolutum*, *Passerina vulgaris, Eriocephalus racemosus, Senecio halimifolius, Rhus laevigata, Nylandtia spinosa, Salvia africana-lutea, Phylica stipularis*, *Carpobrotus acinaciformis,* shorter restios, and a variety of herbs and grasses.

Study species

The 14 study species were a subset (based on sample size of nests) of the ground- and shrub-nesting species constituting the terrestrial (i.e. non-wetland) breeding-bird community in Koeberg Nature Reserve. These species were Cape Bulbul (*Pycnonotus capensis*), Cape Robin (*Cossypha caffra*), Karoo Robin (*Erythropygia coryphoeus*), Chestnut-vented Titbabbler (*Parisoma subcaeruleum*), Grassbird (*Sphenoeacus afer*), Karoo Prinia (*Prinia maculosa*), Grey-backed Cisticola (*Cisticola subruficapilla*), Bar-throated Apalis (*Apalis thoracica*), Long-billed Crombec (*Sylvietta rufescens*), Lesser Double-collared Sunbird (*Nectarinia chalybea*), Cape White-eye (*Zosterops pallidus*), Bokmakierie (*Telophorus zeylonus*), and Cape Bunting (*Emberiza capensis*), all of which defended breeding territories, and the non-territorial Yellow Canary (*Serinus flaviventris*). Average territory sizes ranged from 1.2ha for Karoo Prinia to 30ha for Bokmakierie (P Lloyd, unpubl. data). Other species recorded nesting at lower density include Red-faced Mousebird (*Uricolis indicus*), Speckled Mousebird (*Colius striatus*), White-backed Mousebird (*Colius colius*), Cape Penduline Tit (*Anthoscopus minutus*), Layard's Titbabbler (*Parisoma layardi*), Fiscal Shrike (*Lanius collaris*), Malachite Sunbird (*Nectarinia famosa*), Yellow-rumped Widow (*Euplectes capensis*), White-throated Canary (*Serinus albogularis*) and Cape Sparrow (*Passer melanurus*). The breeding territories of most individuals studied incorporated areas of shorter shrubland and shrub-thicket patches, meaning they had access to the full range of nest-site microhabitats.

Data collection procedures

The study was conducted during the breeding season (August–November 2002). Nests were located using parental behaviour, usually during the building stage, and monitored at 1–3 day intervals thereafter to determine nest fate. After termination or completion of the nest attempt, nest-site variables were measured at two spatial scales: (1) at the nest site, and (2) within the nest patch. The nest site was defined as that area within a 1m radius of the nest, whereas the nest patch was that area within a 5m radius of the nest.

Nest-site variables

Nest-site variables we measured included: (1) substrate type (e.g. plant species, grass or ground), (2) nest height above ground, determined using a measuring stick (zero for ground nests), (3) substrate or plant height, (4) distance of nest from lateral edge of foliage, and (5) nest concealment. Concealment was determined by estimating the percentage of the nest visible 1m from the nest at nest height in the four cardinal directions, and from 1m above the nest.

Nest-patch variables

Nest-patch variables included nest-patch heterogeneity (number of plant species in the nest patch), and percentage plant cover at each of four height intervals (10cm, 50cm, 100cm, 200cm) along each of eight, evenly spaced 5m radii centred on the nest. These eight measurements were averaged for each height interval. Using a 5m length of string strung between two vertical poles, percent cover was estimated as the proportion of the string that was surrounded by vegetation within 5cm of each height interval. Percent cover was estimated separately for each plant species, and the total number of these species (at all radii) provided the estimate of nest-patch heterogeneity.

Data analysis

Habitat variables were analysed using correlation analysis to reduce the number of variables. Among the nest-site variables, nest height was correlated with nest-plant height ($r = 0.77$, $P < 0.05$), so these were combined to produce a new variable, relative nest height (ratio of nest height to nest-plant height). This new variable was correlated with nest height ($r = 0.57$, $P < 0.05$) but not with nest-plant height, so nest height was excluded from the analysis. The five measurements of concealment (from the four cardinal directions and from above) were correlated with each other, so the average for this was used in the analysis. All five nest-patch variables were included in the analysis (nest-patch heterogeneity and the four measures of vegetation cover).

Univariate analysis of variance, entering species as a fixed factor and habitat variable as a dependent variable, repeated for each of 10 habitat variables (nest height, nest-plant height, relative nest height, distance to lateral foliage edge, average nest concealment, cover at each of four height intervals, and nest-patch heterogeneity), was used to test for overall differences among the nest sites of the 14 species. Habitat variables that discriminated between species were identified using Stepwise Discriminant Function Analysis (SDFA). Wilks' Lambda and F-tests were used to determine the combination of variables providing the best group separation. Co-variance matrices were tested for homogeneity using Box's *M* criterion. The between-group matrices often showed significant heteroscedasticity ($P < 0.05$). Consequently, we based the SDFA on pooled within-group co-variance matrices. Mahalanobis distance (minimum D^2) between group centroids was used as the criterion for maximising separation of the species. Standardised co-efficients were obtained from SDFA to determine the partial contributions of each variable to the discriminant function. Factor structure co-efficients determined correlations of variables with the discriminant functions. Means of canonical variables were used to determine the groups best identified (discriminated) by the discriminant function.

