

Impacts of a South African coastal golf estate on shrubland bird communities

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Golf courses and estates are one form of development threatening coastal vegetation in South Africa's Cape Floristic Region. They occupy substantial tracts of land, fragmenting indigenous vegetation. This study investigates the effects on bird community structure and function of replacing natural Strandveld vegetation with a 170-ha golf estate in which 46 ha of Strandveld vegetation was retained in conditions ranging from pristine to moderately degraded. Bird assemblages of the remaining Strandveld patches in the golf estate were compared with those of an adjacent Strandveld conservation area. Field work was conducted during the birds' breeding season, in October and November 2005. The golf estate was more species rich overall, but many species were uncommon, several were present only as a consequence of the creation of new habitats, and species were not evenly distributed across the remaining Strandveld fragments. Bird diversity and abundance were significantly higher in the adjacent conservation area. It is estimated that more than 8500 individual birds were displaced by construction of the golf estate and four Strandveld species were not represented at all within the estate. Within the estate, species richness rose with increasing Strandveld patch size and the minimum area of continuous pristine vegetation required to maintain the natural species assemblage was estimated at 51 ha. The golf estate was characterized by a high proportion of generalist and granivorous species, but at the cost of reduced numbers of frugivores and nectarivores. Energy flow through the bird communities in the two areas was thus markedly different, and pollination and fruit dispersal potential within the golf estate were reduced substantially. Golf courses and golf estates inevitably will not substitute for the natural habitats they have replaced, but careful design with input from ecological theory can reduce the adverse effects of fragmentation.

Introduction

The Cape Floristic Region, one of the world's 34 terrestrial biodiversity hotspots,¹ is threatened by habitat loss from agriculture, rapid and intensive development and the spread of invasive alien species.^{2–6} All of these threats are predicted to intensify, a trend evident in other regions with Mediterranean-type climates.^{6,7}

Golf courses and golf estates are one such form of development that is increasing in the Cape Floristic Region, particularly in the coastal lowlands.⁸ This is a trend with potentially serious biodiversity implications because natural coastal vegetation is susceptible to fragmentation, largely because it occurs in a narrow band.^{8,9}

Environmental implications of the global 'golfing boom' (there are approximately 31 500 golf courses worldwide¹⁰) include habitat and species loss, high water consumption, excessive runoff and soil erosion, chemical contamination of soil, surface water and ground water, and peripheral urbanization.^{8,11,12} Golf courses on average occupy 50–60 ha,¹² while golf estates, which

include housing components, may be up to 1000 ha in extent.⁸ In the Western Cape province alone, which includes most of the Cape Floristic Region, there are 106 existing or approved golf courses/estates covering approximately 4888 ha, with an additional 6264 ha in the construction or planning phase (calculated from ref. 8).

A few studies have investigated the effects of golf courses on local biodiversity elsewhere in the world,^{10,12–18} but their findings have varied. Many have used birds as the taxon for study because bird diversity and distribution are strongly influenced by vegetation composition and structure.^{19,20} Furthermore, birds are considered to be useful indicators of biodiversity trends,^{21–25} not least because they play important ecological roles such as pollination and seed dispersal²⁶ and, on small scales (1–10 km) in particular, are expected to mirror the responses of some other taxa, such as butterflies.¹⁴

Most studies of the biodiversity impacts of golf estates/courses emanate from the northern hemisphere, where such developments can provide a habitat refuge for native species when sited within an agricultural or urban matrix. However, in comparison with natural habitats, golf courses are typically species poor.^{12–14} Although overall richness is comparable in some cases,¹² assemblages are not, with golf courses supporting more generalist species (urban exploiters) and fewer sensitive species (urban avoiders).¹³ Species richness can potentially increase in anthropogenically altered landscapes²⁷ due, for example, to encroachment of invasive and ecotonal species. However, species native to the area are more likely to decrease in diversity and/or abundance.^{28–31}

Where natural vegetation is replaced by a different land use, several consequences of altered land use can be predicted. These include isolation of fragments both from each other and from potential source pools, coupled with alteration in microclimates and increased risk of invasion.^{31,32} The severity of these impacts will depend on the size, shape and position of fragments, the nature of the matrix, the time since isolation and the degree of fragment connectivity.^{31,33,34} The distribution of birds in the landscape will also alter in response to changes in the distribution and abundance of resources such as food, water and nesting sites, which are predicted to change resource availability patterns in ways beneficial to some species and detrimental to others. Ultimately, changes in habitat and species composition are predicted to change patterns of energy flow through the system, which may have implications at several trophic levels.

This study compares the avian species assemblages of fragmented natural vegetation within a golf estate and an adjacent conservation area which represents the habitat that the golf estate replaced. Specifically, the study addresses the following questions. 1) Can a golf estate approximate the structure and function of the bird assemblages in the habitat it replaced; 2) how do habitat fragmentation and quality affect bird assemblages in the golf estate; 3) do different dietary guilds respond differently to the golf estate environment; and 4) are there implications for energy flow and hence ecological processes in the system?

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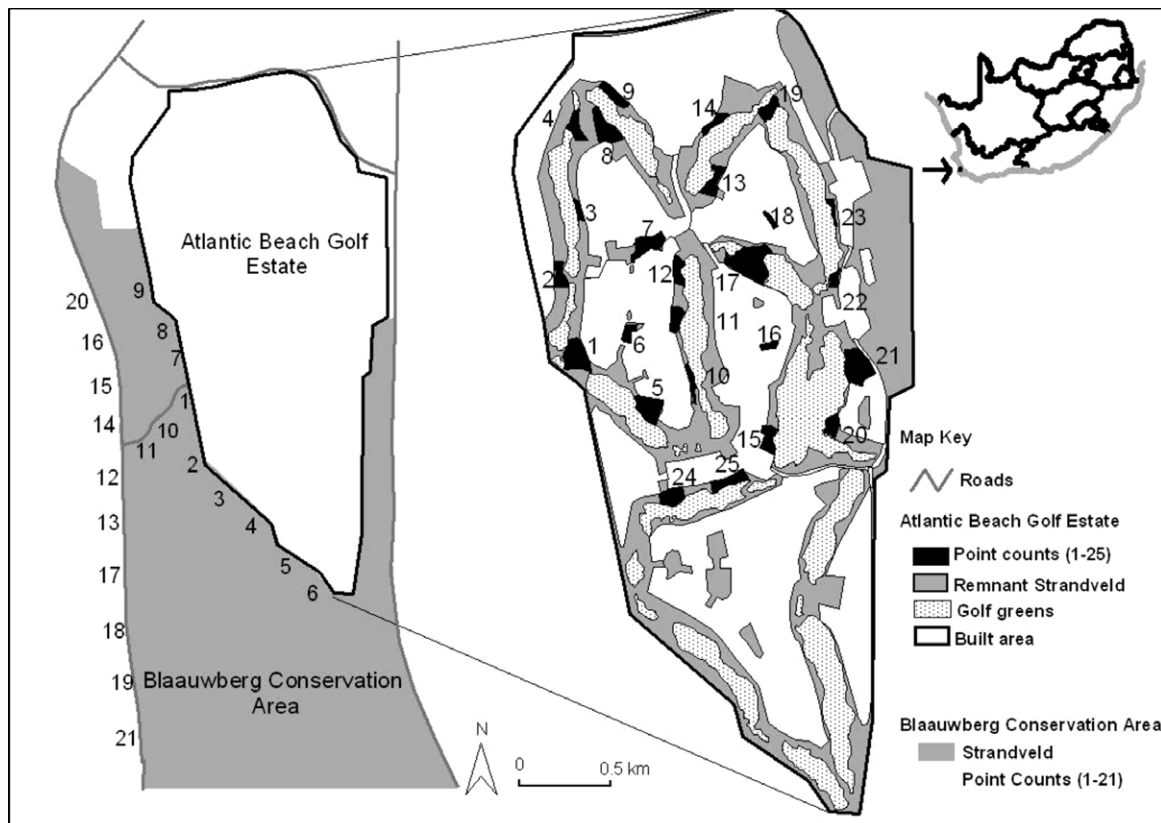


