

Bird diversity and density in south african forests

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Summary. Afromontane woodlands are fairly continuous in eastern Cape Province of southern Africa, but occur as increasingly smaller and more isolated patches towards Cape Town in the southwest. These habitat patches are similar in both vegetation structure and floristic composition. Although bird species numbers in the patches decline three-fold from east to west to 15 species at Table Mountain, total bird density remains roughly constant, and bird density per species increases threefold as species diversity declines by the same factor.

A few species, especially frugivores, seedeaters and nectarivores, may be restricted to the larger more easterly woodlands because their food resources are so restricted. Some species, perhaps the sallying flycatchers, may be more abundant in the western species-poor habitat patches because of the higher productivity in their food supplies, but evidence for this view is scant. Some guilds, most notably foliage insectivores and slow-searching omnivores, exhibit good density compensation, such that the elevated densities of species in impoverished woodlands are predictable from densities and overlaps in foraging ecology at the species-rich sites. The guild of foliage insectivores "warbler-types," declines in size serially from east to west at five sites: 5 spp-4-3-2-1; in this guild food resources are best matched amongst sites, and the predictions allowed, of the structure and composition of the increasingly smaller species subsets, are most detailed.

Introduction

Forest vegetation is presently of very limited extent in western Cape Province, occurring mostly as patches on the

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southern foothills of the mountains ranked along the Indian Ocean coast (Fig. 1). The forest is contiguous over hundreds of hectares in the Knysna region, but thence west-south-west the patches become smaller and more isolated from each other, ending with stands of a few hectares in the gullies on the eastern slopes of Table Mountain.

This forest vegetation is related to that of the Afromontane region by White (1978), who gives a comprehensive treatment of its biogeography. From Knysna these forests extend northerly to the Drakensberg and occur in amplified form at higher elevations on Mt. Kenya and Mt. Kilimanjaro. At lower elevations in Moçambique, the flood-plain forests extend southwest down the coast, and elements of this type of vegetation meet the Afromontane forest at Alexandria, which is a mixture of the two (Moll and White 1978).

The smaller and more isolated patches of the southern Cape forest west of Knysna were investigated by MacKenzie (1978), who analysed diversity, density and the site preferences of the dominant plants at a series of seven sites between Knysna and Cape Town. His results show that the number of major woody plant species decreases towards the Cape from 50 to 31, and that the composition of the forests changes chiefly by a subtraction of species from northeast (Knysna) to southwest. These changes can be interpreted as effects of increasing isolation and decreasing stand size towards the southwest, changes that correspond to a peninsular or island effect in the usual biogeographic sense as the flora attenuates away from its center of distribution. However, climatic differences exist between the ends of the series of forest patches; especially relevant is an increase of total rainfall by 50% and a decrease in the frequency of summer rains as one moves SW into the Mediterranean climatic zone around the Cape proper (McKenzie 1978). This may account in part for the restriction of some trees to the northeastern areas, but it is difficult to separate

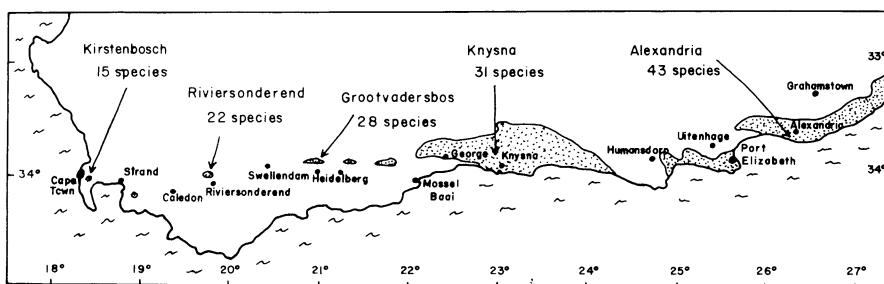


Fig. 1. Map showing the locations of five forest study sites in Southern Africa and numbers of bird species censused at each site

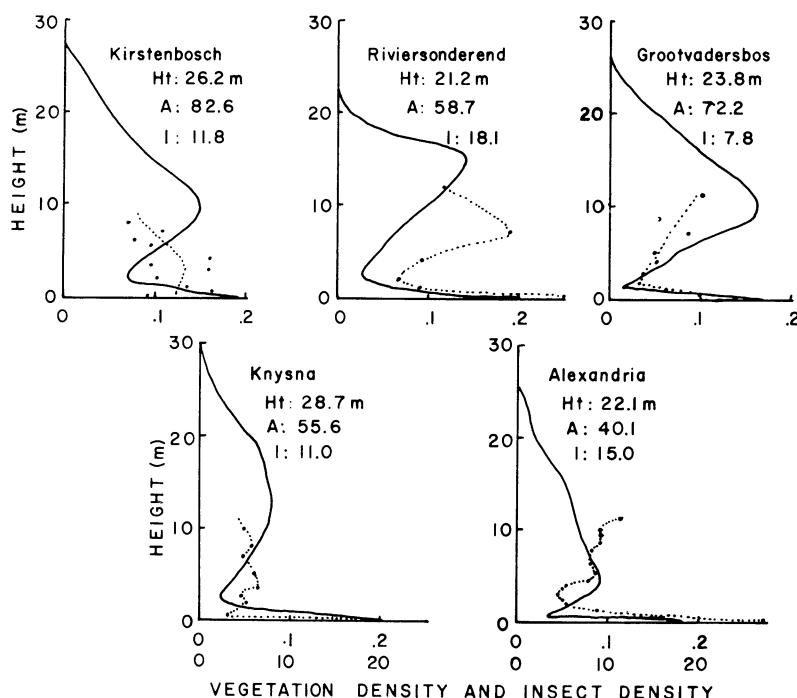


Fig. 2. The foliage profile, a plot of vegetation density against height, is given for each of five forest sites as the solid line in the figures. The dotted line indicates numbers of insects caught on sticky plaques at different heights in the forests (see scale at bottom of Figure). Numbers on forest height H_t , area under the foliage profile A and mean numbers of insects I are also included

a climatic effects from factors related to area alone in these habitat islands.

The recent historical perspective tends to further the view that isolation and exploitation rather than climatic change limit tree species distributions. Since early colonial times, the first settlers had to push further northeast from the depleted forest near Cape Town for the selected timbers necessary for wagon wheels and axles. This adds a further factor; some trees now scarce in or absent from the southwestern Cape were once more abundant there, and a combination of burning in the fynbos vegetation that replaces logged forests and the lack of reinvasion opportunities for forest trees may account in part for some restricted tree distributions (Moll et al. 1980). Thus tree species diversity in the southwestern Cape may be reduced by at least 3 factors: heavier logging in colonial times, lack of summer rainfall, and the island, peninsular or "isolation" effect.

In less recent times, evidence suggests that the Pleistocene pluvials enhanced the distribution of the Afromontane forests (Deacon 1979). There is at least the possibility that forests that are now isolated patches were contiguous with other such patches, but prevailing opinion is that the forests probably did not form a continuous belt from Knysna to the Cape Peninsula (H.J. Deacon, pers. comm.). But relative to their extent over recent geological time the forests now occupy a series of relictual patches, with those on the Cape Peninsula most isolated and those in the Knysna region least isolated from larger tracts of contiguous habitat.

From the point of view of the bird-watcher and perhaps also of the birds, the forests between the Cape Peninsula and the Eastern Cape seem relatively similar in structure. The tallest trees generally reach 30 m in height, and the canopy is more or less continuous between 10 m and 20 m. The undergrowth is open and easily walked through, dominated by ferns, such low shrubs as *Trichocladus* and *Diospyros*, and of course the samplings of canopy trees. Only in Alexandria (see Fig. 2) is the aspect of the forest rather

different, with the bulk of the canopy somewhat lower and a greater incidence of vines (especially *Vitis* and *Rhoicissus*). I capitalized on the overall similarity in forest structure in conjunction with the island-like nature of the forests patches to investigate forest bird diversity and community structure at 5 sites between Cape Town and Alexandria.

Aims

To birds that live only in forests and avoid lower vegetation, such as fynbos, between the forests, suitable habitat is distributed as a chain of island-like areas of increasing isolation and smaller extent from the eastern Cape to Table Mountain. I ask the following questions. 1. To what extent are the forests like true islands to the birds, and show in the classical fashion a reduced species diversity in more isolated patches? 2. To what extent do the forest patches present similar habitat for forest birds, in terms both of the structure of the vegetation and of the food resources available to birds? 3. If bird diversity decreases with isolation as predicted by most island models (Case and Cody 1983) to what extent do birds typical of fynbos or other non-forest habitat invade the forests and occupy ecological roles analogous to those of forest-restricted species? 4. With varying bird species numbers in forests, to what extent do smaller numbers of species occupy broader niches, and show density-compensation (eg. MacArthur, Diamond and Karr 1972; Wright 1980) for absent forest bird species? 5. If density compensation exists, is it ubiquitous among broadly distributed birds, or restricted to certain species, guilds or niches?

Methods

Between October 21 and December 12, 1979 I studied forest birds at the five sites marked in Fig. 1. These sites, from southwest to northeast, are Skeleton Gorge, at the Kirsten-

bosch Botanical Gardens on Table Mountain; in the Oubos forest of the Riviersonderend Mountains $2\frac{1}{2}$ km N of the Groenwald farm 40 km east Caledon; in the Department of Forestry's Grootvadersbos forest north of Heidelberg; in the Knysna Forest 4 km west of the Deepvalle Forest Station; in the Alexandria Forest around 6 km SE of the forest station S of Alexandria (same site as that of Harkus 1977). I spent from 6 to 10 days at each site.