The discriminant function analyses included dummy variables representing the nest-plant species or substrate type in which the nest was placed in or under. Habitat variables used in the SDFA analysis were: nest-plant height, nest-plant species, relative nest height, nest distance from plant foliage edge, average concealment, nest-patch heterogeneity and the average percentage vegetation cover at the four height intervals.

All analyses were performed using the STATISTICA software version 6 (Statsoft Inc. 2002). Means are presented ± standard deviations. Significance levels were set at $P < 0.05$ for all analyses. Percentage data were arcsine-transformed to meet assumptions of normality.

Results

Comparison of nest-site characteristics among bird species

Nest height, nest-plant height, and relative nest height

Although there was broad overlap among individual species along the gradient of available nest heights, nest heights differed significantly ($F_{13} = 37.8$, $P < 0.001$) among the species (Figure 1). At the two extremes, the Karoo Robin, Grassbird, Grey-backed Cisticola, Cape Bunting and Cape Robin nested relatively low (mean nest height 0.18–0.51m), whereas the Cape Bulbul, Lesser Double-collared Sunbird and the Cape White-eye nested relatively high (mean nest height 1.02–1.65m). The remaining species nested at intermediate heights.

The heights of the plants in which the nests were placed in, or under, also differed significantly among the species ($F_{13} = 25.4$, $P < 0.001$), although there was overlap among individual species (Figure 2). The Karoo Robin, Grassbird, Grey-backed Cisticola and Cape Bunting usually nested in relatively short plants (mean nest-plant heights 0.64–0.91m), whereas the Long-billed Crombec, Cape Bulbul, Lesser Double-collared Sunbird and the Cape White-eye nested most frequently in tall plants (mean nest-plant heights 1.66–2.18m). The rest of the species usually nested in plants with intermediate heights.

The species differed significantly in the relative heights at which they placed their nests ($F_{13} = 12.0$, $P < 0.001$; Figure 3). Nests of Cape White-eye, Yellow Canary, Karoo Prinia, Lesser Double-collared Sunbird and Bar-throated Apalis were usually placed towards the top of nest plants (mean relative height >0.65m). Grassbird, Karoo Robin and Long-billed Crombec usually nested within the lower half of nest plants, with the remainder of species at intermediate relative heights.

Distance of the nest from lateral foliage edge

Although most of the species were generalists, nesting at a wide range of distances from the lateral edge of plant foliage, there were significant differences in the distances from the edge at which the different species placed their nests ($F_{13} = 6.24$, $P < 0.001$; Table 1). Cape Bunting, Grey-backed Cisticola, Karoo Robin, Yellow Canary, Grassbird, and Bar-throated Apalis often nested near the lateral edge of

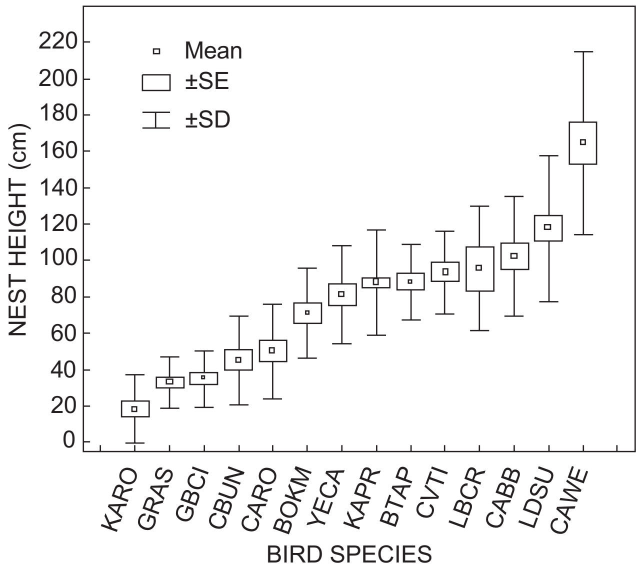

Figure 1: Comparison of nest heights among 14 bird species breeding in Koeberg Nature Reserve (ANOVA $F = 37.8$, $P < 0.001$). KARO = Karoo Robin, GRAS = Grassbird, GBCI = Grey-backed Cisticola, CBUN = Cape Bunting, CARO = Cape Robin, BOKM = Bokmakierie, YECA = Yellow Canary, KAPR = Karoo Prinia, BTAP = Bar-throated Apalis, CVTI = Chestnut-vented Titbabbler, LBCR = Long-billed Crombec, CABB = Cape Bulbul, LDSU = Lesser Double-collared Sunbird, CAWE = Cape White-eye.

