Effects of alien woody plant invasion on the birds of Mountain Fynbos in the Cape of Good Hope Nature Reserve

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The density, biomass, species richness and composition of birds in plots in two Mountain Fynbos plant-species assemblages (Tall Mixed Fynbos and Restionaceous Tussock Marsh), infested with alien woody plants (mainly Australian *Acacia* spp.) at the Cape of Good Hope Nature Reserve, South Africa, were compared with those of uninfested plots. The relative density of frugivorous and granivorous birds tended to increase, but total bird density did not change significantly with increasing density of *Acacia cyclops* in Tall Mixed Fynbos. However, the density of nectarivorous birds decreased with increasing *A. cyclops* infestation as a result of the elimination of their food plants (proteaceous and ericaceous shrubs). Thus, alien woody plants have the capacity to disrupt the putative avian nectarivore – indigenous plant pollination relationship. Dense infestations of mixed alien species in Restionaceous Tussock Marsh supported fewer nectarivorous birds, but more granivores and insectivores than did uninfested vegetation. Moreover, bird species more typical of woodland and thicket (and absent from uninfested fynbos vegetation), notably large granivores, were found in dense mixed-alien infestations of this plant-species assemblage.

Die digtheid, biomassa, spesierykheid en -samestelling van voëls in persele in twee bergfynbosplantspesiegroepe (Hoë Gemengde Fynbos en Restioonagtige Polvlei) vervuil met uitheemse houtagtige plante (hoofsaaklik Australiese *Acacia* spp.), in die Kaap die Goeie Hoop-Natuurreservaat, Suid-Afrika, is vergelyk met dié van onvervuilde persele. Die relatiewe digthede van vrugte- en saadvretende voëls het effens toegeneem, alhoewel totale voëldigtheid nie betekenisvol deur toenemende *Acacia cyclops*-digthede in Hoë Bergfynbos beïnvloed is nie. Nietemin het digthede van nektarvretende voëls afgeneem met toenemende *A. cyclops*-vervuiling as gevolg van die verdringing van hul voedselplante (protea- en erika-agtige struike). Gevolglik het uitheemse houtagtige plantvervuilings die vermoë om die veronderstelde nektarvretende voëls – inheemse plant-bestuiwingsverhouding te ontwrig. Digte gemengde uitheemse spesievervuilings in Restioonagtige Polvleie het minder nektarvretende voëls, maar meer saad- en insektevretende voëls as onvervuilde plantegroei, onderhou. Verder is voëlspesies, wat meer tipies van boswêreld en digbos is (en afwesig is in onvervuilde fynbosplantegroei), vernaamlik groot saadvreters, in digte gemengde-uitheemse vervuilings van hierdie plantspesiegroep gevind.

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Alien woody plants were introduced into South Africa, predominantly in the eighteenth and nineteenth centuries, for drift-sand stabilization, timber and ornamental use (Shaughnessy 1986). Many species have since become invasive, and the Fynbos Biome is now more severely infested with alien vegetation than any other southern African biome (Macdonald 1984).

Alien woody vegetation forms dense stands which exclude indigenous vegetation (Taylor, Macdonald & Macdonald 1985; Richardson & van Wilgen 1985). Although there has been little research on birds in alien-infested fynbos vegetation, in an analysis of lists of the bird species recorded from alien *Acacia* thickets in the south-western Cape Province, Winterbottom (1970) found that species richness was lower in alien infestations than in uninfested fynbos, with 30% of the dominant bird species of infested vegetation being '...derived from indigenous forest'. As alien monocultures can provide inimical habitat for birds (Winterbottom 1970; Cody 1975), a decrease in overall avian species richness, density and biomass would be expected where the heterogenous fynbos vegetation is increasingly infested by alien woody plants.

Bird density and species richness in undisturbed fynbos vegetation are low (Winterbottom 1966; Siegfried 1983; Siegfried & Crowe 1983). However, large numbers of nectarivorous birds, notably the Cape sugarbird *Promerops cafer* and sunbirds (Nectariniidae), may rely on the inflorescences of members of the families Proteaceae and Ericaceae as an important food source (Rebelo 1987). Moreover, in feeding from these plants, these birds appear to play an important role in their pollination (Rebelo, Siegfried & Crowe 1984). Therefore, since alien woody plants suppress the densities of indigenous plants, in addition to an overall decrease in bird-species richness, a decrease in avian nectarivore density may also be expected in alien-infested fynbos. The spread of alien *A. cyclops* is apparently enhanced by dispersal of the seeds by frugivorous birds (Glyphis, Milton & Siegfried 1981), and since there are few ornithochorous plants and frugivorous birds in uninfested Mountain Fynbos (Siegfried 1983), an increase in frugivorous-bird abundance and/or species richness might be an expected response to alien *A. cyclops* infestation.

Although the factors controlling the density and diversity of fynbos invertebrates are poorly understood (Jarvis 1979), positive correlations between insect abundance and foliage density have been reported in other vegetation types (e.g. Murdoch, Evans & Peterson 1972; Koen & Crowe 1987). Thus, if vegetation density is increased by alien infestation, a rise in invertebrate abundance may be expected and, consequently, an increase in the density of insectivorous birds. Moreover, alien *Acacias* also produce copious, long-lived seeds which accumulate in large seed-banks in or on the soil (Milton & Hall 1981; Holmes, Macdonald & Juritz 1987). Since such seeds are potentially available to avian granivores, an increase in this feeding guild would also be anticipated in alien-infested fynbos.

The aims of this study were to assess the effects of alien woody plant infestation on avian assemblages of two Mountain Fynbos plant-species assemblages (Tall Mixed Fynbos and Restionaceous Tussock Marsh; Taylor 1984). Specific attention is directed at the following hypotheses:

(1) Total bird-species richness, density and biomass will decrease as alien infestation increases.
(2) Bird-species turnover will increase with increasing alien infestation, such that typical fynbos birds will be replaced by thicket or woodland species.
(3) The relative density of frugivorous birds will increase in areas of high *Acacia cyclops* infestation.
(4) The relative density of nectarivorous species will decrease as alien infestation increases.
(5) The relative density of insectivorous birds will increase as alien infestation increases.
(6) The relative density of the granivorous birds which can eat alien seeds will increase as alien infestation increases.