Birds were censused on study sites selected for homogeneity of vegetation, between 5 ha and 10 ha in size, gridded in colored forestry tape for the purposes of mapping birds and estimating their densities. Records were accumulated on study area maps until species identities, locations and densities were judged complete, when no new records were added from day to day. Most species bred on the study sites, territorial activity and singing were high, and many nests were found. Such species are most easily censused, and include all of the insectivorous birds and many generalized ground foragers such as bulbuls and thrushes. Other birds, especially frugivores, were more widely ranging, and while they foraged regularly in the study sites, their densities are only broadly estimated. Note that, since final census estimates are made by the accumulation of point records

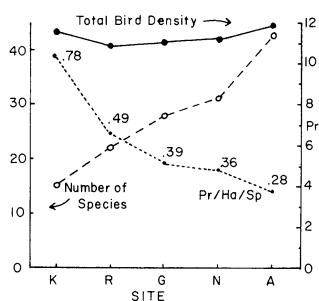


Fig. 3. Numbers of bird species (ordinate at the left), total bird density (ordinate at the right) and bird pairs/hectare/species (dotted line and included figures) at five forest sites

on the site maps, there are no estimates of confidence around census data, only a "best estimate" which is derived in exactly similar fashion amongst sites.

In addition to census data of species numbers and densities, I collected observations on foraging heights of birds. Most insectivorous birds were feeding either young in the nest or recently fledged juveniles, and my data on these species are quite adequate. Other species, especially those nesting elsewhere or with cryptic habits (litter-scratching in the thicker bush), are less well categorized in terms of feeding heights and methods, and will be discussed in more general terms.

A foraging observation was recorded if a bird foraged for at least 20 s without distraction, after which its presence in a vegetation layer was recorded or apportioned amongst layer if its activity spanned several. The limits of horizontal layers are shown in e.g. Fig. 4 for the foliage insectivores, remained constant amongst sites and bird guilds, and are those used also to describe the distribution of vegetation over height. The numbers of foraging height observations, as defined above, averaged 33.8 ± 21 for all bird species, and for the three bird guilds treated in detail in this paper are: foliage insectivores, average 39.4 observations/species; flycatchers, 33.6 observations/species; slow-searching omnivores, 22.6 observations/species.

At each site I constructed a foliage profile (see, e.g., Cody 1974) of the vegetation based on observations at 20 randomly selected points within the study site. At each such point, four orthogonal directions are established, and along each direction the horizontal distance to vegetation that will half cover a vertically-held board is estimated, at a sequence of heights above ground level. These heights are $1/2, 2, 4, 7, 10, 15, 20, 25, 35, 50, 69, 80$ and 100 feet above the ground (see Fig. 4 for metric equivalents). Vegetation density is the reciprocal of the horizontal distances, and the foliage profile is drawn as an average of 80 density estimates at each of 13 heights. In this way the density of vegetation over height may be compared between sites.

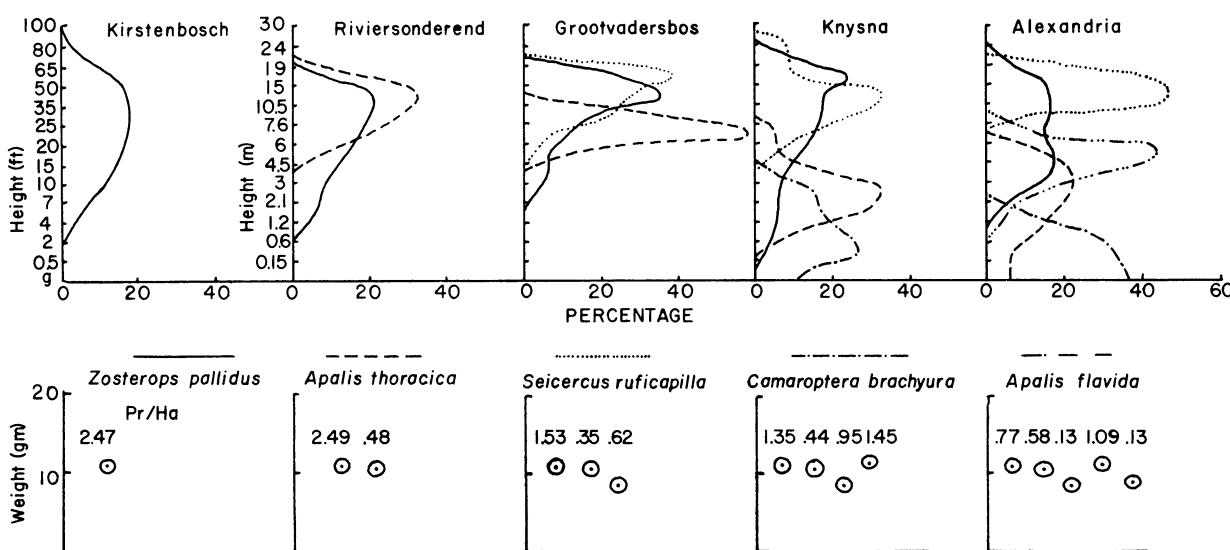


Fig. 4. Foraging height distributions of five species of foliage insectivorous birds at five sites, from the one-species system at the small and isolated Kirstenbosch forest to the five-species system in the east at Alexandria. Abscissa in upper Figures is percentage of foraging time spent within the height intervals shown on the ordinate. Below are species weights, and the densities of the five species in pr/ha at each site, ordered as are the captions above

I estimated the food availability for the insectivorous birds using Tanglefoot traps, 10 × 10 cm white plaques coated with a sticky resin and hung at various heights in the vegetation between the ground and 12 m. Ten plaques were used at each of four stations at each study area. The utility and replicability of these catches and their relevance to insectivorous bird densities are discussed elsewhere (Cody, MS), but here these figures are used in a strictly comparative fashion to estimate intersite differences in insect densities. Of course the insect catches vary with season, and are used here to estimate potential intersite differences at the peak of the bird breeding season.

Results

Census results

The species and densities of birds at the five sites censused are given in Table 1. Sites are ranked in the Table from southwest to northeast, from forests most isolated from the larger contiguous forest regions to those least isolated. Likewise bird species are ranked from those of the southwestern forests to those occurring only in the northeastern forests. In addition to the birds listed in Table 1, at each site there are raptors, aerial feeders such as swallows and swifts, and cuckoos, but I paid little attention to them; the cuckoos are a particularly obvious element of the Alexandrian avifauna, and in the middle of the day the predominant bird noises are the calls from four species of cuckoo. Martin et al. (1979) published bird censuses of the Riviersonderend and Grootvadersbos forests, with very similar results to mine.

The most noticeable aspect of Table 1 is that species numbers increase from southwest to northeast, from 15 spp. in Kirstenbosch to 43 spp. at Alexandria. From Kirstenbosch through Riviersonderend to Grootvadersbos species numbers are steadily augmented (15 → 22 → 28) with all species at Kirstenbosch being still present at Grootvadersbos. The species list at Knysna is further increased, but species turnover is involved; the 31 spp. at Knysna include 10 spp. not found in Grootvadersbos, and 7 at Grootvadersbos are not on the Knysna list (although 4 of these reappear at Alexandria). An additional 11 new species occur at Alexandria, whereas only three Knysna species are not represented in the Alexandria total. Thus the forest bird faunas to the southwest are derived from the more diverse faunas in the northeast chiefly through a process of attrition, with more and more species presumably being filtered out with increasing insolation of the forests.

Despite the lower diversity in the southwestern forests, it appears that only a few birds typical of non-forest habitats enter the forests there but are excluded from the forest elsewhere. The first two species listed, Cape canary and Cape turtle dove, seem the only good examples; although their ranges extend east beyond the Knysna and Alexandria forests, they were found in only the southwestern, low-diversity, forests. The first 9 species listed (9/15) of the Kirstenbosch birds are birds with habitat ranges in the southwestern Cape that include non-forest habitat, particularly fynbos and *Brabeium-Podalyria* riparian woodland, and some of these reach higher densities in fynbos than they do in the forest at Kirstenbosch (see Cody 1975). In contrast, a large majority of the Knysna and Alexandria species occupy forest exclusively (31/43 of the Alexandria total);

it seems likely that some of the forest occupants at Kirstenbosch are as dependent on other habitats as on the forest per se, and perhaps owe their persistence in isolated forest to the widespread availability of usable fynbos in the vicinity.

Comparisons of bird species numbers between forests depend heavily on assumptions that the forests are comparable to the birds, and in practice this means comparability in term of the structure of the vegetation and its productivity (Cody 1981). Many studies, beginning with MacArthur's diversity studies in the early 60's, have emphasized the dependence of bird species diversity in general and of specific habitat preferences in birds in particular on structural characteristics of the habitat (see reviews in Cody 1974, 1981; and Cody and Walter 1976, Cody 1978a for examples of detailed studies of species' habitat preferences with respect to vegetation). In Fig. 2 I give the foliage profiles of the five sites studied, and differences in vegetation structure are readily apparent. The tallest forest is Knysna (ht = 28.7 m), with Kirstenbosch and Grootvadersbos intermediate, and the Riviersonderend and Alexandria forests lower (ht = 21.2 and 22.1 m respectively). More substantial are the differences in the total amount of vegetation, estimated by the area A under the foliage profiles and varying by a factor of two between Kirstenbosch and Alexandria, and mean vegetation density measured as A/ht, which declines from 0.96 at Kirstenbosch to 0.55 at Alexandria. Differences in total amount of vegetation follow differences in total precipitation, with less leaf area supported in the drier eastern forests (Fig. 2).