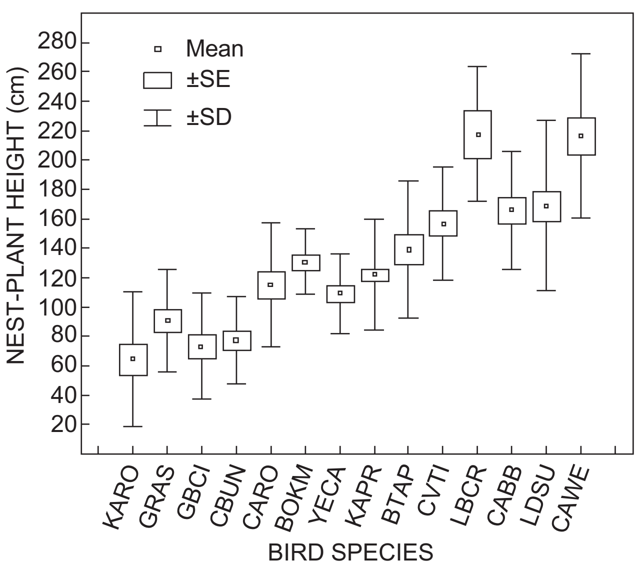

Figure 2: Comparison of nest-plant heights among 14 bird species (ANOVA $F = 25.4$, $P < 0.001$). Species abbreviations as in Figure 1.

plant foliage (mean distances 0.22–0.37m), whereas Cape White-eye and Long-billed Crombec nested in locations far away from the lateral foliage edge (mean distances 1.07–1.47m).

Concealment of the nest

Generally, there was little variation in nest concealment, since most species had mean concealment ranging from 30–55% (Figure 4). However, nest concealment in the immediate vicinity of the nest was significantly different among the species (F_{13} = 9.29, P < 0.001). Long-billed Crombec nests are clearly outliers, in that they are by far the least concealed (mean concealment = 8%). By contrast, Grassbird, Bokmakierie and Yellow Canary stand out as having the most concealed nests (mean concealment 64–76.4%). Because all species studied were nesting concurrently, and most nests were sited in mature, evergreen perennials, differences in nest concealment were not due to time of season.

Nest-plant species (substrate type)

In general, all birds used a range of plant species as nesting substrates (Appendix 1). However, the subset of substrate types chosen differed among the 14 bird species (Figure 5). One group of species (Cape Bulbul, Bar-throated Apalis, Cape White-eye, Chestnut-vented Titbabbler, Long-billed

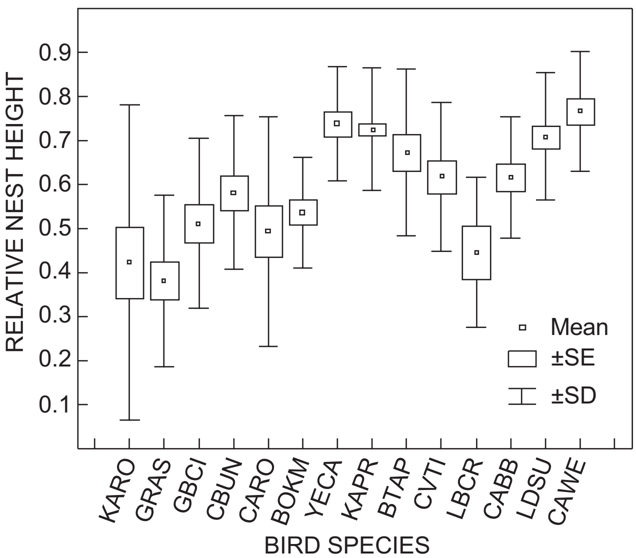

Figure 3: Comparison of relative nest heights among 14 bird species (ANOVA F = 12.0, P < 0.001). Species abbreviations as in Figure 1

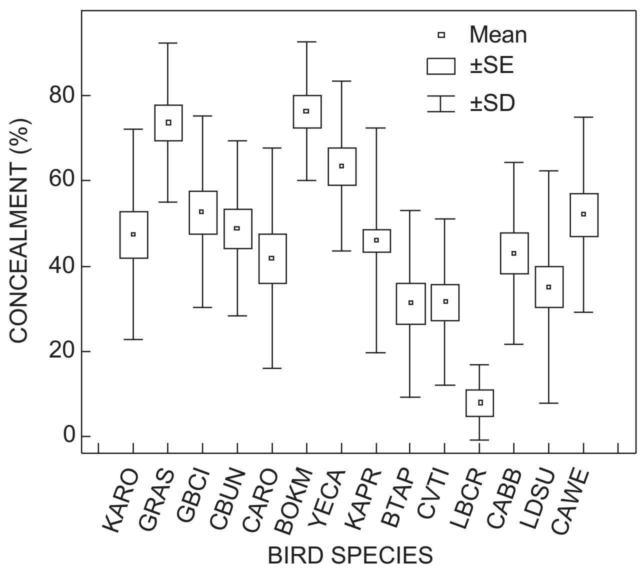

Figure 4: Comparison of average nest concealment among 14 bird species (ANOVA F = 9.29, P < 0.001). Species abbreviations as in Figure 1