Fig. 1. Study area showing Atlantic Beach Golf Estate (outlined in black) nested within the northern section of Blaauwberg Conservation Area. Point count numbers are indicated for Atlantic Beach Golf Estate (1–25), with the fragment in black, and Blaauwberg Conservation area (1–21).

Study areas

The study sites were Blaauwberg Conservation Area (18°45'E, 33°77'S) and Atlantic Beach Golf Estate (18°45'E, 33°75'S), which lie adjacent to one another on the west coast of South Africa in the Western Cape province, 24 km north of Cape Town (Fig. 1). The climate is Mediterranean, with hot, dry summers (October–April) and cool, wet winters (May–September). The vegetation at both sites is Cape Flats Dune Strandveld,³⁶ formerly known as Dune Thicket.⁹ It is a fire-climax shrubland, returning to thicket dominance after 10 to 12 years.³⁷ Atlantic Beach Golf Estate, where construction started in 1999 but is not yet completed, was carved out of what is now the 1000-ha Blaauwberg Conservation Area and retains fragments of natural vegetation totalling approximately 46 ha, that are demarcated as 'conservation areas'. The fairways and greens are planted with a *Cynodon* grass hybrid, gulf green (*C. dactylon* × *C. transvaalensis*), as well as Kikuyu grass, *Pennisetum clandestinum*. Fire is excluded from the golf estate. In most parts of the conservation area—particularly within the study area—the natural vegetation is mature, having not burnt for at least 50 years (although large areas did burn a few weeks after the completion of this study!).

Methods

Data were collected during the breeding season of 2005, in October and November. Only birds directly utilizing Strandveld were recorded, thus predominantly aerial taxa such as swifts, swallows and martins were excluded from analyses. Birds in the golf estate that used exclusively fairways, gardens and water features were also excluded. The time of data collection was standardized between dawn and 10:00 and data were collected on days with no rain, no strong winds and no high temperatures.

The Point Count method was chosen as the most appropriate for determining relative densities of birds.³⁸ Owing to the

impenetrable nature of the vegetation, semicircular point counts were made by standing at the edge of the vegetation facing into the patch. Small and narrow patches were surveyed in the same manner, resulting in a count of the entire patch. To select sites separated by at least 200 m,³⁸ point counts in the golf estate were chosen by overlaying a 200 × 200 m grid on a map of the estate and identifying the closest patch of vegetation to the centre of each square, regardless of patch size. Twenty-five point counts were sited in the golf estate (sites A1–A25), mostly in the northern half of the estate because the southern half was still very disturbed by ongoing building (Fig. 1). Twenty-one point counts were sited in the conservation area (sites B1–B21), all 200 m apart. They were distributed along the fence line of the conservation area and along the coastal road (Fig. 1). Six replicate point counts were made at each site, each on a different day, and each lasting for 10 minutes, preceded by a 3-minute 'relaxation period'. Using Zeiss 10 × 40B binoculars and call-back tracks of 16 inconspicuous but responsive taxa, species and number of individuals were recorded, and distance from observer estimated when birds were first seen. Call-backs were played with a mini-iPod MP3 player set to constant volume. Calls were played once each with 15 seconds of silence in between. Counts were randomized such that counts at each site were not made at the same time of day, nor were sites visited successively in a regular pattern.

Grey-backed cisticola (*Cisticola subruficapilla*) and Levallant's cisticola (*C. tinniens*) were treated as a single unit in analyses (the former is common and the latter rare and dependent on patches of damp vegetation) due to difficulty in distinguishing them under some conditions in the field. There was only one observer, nullifying the problem of between-observer bias. Within the golf estate, a rapid assessment of vegetation quality and structural diversity was undertaken within the vicinity of each point

count. Because the assessment was largely subjective, based on species occurrence and diversity, and structural diversity, the vegetation was crudely ranked as being of low, medium or high quality. At one end of the spectrum, low quality patches were characterized by low cover and species richness of indigenous shrubs, and the presence of alien grasses. At the other extreme, high quality patches had equivalent vegetation structure to the conservation area (Appendix 1).

A 2004 Orthophoto (City of Cape Town) was used in the Geographic Information System Arcview 3.3 to digitize remnant Strandveld patches in the golf estate, as well as to measure areas of patches and point counts. Distances of each site from the nearest water and from the conservation area were also calculated (Appendix 1).

Total observed species richness and numbers of each species were calculated per point count and as an overall total for the conservation area and the golf estate. Species diversity was calculated for each site using the Shannon-Wiener diversity index (H') and the Brillouin Index ($\hat{H}$).^{39,40} The Shannon-Wiener Index measures the amount of uncertainty that surrounds the prediction of the identity of the next individual recorded, so that the larger the value of H' , the greater the uncertainty.⁴⁰ The Brillouin Index is not restricted for use in samples where the total number of species should be known (as is the case with the Shannon-Wiener Index). Both indices are most sensitive to changes in the representation of rare species in the community, and both increase as the number of rare species increases.⁴⁰ The measure of evenness, based on the Brillouin Index,^{39,40} was also calculated: when all species are equally abundant, evenness is maximal.

Not all species were equally detectable. To calculate relative species densities ($n \text{ ha}^{-1}$), the numbers of individuals of each species recorded were plotted against the distance at which they were observed. For each species, the distance at which detectability started to diminish was determined from these curves. This distance was used as the effective radius of the point count for the calculation of density, assuming that all individuals of species X within that radius were detected. Most point counts within the golf estate were in patches of vegetation whose radii were less than the acceptable detection radius; in these cases, density calculations were based purely on patch area.