Study area

Fieldwork was carried out at the Cape of Good Hope Nature Reserve (CGHNR), (34°15'S / 18°25'E) in the south-western Cape Province. The vegetation of the reserve comprises Mountain Fynbos (Moll, Campbell, Cowling, Bossi, Jarman & Boucher 1984), which in turn is made up of a number of distinct plant-species assemblages, including extensive areas of Tall Mixed Fynbos and Restionaceous Tussock Marsh (Taylor 1984). Tall Mixed Fynbos comprises an understorey dominated by Restionaceae and ericoid and other fine-leaved shrubs, with *Mimetes fimbriifolius* and *Leucospermum conocarpodendron* being characteristic overstorey species. Restionaceous Tussock Marsh comprises predominantly a dense understorey of Restionaceae and decumbent dwarf shrubs with emergent proteoid shrubs, notably *Mimetes hirtus* and *Leucadendron laureolum*. Much of the reserve is infested with alien woody plants, particularly *Acacia cyclops* (Taylor *et al.* 1985; Macdonald, Graber, De Benedetti, Groves & Fuentes 1988).

Materials and methods

Study plots of 1 ha each were marked out in an area of Tall Mixed Fynbos infested with various levels (< 1%, 10%, 18%, 42%, 50% and 72% projected canopy cover) of *Acacia cyclops*, and in Restionaceous Tussock Marsh infested with 0%, 25%, 50% and 100% of a mixture of alien woody plant species (*A. longifolia, A. saligna, Eucalyptus lehmanni* and *Pinus* spp.).

Bird counts

Birds were counted by walking slowly along a zig-zag route (following a different path on each visit) through each plot. Birds known to have entered the plot after commencement of the count were not counted. Nocturnal species roosting by day, wide-ranging raptorial species and aerial foragers [e.g. swifts (Apodidae) and swallows (Hirundinidae)], were not counted. Counts were carried out between three and 10 times per month, mostly before midday and under dry and relatively windless (< F. 5 Beaufort Scale) conditions.

Birds were counted between June 1984 and April 1986 in the 10%, 42% and 72% *Acacia cyclops*-infested plots and the 100% mixed-alien plot, between June 1985 and April 1986 in the < 1%, 18% and 50% *A. cyclops*-infested, and between June 1985 and January 1986 in the three remaining mixed-alien plots. Avian species richness, density and biomass were calculated for each visit. Bird body masses were obtained from birds mistnetted at the reserve (M. W. Fraser, unpublished data) or from Maclean (1985). To assess the effects of alien infestation on avian trophic structure, birds were grouped into feeding guilds (nectarivore, insectivore, frugivore, granivore and folivore) after Siegfried (1983).

Statistical methods

Correspondence analysis (Greenacre 1984; Underhill & Peisach 1985) was employed to detect possible relationships between the avifaunas of each plot and densities of their component bird species. In the results of correspondence analyses, the inertia statistic reflects the degree to which a particular variable determines the overall positioning of the points displayed. Jaccard and Czekanowski similarity coefficients (Southwood 1978) were calculated to illustrate the degree of similarity between bird species assemblages and provide an index of the change in species composition with increasing alien infestation.

Friedman two-way analysis of variance by ranks (Conover 1971) was used to assess the significance of variation in the density of avian feeding guilds and monthly variation in overall bird density in plots infested with *Acacia cyclops*.

Resource availability

Invertebrates were sampled from January to December 1985 using sticky traps (Cody 1983). Between seven and 18 (depending on the height of the vegetation) 10 × 20 cm perspex plaques coated with Formex (a sticky resin used commercially as an insect guard on fruit trees) were suspended at 20-cm intervals from ground to canopy level to intercept aerial invertebrates. A pitfall trap (450 ml glass jar containing approximately 200 ml glycerol in alcohol solution) for sampling ground invertebrates was sited at the base of each set of plaques. Three sampling stations were installed within each of the 10%, 42% and 72% *A. cyclops*-infested plots and one sampling station in the 100% mixed-alien infestation and were operated for three to eight days a month.

The densities of mature *Leucospermum conocarpodendron* and *Mimetes fimbriifolius* bushes (food plants of avian nectarivores) were recorded in each plot, and their flowering phenology was monitored to determine any relationship between numbers of plants and nectarivorous birds. To assess any relationship between alien fruit availability and the density of frugivorous birds, fruit loss from *A. cyclops* pods was recorded weekly on tagged branches of five bushes in each of the 10%, 42% and 72% infested plots. Litter traps were placed beneath each tagged branch to intercept fallen fruits and thus determine whether fruit loss was attributable to dehiscence (the number of fruits in the trap equalling the number lost from the pods) or predation (the number of fruits in the traps being less than that lost from pods).

Vegetation structure

Since bird community structure may be influenced by vegetation structure (Cody 1975, 1983), foliage profiles and half-heights (Cody 1983) were constructed using a density board in all the *A. cyclops*-infested plots and the 100% mixed-alien plot. Projected canopy cover of alien vegetation was measured along forty 10-m transects within these plots. The remaining mixed-alien plots were destroyed by fire in February 1986 before their profiles were measured. In these three plots, the prefire projected canopy cover of the alien vegetation was estimated to be 0%, 25% and 50% respectively.

Results

Tall Mixed Fynbos infested with *Acacia cyclops*

Birds

Twenty-two bird species were recorded in plots infested with *A. cyclops* (Table 1). Eight species (36%) were found at all levels of infestation, and four (18%) (Cape bulbul *Pycnonotus capensis,* Cape robin *Cossypha caffra,* southern boubou *Laniarius ferrugineus* and Cape siskin *Serinus totta* were absent from only the least infested (< 1%) plot. Four species were recorded in only one plot. Six species found in Tall Mixed Fynbos infested with *A. cyclops* were absent from the Restionaceous Tussock Marsh infested with mixed aliens. The eight bird species found at all levels of *A. cyclops* infestation represented four feeding guilds.

Similarity coefficients between bird-species assemblages were high among all levels of infestation, but lowest between the least (< 1%) infested and the other plots (Table 2). Avian density was highly variable between plots, but was highest overall in the 10% infested plot (Table 1). Differences in mean density between plots were not significant (Spearman rank correlation: r_s = 0,18; 4 *df*). Moreover, monthly bird density did not differ significantly between plots (Friedman Test χ^2_5 = 9,0 N.S.).