Table 1: Means ± SD of nest-patch heterogeneity (total number of shrub species within a 5m radius of the nest), average nest-patch vegetation cover at four height intervals and distance of nest from lateral foliage edge (NDE) for the nest sites of 14 species. Nest sample size in parentheses

Variable	Nest-patch heterogeneity	Cover at 10cm (%)	Cover at 50cm (%)	Cover at 100cm (%)	Cover at 200cm (%)	NDE (cm)
Karoo Robin (20)	5.9 ± 2.4	55.2 ± 20.3	37.9 ± 19.1	6.2 ± 7.9	0.0 ± 0.0	32.8 ± 59.5
Cape Bunting (20)	4.6 ± 1.7	70.8 ± 9.9	53.6 ± 20.1	9.9 ± 13.6	0.0 ± 0.0	22.7 ± 10.4
Grey-backed Cisticola (20)	4.4 ± 1.7	60.8 ± 15.8	29.7 ± 22.6	3.9 ± 6.4	0.0 ± 0.0	24.9 ± 27.3
Grassbird (20)	4.5 ± 1.5	73.0 ± 14.7	49.3 ± 18.6	6.8 ± 8.7	0.5 ± 1.7	36.1 ± 23.0
Yellow Canary (22)	4.5 ± 1.3	64.5 ±17.7	49.2 ± 21.3	15.3 ± 15.1	0.0 ± 0.0	35.0 ± 26.0
Bokmakierie (20)	4.1 ± 1.4	69.1 ± 13.3	50.8 ± 21.2	20.2 ± 21.1	0.1 ± 0.6	79.7 ± 51.4
Cape Robin (20)	5.4 ± 2.1	54.7 ± 21.2	49.6 ± 26.7	21.4 ± 20.5	0.4 ± 0.8	52.5 ± 66.2
Bar-throated Apalis (21)	5.7 ± 2.4	59.4 ± 17.6	61.4 ± 15.6	31.4 ± 14.9	2.7 ± 7.7	36.7 ± 31.3
Chestnut-vented Titbabbler (20)	4.5 ± 1.9	72.4 ± 17.2	69.9 ± 15.4	31.2 ± 20.6	2.8 ± 10.7	90.3 ± 64.8
Karoo Prinia (99)	5.2 ± 1.6	68.0 ± 14.9	56.3 ± 19.5	17.9 ± 19.6	1.6 ± 7.7	50.2 ± 46.0
Cape Bulbul (20)	4.5 ± 1.4	80.3 ± 8.6	81.6 ± 11.0	50.6 ± 24.8	6.8 ± 17.4	92.3 ± 61.2
Lesser Double-collared Sunbird (33)	5.3 ± 1.7	62.7 ± 17.8	60.7 ± 23.1	31.4 ± 27.8	6.4 ± 16.3	75.3 ± 90.9
Cape White-eye (20)	4.7 ± 2.0	74.4 ± 18.7	73.4 ± 17.9	51.8 ± 26.1	16.2 ± 18.7	107.2 ± 105.8
Long-billed Crombec (8)	2.9 ± 2.0	59.7 ± 11.6	71.8 ± 17.3	62.0 ± 29.8	35.4 ± 48.1	146.9 ± 104.4
ANOVA F	3.0	8.2	6.4	2.8	1.8	6.2
P	<0.001	<0.001	<0.001	<0.001	0.04	<0.001