Species assemblages were analysed using cluster analysis and non-metric multi-dimensional scaling programs in the software package PRIMER 5.0.⁴¹ Between-site similarity was assessed using the Bray-Curtis similarity coefficient,⁴² for both presence-absence data and relative density. SIMPER (similarity percentages analysis) was used to determine which species contributed most towards dissimilarity between sites.

Data were further analysed using STATISTICA 7.0.⁴³ Student's t -tests for independent samples (after testing for normality)⁴⁴ were used to investigate further the differences between sites in the golf estate and the conservation area. These tests were made for species richness, diversity, evenness and density. MacArthur's Broken-stick Model³⁹ was fitted to the data to produce species-abundance curves for the conservation area and the golf estate. A Student's t -test for independent samples was performed to determine if there was an overall difference in the average density of birds between the golf estate and the conservation area. A Wilcoxon signed-rank test⁴⁴ was used to test whether there was a difference in the abundances of all species between the golf estate and the conservation area. The average density of birds per hectare in the golf estate and the conservation area was calculated in order to estimate the number of birds displaced from the golf estate by habitat loss.

To determine if fragment size within the golf estate influenced species richness, semi-log species-area curves were constructed, both with and without those species unique to the golf estate. The equation from the latter relationship was used to calculate the minimum fragment size required to support all species present in the conservation area. This was calculated both for all fragments and for only those fragments with high-quality vegetation (Appendix 1). To assess whether environmental factors apart from patch size influenced the spatial distribution of birds within the golf estate, a stepwise multiple regression was performed between species richness and the environmental attributes of each site (Appendix 1). Lastly, the average body mass of each species⁴⁵ was used to determine whether a relationship existed between habitat fragment size and bird body mass: the area of the smallest patch in which each species was recorded (Appendix 2) was regressed against body mass, with the expectation that the largest species would be confined to the largest patches.

To assess whether fragmentation within the golf estate has ecological implications beyond impact at the species level, dietary guilds were compared between the two sites. Species were categorized into one of six dietary guilds (see Appendix 3 as online supplement).⁴⁵ Student's t -tests for independent samples (after testing for normality)⁴⁴ were used to compare species richness and total density of birds within each guild between the conservation area and the golf estate.

The effect of fragment size on the proportional representation of dietary guilds was analysed through regression. The proportion of species in each guild present at each site was $\log_{10}$ transformed and regressed against $\log_{10}$ fragment area. To obviate the problem of logging zero values, a constant of 0.23 was added to all values being logged.⁴⁶

For each species, field metabolic rate (FMR) was calculated using the most appropriate equation from Nagy *et al.*⁴⁷ (Appendix 2). FMR was multiplied by the density of each species. These values were then totalled for each guild both in the golf estate and in the conservation area. The proportion that each species contributed to overall FMR was calculated.

Results

Structural differences in bird communities

Forty-four species were identified in the entire study area: 10 of these are endemic and nine near-endemic to southern Africa, but none is currently threatened or endangered.⁴⁵ Thirty species were shared between the golf estate and the conservation area (Appendix 3). Four species were recorded only in the conservation area and ten species were recorded only in the golf estate (Table 1).

Based on presence-absence data alone, there was a discernible difference between the species composition of the conservation

Table 1. Species recorded only at sites in either the conservation area or the golf estate.*

Conservation area only	Golf estate only
Grey-winged francolin	Speckled pigeon
Black-shouldered kite	Red-eyed dove
Cape grassbird	Cape turtle-dove
Pied crow	Laughing dove
	Spotted thick-knee
	Cape wagtail
	Blacksmith lapwing
	Common moorhen
	Common waxbill
	Pin-tailed whydah

*Scientific names are detailed in Appendix 3 as online supplement.

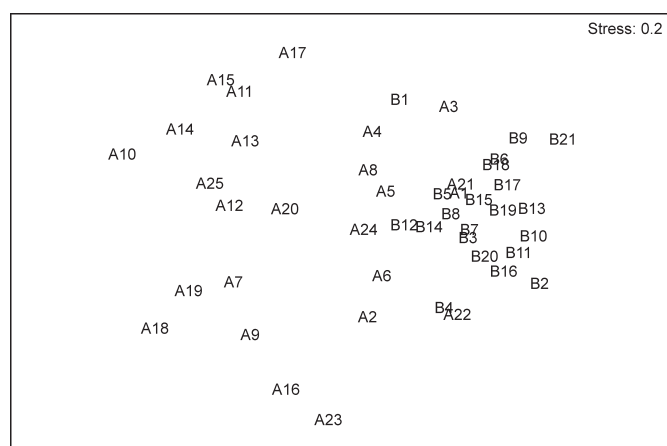


Fig. 2. Multidimensional scaling ordination plot between all sites in the conservation area (B1–B21) and the golf estate (A1–A25), based on species presence–absence. (An MDS plot based on species' densities showed a similar pattern, but with a less tightly packed clustering of conservation area sites.)

area and the golf estate (Fig. 2). Sites in the conservation area supported similar species assemblages, clustering together in the analysis. Golf estate sites fan out from the cluster of conservation area sites with a few sites (A1, A4, A6, A8 and A21) being very similar to the conservation area. These latter sites were either close to the conservation area or were relatively large, with vegetation similar in quality to that of the conservation area (Fig. 1, Appendix 1).

Based on presence–absence data, the species that contributed the most to the average dissimilarity in the SIMPER analysis were red-faced mousebird, southern masked-weaver and southern double-collared sunbird. Based on density, however, the species that contributed most to the average dissimilarity was the southern double-collared sunbird, followed by cisticola species and Karoo prinia.

Inter-site differences evident in the multivariate analysis (Fig. 2) were supported by a significantly higher species richness ($t = -3.13$, $P < 0.01$) and diversity in the conservation area, the latter being reflected in significant differences in both the Shannon-Wiener ($t = -2.33$, $P < 0.01$) and Brillouin indices ($t = -3.42$, $P < 0.01$). The rank–abundance plot further supports this distinction (Fig. 3). There was, however, no significant difference between the two areas in terms of either evenness ($t = 1.82$, $P = 0.08$), or average bird density ($t = -1.52$, $P = 0.09$).

Species shared between the golf estate and the conservation area occurred at significantly higher density in the conservation area ($t = 352$, $P < 0.05$). Thus, although there was little difference between the overall density of birds in Strandveld vegetation in the two areas, there were significant differences in the relative densities of different species (Table 2).