Bird species diversity has been shown positively correlated to both the vegetation height and a simple index of the equitability of distribution of vegetation density over height, the "half-height". In an earlier paper (Cody 1975), bird species numbers S in a variety of vegetation types in western Cape Province are related to the principle component of vegetation height and half-height, H, by the relation

$$S = \frac{a}{1 + be^{-cH}}.$$

Based on this relation and a span of H between 1.865 (Alexandria) and 1.975 (Knysna), the expected numbers of bird species S in the five sites can be expected to vary between only 24.81 and 24.84 species (<1%; observed: 287%); further the observed differences in species numbers are uncorrelated with the differences expected from structural dissimilarities among the forests. Clearly the structural differences here play at best a very minor role in determining bird species numbers in these forests.

Differences in total amount of vegetation (area under foliage profile) may affect bird diversities to a minor degree only, but have been found to be a more important contribution to bird densities (Cody 1980). This possible relation will be discussed in the following section.

Bird densities

Table 1 gives the total bird densities of those species censused at each site. In contrast to the wide differences in species numbers, the total bird densities vary very little (Fig. 3). The lowest and the highest densities, at Riviersonderend and Alexandria respectively, differ by only 10%; given an inherent potential for some inaccuracy in bird species counts, differences as small as 10% seem insignificant. The uniformity of total bird density among sites is particularly striking given that species numbers among sites

Table 1. Densities of bird species, in pairs per hectare, foraging regularly in five Afromontane woodland sites listed from west to east, Kirstenbosch (Cape Town) to Alexandria

Bird species	Kirstenbosch	Rivier-sonderend	Groot-vandersbos	Knysna	Alexandria
1 Cape canary <i>Serinus canicollis</i>	0.89	0.30	0.37		
2 Cape turtle dove <i>Streptopelia capicola</i>	0.25	0.42	0.37		
3 Red-winged starling <i>Onychognathus morio</i>	0.12	0.05	0.10	0.02	
4 Lesser double-collared sunbird <i>Cinnyris chalybeus</i>	0.10	0.12	0.10	0.22	
5 Cape robin <i>Cossypha caffra</i>	0.99	0.12	0.10	—	0.06
6 Cape batis <i>Batis capensis</i>	1.42	0.84	0.96	0.50	0.48
7 Cape white-eye <i>Zosterops pallidus</i>	2.47	2.49	1.53	1.35	0.77
8 Boubou shrike <i>Laniarius ferrugineus</i>	0.35	0.35	0.25	0.28	0.53
9 Olive thrush <i>Turdus olivaceus</i>	0.96	0.48	0.35	0.08	0.06
10 Dusky flycatcher <i>Muscicapa adusta</i>	1.07	0.72	0.42	0.28	0.26
11 Paradise flycatcher <i>Tersiphone viridis</i>	0.88	0.42	0.57	0.42	0.35
12 Sombre bulbul <i>Andropadus importunus</i>	1.42	1.20	0.72	1.24	0.83
13 Red-eyed turtle dove <i>Streptopelia semitorquata</i>	0.17	0.30	0.30	—	0.16
14 Rameron pigeon <i>Columba arquatrix</i>	0.35	0.17	0.37	0.20	0.04
15 Cinnamon dove <i>Aplopelia larvata</i>	0.25	0.25	0.35	0.17	0.15
16 Greater double-collared sunbird <i>Cinnyris afer</i>		1.07	0.77	0.56	0.32
17 Bar-throated apalis <i>Apalis thoracica</i>		0.48	0.35	0.44	0.58
18 Olive woodpecker <i>Mesopicos griseocephalus</i>		0.25	0.30	0.22	0.25
19 Grey cuckoo-shrike <i>Coracina caesia</i>		0.30	0.35	0.31	0.23
20 Blue-mantled flycatcher <i>Trochocercus cyanomelas</i>		0.15	0.30	—	0.13
21 Forest canary <i>Serinus scotops</i>		0.12	0.62	0.07	0.37
22 Swee waxbill <i>Coccycygia melanotos</i>		0.12	0.12	—	—
23 Tambourine dove <i>Turtur tympanistria</i>			0.15	—	0.10
24 Olive bush shrike <i>Chlorophoneus olivaceus</i>			0.10	0.05	—
25 Fork-tailed drongo <i>Dicrurus adsimilis</i>			0.15	0.07	0.07
26 Yellow-throated warbler <i>Seicercus ruficapilla</i>			0.62	0.95	0.13
27 Terrestrial bulbul <i>Phyllastrephus terrestris</i>			0.15	0.28	0.51
28 Cardinal woodpecker <i>Dendropicos fuscesens</i>			0.05	0.05	0.10
29 Buff-spotted flufftail <i>Sarothrura elegans</i>				0.12	0.02
30 Red-billed wood-hoopoe <i>Phoeniculus purpureus</i>				0.12	0.07
31 Bleating bush warbler <i>Camaroptera brachyura</i>				1.45	1.09
32 Black-headed oriole <i>Oriolus larvatus</i>				0.40	0.32
33 Narina trogon <i>Apaloderma narina</i>				0.27	0.25
34 Chorister robin <i>Cossypha dichroa</i>				0.44	0.42
35 Starred robin <i>Pogonochichla stellata</i>				0.11	0.26
36 Black cuckoo-shrike <i>Campethaga phoenicea</i>				0.06	0.06
37 Knysna loerie <i>Tauraco corythaix</i>				0.20	0.25
38 Puff-backed shrike <i>Dryoscopus cubla</i>				0.31	0.36
39 Grey sunbird <i>Cyanomitra veroxii</i>					0.54
40 Brown robin <i>Tychaeodon signata</i>					0.51
41 Forest weaver <i>Symplectes bicolor</i>					0.45
42 Collared sunbird <i>Anthreptes collaris</i>					0.45
43 Yellow-throated apalis <i>Apalis flavida</i>					0.13
44 Emerald-spotted wood-dove <i>Turtur chalcospilos</i>					0.06
45 Square-tailed drongo <i>Dicrurus ludwigii</i>					0.06
46 Trumpeter hornbill <i>Bycanistes bucinator</i>					0.05
47 Black-collared barbet <i>Lybius torquatus</i>					0.05
48 Red-fronted tinker-barbet <i>Pogoniulus pusillus</i>					0.05
49 White-breasted coucal <i>Centropus superciliosus</i>					0.02
Total species number:	15	22	28	31	43
Total bird density: pr/ha	11.69	10.72	10.99	11.24	11.84
pr/ac	4.73	4.34	4.45	4.55	4.79
PR/HA/Species:	0.78	0.49	0.39	0.36	0.28

vary nearly three-fold. Although Alexandria has the highest species count and the highest total bird density, there seems to be no general relation among sites between species numbers and total density. An interpretation of the invariance of total bird density follows.

Birds have a well-developed potential for habitat selection, and will be found breeding only in those habitats that

supply their needed resources above some critical threshold level. They have in addition the behavioral flexibility to defend smaller territories, and live in higher densities, where resources are more abundant. Three factors can be considered independently to affect resource abundance: the structure of the vegetation, which supplies foraging sites and perches from which to search or sally; the abundances of

food per se; and the extent to which foraging sites and food are exploited by other species with overlapping requirements – the effects of competitors.

Treating these factors in turn, vegetation has been shown to affect bird density. In areas of continuous and smoothly varying vegetation cover, where the total vegetation density varies smoothly, bird densities increase with increasing vegetation density. These effects are in general difficult to measure independently from changes in bird species numbers, with changing vegetation, but in Moroccan maquis (chapparral or fynbos) I found that variations in vegetation density per se accounted for 24% of variation in total bird density (Cody 1980). While I have no basis for precise, quantitative predictions, structural differences among the five forest sites would lead us to expect considerably lower total bird densities in Alexandria with the lowest $A=40.1$, and considerably higher bird densities at Kirstenbosch and Grootvadersbos, predictions clearly not verified. Thus similarities in total bird densities among sites are due to vegetation structure similarities among sites, nor does vegetation structure act in a way to offset declining species numbers and boost density.

The availability of food for insectivorous birds varies both between habitats and within habitats from year to year. A rough estimate of this availability is provided by the Tanglefoot catches made in the five forest sites as shown in Fig. 2. A total of 25 plaques were distributed from the ground to 12 m in each site. The mean numbers of insects caught per plaque side varied between a high of 18.1 insects at Riviersonderend to a low of 7.8 insects in Grootvadersbos. Insect density varied approximately with the vegetation density within sites, being particularly high at ground level, falling to the lowest levels between heights of 1/2–2m where vegetation densities were low, and generally increasing with above this with increasing vegetation density up into the subcanopy. These figures at best give crude information on what is available to the birds, and the variability amongst them must be interpreted empirically. At a site in pine-oak woodland in Arizona, I found that year-to-year variations in insect catches with Tanglefoot boards were 8-fold between 1970 and 1979, and were positively correlated with year-to-year variations in bird densities. From these limited data it seems that such changes in insect density correspond to about a doubling of total bird density (Cody 1981). Again, from the Moroccan maquis study cited above, the correlation between total bird density and Tanglefoot insect catches was 0.88, teaching us to expect that, all other things being equal, sites with higher insect catches should support higher bird density. Using the 4:1 insects:birds relation above, the African forests might vary from 91% (Grootvadersbos) to 113% (Riviersonderend) of the Kirstenbosch bird density, figures that obviously fail to explain either density similarities or density differences.