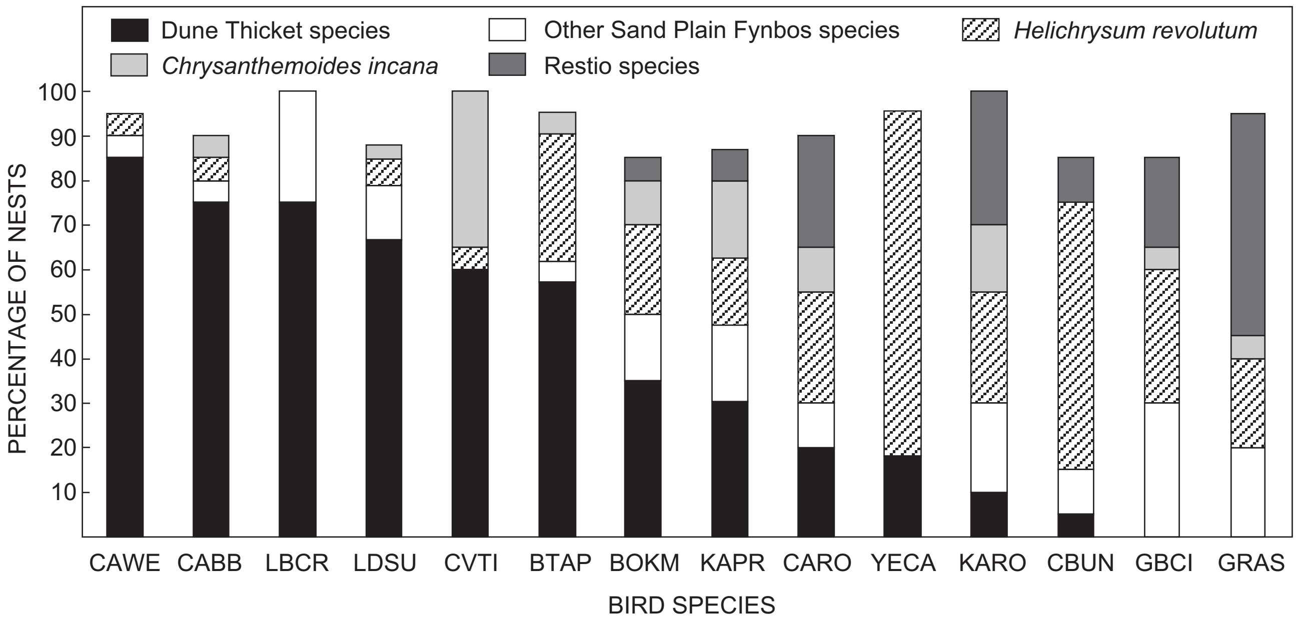

Figure 5: Percentage of nests of 14 bird species placed in plant species associated with either Dune Thicket (thicket species), or Sand Plain Fynbos (*Chrysanthemoides incana*, *Helichrysum revolutum*, restios and other short-shrubland plants). Species abbreviations as in Figure 1

Crombec and Lesser-Double-collared Sunbird) nested predominantly in tall-shrub species that are primarily associated with Dune Thicket, but also grow as isolated plants scattered in Sand Plain Fynbos. A second group (Grey-backed Cisticola, Grassbird, Cape Bunting, Cape Robin, Bokmakierie, Karoo Prinia and Yellow Canary) nested predominantly in plant species associated with the shorter, open Sand Plain Fynbos. A few species exhibited a strong preference for particular nest-plant species within each vegetation type. For example, Cape Bunting and Yellow Canary usually selected *Helichrysum revolutum* (60% and 77.3% of nests), whereas the Grassbird usually selected restios (50% of nests).

Comparison of nest-patch variables between species

Vegetation cover

Vegetation cover at all four height intervals was significantly different among the nest sites of species ($F_{13} > 1.8$, $P < 0.04$ for all heights). Species that typically nested in plant species associated with the taller Dune Thicket (Long-billed Crombec, Cape White-eye, Cape Bulbul, Lesser Double-collared Sunbird, Chestnut-vented Titbabbler and Bar-throated Apalis) had relatively high mean vegetation cover at the 100cm and 200cm height intervals (Table 1). Species that typically nested in plant species associated with the more open, shorter Sand Plain Fynbos shrubland (Grey-backed Cisticola, Karoo Robin, Grassbird and Cape Bunting) had low vegetation cover at these heights.

Nest-patch heterogeneity

Although there was little variation among most species, nest-patch heterogeneity was significantly different among the 14 species ($F_{13} = 3.0$, $P < 0.001$). The Long-billed Crombec was the outlier, with low nest-patch heterogeneity (mean 2.9), largely because it typically nested within particularly large shrubs that occupy most of the cover around the nest patch.

Nest-site partitioning among the species

No two species nested in sites that were consistently similar across the range of habitat variables considered, indicating that all species differed somewhat in overall nest-site characteristics. SDFA yielded seven significant canonical axes that differentiated nest sites of the different species ($X^2 > 45.6$, $P < 0.02$ for all axes; Mahalanobis: $F > 1.7$, df = 10.340, $P < 0.05$ for all pair-wise comparisons except for that between Grey-backed Cisticola and Cape Buntings, where $P > 0.06$). Three non-significant canonical axes were also produced ($P > 0.09$ for all three axes).