Average densities of birds in Strandveld patches in the golf estate and in the conservation area were 80.2 (68.0 excluding golf estate-restricted species) and 95.9 birds/ha, respectively. Assuming that bird density in the conservation area approximates that which would have occurred in the golf estate area prior to its construction, the resultant displacement of Strandveld birds

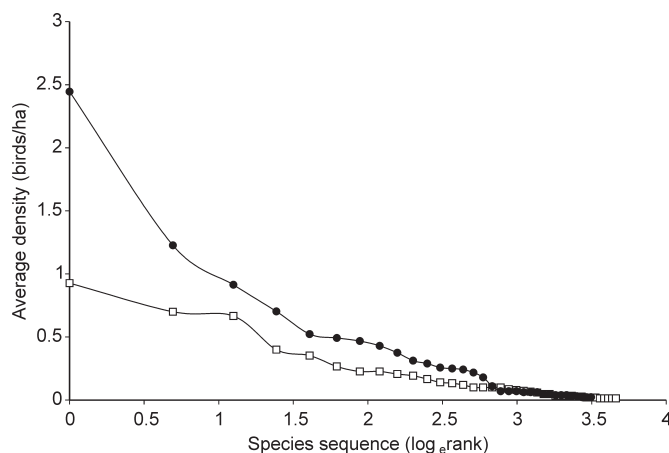


Fig. 3. Rank abundance plot (Broken-stick Model, based on average densities) for the conservation area (●) and the golf estate (□), where the density for each species is ranked highest to lowest.

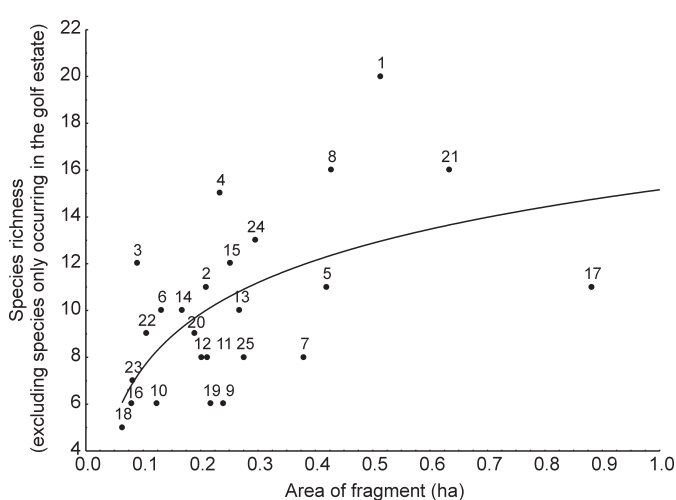


Fig. 4. Semi-log species–area curve for species richness in habitat fragments in the golf estate.

(excluding those unique to the golf estate) from the golf estate can be crudely calculated as: (average density in conservation area $\times$ area of the golf estate) – (average density remaining in golf estate fragments $\times$ combined area of golf estate fragments) = 8766 birds (equivalent to an average across the entire golf estate of 71 birds/ha).

Fragmentation effects within the golf estate

In the golf estate, species richness (all species) and fragment size were positively correlated ($r = 0.56$, $P < 0.01$), irrespective of vegetation quality. Repeating the regression for only those species shared with the conservation area ($r = 0.55$, $P < 0.01$; Fig. 4) allows prediction of the minimum patch size (556 hectares) that would retain these species. However, if only patches of high-quality vegetation are included in the analysis, the predicted minimum patch size for 100% representation of

Table 2. Abundance ratios of selected species occurring both in the golf estate and the conservation area.

Species proportionally more abundant in the golf estate		Species proportionally more abundant in the conservation area	
Cape spurfowl	20.0	Cape bunting	10.7
Cape sparrow	14.3	Yellow bishop	7.1
Southern red bishop	5.3	Layard's tit-babbler	4.5
Common fiscal	3.7	Cape bulbul	4.5
Speckled mousebird	2.1	Karoo scrub-robin	4.1

Table 3. Student's *t*-tests comparing species richness (SR) and density (ha⁻¹) of birds, and differences between total field metabolic rate (FMR, kJ ha⁻¹ day⁻¹) for the six dietary guilds, between the golf estate and the conservation area: positive values indicate higher values in the conservation area).

Dietary guild	SR	Density	FMR
Frugivore	2.32*	3.55**	982
Granivore	2.79**	0.29	-213
Invertebrate feeder	3.23**	0.98	-368
Generalist	-2.85**	-2.44*	-1490
Nectarivore	2.15*	2.42*	661
Carnivore	2.66*	-0.49	37
Total	N/A	N/A	-391

**P* < 0.05, ** *P* < 0.01.

species is reduced to 51 hectares ($r = 0.67$, $P < 0.05$), highlighting the importance of vegetation quality as well as patch size. Stepwise multiple regression of species richness against ($\log_{10}$) area, distance from the conservation area, and distance from the nearest water source indicated that patch area is overridingly the most important explanatory variable of species richness ($\beta = 0.586$, $P < 0.05$). In the regression, distance from the nearest water was removed first, followed by distance from conservation area: neither made a significant contribution to explaining variance. Contrary to prediction, there was no significant relationship ($r = 0.10$, $P = 0.56$) between bird body size and the minimum area of a fragment in which a particular species occurred; that is, the largest species were not confined to the largest fragments.

Functional differences in bird communities

Differences in the proportional representation of species in different guilds indicate that some guilds are favoured by the altered golf estate environment whilst others are not (Table 3). Species richness and density of both frugivores and nectarivores were significantly higher in the conservation area. Granivores, invertebrate feeders and carnivores were significantly more species rich in the conservation area but did not differ in density between the two areas. The species richness and density of generalists were, however, significantly higher in the golf estate.

Within the golf estate, increasing fragment size resulted in a significant increase in the number of frugivore, insectivore and generalist species ($r = 0.56$, $P < 0.01$; $r = 0.52$, $P < 0.01$; $r = 0.48$, $P < 0.05$, respectively).

The combined FMR for the six dietary guilds was higher in the golf estate than in the conservation area by 391 kJ ha⁻¹ day⁻¹. However, the combined FMRs of frugivores, nectarivores and, to a lesser degree, carnivores were greatest in the conservation area (Table 3). The higher assemblage FMR in the golf estate is due to the greater contribution by generalists and to a lesser degree invertebrate feeders and granivores (Table 3). Species contributing the most to FMR in the golf estate were Cape sparrow, Cape spurfowl, blacksmith lapwing and southern double-collared sunbird, while those contributing the most in the conservation area were southern double-collared sunbird, Cape bulbul, Karoo prinia, malachite sunbird and common starling (Table 4).

Discussion

Bird assemblages of the golf estate and the adjacent conservation area differed substantially. Key environmental features, including available habitat and vegetation quality influenced not only species' presence, but also their relative abundance. Both bird diversity and density per unit area of 'natural' vegetation were higher in the conservation area (Figs 2, 3), and more than 8500 birds were estimated to have been displaced by loss of

Table 4. Species that contributed the most to differences in energy flow between the golf estate and the conservation area.