Although both structural differences and differences in apparent insect availability are measured among the five forest sites, neither seem to be of the magnitude greatly to affect the total bird densities at each site. And yet, with the empirical observations that total bird density remains nearly constant while bird species numbers vary nearly three-fold, bird density per species obviously must be quite different from one site to another. These figures are given at the bottom of Table 1 and shown in Fig. 3, and range from almost 0.8 pr/ha/sp at Kirstenbosch to just under 0.3 pr/ha/sp in Alexandria. Ruling out a major role for

the several alternative explanations, I feel the differences in density/species among sites can be confidently attributed to the site differences in species numbers. At the sites of high bird diversity, resources are divided among more species and the share of each species is small; at sites with lower consumer diversity, the species present can avail themselves of resources that would otherwise have gone to absent competitors, and they are thereby able to maintain higher densities. This concept of density compensation has been in the ecological literature for many years (Crowell 1962; MacArthur et al. 1972; Case 1975; see Wright 1980 for recent synthesis), but data gathered from controlled sites are few. We can reasonably estimate that, in order to obtain mean densities per species of three times those of the Alexandria site at the Kirstenbosch forest, we would require insect densities perhaps a dozen times greater there and vegetation densities several times greater there than at Alexandria. Both of these possibilities can be safely dismissed, and it appears that competitive release in the lower-diversity communities has permitted their higher species densities.

It remains likely that resources other than insects can affect total bird density. The incidence of non-insectivorous birds in these forest communities is higher towards the Alexandria end of the series of forests. For example, species such as Knysna loeries, trumpeter hornbills, red-fronted tinker barbets, black-headed orioles and red-billed hoopoes contribute to total bird density at Knysna and especially at Alexandria, and it appears that such largely frugivorous or vegetarian species might depend on resources not available in the southwest Cape forests. This makes the point of density compensation all the more strongly, for the densities of insectivorous birds in the southwestern forests must be very much greater than those of conspecific or analogous populations in the northeast. In general, not all of the species of low-diversity communities are expected to be involved in density compensation, and examination of Table 1 identifies those species that have greatly increased densities in the species-poor sites. The questions of which species can density-compensate and which not are discussed at the "guild" level in the following sections.

The foliage insectivores

An important and reasonably discrete guild in these forest bird communities are the foliage insectivores, birds which search actively in the foliage for chiefly insect prey. There are five such species at Alexandria, (Cape white-eye, bar-throated apalis, yellow-throated apalis, bleating bush warbler and yellow-throated warbler), but at each successive site to the west a species is lost, so that by Kirstenbosch a single species, Cape white-eye, remains. All are similar in size, and differ mainly by their foraging at different height in the vegetation (see Fig. 4). Other insectivorous birds are excluded from this guild because of differences in foraging behavior or body size; for example, the mostly insectivorous forest weaver at Alexandria (at 34.6 g) is three times the weight of the white-eye and moves far more slowly through the vegetation.

The summed densities for the guild are more or less constant among sites, with the exception of higher density at Knysna, where the vegetation is significantly taller (Fig. 5). For the white-eye, density decreases from 2.5 pr/ha where it occurs alone and with a single additional species, down to one third this level where it coexists with 4 addi-

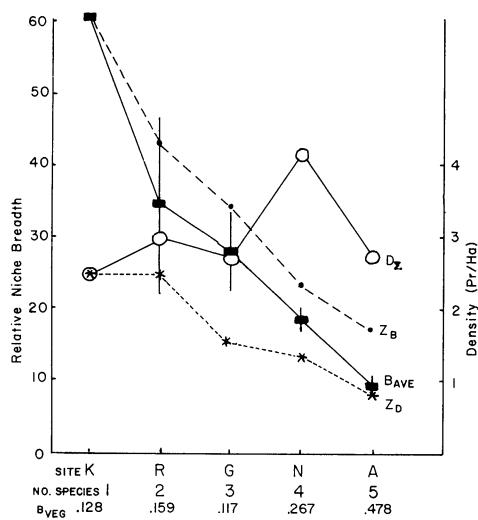


Fig. 5. Densities and niche breadths of foliage insectivores at five forest sites. Open circles: total guild density D_{Σ} (1–5 species); asterisks: density Z_B of the Cape white-eye *Zosterops pallidus*, decreasing with increasing guild size; black bars: means and standard errors of niche breadth over foraging height B_{AVE} for the foliage insectivore guild; small dots and dashed line: decreasing niche breadth Z_B of *Zosterops* with increasing guild size

tional species. This trend of declining density in higher-diversity systems is followed by none of the other species; bar-throated apalis, for example, is commonest at Alexandria (the 5-species system), and uniformly less common to the west. Also shown in Fig. 5 are niche breadths, the average for the community as a whole and of the white-eye in particular. Niche breadths B_j are calculated from the foraging height distributions of Fig. 4, as $1/\sum p_i^2$, where the p_i are the proportions of time a species spends in a horizontal layer of vegetation i . But since the equitability of the vegetation distribution amongst these layers varies between sites, the B_j are corrected by dividing by $B_V = 1/\sum p_i^2$, a site-specific measure of this equitability where p_i = the amount of vegetation in the layers i . This gives a relative niche breadth B_j/B_V for each species, and its average is plotted in Fig. 5. The average niche breadth in the guild decreases with increasing species number, and specifically the niche breadth of the white-eye over vegetation height decreases 3-fold, as does its density, from the 1-species to the 5-species community.

I next enquire whether the structure of the foliage insectivore guild at Alexandria enables us to predict which species will drop out most readily with the increasing isolation of the forests to the west. I do this by examining various subsets of the 5-species guild, based on the data on foraging height distributions in Fig. 4. For each species pair, the foraging height distributions can be used to generate a value of foraging height overlap, with a range from 0 to 1, which represents the area common to the two foraging height curves. These values are arranged in the symmetrical 5×5 community overlap matrix A as shown in Fig. 6. If these 5 species are at equilibrium, then they will satisfy the matrix equation $K = AX$, where X is the (observed) matrix of putative equilibrium values estimated in the forest, and K is the vector of (calculated) carrying capacities that satisfy the equation.

ALEXANDRIA Foliage Insectivores

$$\begin{array}{c} K = A X \\ \text{Species } Z \quad \begin{bmatrix} 1.12 \\ 1.27 \\ 0.42 \\ 1.28 \\ 0.81 \end{bmatrix} = \begin{bmatrix} 1 & .38 & .38 & .02 & .51 \\ .38 & 1 & 0 & .31 & .51 \\ .38 & 0 & 1 & 0 & 0 \\ .02 & .31 & 0 & 1 & 0 \\ .51 & .51 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} .77 \\ .58 \\ .13 \\ 1.09 \\ .13 \end{bmatrix} \end{array}$$

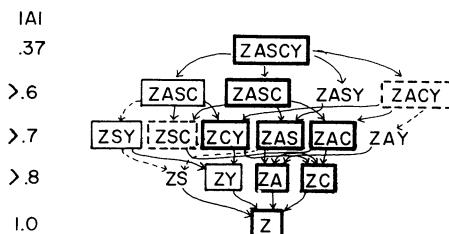


Fig. 6. Analysis of 5-species foliage insectivore guild at Alexandria. Above, the guild is represented by the matrix A of foraging height overlaps and the vector X of observed densities, from which is calculated the vector K of species' carrying capacities. Species abbreviations are Z : *Zosterops pallidus*; A : *Apalis thoracica*; S : *Seicercus ruficapilla*; C : *Camaroptera brachyura*; Y : *Apalis flavida*. Below, the likely breakdown of the 5-species community into smaller subsets is shown, based on the feasibility of the subsets, the relative abundances of species in the subsets, and the values of the determinants of each subset. Unboxed subsets are unfeasible, those with dashed boxes marginally feasible, and those with heavy boxes have the higher determinant values as indicated by the column at the left. The likely degeneration of the $\{ZASCY\}$ guild is to $\{ZASC\}$, then to either of $\{ZCY\}$, $\{ZAS\}$ or $\{ZAC\}$, then to $\{ZA\}$ or $\{ZC\}$ and then $\{Z\}$. The observed degeneration, with increasing forest isolation, is $\{ZASCY\} \rightarrow \{ZASC\} \rightarrow \{ZAS\} \rightarrow \{ZA\} \rightarrow \{Z\}$. See text for further explanation

There are a variety of ways in which the stability of the various subsets of this community can be tested, using the vector K and the matrix A . Suppose, for example, we generate a three-species subset $\{ZAS\}$ by “removing” species C and Y from the 5-species set $\{ZASCY\}$. Here Z denotes *Zosterops pallidus*, A : *Apalis thoracica*, S : *Seicercus ruficapillus*, C : *Camaroptera brachyura* and Y : *Apalis flavida*. The subset $\{ZAS\}$ will be feasible only if all three of the new equilibrium values X are positive. If it is feasible, the robustness of the subset's stability, that is, continued persistence in the face of environmental perturbations, can be estimated by a) the return time of the subset to equilibrium following a displacement from equilibrial densities; b) the likelihood of one or more species going to extinction following changes in the carrying capacities K of the three component species; c) the value to the determinant of A , $|A|$. If a subset is likely to be persistent and stable, then its return time to equilibrium will be rapid, the component species will persist despite changes in their carrying capacities (that is, “feasible” K -space is relatively large), and the determinant of the subset's overlap matrix will be high (approaching the maximum value 1).