In the correspondence analysis of the plots infested with *A. cyclops* (Figure 1), the first axis accounts for 48% of the inertia and contrasts the densities of three nectarivores (Cape sugarbird, malachite sunbird *Nectarinia famosa* and orangebreasted sunbird *N. violacea*) which are associated with low levels of *A. cyclops* infestations

Table 1 Mean avian density and species richness in *Acacia cyclops* infested Tall Mixed Fynbos

	Density of birds per plot in plots with increasing *Acacia cyclops* density (% projected canopy cover)					
Species	< 1	10	18	42	50	72
Cape turtle dove *Streptopelia capicola* (G)*	–	0,03	–	0,07	0,04	0,03
Speckled mousebird *Colius striatus* (Fo)	–	–	–	0,02	–	–
Ground woodpecker *Geocolaptes olivaceus* (I)	–	–	0,08	–	–	–
Cape bulbul *Pycnonotus capensis* (Fr)	–	0,06	0,23	0,27	0,25	0,53
Olive thrush *Turdus olivaceus* (I)	–	0,01	–	0,02	–	–
Cape robin *Cossypha caffra* (I)	–	0,14	0,08	0,38	0,15	0,45
Grassbird *Sphenoeacus afer* (I)	0,03	0,02	–	0,03	–	–
Longbilled crombec *Sylvettia rufescens* (I)	–	–	–	–	0,08	–
Greybacked cisticola *Cisticola subruficapilla* (I)	0,14	0,14	0,10	0,15	0,04	0,05
Spotted prinia *Prinia maculosa* (I)	0,46	0,72	0,40	1,47	0,54	0,64
Southern boubou *Laniarius ferrugineus* (I)	–	0,02	0,02	0,18	0,06	0,19
Bokmakierie *Telephorus zeylonus* (I)	–	0,09	–	0,02	–	0,02
Redwinged starling *Onychognathus morio* (Fr)	0,16	0,51	0,12	0,07	0,61	0,17
Cape sugarbird *Promerops cafer* (N)	0,40	1,10	0,22	0,13	0,23	0,13
Malachite sunbird *Nectarinia famosa* (N)	0,11	0,13	0,05	0,12	0,08	0,02
Orangebreasted sunbird *N. violacea* (N)	1,76	1,50	1,27	0,92	1,04	0,41
Lesser doublecollared sunbird *N. chalybea* (N)	0,22	0,19	0,35	0,41	0,21	0,20
Cape white-eye *Zosterops pallidus* (I)	–	0,12	–	0,17	0,08	0,57
Cape weaver *Ploceus capensis* (G)	–	–	–	–	0,04	–
Cape siskin *Serinus totta* (G)	–	0,09	0,37	0,08	0,33	0,13
Yellow canary *Serinus flaviventris* (G)	–	0,01	–	0,05	–	–
Cape bunting *Emberiza capensis* (G)	0,08	0,09	0,10	0,08	0,08	0,15
Plot-specific species	0	0	0	1	2	0
Total mean density (birds per ha ± *SD*)	3,3 ±2,2	5,0 ±4,4	3,4 ±3,4	4,6 ±3,0	3,8 ±4,3	3,7 ±2,7
Number of species	9	18	13	19	16	15

* Feeding guilds: Fo = Folivore, Fr = Frugivore, G = Granivore, I = Insectivore, N = Nectarivore.

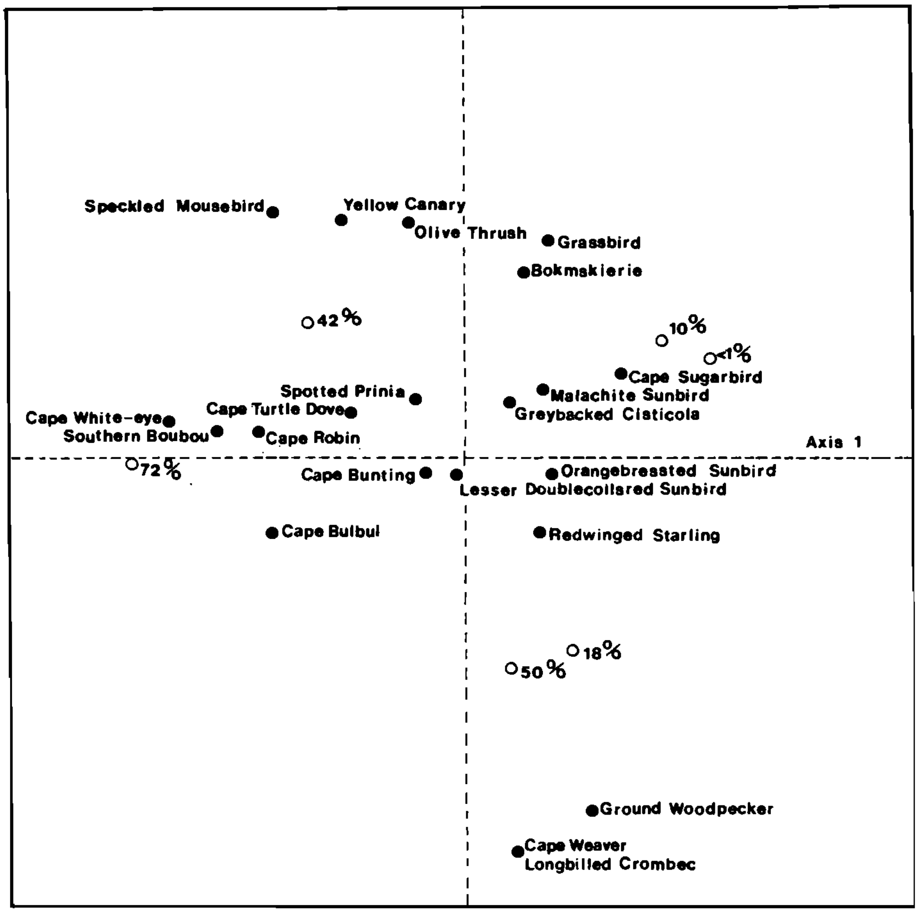

Figure 1 Results of correspondence analysis of bird-species densities (closed circles) in six levels of *Acacia cyclops* infestation (open circles) in Tall Mixed Fynbos at the Cape of Good Hope Nature Reserve.