	Percentage contribution to energy flow	
	Golf estate	Conservation area
Cape sparrow	12.7	1.2
Cape spurfowl	12.0	1.2
Blacksmith lapwing	9.7	0
Southern double-collared sunbird	9.2	15.4
Karoo prinia	7.7	9.0
Cisticola spp.	5.5	3.8
Southern red bishop	4.2	0.8
Yellow canary	3.1	4.0
Cape bulbul	3.0	15.0
White-backed mousebird	2.6	3.3
Malachite sunbird	2.4	6.1
Cape robin-chat	1.8	4.3
Common starling	1.7	4.5
Cape white-eye	1.2	4.0
Karoo scrub-robin	0.8	3.3

habitat. In the golf estate, bird assemblages in some habitat patches approximated those in the conservation area (Fig. 2), but they were outnumbered by sites that included species not normally encountered in Strandveld at the cost of those predicted to be there. For example, the addition of trees, water points and built structures benefits generalists,⁴⁸ water-dependent species such as spotted thick-knee and blacksmith lapwing, and also granivores, such as doves.⁴⁵ Similar responses to ex-urban development have been reported from other systems.⁴⁹ A few species accounted for a large proportion of the differences between sites in terms of both presence/absence (southern masked-weaver, southern double-collared sunbird) and relative density (southern double-collared sunbird, Karoo prinia and cisticola spp.). Southern masked-weavers occurred at only one site in the conservation area but were common throughout the golf estate. By contrast, southern double-collared sunbirds occurred in all sites in the conservation area but in much higher densities than at the 19 sites where they were present in the golf estate.

Fragment size was the overriding factor influencing species' occurrence in patches of 'natural' habitat in the golf estate, explaining 55% of the variance. Distance to water was not a significant predictor of overall species richness, nor was distance from the conservation area, indicating that the golf estate matrix is permeable to most species. This is probably due to the relatively small size of the golf estate, proximity to the source pool and proximity of patches within the golf estate. Although it was predicted that large species would have been the most susceptible to displacement as a result of habitat fragmentation,⁵⁰ there was no relationship between body size and fragment size.

Some very small fragments in the golf estate (e.g. A6) had similar species composition to the conservation area, although they were relatively species poor (Fig. 2), indicating that even a small fragment of pristine vegetation can accommodate a subset of the natural species assemblage. Even fragments that were essentially parts of corridors (e.g. A3) supported some birds, indicating that the corridors were either facilitating some movement and/or provided territories for some birds. However, relaxation effects (*sensu* Diamond⁵¹) may not yet have occurred (the golf estate has been in existence only since 1999) and species numbers and density may still decrease^{31,52,53} because the small size and the shape of many remnants will render them highly susceptible to edge effects.^{31,54,55} Some such effects are already evident, including invasion of natural vegetation by Kikuyu grass.

Although, collectively, fragments in the golf estate contained the majority of Strandveld species, the densities of most species were much lower than in the conservation area. Theoretically, a patch of approximately 51 ha of high-quality vegetation within the golf estate would be adequate to accommodate the species complement of the conservation area (although this would probably be dependent on the conservation area remaining intact). However, if the vegetation was of poorer quality (i.e. the 'average' quality of the remaining golf estate vegetation), a patch 3.3 times the size of the golf estate would be required. In order to maximize the recreational/residential area within a golf estate, this indicates that land set aside for conservation needs to be maintained in as pristine a state as possible in the long term, requiring effective control of alien invasive fauna and flora as well as the maintenance of natural ecological processes such as fire, water and nutrient regimes.^{56,57} All three of these latter processes are altered in a golf estate situation and are particularly strongly affected when the vegetation is fragmented. For example, although the vegetation in the Cape Floristic Region is fire climax, to date there is not one example of a controlled fire having been started on a golf estate in the region.⁸ Soil nutrient enrichment from fertilizers, and altered water regimes from sprinkler systems are also highly likely to affect remnant vegetation, particularly by favouring alien invasive species such as Kikuyu grass.⁵⁸ Based on other studies, species in small habitat fragments may have lower reproductive output⁵⁹ or elevated mortality, which could lead to these fragments being or becoming population sinks.³² Elevated mortality, for example, could stem from reduced cover from predators, but perhaps the greatest predation risk comes from domestic cats, *Felis catus*, which are common on the golf estate and are well documented as important predators of birds.⁶⁰

There are important ecological implications behind the differences in bird assemblages between the golf estate and the conservation area. The loss of birds is non-random, and is linked in part to diet. The golf estate favours granivores (as also happens in gardens⁶¹) and generalists, especially those associated with water, such as the southern masked-weaver. It also favours species that benefit from ecotonal habitats, such as Cape spurfowl.⁶² The golf estate, however, has a negative effect on nectarivores and frugivores. Whether this is due to spatial (territorial) or nutritional (lack of food) limitation is likely species specific. The impacts on nectarivores and frugivores are likely to be particularly ecologically important because of the roles these species play as pollinators of some Strandveld plants⁶³ and especially as seed dispersers.^{64,65}

Fragment size appears to be the main factor influencing the density of nectarivores. Similar results have been reported (also during the breeding season) for southern double-collared and malachite sunbirds in renosterveld fragments,^{66,67} and for southern double-collared sunbirds in the Karoo.⁶¹ Sunbirds rely on both insects and nectar in the breeding season,⁶⁸ therefore either resource could be limiting their use of small patches in the golf estate. Regardless of the proximate cause, the loss of these key fynbos pollinators from fragments will affect plants that rely on them: *Microloma sagittatum*, for example, is pollinated exclusively by southern double-collared sunbirds.⁶⁹

Dietary guild-level responses to fragmentation have been reported elsewhere. Birds found to be vulnerable to fragmentation have included insectivores,⁷⁰ those with large spatial requirements such as frugivores^{50,71–73} and those with specialized food or habitat requirements.^{50,71,74} As a semi-independent test of these findings in a situation where vegetation diversity was greater inside than outside a golf estate, Tanner and Gange

found that golf estates had a higher proportion of insectivores and a lower proportion of generalists than surrounding farmland.¹⁰

In the golf estate, much more energy per unit area was channelled through granivores, invertebrate feeders and generalists than was the case in the conservation area. Excluding species favouring disturbed or aquatic microhabitats, however, more energy per unit area was channelled through birds in the conservation area. Thus, not only have the pathways of energy flow changed, but as a necessary corollary, there must have been changes associated with pollination, fruit dispersal and predation, indicating a shift away from a naturally functioning system. What appears on the surface to be an 'ecologically friendly' golf estate, masked by a species-rich bird community, therefore, is in fact deficient in terms of the primary aims of conservation, namely to conserve pattern and process in order to maintain natural biodiversity.