The first significant canonical axis was the most important in the discrimination of the 14 species (Eigenvalue = 1.66, Wilks' lambda = 0.108, $X^2 = 780.2$, $P < 0.001$). The variables that contributed most to this axis (viz. those that had high standardised co-efficients, and usually with high factor co-efficients) included (in order of importance) substrate or nest-plant height, relative nest height, vegetation cover at 1.0m and 2.0m above ground, substrate type and concealment (2).

Generally, nest sites were correctly classified by SDFA more frequently than not, with overall classification success of 52.6%, markedly better than a random classification of 11.8% (3). Among individual species, the classification was 2–13 times better than a random classification (Table 3). Among species with a higher frequency of misclassifications, Lesser Double-collared Sunbird nests were misclassified as Cape Bulbul and Cape White-eye at 2–3 times the expected rate; Cape Bulbul nests were misclassified as Cape White-eye, Lesser Double-collared Sunbird and Bar-

Table 2: Standardised co-efficients for canonical variables and factor structure co-efficients (pooled within-group correlations) for the first canonical root (axis) discriminating between the nest sites of 14 species. Variables are listed in the order in which they were entered into the SDFA model

Variables	Wilks' partial lambda	P	Co-efficients for Root 1 Standardised	Co-efficients for Root 1 Factor structure
Substrate height	0.564	0.000	–0.892	–0.706
Relative nest height	0.631	0.000	–0.650	–0.378
Concealment	0.765	0.000	0.170	0.215
Cover at 10cm	0.824	0.000	0.058	0.049
Nest-plant species	0.859	0.000	–0.183	–0.216
Cover at 50cm	0.880	0.000	–0.041	–0.068
Patch heterogeneity	0.911	0.002	–0.126	0.008
Distance from edge	0.941	0.075	–0.051	–0.278
Cover at 100cm	0.947	0.134	–0.207	–0.094
Cover at 200cm	0.950	0.166	0.188	0.051

Eigenvalue = 1.66

throated Apalis at twice the expected rate; Cape Robin nests were misclassified as Cape Bunting at three times the expected rate; Grey-backed Cisticola nests were misclassified as Cape Bunting, Cape Robin and Grassbird at 2–3 times the expected rate, and Chestnut-vented Titbabbler nests were misclassified as Cape Bulbul and Bar-throated Apalis at twice the expected rate. All the variables included in the analysis were recognised by SDFA as being important in the discrimination of the 14 species. However the variables that were significantly important ($P < 0.05$) in the classification of the species included substrate or nest-plant height, relative nest height, concealment, vegetation cover at 0.1m above ground, substrate type or nest-plant species, vegetation cover at 0.5m above ground and nest-patch heterogeneity (Table 2).

Discussion

Although there was broad overlap among bird species in each of the nest-site habitat variables considered in this study (Figures 1–5), the success of the SDFA in correctly classifying species (Table 3) provides strong evidence of nest-site partitioning in this community, given that all species had access to the full range of potential nest sites. Three of the four most important variables in the SDFA (substrate height, cover at 1m, cover at 2m) are features that distinguish plant species associated primarily with Dune Thicket (large, tall shrubs, often aggregated into thicket patches) from plant species associated with Sand Plain Fynbos (open, with shorter shrubs), suggesting species differ primarily in their selection of habitat patch for nesting in (Figure 5). Thus, there was one group of species (Cape White-eye, Cape Bulbul, Long-billed Crombec, Lesser Double-collared Sunbird, Bar-throated Apalis and Chestnut-vented Titbabbler) that nested mostly in plant species associated with Dune Thicket, and a second group of species (Bokmakierie, Cape Robin, Karoo Prinia, Yellow Canary, Karoo Robin, Grey-backed Cisticola, Grassbird and Cape Bunting) that nested mostly in plant species associated with open areas of Sand Plain Fynbos.

Relative nest height, substrate type and concealment were important for distinguishing sites within a patch (Table 2). Although there was less variation in the distance from the lateral foliage edge, nest concealment and the nest-patch heterogeneity among species, these characteristics also contributed to the differentiation of the nest sites by SDFA (Table 2). This suggests that all the variables considered in this analysis play some role in nest-site partitioning.

Among the species that nested most frequently in species associated with Dune Thicket, Long-billed Crombec usually selected locations in the relatively open centre (away from the edge) of very large shrubs or thicket patches. Unlike Bar-throated Apalis and Chestnut-vented Titbabbler, the rest of the species in this cluster rarely nested outside of species associated with Dune Thicket. When nesting outside of Dune Thicket, Bar-throated Apalis invariably nested in *Helichrysum revolutum*, whereas Chestnut-vented Titbabbler invariably nested in *Chrysanthemoides incana*. Cape White-eye and Cape Bulbul usually nested in the centre (away from the edge) of patches that are often more dense than those in which Lesser Double-collared Sunbird nested in. Cape White-eye nested in well-concealed positions just under or within the foliage crown, whereas Cape Bulbul nested lower within the plant.