Table 2 Jacard (upper half-matrix) and Czekanowski (lower) similarity coefficients between avian species composition of *Acacia cyclops* infested Tall Mixed Fynbos

Percent infestation	0	10	18	42	50	72
0		0,50	0,57	0,47	0,47	0,50
10	0,66		0,66	0,95	0,70	0,83
18	0,73	0,77		0,60	0,71	0,73
42	0,64	0,97	0,75		0,66	0,79
50	0,64	0,82	0,83	0,80		0,82
72	0,66	0,85	0,78	0,88	0,90	

Table 3 Avian standing-crop biomass in infested Tall Mixed Fynbos

Acacia cyclops (% projected canopy cover)	Biomass ± *S.E.* (mean g ha^{-1})
<1	64,9 ± 14,0
10	161,1 ± 24,2
18	73,8 ± 19,9
42	96,9 ± 10,4
50	143,6 ± 34,6
72	101,6 ± 9,6

against the Cape bulbul, Cape robin, southern boubou, and Cape white-eye *(Zosterops pallidus)* which are associated with the 42% and 72% infestations. Along the first axis, the plots are ordered with respect to a decreasing level of infestation, except that the 42%- and 50%-infested plots are interchanged. The second axis, which accounts for a further 21% of the inertia, contrasts the relative abundance of Cape sugarbirds in the 10%-infested plot (where the density of proteaceous shrubs is highest) with that of the Cape siskin in the 18% and 50% infestations.

Avian biomass did not display a consistent trend with increasing infestation (Spearman rank correlation, r_s = 0,37; 4 *df*, N.S.), but was highest in the 10%-infested plot (Table 3) where Cape sugarbirds, sunbirds and redwinged starlings *Onychognathus morio* accounted for much of the overall avian density and biomass. Indeed, the redwinged starling made the greatest contribution to avian biomass in all plots. It is noteworthy that the redwinged starling, although classified as a frugivore, was observed feeding exclusively from proteaceous inflorescences, presumably on nectar and insects, even when ripe *A. cyclops* fruits were available. It and the Cape bulbul were the only frugivorous species recorded and, although occurring at relatively low absolute (never more than 0,86 birds ha^{-1} and relative (maximum contribution to overall avian density of 20%) densities, their density increased significantly (Friedman Test $\chi^2_5 = 18{,}28$; $p < 0{,}01$) with increasing alien infestation. The density of nectarivores (Cape sugarbird and three sunbird species) was significantly correlated ($r_s = 0{,}98$; $p < 0{,}05$; 4 *df*) with the number of flowering *Leucospermum conocarpodendron* and *Mimetes fimbriifolius* shrubs. Thus, the density of these nectarivores decreased significantly (Friedman Test $\chi^2_5 = 38{,}3$; $p < 0{,}01$) with increasing infestation by *A. cyclops* (Figure 2). Density of insectivores varied considerably between plots (Figure 2) and, although not displaying a consistent trend, was significantly higher (Friedman Test $\chi^2_5 = 15{,}6$; $p < 0{,}01$) in heavily infested plots (notably the 42% infested) and lowest in the least infested plot. Granivore density was low, relative to other feeding guilds, but was highest in the heavily infested Plots (Figure 2) (Friedman Test $\chi^2_5 = 17{,}38$; $p < 0{,}01$).

In terms of avian density, the dominant species in the < 1%-, 10%-, 18%- and 50%-infested plots was the orangebreasted sunbird. In the 40%- and 72%-infested plots an insectivore, the spotted prinia *Prinia maculosa*, occurred at the highest density.

Vegetation structure and resource availability

Although the foliage profiles and half-heights of the vegetation differed between the *Acacia cyclops*-infested plots (Figure 3), invertebrate densities were similar (Figure 4). The number of proteaceous shrubs was highest in the 10%-infested plot, decreasing thereafter with increasing alien infestation. In all plots, flowering of proteaceous shrubs extended from July to December, with the greatest number of open inflorescences found in November. In the 10%-infested plot bird density was highest in November, with 78% of the birds recorded in that month being nectarivores. Pods of *A. cyclops* opened in mid-summer to display ripe fruits which remained on the bushes throughout the year. No removal by frugivores of fruits from tagged bushes was observed and fruit loss was accounted for by the number of fruits intercepted by litter traps.

Mixed-alien infestation

Birds

Twenty-three bird species were recorded in Restionaceous Tussock Marsh infested with mixed aliens (Table 4). Four species (three sunbird species and Cape white-eye) were found at all levels of infestation. Interplot similarity values (Table 5) for the bird-species assemblages of mixed-alien infestations varied markedly, but were lower than those between plots infested by *Acacia cyclops* (Table 2). About a third of the 23 bird species recorded in the 0–100%-infested Restionaceous Tussock Marsh plots were absent from the *A. cyclops* infestations. With the exception of one insectivore (dusky flycatcher *Muscicipa adusta*), these were relatively large-bodied, granivorous species. Four of these (helmeted guineafowl *Numida meleagris*, Cape francolin *Francolinus capensis*, redeyed dove *Streptopelia semitorquata*

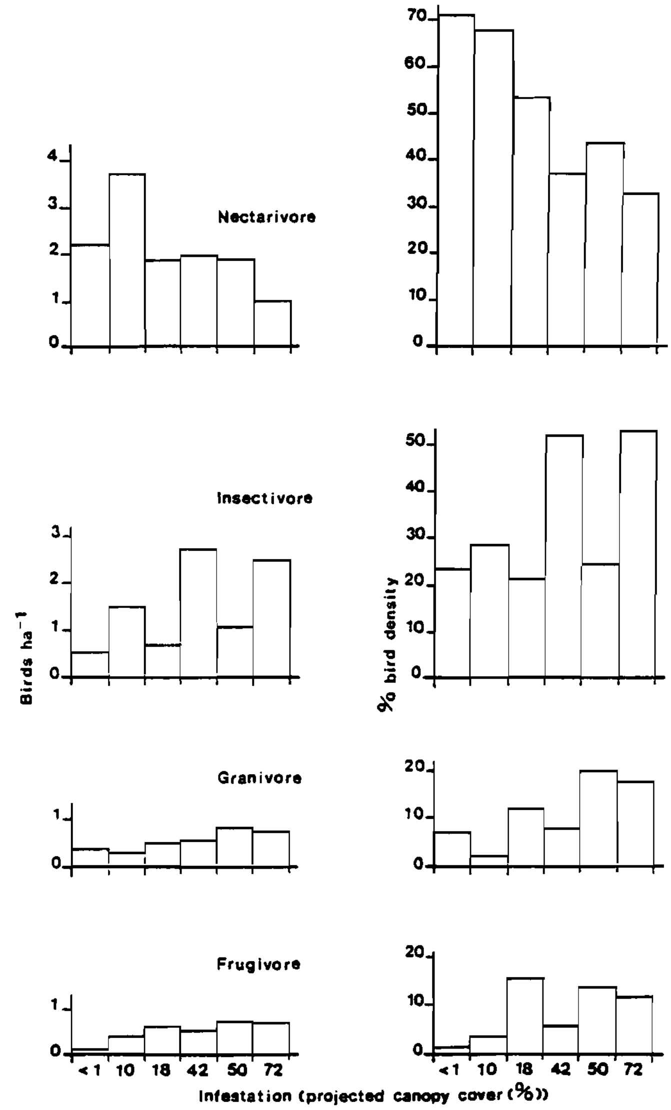

Figure 2 Absolute (left) and relative (right) contribution of avian feeding guilds to bird density in *Acacia cyclops* infested Tall Mixed Fynbos at the Cape of Good Hope Nature Reserve.