Conclusions

A golf course/estate will never substitute for natural habitat because a significant proportion of natural habitat is lost in its construction. Answers to the question of how golf courses/estates influence biodiversity are likely to differ on a case-by-case basis, depending on the matrix surrounding the development. For example, where golf estates are replacing land that had already been adversely transformed, such as old mine sites or monoculture, they can play an important role in promoting biodiversity.^{10,18}

In the Cape Floristic Kingdom, however, the reverse is typically the case, with developments having being carved out of pristine or near-pristine habitats. Based on the findings of this study, in terms of both diversity and ecosystem functioning, those that are still in the planning phase would be better advised to maintain natural vegetation in the form of fewer, large areas rather than a plethora of small patches and ribbons.^{54,55}

This project was funded by the DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town. The study would not have been possible without the permission granted to work on the properties of both Atlantic Beach Golf Estate and Blaauwberg Conservation Area. We thank Francois Brand and Morise Peterson for help and advice on numerous aspects about the golf estate, Clifford Dorse for helping to assess vegetation quality, the City of Cape Town for allowing use of an Orthophoto of the area, Thomas Birch for statistical advice and Vanessa Stephen for help in the field.

Received 8 August. Accepted 16 December 2006.

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Appendix 1. Attributes of sites in the golf estate, where vegetation quality was scored as being of low (L), medium (M) or high (H) quality.

Site in golf estate	Area (ha)	Distance to conservation area (m)	Distance to nearest water (m)	Quality of vegetation
A1	0.51	9	253	H
A2	0.21	62	33	H
A3	0.09	173	207	M
A4	0.23	343	17	H
A5	0.42	145	133	H
A6	0.13	183	93	H
A7	0.38	290	56	M
A8	0.43	377	16	M
A9	0.24	490	63	M
A10	0.12	303	29	L

Appendix 1 (continued)

A11	0.21	307	0	M
A12	0.20	395	0	M
A13	0.27	528	0	M
A14	0.17	606	2	L
A15	0.25	464	140	L
A16	0.08	525	183	M
A17	0.88	554	102	M
A18	0.06	694	167	L
A19	0.22	775	27	H
A20	0.19	655	102	M
A21	0.63	745	237	H
A22	0.11	775	420	M
A23	0.08	878	340	M
A24	0.30	160	0	H
A25	0.28	309	103	M

Appendix 2. Groups used for allometric equations for the calculation of field metabolic rate (FMR),⁴⁷ and the smallest fragment in which each species is found in the golf estate.

Species	Group used for allometric equation for calculation of FMR (Nagy <i>et al.</i> ⁴⁷)	Smallest fragment (in the golf estate) containing the species (ha)
Frugivores		
Speckled mousebird	Temperate bird	0.23
White-backed mousebird	Desert bird	0.11
Red-faced mousebird	Desert bird	0.23
Acacia pied barbet	Desert bird	0.22
Cape bulbul	Passerine	0.09
Granivores		
Speckled pigeon	Temperate bird	0.25
Red-eyed dove	Temperate bird	0.17
Cape turtle-dove	Temperate bird	0.08
Laughing dove	Temperate Bird	0.06
Southern red bishop	Passerine	0.06
Common waxbill	Passerine	0.30
Pin-tailed whydah	Passerine	0.25

Appendix 2 (continued)

Yellow canary	Passerine	0.08
White-throated canary	Passerine	0.38
Cape bunting	Passerine	0.30
Invertebrate feeders		
Spotted thick-knee	Charadriiform	0.88
European bee-eater	Insectivore	0.21
Cape robin-chat	Passerine	0.06
Chestnut-vented tit-babbler	Passerine	0.09
Layard's tit-babbler	Passerine	0.23
Bar-throated apalis	Passerine	0.09
Long-billed crombec	Passerine	0.51
Cape grassbird	Passerine	N/A
Cisticola spp.	Passerine	0.09
(grey-backed cisticola and Levallant's cisticola)		
Karoo prinia	Passerine	0.06
Cape wagtail	Passerine	0.08
Karoo scrub-robin	Passerine	0.23
Blacksmith lapwing	Charadriiform	0.17
Generalists		
Grey-winged francolin	Galliform	N/A
Cape spurfowl	Galliform	0.09
Common moorhen	Omnivore	0.21
Common starling	Passerine	0.11
Cape white-eye	Passerine	0.08
Cape sparrow	Passerine	0.06
Cape weaver	Passerine	0.08
Southern masked-weaver	Passerine	0.09
Yellow bishop	Passerine	0.09
Brimstone canary	Passerine	0.42
Nectarivores		
Malachite sunbird	Passerine	0.08
Southern double-collared sunbird	Passerine	0.08
Carnivores		
Black-shouldered kite		N/A
Common fiscal	Passerine	0.12
Bokmakierie	Passerine	0.06
Pied crow	Passerine	N/A

Supplementary material to:

Fox S-J.C. and Hockey P.A.R. (2006). Impacts of a South African coastal golf estate on shrubland bird communities *S. Afr. J. Sci.* **103**, 27–34.

Appendix 3. Densities (birds ha⁻¹) of each species, according to guild, at each site in the golf estate (A) and the conservation area (B).