I used the results of a simulation analysis by T. Case to ascertain that these three estimates of subset stability are not independent. These simulations were conducted on the Alexandrian subsets of foliage insectivores, and also on subsets of the 4-species Knysna system. Returns times

KNYSNA Foliage Insectivores

$$\begin{array}{ccc} K & = & A \\ \text{Species: } Z & \left[\begin{array}{c} 2.48 \\ 1.70 \\ 1.93 \\ 1.98 \end{array} \right] & = \left[\begin{array}{cccc} 1 & .31 & .70 & .22 \\ .31 & 1 & .10 & .50 \\ .70 & .10 & 1 & 0 \\ .22 & .50 & 0 & 1 \end{array} \right] \left[\begin{array}{c} 1.37 \\ .46 \\ .92 \\ 1.45 \end{array} \right] \end{array}$$

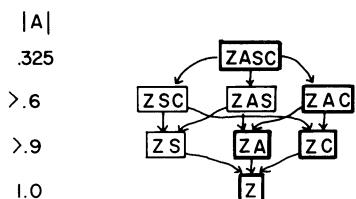


Fig. 7. Analysis of 4-species foliage insectivore guild at Knysna. See preceding figure for explanation of species abbreviations. The most likely breakdown of the guild is from {ZASC} to {ZAC} → {ZA} → {Z}. See text for further explanation

to equilibrium (RT), the average computed from ten displacements from equilibrium for each subset, are related to the subset determinant by the equation $\log(RT) = 1.729 - 0.815|A|$, $R^2 = 82\%$, and relative K-space is related to the determinant by the equation $\log(\text{Rel. } K\text{-space}) = 2.760|A| - 2.660$, $R^2 = 89\%$. Thus subsets with high determinant values return to equilibrium faster following displacements, and are stable over larger relative K-space than are subsets with smaller determinants. I use only the value of the determinant in estimating which subsets are likely to be found in lower-diversity communities.

The likely degeneration of the Alexandria guild is shown in Fig. 6. Arrows show the most likely pathways, and dashed arrows less likely paths. Unboxed combinations are unfeasible ({ZASY}, {ZAY}, {ZS}), and combinations with dashed boxes unlikely since one of the members has an equilibrium density of less than 0.1 pr/ha ({ZACY}, {ZSC}). Note that only subsets than include the ubiquitous *Zosterops* are analysed. Combinations boxed with the heavier lines are those with higher determinants, the limits of which are shown at the left of the chart. The analysis shows that a likely path of degeneration is {ZASCY} → {ZASC} → {ZAS} → {ZA} → {Z}, which is in fact just the order in which these species drop out in forests to the west of Alexandria.

In Fig. 7 a similar analysis is worked out with the Knysna 4-species guild. Here, based on the larger determinant of {ZAC} (0.634, versus 0.447 for {ZAS}), the most likely path is {ZASC} → {ZAC} → {ZC} or {ZA} → {Z}, which is at variance with the observations, but which is in fact a likely pathway in the Alexandrian community. This result suggests that, while subsets {ZAC} and {ZC} were not found in this study, they might occur in isolated forest patches and should be looked for. The idea that alternative subsets of competition communities might be almost equally likely and stable is relevant here (Gilpin and Case 1976; Case and Casten 1979).

Matching bird utilization curves to the foliage profile

The theory of resource utilization predicts that competition will minimize unused resources by selecting for species

whose utilization curves, in concert, match the resources provided by the habitat: $\{P - \sum_i X_i U_{ij}\}$ will be minimized, (MacArthur 1970; Case 1980), through adjustment of the vector of equilibrium densities X_i of species i . P represents a production curve over resource states j , and each species has a specific utilization of these resources U_{ij} . Although the data on density and distribution of insects over vegetation height is unsufficient to use as a direct measure of the resources available to the insectivorous bird community, I shall use the density and distribution of the vegetation itself as an estimate of "resources". Previous studies have shown that vegetation density has an important influence on where insectivorous birds forage, although sometimes the distribution of insects through the vegetation is not congruent with the distribution of vegetation itself (e.g. Fig. 24h, Cody 1978; Fig. 2, Cody 1980). The limited data on insect densities over height shown in Fig. 2 show little consistency in pattern among sites; insect densities are significantly correlated with vegetation density at three sites, Alexandria, Knysna and Riviersonderend, but not at the remaining two sites, and are uncorrelated with the amount of vegetation within a height interval at all sites (see Table 2).

I ask first how individual species' utilization curves are related to the distribution of vegetation, both to the mean vegetation density (X_1) in a height interval, and the amount of vegetation within that interval (X_2). These correlations are shown in the upper left part of Table 2. Just one species (*Camaroptera brachyura*) forages within the levels of dense X1-vegetation, with significant positive correlation between its frequency distribution U_C and vegetation density X_1 ; the tendency in *Zosterops* and *Seicercus* is to avoid dense vegetation (negative correlations). On the other hand, *Zosterops* foraging activity is highly correlated with those layers that contain large amount of vegetation ($U_Z \times X_2$ correlated) at all sites, as is that of *Seicercus*; *Camaroptera* forages in layers where there is little (but dense) vegetation overall, but *Apalis thoracica* alters its foraging among sites. *A. thoracica* is not found where the most vegetation is concentrated at Alexandria and Knysna (negative correlations), but shifts increasingly to these layers in the 3-species and 2-species sites, suggesting that these situations with fewer species permit such a shift.

Taking the insectivore guild as a whole, I correlate 4 increasingly realistic measures of bird utilization to aspects of vegetation distribution. Firstly Y_1 is the distribution of foraging activity U_{ij} summed over species i : $\sum_i U_{ij}$. This measure takes no account of the differences in abundance among species, which is corrected in $Y_2: \sum_i X_i U_{ij}$. But then larger species remove more insect prey and exert a greater effect than do smaller species, and weighting each species' contribution to overall bird utilization by its weight W adjusts for this: $Y_3: \sum_i W_i X_i U_{ij}$. Bird weight to the power 0.71 is a current figure (King 1974) that reflects how field metabolic rate increases at a decreasing rate with body size: $Y_4: \sum_i W_i^{0.71} X_i U_{ij}$. In Table 2 (lower left-hand columns) it is seen that each more refined measure of utilization is increasingly correlated with vegetation density; overall bird utilization is high where vegetation density is high, and adjusting foraging frequency by bird density and then by body size greatly improves the match. A posteriori, it seems that the factor $W^{0.71}$ overestimates the field metabolic rate of these birds, and weights larger species too strongly; as

Table 2. Correlation coefficients between foliage insectivore species (column at left) and vegetation characteristics at each of five forest sites (row at the top). Sites are A: Alexandria, 5 spp.; N: Knysna, 4 spp.; G: Grootvadersbos, 3 spp.; R: Riviersonderend, 2 spp.; K: Kirstenbosch, 1 sp. Species are Z: *Zosterops pallidus*, A: *Apalis thoracica*, S: *Seicercus ruficapilla*, C: *Camaroptera brachyura*, Y: *Apalis flavigularis*. Top part of the table gives the correlations between individual species foraging distributions and vegetation profile density (left third), amount of vegetation (centre third) and the combination of these two (right third). The second part of the table gives correlation coefficients between four measures of guild utilization Y_i and vegetation: $Y_1 = \sum_{ij} U_{ij}$, the sum of foraging percentages U_{ij} at heights j over species i ; $Y_2 = \sum_{ij} X_i U_{ij}$, with each species weighted by its abundance X_i ; $Y_3 = \sum_{ij} W_i^{0.71} X_i U_{ij}$, with each species additionally weighted by its weight W_i ; $Y_4 = \sum_{ij} W_i^{0.71} X_i U_{ij}$, where species weight W is raised to the power 0.71. The lowest line of the table shows how estimates of insect density over height correlates with vegetation measures over height. In the left two-thirds of the table, values above 0.523 are significant at the 5% level ($n=13$, 1 independent variable); in the right third of the table (two independent variables) values above 0.627 have the same significance

Species	Correlations with foliage profile, or veg. density: X_1					Correlations with amount of vegetation per layer: X_2					Multiple correlations with veg. density + amount: $X_1 + X_2$				
	Site: A 5	N 4	G 3	R 2	K 1	A 5	N 4	G 3	R 2	K 1	A 5	N 4	G 3	R 2	K 1
Z	-0.182	-0.449	0.547	-0.034	-0.343	0.779	0.738	0.956	0.664	0.677	0.790	0.748	0.957	0.681	0.714
A	0.153	-0.251	0.531	0.154		-0.352	-0.541	0.256	0.921		0.370	0.743	0.536	0.922	
S	-0.163	-0.306	0.438			0.796	0.912	0.886			0.809	0.740	0.893		
C	0.808	0.603				-0.392	-0.449				0.886	0.478			
Y	0.021					0.018					0.245				
Y_1	0.400	-0.218	0.668	0.084	-0.343	0.450	0.196	0.847	0.859	0.677	0.627	0.579	0.871	0.862	0.714
Y_2	0.888	0.010	0.606	0.009	-0.343	-0.129	0.393	0.950	0.746	0.677	0.891	0.564	0.943	0.756	0.714
Y_3	0.903	0.115	0.612	0.007	-0.343	-0.157	0.238	0.950	0.743	0.677	0.910	0.480	0.951	0.753	0.714
Y_4	0.901	0.086	0.610	0.007	-0.434	-0.164	0.281	0.950	0.697	0.677	0.905	0.523	0.946	0.755	0.714
Insects:	0.952	0.784	0.384	0.966	-0.050	-0.324	-0.218	0.289	-0.159	-0.481					

the exponent of W is decreased down to 0.29, the correlation in the Y_4 row increases to 0.913 (Alexandria) and 0.273 (Knysna), but the low Y_4 correlations at Riviersonderend and Kirstenbosch are not much improved.