and laughing dove *S. senegalensis*) were restricted to the 100% mixed-alien infestation where they were responsible for the high avian biomass recorded in this plot (Table 6).

Avian density was highest in the two most densely infested plots (Table 4). In a correspondence analysis based on species density (Figure 5), the first two axes accounted for 63% and 37%, respectively, of the inertia, i.e. the data matrix is well displayed in two dimensions. Along axis 1, the plots are ordered with respect to level of alien infestation, with the largest contributions to the inertia being made by Cape sugarbird and orangebreasted sunbird, which are associated with low infestation levels. The most important feature of the display is the contrast between the 100%-infested plot and the three lesser infestations. This contrast is due particularly to the high relative density of the Cape sugarbird in the uninfested plot and the restriction of seven species (helmeted guineafowl, Cape francolin, redeyed dove, laughing dove, speckled mousebird *Colius striatus*, olive thrush

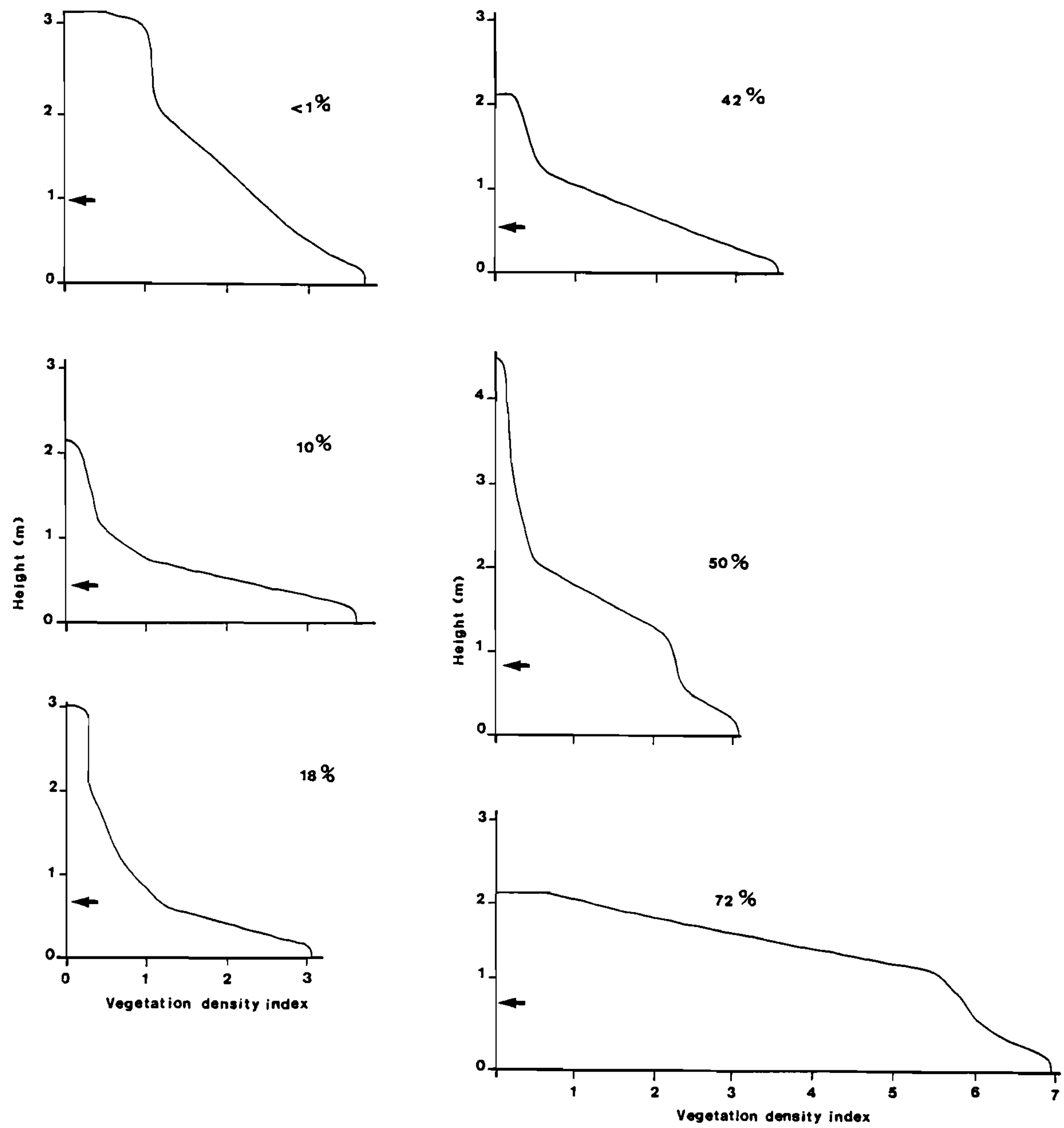

Figure 3 Foliage profiles of *Acacia cyclops* infested Tall Mixed Fynbos at the Cape of Good Hope Nature Reserve. The arrows indicate the half-height of the vegetation and the percentages the projected canopy cover of the alien vegetation.

Turdus olivaceus and dusky flycatcher), to the 100% infestation.

In contrast with the other nectarivores, the lesser doublecollared sunbird *Nectarinia chalybea* makes a relatively small contribution to the analysis. The contrast between the 100% infestation and the nectarivore density in the other plots is again borne out in axis 2. Here high densities of orangebreasted and malachite sunbirds in the 50% infestation contrast with the absence of Cape sugarbird from this plot and emphasize the sugarbird's high density in the uninfested plot. The contribution of malachite sunbird is particularly high in this respect. This correspondence analysis ordination further illustrates the relationships between the bird-species densities in each mixed-alien infestation. The 25% and 50% infestations show greater similarity to each other than the 0% and 100% infestations. The proximity of malachite and orangebreasted sunbirds demonstrates their similar pattern of occurrence.