(A) Species	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12	A13	A14	A15	A16	A17	A18	A19	A20	A21	A22	A23	A24	A25
Frugivores																									
Speckled mousebird <i>Colius striatus</i>				2.28				1.56																	
White-backed mousebird <i>C. colius</i>	5.35			8.71			2.65				13.26		15.92		2.65					5.35	13.26	7.96			2.65
Red-faced mousebird <i>Urocolius indicus</i>				3.43				5.93													8.49				
Cape bulbul <i>Pycnonotus capensis</i>	1.33	3.36	5.28		3.98	2.15	0.86	1.33	1.73										5.72	0.79	5.67	6.31		5.35	3.85
Granivores																									
Speckled pigeon <i>Columba guinea</i>															5.93										
Red-eyed dove <i>Streptopelia semitorquata</i>														2.14	1.70										
Cape turtle-dove <i>S. capicola</i>															2.94							4.24			
Laughing dove <i>S. senegalensis</i>														4.28				3.43							
Southern red bishop <i>Euplectes orix</i>								5.35	5.35		23.87	2.65	5.35	39.85	5.35			4.36	29.18	5.35				7.96	
Common waxbill <i>Estrilda astrild</i>																								3.40	
Pin-tailed whydah <i>Vidua macroura</i>															11.88										
Yellow canary <i>Crithagra flaviventris</i>	9.62	2.46		4.13	12.30	16.53	2.46					14.44				2.66				4.81	14.44	7.22		4.81	
White-throated canary <i>C. albogularis</i>	3.27						3.27														16.36				
Cape bunting <i>Emberiza capensis</i>	3.18																							1.36	
Invertebrate feeders																									
Spotted thick-knee <i>Burhinus capensis</i>																	3.40								
European bee-eater <i>Merops apiaster</i>		1.85																							
Cape robin-chat <i>Cossypha caffra</i>	1.96	0.96	3.47	2.49	1.84	2.49	0.99	0.92										3.33			2.75	4.73		1.84	
Chestnut-vented tit-babbler <i>Parisoma subcaeruleum</i>			6.28		6.28																12.56				
Layard's tit-babbler <i>Parisoma layardi</i>	2.94																							5.88	
Bar-throated apalis <i>Apalis thoracica</i>	5.35		8.88			4.36			2.65												13.26	5.35		2.65	
Long-billed crombec <i>Sylvietta ruficapilla</i>																					5.41				
Cisticola spp. (grey-backed cisticola <i>Cisticola subruficapilla</i> and Levaillant's cisticola <i>Cisticola tinniens</i>)	11.14		3.73	1.44	7.34					13.48	33.43	7.34	36.71	14.69	14.69		14.69			11.14	3.67			14.69	
Karoo prinia <i>Prinia maculosa</i>	5.35	18.57	14.84	13.67	7.96	43.56	5.35	13.26	15.92	7.42	13.26	5.35	7.96	5.69	21.23	8.54		4.36	7.96	13.26	1.61	1.61	16.00	1.61	1.61
Cape wagtail <i>Motacilla capensis</i>														8.77			8.77					8.77			
Karoo scrub-robin <i>Cercotrichas coryphoeus</i>	1.35			6.84	4.68			5.41													1.35				
Blacksmith lapwing <i>Vanellus armatus</i>														26.5			17.67								
Generalists																									
Cape spurfowl <i>Pternistes capensis</i>		1.57	6.44	3.29				3.14			9.73	1.69	1.57		9.42		1.57								1.65
Common moorhen <i>Gallinula chloropus</i>											1.73														
Common starling <i>Sturnus vulgaris</i>	1.73						0.96					1.21	1.73	4.39	0.97		1.73			0.92		3.16			
Cape white-eye <i>Zosterops virens</i>			5.92													5.69					13.26	1.61			
Cape sparrow <i>Passer melanurus</i>		22.69	2.25	6.85	11.88	2.56	5.93	1.19	3.40	5.79	1.73	37.49	13.58	12.84	16.98	6.50	8.49	13.78	5.93		6.80		3.13	1.19	8.72
Cape weaver <i>Ploceus capensis</i>	2.65		2.97	8.71		4.36	5.35						2.65	8.54	2.65	2.85	5.35			2.65				2.65	
Southern masked-weaver <i>P. velatus</i>			3.17	27.65			5.88				8.82	5.88	14.70		5.88				2.94					5.88	
Yellow bishop <i>Euplectes capensis</i>			7.37																						
Brimstone canary <i>Crithagra sulphuratus</i>	2.65				2.65																				
Nectarivores																									
Malachite sunbird <i>Nectarinia famosa</i>		5.35	2.97	8.71		17.42							2.65	2.85	2.65						7.96		8.00	2.65	
Southern double-collared sunbird	26.20	3.27	1.27	24.47	45.85	34.26					6.55	3.27	3.27	9.98	6.55	6.65			32.75	3.27	3.27	9.82	13.52	45.85	19.65
<i>Cinnyris chalybeus</i>																									
Carnivores																									
Common fiscal <i>Lanius collaris</i>		5.35	2.97							18.54				2.85	2.65										2.65
Bokmakierie <i>Telophorus zeylonus</i>			3.65	2.83	2.36	2.83				2.38	2.76						3.54	6.67							
(B) Species	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15	B16	B17	B18	B19	B20	B21				
Frugivores																									
Speckled mousebird <i>Colius striatus</i>								1.56																	
White-backed mousebird <i>Colius colius</i>			4.55		23.87	7.96	1.61	7.96		15.92					5.35			2.65			9.35				
Red-faced mousebird <i>Urocolius indicus</i>	15.28					8.49			8.49									1.70							
Acacia pied barbet <i>Tricholaema leucomelas</i>						4.14																			
Cape bulbul <i>Pycnonotus capensis</i>	1.33	8.63	8.53	5.35	11.94	9.95	3.98	6.63	5.97	8.63	8.63	14.21	6.63	1.61	9.28	7.96	3.98	32.49	7.29	6.63	11.19				
Granivores																									
Southern red bishop <i>Euplectes orix</i>							2.65	5.35	13.26																
Yellow canary <i>Crithagra flaviventris</i>		9.62	2.62		2.46	12.30	4.81	9.62	12.30	4.81	4.81	2.62		4.81	19.25	7.22		2.46	4.81		5.46				
White-throated canary <i>Crithagra albogularis</i>		3.27	14.35		9.82		3.27	3.27					6.55		9.82	3.27	3.27		3.27	9.82	5.23				
Cape bunting <i>Emberiza capensis</i>	3.18	4.14	1.78		5.19	2.72	1.36	1.36	5.19	2.72			1.36		1.36	2.72		1.36	1.36	3.18	1.78				
Invertebrate feeders																									
European bee-eater <i>Merops apiaster</i>	0.87									1.73															
Cape robin-chat <i>Cossypha caffra</i>	4.59	2.75	3.15	0.92	1.84		3.67	6.42	2.75	3.67	4.59	3.93	1.84	2.75			0.92	7.34	3.67	2.75	3.45				
Chestnut-vented tit-babbler <i>Parisoma subcaeruleum</i>									18.83	6.28															
Layard's tit-babbler <i>P. layardi</i>			5.39				2.94							2.94	2.94	2.94	2.94	8.82			4.40				
Bar-throated apalis <i>Apalis thoracica</i>		2.65	9.95	2.65		7.96		5.35		2.65			2.65	5.35	2.65		7.96				4.30				
Long-billed crombec <i>Sylvietta ruficapilla</i>																									

Supplementary material to:

Fox S-J.C. and Hockey P.A.R. (2006). Impacts of a South African coastal golf estate on shrubland bird communities *S. Afr. J. Sci.* **103**, 27–34.

Appendix 3. Densities (birds ha⁻¹) of each species, according to guild, at each site in the golf estate (A) and the conservation area (B).