Correlations between bird utilization and vegetation density are strongest at Alexandria, and in general weaken to non-significance across the Table (Table 2). Regarding the other two sites where insect density is correlated with vegetation density, at Knysna correlations improve from Y_1 to Y_3 but remain insignificant, and at Riviersonderend correlation are close to zero throughout. In contrast, correlations between bird utilization and amount of vegetation improve from left (5-spp) to right (increasingly fewer species) in Table 2, lower right. The reason for low guild correlations in Alexandria and Knysna appears to be the inclusion of *Apalis thoracica* and *Camaroptera brachyura* in these diverse communities (see above in table). The former appears to be excluded from vegetation layers where most of the vegetation is found, and the latter is restricted to lower levels where the vegetation is dense but not voluminous.

Predictions of bird densities in low diversity forests

A final use to which the insectivore guild can be put is to test theoretical predictions of species densities in the lower diversity forests to the west based on densities and overlap matrices in the higher diversity forests to the east. Each site's data can be used to predict the new equilibrium densities of each species extant to the west; this produces 20 predicted density values, which are compared to the 20 observed values. Predicted and observed values are related by the equation (Actual density) = 0.458 + 0.777 (Predicted density), which is highly significant ($F_{1,18}=17.90$; $P<0.001$) and its slope not significantly different from unity ($t=1.215$, $P\simeq 0.25$). In general the predictions from the

Knysna data are far better than the predictions from the Alexandria data: *Zosterops* predicted densities in Grootvadersbos, Riviersonderend and Kirstenbosch are respectively 1.68, 2.15 and 2.47, compared to observed values of 1.53, 2.49 and 2.47. *Seicercus* is predicted at 0.63 in Grootvadersbos, observed at 0.62, but *Apalis* is consistently overestimated, by a factor of 2 to 3. Overall, the Knysna data predict densities within $\pm 20\%$ of the observed values. The Alexandria-based predictions are much wider of the mark, chiefly because *Zosterops* is predicted to be much scarcer than it actually is, by up to a factor of 3, and *Seicercus* is likewise underestimated. As with the Knysna data, *Apalis* is overestimated in less diverse forests. The conclusion seems inescapable that, because the Alexandrian forest is less like forests to the west than is Knysna, predictions based on Alexandrian observations are therefore less successful. Note that such predictions assume that a) carrying capacities remain the same, and that b) overlap values remain constant too, assumptions that are less likely to be upheld if either vegetation (amount, density and distribution over height) or insect density and distribution change among sites. Clearly the propensity for niche shifts in vertical foraging distributions will temper the predictions, and it appears that most species are flexible in this characteristic.

The sallying flycatchers

A second guild for which adequate data on foraging heights were obtained is the sallying flycatchers. These are species which forage largely by perching and waiting for insect prey to fly by, and glean foliage to a much more limited extent than do the foliage insectivores. In contrast to the foliage insectivores, species numbers show no pattern with increasing isolation of the site: A total of four species are involved (dusky flycatcher, *Muscicapa adusta*; paradise fly-

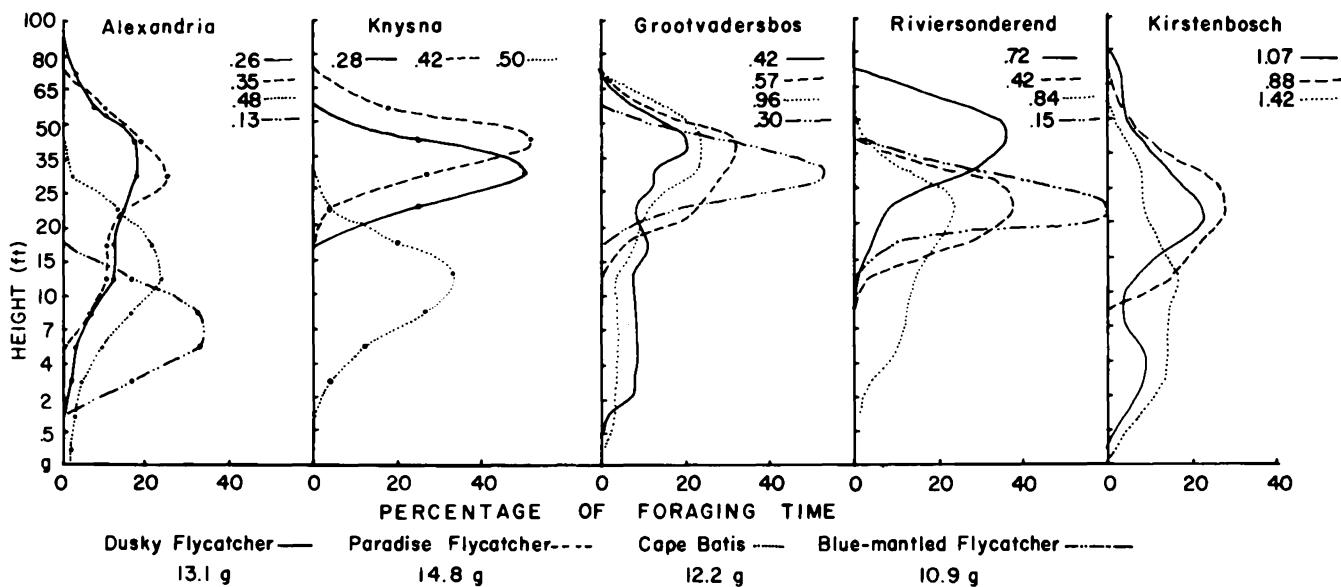


Fig. 8. Distributions of foraging activity over height for four species of sallying flycatchers. The density of each species at each site is given, in pr/ha, beside its line code above, and the weights of species are shown below. See Fig. 4 for ordinate in m

catcher *Terpsiphone viridis*; Cape batis *Batis capensis* and blue-mantled flycatcher *Trochocercus cyanomelas*), with the first three species occurring at all sites and the fourth not censused at Knysna and Kirstenbosch. The densities of the more widespread species are highest at Kirstenbosch, and show general trends of decreasing density to the east. Total flycatcher density increases from 1.2 pr/ha in Alexandria and Knysna, to around 2.2 pr/ha at Grootvadersbos and Riviersonderend, to 3.4 pr/ha in Kirstenbosch; inclusion of flycatching drongos (*Dicrurus adsimilis*) in the guild in the east would not alter the trend to increasing density in the west. The reasons for this increase seem most likely to be greater prey availability in the western areas, but my evidence for this interpretation is lacking, and I can cite only increased rainfall and increased amounts of vegetation in the west (see next paragraph) as a possible explanation.

Patterns of foraging segregation amongst the flycatchers are likewise not clearcut (Fig. 8). There seems to be more foraging activity lower in the forest at Alexandria, a site with more low vegetation, and less foraging at lower levels at Grootvadersbos, where the vegetation at lower levels is reduced. Note that there are not substantial size differences among the flycatchers (Fig. 8), but there may be further behavioral or foraging site differences amongst species that I did not measure. Overall flycatcher utilization, measured as $\sum_i W_i^{0.71} X_i U_{ij}$ increases with the amount of vegetation in a layer (Fig. 9), and thus the flycatchers may respond more directly to the distribution of vegetation over height than to height per se. This helps to explain why different species shift their foraging ranges from site to site (as vegetation changes), but more detailed information on both vegetation and flycatcher foraging is required to elucidate this point.

The slow-searching omnivores

This third guild consists of birds whose foraging is best described as slow searching; they are large, some eat fruit as well as insects, and include two shrikes (*Laniarius ferrugineus*, *Dryoscopus cubla*), two bulbuls (*Adnropadus impotens*, *Phyllastrephus terrestris*) and two cuckoo-shrikes (*Coracina caesia*, *Campephaga phoenicea*). The foraging height distributions, weights and densities of these species are shown in Fig. 10. A seventh member of the guild is the olive bush shrike *Chlorophoneus olivaceus*, but it is rare (at the three eastern-most sites), and I was unable to collect foraging data on it.