As in *Acacia cyclops*-infested fynbos vegetation, the relative density of nectarivores tended to decrease with increasing alien infestation in Restionaceous Tussock Marsh plots (Figure 6). For example, the Cape sugarbird, the most abundant species in the uninfested plot, occurred only rarely in the more infested plots. However, nectarivore density was not significantly correlated with increasing mixed-alien infestation (Spearman rank correlation: r_s = 0,20, N.S.; 4 *df*). Granivores were very scarce in or absent from the three less infested mixed-alien plots, but their density increased significantly with increasing infestation (Spearman rank correlation: r_s = 1,0; $p < 0,05$; 4 *df*). In the 100% infestation, this guild contributed 28% to avian density and comprised 35% of bird-species richness. Insectivore density increased as

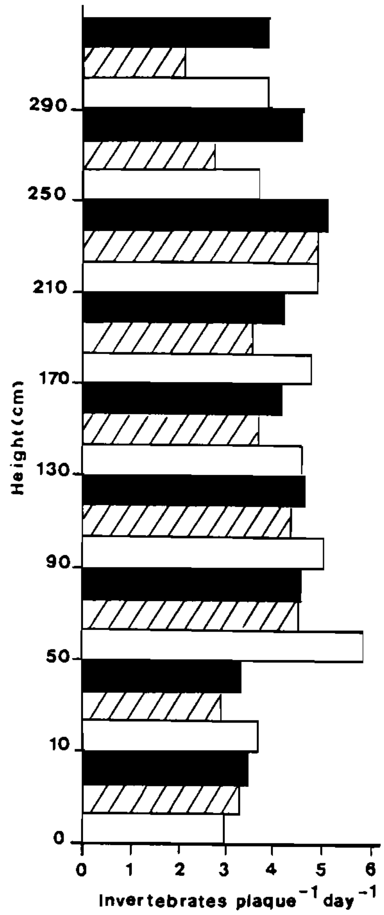

Figure 4 Invertebrate abundance at different strata in *Acacia cyclops* infested Tall Mixed Fynbos at the Cape of Good Hope Nature Reserve. Open bar = 10% projected canopy cover of *Acacia cyclops*, hatched bar = 42%, solid bar = 72%.

alien infestation increased (Spearman rank correlation: $r_s = 1,0$; $p = 0,05$; 4 *df*). Five times as many species of this feeding guild were present in the 100%-infested plot as in the uninfested plot.

Vegetation structure and resource availability

A foliage profile for the 100% mixed-alien infestation is given in Figure 7. Foliage density and height were not quantified in the three other plots but apparently increased with increasing infestation. Ground invertebrate abundance in the 100%-infested plot was high relative to aerial taxa, which showed little variation with height (Figure 8).

Discussion

Hypothesis 1: Total bird-species richness, density and biomass will decrease as alien infestation increases

Results from this study do not support this hypothesis. The sustained ability of Tall Mixed Fynbos vegetation to support similar densities of birds despite increasing *Acacia cyclops* densities implies a maintenance of resource levels. This is borne out by invertebrate abundance, but not by nectar availability as proteaceous

Table 4 Mean avian density and species richness in mixed alien infested Restionaceous Tussock Marsh

	Density of birds per plot in plots with increasing mixed-alien density (estimated percentage projected canopy cover)			
Species	0	25	50	100
Cape francolin *Francolinus capensis* (G)*	–	–	–	0,08
Helmeted guineafowl *Numida meleagris* (G)	–	–	–	0,31
Redeyed dove *Streptopelia semitorquata* (G)	–	–	–	0,01
Cape turtle dove (G)	–	–	0,20	0,97
Laughing dove *Streptopelia senegalensis* (G)	–	–	–	0,04
Speckled mousebird (Fo)	–	–	–	0,01
Cape bulbul (Fr)	–	0,04	0,04	0,17
Olive thrush (I)	–	–	–	0,12
Cape robin (I)	–	0,04	0,12	0,56
Grassbird (I)	0,12	0,12	–	–
Greybacked cisticola (I)	–	0,04	–	–
Spotted prinia (I)	0,28	0,24	0,20	–
Dusky flycatcher *Muscicapa adusta* (I)	–	–	–	0,01
Southern boubou (I)	–	–	0,08	0,47
Bokmakierie (I)	–	–	0,04	–
Cape sugarbird (N)	1,0	0,12	–	0,06
Malachite sunbird (N)	0,08	0,56	1,36	0,35
Orangebreasted sunbird (N)	0,36	0,88	2,08	0,04
Lesser doublecollared sunbird (N)	0,04	0,16	0,32	0,60
Cape white-eye (I)	0,08	0,40	1,24	1,29
Cape weaver (G)	–	–	0,04	–
Yellowrumped widow *Euplectes capensis* (G)	0,20	–	–	–
Common waxbill *Estrilda astrild* (G)	0,08	–	–	0,05
Plot-specific species	1	1	2	7
Total mean density (birds per ha ± *SD*)	2,2 ±0,6	2,6 ±0,6	5,7 ±1,1	5,1 ±0,4
Species richness	9	10	11	17

* Feeding guilds: Fo = Folivore, Fr = Frugivore, G = Granivore, I = Insectivore, N = Nectarivore.