(A) Species	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12	A13	A14	A15	A16	A17	A18	A19	A20	A21	A22	A23	A24	A25
Frugivores																									
Speckled mousebird <i>Colius striatus</i>				2.28				1.56																	
White-backed mousebird <i>C. colius</i>	5.35			8.71			2.65				13.26		15.92		2.65					5.35	13.26	7.96			2.65
Red-faced mousebird <i>Urocolius indicus</i>				3.43				5.93													8.49				
Cape bulbul <i>Pycnonotus capensis</i>	1.33	3.36	5.28		3.98	2.15	0.86	1.33	1.73										5.72	0.79	5.67	6.31		5.35	3.85
Granivores																									
Speckled pigeon <i>Columba guinea</i>															5.93										
Red-eyed dove <i>Streptopelia semitorquata</i>														2.14	1.70										
Cape turtle-dove <i>S. capicola</i>															2.94								4.24		
Laughing dove <i>S. senegalensis</i>														4.28				3.43							
Southern red bishop <i>Euplectes orix</i>								5.35	5.35		23.87	2.65	5.35	39.85	5.35			4.36	29.18	5.35				7.96	
Common waxbill <i>Estrilda astrild</i>																								3.40	
Pin-tailed whydah <i>Vidua macroura</i>															11.88										
Yellow canary <i>Crithagra flaviventris</i>	9.62	2.46		4.13	12.30	16.53	2.46					14.44				2.66				4.81	14.44	7.22		4.81	
White-throated canary <i>C. albogularis</i>	3.27						3.27														16.36				
Cape bunting <i>Emberiza capensis</i>	3.18																							1.36	
Invertebrate feeders																									
Spotted thick-knee <i>Burhinus capensis</i>																	3.40								
European bee-eater <i>Merops apiaster</i>		1.85																							
Cape robin-chat <i>Cossypha caffra</i>	1.96	0.96	3.47	2.49	1.84	2.49	0.99	0.92										3.33			2.75	4.73		1.84	
Chestnut-vented tit-babbler <i>Parisoma subcaeruleum</i>			6.28		6.28																12.56				
Layard's tit-babbler <i>Parisoma layardi</i>	2.94																							5.88	
Bar-throated apalis <i>Apalis thoracica</i>	5.35		8.88			4.36			2.65												13.26	5.35		2.65	
Long-billed crombec <i>Sylvietta ruficapilla</i>																					5.41				
Cisticola spp. (grey-backed cisticola <i>Cisticola subruficapilla</i> and Levaillant's cisticola <i>Cisticola tinniens</i>)	11.14		3.73	1.44	7.34					13.48	33.43	7.34	36.71	14.69	14.69		14.69			11.14	3.67			14.69	
Karoo prinia <i>Prinia maculosa</i>	5.35	18.57	14.84	13.67	7.96	43.56	5.35	13.26	15.92	7.42	13.26	5.35	7.96	5.69	21.23	8.54		4.36	7.96	13.26	1.61	1.61	16.00	1.61	1.61
Cape wagtail <i>Motacilla capensis</i>														8.77			8.77					8.77			
Karoo scrub-robin <i>Cercotrichas coryphoeus</i>	1.35			6.84	4.68			5.41													1.35				
Blacksmith lapwing <i>Vanellus armatus</i>														26.5			17.67								
Generalists																									
Cape spurfowl <i>Pternistes capensis</i>		1.57	6.44	3.29				3.14			9.73	1.69	1.57		9.42		1.57								1.65
Common moorhen <i>Gallinula chloropus</i>											1.73														
Common starling <i>Sturnus vulgaris</i>	1.73						0.96					1.21	1.73	4.39	0.97		1.73			0.92		3.16			
Cape white-eye <i>Zosterops virens</i>			5.92													5.69					13.26	1.61			
Cape sparrow <i>Passer melanurus</i>		22.69	2.25	6.85	11.88	2.56	5.93	1.19	3.40	5.79	1.73	37.49	13.58	12.84	16.98	6.50	8.49	13.78	5.93		6.80		3.13	1.19	8.72
Cape weaver <i>Ploceus capensis</i>	2.65		2.97	8.71		4.36	5.35						2.65	8.54	2.65	2.85	5.35			2.65				2.65	
Southern masked-weaver <i>P. velatus</i>			3.17	27.65			5.88				8.82	5.88	14.70		5.88				2.94					5.88	
Yellow bishop <i>Euplectes capensis</i>			7.37																						
Brimstone canary <i>Crithagra sulphuratus</i>	2.65				2.65																				
Nectarivores																									
Malachite sunbird <i>Nectarinia famosa</i>		5.35	2.97	8.71		17.42							2.65	2.85	2.65						7.96		8.00	2.65	
Southern double-collared sunbird	26.20	3.27	1.27	24.47	45.85	34.26					6.55	3.27	3.27	9.98	6.55	6.65			32.75	3.27	3.27	9.82	13.52	45.85	19.65
<i>Cinnyris chalybeus</i>																									
Carnivores																									
Common fiscal <i>Lanius collaris</i>		5.35	2.97							18.54				2.85	2.65										2.65
Bokmakierie <i>Telophorus zeylonus</i>			3.65	2.83	2.36	2.83				2.38	2.76						3.54	6.67							
(B) Species	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15	B16	B17	B18	B19	B20	B21				
Frugivores																									
Speckled mousebird <i>Colius striatus</i>								1.56																	
White-backed mousebird <i>Colius colius</i>			4.55		23.87	7.96	1.61	7.96		15.92					5.35			2.65			9.35				
Red-faced mousebird <i>Urocolius indicus</i>	15.28					8.49			8.49									1.70							
Acacia pied barbet <i>Tricholaema leucomelas</i>						4.14																			
Cape bulbul <i>Pycnonotus capensis</i>	1.33	8.63	8.53	5.35	11.94	9.95	3.98	6.63	5.97	8.63	8.63	14.21	6.63	1.61	9.28	7.96	3.98	32.49	7.29	6.63	11.19				
Granivores																									
Southern red bishop <i>Euplectes orix</i>							2.65	5.35	13.26																
Yellow canary <i>Crithagra flaviventris</i>		9.62	2.62		2.46	12.30	4.81	9.62	12.30	4.81	4.81	2.62		4.81	19.25	7.22		2.46	4.81		5.46				
White-throated canary <i>Crithagra albogularis</i>		3.27	14.35		9.82		3.27	3.27					6.55		9.82	3.27	3.27		3.27	9.82	5.23				
Cape bunting <i>Emberiza capensis</i>	3.18	4.14	1.78		5.19	2.72	1.36	1.36	5.19	2.72			1.36		1.36	2.72		1.36	1.36	3.18	1.78				
Invertebrate feeders																									
European bee-eater <i>Merops apiaster</i>	0.87								1.73																
Cape robin-chat <i>Cossypha caffra</i>	4.59	2.75	3.15	0.92	1.84		3.67	6.42	2.75	3.67	4.59	3.93	1.84	2.75			0.92	7.34	3.67	2.75	3.45				
Chestnut-vented tit-babbler <i>Parisoma subcaeruleum</i>									18.83	6.28															
Layard's tit-babbler <i>P. layardi</i>			5.39				2.94							2.94	2.94	2.94	2.94	8.82			4.40				
Bar-throated apalis <i>Apalis thoracica</i>		2.65	9.95	2.65		7.96		5.35		2.65			2.65	5.35	2.65		7.96				4.30				
Long-billed crombec <i>Sylvietta ruficapilla</i>					1.83																				