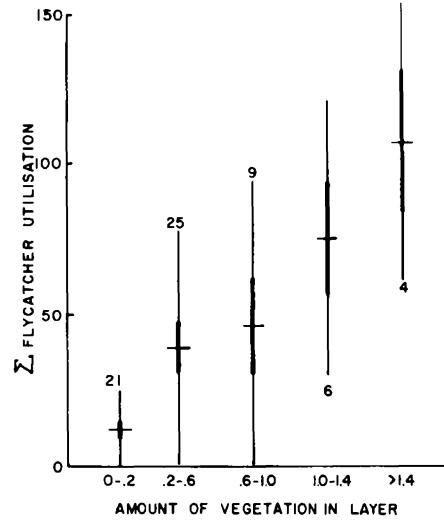


Fig. 9. Flycatcher utilization, derived from foraging activity weighted by species abundance and body size, is shown to increase as the amount of vegetation in a height interval increases, from left to right below. All forest sites are lumped together in this figure. The mean (small horizontal bar), its standard error (thick vertical bar) and standard deviation (thin vertical line) are shown for flycatcher utilization

The slow-searching guild provides an example of partial density compensation. While overall guild density is highest in the two eastern sites with 6 species each, density per species at Kirstenbosch, with just two species, is double

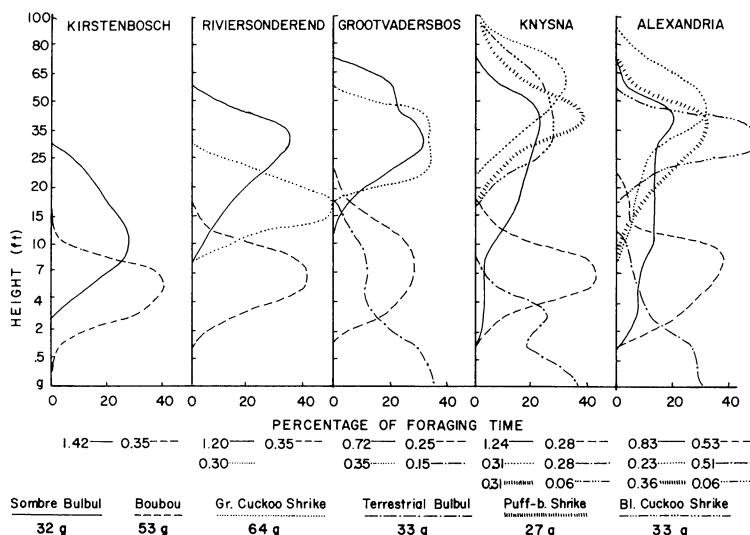


Fig. 10. Distributions of foraging activity over height for six species of the “slow-searcher” guild. Species line codes and weights are shown at the bottom of the figure, above which are the densities of each species at each site, in pr/ha. See Fig. 4 for ordinate in m

Table 3. Mean foraging heights and niche breadths for species of the slow-searcher guild at five forest sites. Sites: *A* Alexandria; *N* Knysna; *G* Grootvadersbos; *R* Riviersonderend; *K* Kirstenbosch. Species: *S* sombre bulbul; *B* boubou shrike; *G* grey cuckoo shrike; *T* terrestrial bulbul; *P* puff-backed shrike; *C* black cuckoo shrike. Mean foraging heights are upper left, and niche breadths lower right

Species	Site				
	A	N	G	R	K
S	6.23 7.79	8.20 6.54	9.39 4.19	8.53 4.05	5.93 4.55
B	4.41 3.47	4.50 2.94	4.72 2.24	4.33 3.13	3.93 3.19
G	9.72 4.85	10.88 3.93	9.01 3.00	7.00 2.67	
T	1.75 5.73	1.77 4.17	2.55 4.12		
P	9.05 4.24	10.12 4.07			
C	9.25 2.46	10.00 4.26			
Guild density:	2.52	2.45	1.47	1.84	1.76
Density/species:	0.42	0.41	0.37	0.61	0.88
Mean niche overlap:	0.30	0.29	0.17	0.19	0.38

what it is at Alexandria (Table 3). In Fig. 10 it is seen that the 2-species system at Kirstenbosch does not use all of the available vegetation profile, cf. foraging ranges to the east, and thus it is not surprising that overall density is lower at Kirstenbosch. This concentration of species in the centre of resource (height) ranges is what is expected from coevolutionary models (Roughgarden 1976; Case 1981) if resource levels are higher in the centre of the height range. Moving from west to east, to higher diversity systems, note that sombre bulbul forages higher with the addition of grey cuckoo shrike at Riviersonderend and that similarly boubou shrike forages higher at Grootvadersbos with the addition there of terrestrial bulbul (see Table 3 for mean forag-

ing heights). Besides such niche shifts, it is clear that niche breadths change also. All commoner species except boubou shrike tend to increase niche breadth in the more diverse communities (Table 3). This result is in contrast to that in the foliage insectivores, diverse sites, in which species tend to narrower niches in more diverse sites, an obvious way by which more species can be accommodated in comparable habitat with similar niche overlaps. With the slow searching omnivores, however, niche breadths are larger at the richer sites and species are more uniformly distributed through out the vegetation.

In this guild body sizes vary considerably (see Fig. 10), from the 27 g puff-backed shrike to the 64 g grey cuckoo shrike. The two bulbul species of *Andropadus* and *Phyllastrephus* are most similar in body size (difference in log (wt)=0.012), but they average only 12% in foraging height overlap. In contrast, the two cuckoo shrikes *Campephaga* and *Coracina* differ in size (by a factor of two) and tolerate large foraging height overlaps (average 0.63). In general, species more similar in body size overlap less in foraging heights ($r=0.182$, significantly positive for $n=30$), but the relation is far from convincing.

The Alexandria and Knysna forests both support the same six species, distributed in similar ways over the vegetation, with similar niche overlaps at each site (means 0.30 and 0.29 respectively, $r=0.97$, $P<0.01$). The matrices of foraging height overlaps can be used, as above, to predict the densities of subsets of this guild at sites to the west with fewer species. These predictions are then tested against observed data, and match according to the equation: Observed density = 1.0031 (predicted density) - 0.124. The fit is remarkable good ($r=0.932$; $R^2=0.869$, $F_{1,7}=43.46$), and the slope is virtually unity. Note however, that the observed densities fall somewhat below the predicted Figures ($a=0.124$ pr/ha rather than 0), although especially for Riviersonderend and Kirstenbosch predictions are very close: predicted for sombre bulbul at Kirstenbosch from Alexandria 1.295 pr/ha, from Knysna 1.611 pr/ha; observed sobre bulbul density: 1.41 pr/ha.

An example of the way in which species in this guild, in concert, spend foraging time in height intervals proportional to the amounts of vegetation is given in Fig. 11. The utilization curve $\sum W_i^{0.71} X_i U_{ij}$; summed over six species

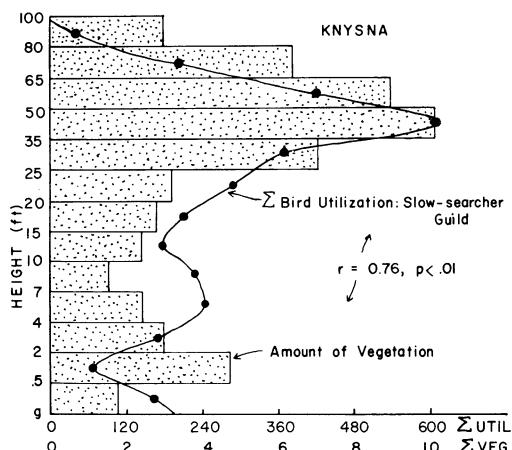


Fig. 11. Amounts of vegetation at each height interval at Knysna are shown by the stippled histogram. The summed utilization of the six species of the slow-searcher guild is given as the solid line, indicating the correspondence between bird utilization and vegetation (correlation coefficient $r=0.75$). See Fig. 4 for ordinate in m

i, is matched with the histogram of vegetation over height; clearly the six species are distributed in a way such that their combined foraging effort is spread over the available foraging sites, and this is certainly less true at sites to the west where the higher cuckoo-shrikes and the lower terrestrial bulbul are absent.

Size segregation in other guilds

I will discuss finally three other bird guilds in which I have insufficient data on foraging heights for detailed analysis, but in which body size differences appear to play an important role. Three such guilds are taxonomically distinguished: the sunbirds Nectariniidae, the pigeons and doves Columbidae, and the thrushes Turdidae. Census data and weights of the species in these three guilds are shown in Fig. 12. The pigeons are at the top of the Figure, with size ranges from the 243 g rameron pigeon to the 62 g emerald-spotted wood dove. A total of six species occur, but rather than tending to a size segregation amongst all six, it appears that the six fall into one of three size modes,

with two species at each mode. The three western sites have two species at each of the larger two modes, and the smallest mode has two species at Alexandria, one at Grootvadersbos, and none further west. Density patterns show no clear trends, in fact the density data themselves are perhaps not worth much in these larger and far-ranging species.

The thrushes are shown in the center of the Figure, with circled densities. At the three westernmost sites there are two species, well segregated by size. The largest of these, the 78 g olive thrush, becomes rare at the two eastern sites, where for the first time the chorister robin, at 43.6 g, makes an appearance. The smaller western thrush, Cape robin (28.8 g), also becomes scarce at the two eastern most sites, but a similarly-sized thrush, brown robin at 32.5 g, is common at Alexandria (but absent from my census site at Knysna). A fifth species, the small starred robin, 21.1 g, is common at the two eastern sites, and the guild shifts from being dominated by olive thrush – Cape robin to a smaller species pair, chorister robin and starred robin, in the east.

The third guild is comprised of 4 species of sunbirds, which again fall into two size modes with two species each, the larger greater double collared sunbird and grey sunbird, at 11.7 g, and the smaller collared sunbird and lesser double collared sunbird, at 7.5 and 8.1 g respectively. Diversity increases from west to east, and density does likewise. At the smaller size mode, the lesser double collared sunbird occupies the 4 western most sites, and gives way to the similarly-sized collared sunbird at Alexandria; at the larger mode, greater double collared sunbird occurs from Riviersonderend through Alexandria, but is absent from Kirstenbosch and is joined at Alexandria by the grey sunbird. These patterns, and those mentioned above, suggest that a) more size modes are occupied in the eastern than in the more isolated western forests; b) coexistence is more likely if species in these guilds are of different body sizes, and c) within a size mode there is a tendency for species to be replaced by others along the west-east range.