Table 5 Jacard (upper half-matrix) and Czekanowski (lower) similarity coefficients for avian species composition in mixed alien infested Restionaceous Tussock Marsh

Level of alien infestation (estimated % projected canopy cover)	0	25	50	100
0		0,70	0,29	0,25
25	0,82		0,50	0,39
50	0,45	0,66		0,36
100	0,38	0,56	0,53	

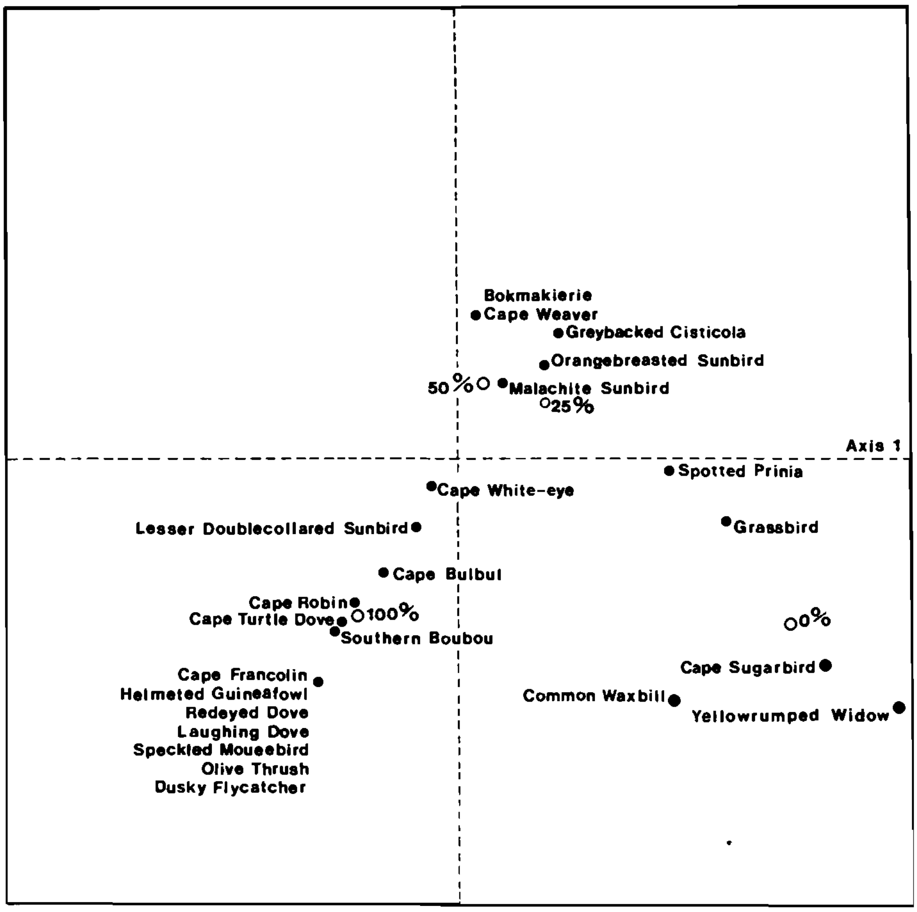

Figure 5 Results of correspondence analysis of bird-species densities (closed circles) in four levels of mixed-alien infestation (open circles) in Restionaceous Tussock Marsh at the Cape of Good Hope Nature Reserve.

Table 6 Avian standing-crop biomass in mixed alien infested Restionaceous Tussock Marsh

Level of alien infestation (estimated % projected canopy cover)	Biomass (Mean g ha^{-1} ± *SD*)
0	37,6 ± 40,9
25	56,9 ± 61,6
50	101,4 ± 100,1
100	709,9 ± 1793,5

shrub density declined with increasing alien infestation. A suppression of resources is, again, not implied by the values for avian biomass.

By contrast, avian density in the most highly infested mixed-alien plot was twice that in uninfested Restionaceous Tussock Marsh, suggesting that resource availability is increased by alien infestation. In the 100% mixed-alien infestation this may be attributable to the height of the vegetation and relatively high invertebrate numbers at ground level. This is supported by the increase in insectivorous birds with increasing infestation. The proportions of each feeding guild in the 100% mixed-alien infestation resemble more closely those found in Strandveld vegetation by Siegfried (1983) than Mountain Fynbos.

Hypothesis 2: Bird-species turnover will increase with increasing alien infestation, such that typical fynbos birds will be replaced by thicket or woodland species

There is little evidence of bird-species replacement with increasing *Acacia cyclops* infestation (Table 3). However, results from the mixed alien infested Restionaceous Tussock Marsh (Table 4) support this hypothesis. Winterbottom (1970) described the birds of *Acacia* stands as a mixture of species from fynbos and scrub forest vegetation types. In the present study, many of the non-nectarivorous bird species of Tall Mixed Fynbos appear to be unaffected by *Acacia* invasion. Assuming that increasing levels of alien infestation is equivalent to moving from one fynbos scrub type to another, this contradicts Cody's (1975) findings that bird-species replacement is relatively rapid under such circumstances. The results from the *Acacia cyclops* infested Tall Mixed Fynbos support Siegfried & Crowe's (1983) suggestion that there is a relaxation of stenotopy in bird species in Mountain Fynbos relative to those which occur in Coastal Fynbos and Strandveld. This may be a consequence of the high number of ecologically equivalent plant species in Mountain Fynbos, in contrast with its floristic heterogeneity.

Four bird species more typical of thicket or woodland than fynbos tend to be more numerous in denser *A. cyclops* infestations but their density is never high. The