Among species that nested low down in open areas of Sand Plain Fynbos, Cape Bunting usually nested within the edge of short shrubs, commonly in *Helichrysum revolutum*. Grassbird and Grey-backed Cisticola usually nested deeper within denser shrubs, in more concealed sites, whereas Karoo Robin usually nested in more open sites, occasionally on the ground, under old tree stumps.

Among the species that nested in plants of both vegetation types, nests for Yellow Canary were usually located in the crowns of dense *Helichrysum revolutum* shrubs in open shrubland, but were occasionally sited in the crowns of species associated with the thicket patches. By contrast, nest sites for Bokmakierie were usually within the centre of dense shrubs. Nest sites for Cape Robin and Karoo Prinia were usually placed in less dense shrub patches, with those of Cape Robin placed mid-way up the plant, whereas those of Karoo Prinia were generally placed higher up, towards the crowns of shrubs.

Table 3: Comparison of the predicted classification of nests to each of 14 species based on 10 nest-site and nest-patch variables *vs* a random classification based on sample size of nests for each species, using discriminant function analysis (based on separate co-variate matrices). The classification for each species is read across its row. Values in bold type indicate correctly classified nests for each species. Nest sample size in parentheses

	Predicted classifications													
Species	KARO	BOKM	CARO	CVTI	YECA	CABB	CBUN	GRAS	CAWE	LBCR	KAPR	LDSU	GBCI	BTAP
Karoo Robin KARO (20)	**45.0**	0.0	5.0	0.0	5.0	0.0	10.0	15.0	0.0	0.0	20.0	0.0	0.0	0.0
Bokmakierie BOKM (20)	0.0	**60.0**	5.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0	5.0
Cape Robin CARO (20)	5.0	0.0	**30.0**	0.0	0.0	5.0	15.0	10.0	0.0	0.0	25.0	0.0	5.0	5.0
Chestnut-vented Titbabbler CVTI (20)	0.0	0.0	0.0	**30.0**	0.0	10.0	5.0	0.0	0.0	0.0	40.0	5.0	0.0	10.0
Yellow Canary YECA (22)	4.5	0.0	0.0	0.0	**54.5**	0.0	0.0	0.0	0.0	0.0	40.9	0.0	0.0	0.0
Cape Bulbul CABB (20)	0.0	5.0	5.0	0.0	0.0	**25.0**	0.0	0.0	10.0	5.0	30.0	10.0	0.0	10.0
Cape Bunting CBUN (20)	5.0	0.0	10.0	0.0	5.0	0.0	**35.0**	5.0	0.0	0.0	25.0	0.0	15.0	0.0
Grassbird GRAS (20)	0.0	15.0	5.0	0.0	5.0	0.0	10.0	**55.0**	0.0	0.0	5.0	0.0	5.0	0.0
Cape White-eye CAWE (20)	0.0	5.0	0.0	0.0	5.0	0.0	0.0	0.0	**65.0**	5.0	10.0	10.0	0.0	0.0
Long-billed Crombec LBCR (8)	0.0	0.0	0.0	12.5	0.0	0.0	0.0	0.0	0.0	**62.5**	0.0	25.0	0.0	0.0
Karoo Prinia KAPR (99)	0.0	4.0	2.0	2.0	4.0	0.0	1.0	3.0	1.0	0.0	**78.8**	2.0	0.0	2.0
Lesser Double-collared Sunbird LDSU (33)	0.0	0.0	3.0	0.0	0.0	12.1	0.0	0.0	15.2	3.0	42.4	**21.2**	0.0	3.0
Grey-backed Cisticola GBCI (20)	5.0	0.0	10.0	0.0	0.0	0.0	15.0	10.0	0.0	0.0	30.0	0.0	**30.0**	0.0
Bar-throated Apalis BTAP (21)	0.0	0.0	0.0	0.0	0.0	0.0	4.8	0.0	4.8	0.0	19.0	4.8	0.0	**66.7**
Random classification (for all species)														
	5.51	5.51	5.51	5.51	6.06	5.51	5.51	5.51	5.51	2.2	27.3	9.09	5.51	5.79

Total correctly classified = 52.6% *vs* random classification = 11.8%

Species breeding at Koeberg experience unusually high nest predation pressure, with daily nest predation as high as 10.7%, and some pairs re-nesting up to 10 times during a three-month breeding season (Martin and Lloyd, unpubl. data). Although density-dependent predation in a multi-dimensional nesting niche space (not just three-dimensional space but also substrate type, distance from edge) could theoretically select for entirely random nest-site selection, differential nest-site selection among species is more likely to arise because of differences in species-specific morphology, physiology, behaviour and nest architecture, which ensure that each species is best adapted to a different type of nest site (James *et al.* 1984, Martin 1998). High, density-dependent nest predation pressure can thus select for limited overlap in nest-site characteristics among co-existing species as a mechanism to inhibit the development of a search image for nest sites of a particular type by a predator (Jeffries and Lawton 1984, Martin 1988b). However, density-dependent predation can also select for variation in nest-site characteristics within a species for the same reason. The extent of this variation is expected to depend on the relative abundance of that species to the total abundance of all other co-existing species. All the species considered in this study at Koeberg had large SDs for all nest-site variables (Table 1, Figures 1–4), suggesting their selection of a relatively wide range of nest sites. However, in the absence of good estimates of relative abundance of the nests of the various species, and the lack of an overall measure of nest-site variability, we cannot address these issues in this study.