Conclusions and summary

In this final section I will summarize the results described above, and draw general conclusions about the patterns

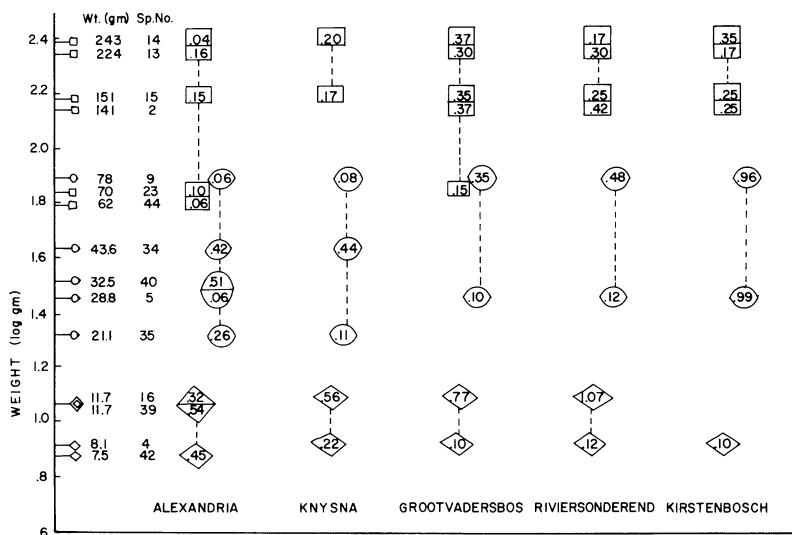


Fig. 12. Weights of species in three guilds at five forest sites. Weights and their logarithms are shown at left, together with the species number as listed in Table 1. Boxed figures are pigeons and doves, encircled figures those of thrushes and robins, and diamond shapes those of sunbirds. Included numbers of species densities, in pr/ha. See text for discussion

Table 4. Observed bird density trend and trends predicted from a variety of known effects on bird density. See text for explanation and discussion

Site	Kirstenbosch	Riviersonderend	Grootvadersbos	Knysna	Alexandria
Observed density:	100%	92%	94%	96%	101%
Pred. from sp. no.:	100%	147%	187%	207%	287%
Pred. from insects:	100%	113%	91%	98%	107%
Pred. from veg.dens.:	100%	71%	87%	67%	49%

of diversity and density observed in the forest sites. With respect first to species numbers, the most important influence appears to be the isolation of the western forest patches in reducing species diversity, an influence akin to the typical island effect widely known for plants and animals alike. Reduced species numbers on habitat islands rather than on real islands have also been described; a few examples are birds on mountaintops (Vuilleumier 1970; Johnson 1975; Mayr and Diamond 1976), mammals on mountaintops (Brown, 1971), plants on mountaintops (Simpson 1974), desert buttes (Cody 1978b) and in forest patches (McKenzie 1978), cave animals in caves (Culver 1970; Vuilleumier 1973), fish in lakes (Barbour and Brown 1974) and insects in thistleheads (Brown and Kodric-Brown 1977). Thus it is neither unexpected nor unusual to find that smaller and more isolated forest patches have fewer bird species. Besides the effects of size and isolation, these forest patches might contain reduced diversity of bird resources. Especially with such birds as nectarivores and frugivores, strong coevolutionary relationships are expected between the consumer and the consumed, and thus any guarantees that such specific resources are uniformly distributed throughout the forest patches are waived. Furthermore it is just such resources, flowering and fruiting plants, that are more uniformly abundant over the seasons where rainfall patterns show less seasonal variation; thus at the Knysna and Alexandria end of the range, where rainfall is more uniform, nectarivores and frugivores are expected a priori to be more common, as they indeed are.

However, for many species resources appear to be as well represented at Kirstenbosch as at Alexandria, and such species include generalized foliage insectivores, slow-searching and larger insectivores, and ground-scratching thrushes, all species of broad diet and unspecialized food requirements. Further, it is the size of the guilds of such species that is smaller at Kirstenbosch, rather than the absence of guild there, indicating that food is available even though fewer species are there to utilize it.

I have next tried to interpret changes in bird densities from east to west in the forest patches, and to isolate the effects of changes in species numbers, and a possible density compensation in consequence of reduced diversity, from other potential influences on bird density. The bald observation that total bird species density changes little from one site to another, despite a three-fold change in species numbers, is represented in the top line of Table 4. If additional species were added purely in consequence of the availability of additional resources available to them, then density/species might remain constant, and total density would increase with increasing species number as shown in the second line of Table 4. Clearly this differs strongly from the observations, and species numbers thus do not reflect the range of resources present. I have two independent lines of evidence that in fact resources may not be

entirely uniform throughout the forest patches, the one more direct from measurements of insect densities, and the other less direct from the amounts of vegetation present at each site. From the former, assuming a doubling in bird density for a four-fold increase in insect density, highest densities of birds are expected at Riviersonderend, and lowest densities at Grootvadersbos. From vegetation densities, in turn, bird densities are expected to be highest at Kirstenbosch and lowest at Riviersonderend (see Table 4). None of these tentative effects on bird density are close to accounting for the observed uniformity of bird density throughout the forest sites, and this brings up the possibility that density compensation takes place within the forests: birds at sites with fewer competitors reach higher densities through access to resources that go to other species at more diverse sites.

To more closely investigate this possibility, and to ask whether density compensation occurs uniformly across bird communities as is suggested by the uniformity of total densities across forest sites, I subdivide the bird community into guilds of ecologically related species. In the first, the foliage insectivores, density compensation appears complete: despite changing guild size from 1 species to 5 species, total guild density remains more or less constant. Furthermore, predictions of bird densities in low-diversity forests based on niche overlaps and densities in high-diversity forests are quite successful, although moderated by variations in vegetation density and perhaps insect abundance. As theoretically expected, niche breadths decrease in higher-diversity communities, and overall the guild behaves in a satisfactorily orderly fashion.

The sallying flycatchers present a different picture. Perhaps because they are the most mobile element of the forest community, with extensive migrations, flycatcher diversity shows no consistent east-west trend. Like the foliage insectivores, these species are all similarly sized, but any possible trend for higher density per species where there are fewer species is masked by a strong increase of guild density from east to west. Apparently, these birds are an example of species whose resources are not constant across the forests and, perhaps due to higher rainfall totals in conjunction with increased amount of forest vegetation, the flycatchers find more food and maintain higher densities in the western sites. Since diversities change little in this guild, density compensation is neither expected nor observed.

Density compensation shows up again in the guild of slow-searchers, the bulbuls, shrikes and cuckoo-shrikes. But these species are of different body sizes, by a factor of over 2, and for such species density compensation is not expected to be complete as it might be in species of similar size. This guild exemplifies partial density compensation, with guild density higher where more species are present, but density/species higher where fewer species are found. Further, niche breadths do not increase at sites with fewer

species as they do for foliage insectivores, and fewer species utilize much less of the foliage profile than is used where there are more species present.

In three remaining guilds ecological segregation seems to be largely by size: the pigeons and doves, thrushes and sunbirds. Both pigeons and thrushes collectively are more abundant at the species-poor end of the range of sites, as are the flycatchers, and the reasons for this are equally obscure. Sunbirds, on the other hand, become more numerous as species and as individuals in the east, and there is no evidence that density compensation occurs. Curiously, the sizes of species in these guilds are not nearly uniformly segregated, but show a tendency to cluster two species to a size mode. Thus there are two large pigeons, two medium sized and two small species. Similarly there are two large sunbirds and two small sunbirds. In the last guild, the two smaller species do not overlap at forest sites; the lesser double collared sunbird occupies the four western sites and is replaced by the collared sunbird at Alexandria. The more widely distributed of the larger species pair, the greater double collared sunbird, declines in density from west to east, and this appears to be independent of the co-occurrence at Alexandria of the same-sized grey sunbird. With the thrushes, the situation is less simple, with the species pair olive thrush-Cape robin dominating in the west and the species trio brown robin-chroister robin-starred robin dominating in the east. Both of the first-mentioned two decline in density from west to east, but this decline takes place before they encounter additional thrush species, and appears therefore to be independent of interspecific competition and density compensation.

The study shows that density compensation, strongly suggested from the original data of Table 1, is a phenomenon limited to few guilds, may be detected as complete (foliage insectivores) or partial (slow-searcher) density compensation, and that other guilds, particularly those in which size-segregation is common, fail to yield any evidence for the phenomenon. The uniformity of total bird density in forest sites from Kirstenbosch to Alexandria thus has several components: density compensation in guilds of generalized species that are larger in the east; higher densities in some guilds, such as thrushes and flycatchers, that are apparently unrelated to interspecific competition and density compensation, and more likely related to higher resource productivity in the western forests; presence of some specialized species, especially of nectarivores, frugivores and herbivores, only in the western forests.

Acknowledgements. The field work reported in this paper was made possible through the generous financial assistance of the John Simon Guggenheim Foundation and the Percy Fitzpatrick Institute of African Ornithology and its director W.R. Siegfried at the University of Cape Town. The Department of Forestry kindly allowed by access to several of the study sites. My wife Daryl Ann assisted with the field work, and the University of California Academic Computing Facility was used at the analytical stage. Ted Case kindly ran computer simulations on community stability and return times. I am very grateful to all of these people and agencies.

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Received January 28, 1983