Results from this study show that species in this community select sites that are generally different from co-existing species. Thus, because of the high density and diversity of breeding birds in this community, management practices should aim to retain as much structural and floristic diversity and patchiness in the vegetation of the reserve as possible. For example, the current approach of not clearing all shrubbery within powerline servitudes (opposite to the management of many servitudes outside of the reserve) is to be encouraged, given that such mechanical clearing dramatically reduces structural and floristic diversity. Only where servitudes cross habitats infested with alien invasive trees/shrubs is the mechanical clearing of these invasives to be encouraged.

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Appendix 1: The distribution of nests (percentage of total for each bird species) among each of the 22 plant species categories used as nest substrates differed significantly among the 14 bird species breeding in Koeberg Nature Reserve. Nest sample size in parentheses

Nest substrate	BOKM (20)	BTAP (21)	CABB (20)	CARO (20)	CAWE (20)	CBUN (20)	CVTI (20)	GBCI (20)	GRAS (20)	KAPR (99)	KARO (20)	LBCR (8)	LDSU (33)	YECA (22)
Chrysanthemoides incana	10.0	0.0	5.0	10.0	0.0	0.0	35.0	5.0	5.0	17.2	15.0	0.0	3.0	0.0
Cissampelos capensis	0.0	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
Eriocephalus racemosus	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0	5.0	5.1	0.0	0.0	0.0	0.0
Euphorbia mauritanica	10.0	4.8	5.0	10.0	0.0	0.0	10.0	0.0	0.0	8.1	5.0	0.0	3.0	4.5
Euclea racemosa	5.0	4.8	5.0	0.0	20.0	0.0	0.0	0.0	0.0	2.0	0.0	12.5	12.1	0.0
Grasses	0.0	0.0	0.0	0.0	0.0	5.0	0.0	20.0	15.0	0.0	0.0	0.0	0.0	0.0
Ground	0.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	15.0	0.0	0.0	0.0
Helichrysum revolutum	20.0	28.6	5.0	25.0	5.0	60.0	5.0	30.0	20.0	15.2	25.0	0.0	6.1	77.3
Metalasia muricata	0.0	0.0	5.0	0.0	5.0	5.0	0.0	0.0	0.0	4.0	0.0	0.0	3.0	0.0
Nylandtia spinosa	0.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0
Olea exasperata	0.0	9.5	15.0	0.0	30.0	0.0	10.0	0.0	0.0	7.1	0.0	37.5	21.2	0.0
Passerina vulgaris	10.0	0.0	0.0	0.0	5.0	0.0	0.0	5.0	0.0	3.0	5.0	0.0	6.1	0.0
Phylica stipularis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
Plecostachys serpyllifolia	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.0	9.1
Asparagus capensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	2.0	0.0	0.0	3.0	0.0
Putterlickia pyracantha	5.0	9.5	10.0	5.0	0.0	0.0	5.0	0.0	0.0	1.0	0.0	0.0	12.1	0.0
Restios	5.0	4.8	0.0	25.0	0.0	10.0	0.0	20.0	50.0	7.1	30.0	0.0	0.0	0.0
Rhus glauca	5.0	28.6	20.0	5.0	20.0	0.0	20.0	0.0	0.0	7.1	0.0	25.0	9.1	4.5
Rhus lucida	0.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.1	0.0
Rhus laevigata	5.0	0.0	15.0	0.0	0.0	0.0	15.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0
Senecio halimifolius	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	25.0	3.0	0.0
Unidentified	15.0	4.8	10.0	10.0	5.0	15.0	0.0	15.0	5.0	13.1	0.0	0.0	12.1	4.5

KARO = Karoo Robin, GRAS = Grassbird, GBCI = Grey-backed Cisticola, CBUN = Cape Bunting, CARO = Cape Robin, BOKM = Bokmakierie, YECA = Yellow Canary, KAPR = Karoo Prinia, BTAP = Bar-throated Apalis, CVTI = Chestnut-vented Titbabbler, LBCR = Long-billed Crombec, CABB = Cape Bulbul, LDSU = Lesser Double-collared Sunbird, CAWE = Cape White-eye