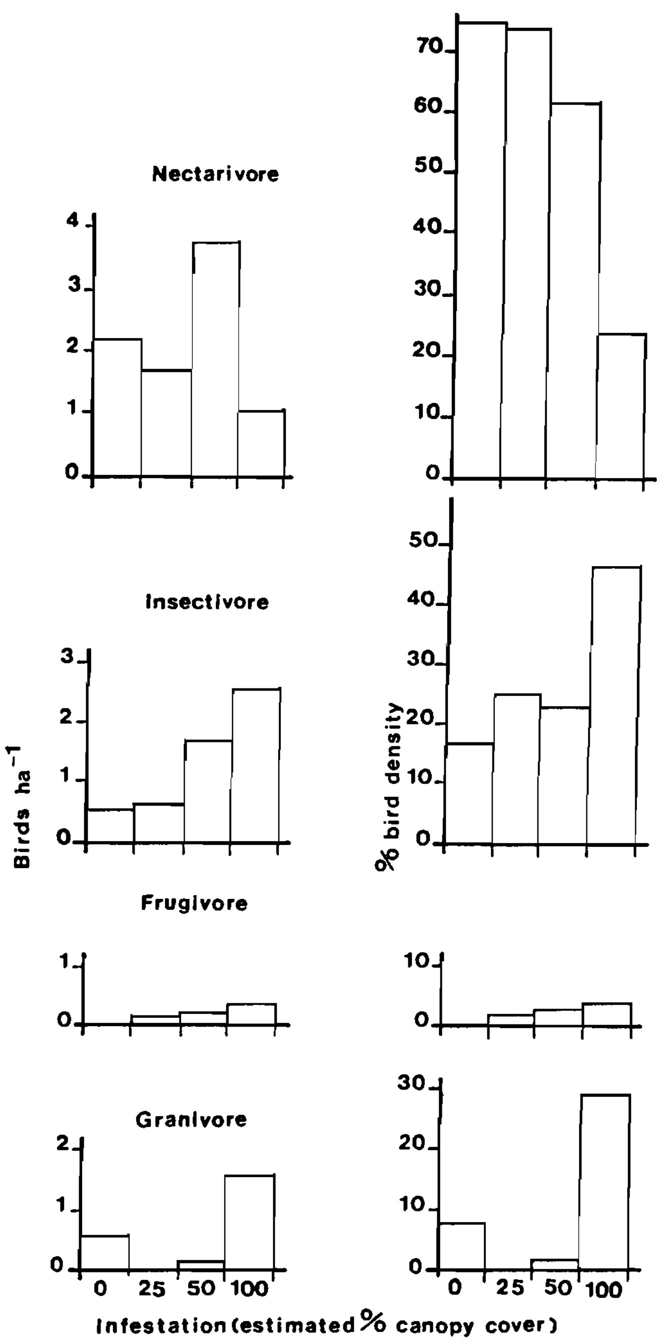

Figure 6 Absolute (left) and relative (right) contribution of avian feeding guilds to bird density in mixed alien infested Restionaceous Tussock Marsh at the Cape of Good Hope Nature Reserve.

same trend is also exhibited by two distinctly non-woodland granivores (Cape siskin and Cape bunting *Emberiza capensis*). Of the woodland species found in the mixed-alien infestation, only the olive thrush was recorded in alien thickets by Winterbottom (1970). The absence of two short vegetation foraging insectivores (grassbird *Sphenoeacus afer* and greybacked cisticola *Cisticola subruficapilla*) from the two most heavily infested plots may be attributable to a thinning of the understorey with increasing height and canopy development of the alien vegetation. The increased density of

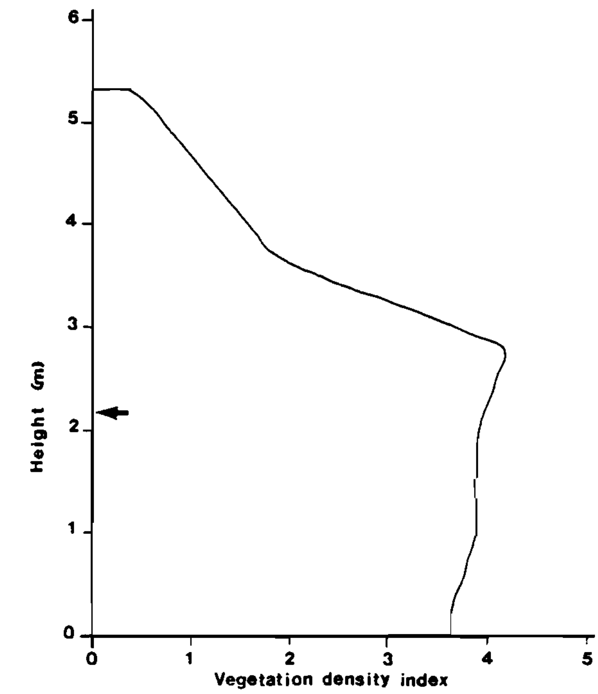

Figure 7 Foliage profile of Restionaceous Tussock Marsh infested with 100% projected canopy cover mixed woody aliens at the Cape of Good Hope Nature Reserve. The arrow indicates the half-height of the vegetation.

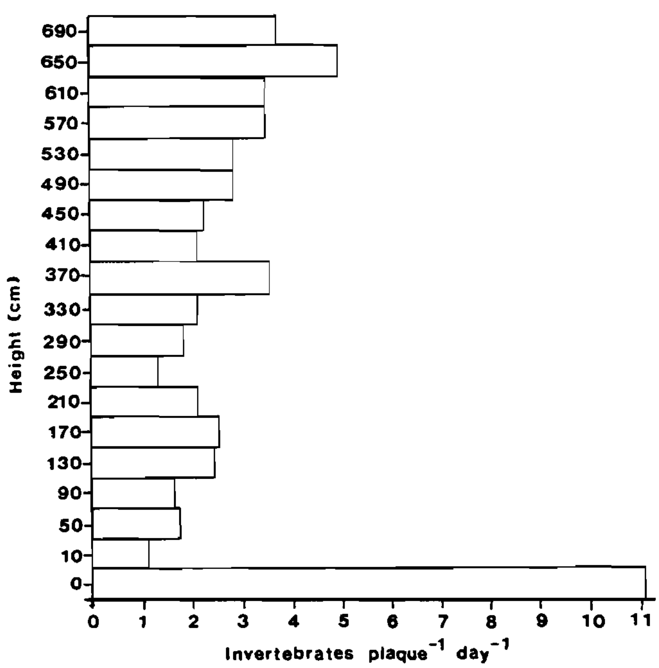

Figure 8 Invertebrate abundance at different strata in 100% mixed alien infested Restionaceous Tussock Marsh at the Cape of Good Hope Nature Reserve.

canopy-foraging Cape white-eyes in the 50%- and 100%-infested plots is to be expected. The helmeted guinea-fowl and redeyed dove recently have expanded their ranges into the Fynbos Biome, a trend which has been attributed in part to alien woody plant invasion (Brooke 1984, 1986).

Hypothesis 3: The relative density of frugivorous birds will increase in areas of high *Acacia cyclops* infestation

Results from this study do not support this hypothesis. The absence of a response by frugivorous birds may relate to high levels of availability of *Acacia cyclops* fruits elsewhere in the reserve, or further afield [this alien is widely distributed in the south-western Cape (Stirton 1987)]. Also, the peninsular location of the study site might not favour large avian influxes. The densities of Cape bulbuls (Table 1) perhaps suggest increased utilization with increasing alien infestation, but this is not supported by the redwinged starling, the only other frugivore recorded. Nor were additional frugivorous species recorded with increasing alien infestation. However, analysis of fresh regurgitated and faecal pellets of the redwinged starling collected at a roost about 1 km away from the study plots indicated that this species fed extensively on *A. cyclops* fruits (M. W. Fraser, unpublished data). As the Cape bulbul and redwinged starling are, in practice, likely to be omnivorous, observed changes in avian trophic structure may not be entirely valid, at least until more is known about the diets of fynbos bird species, especially those with broad dietary ranges.

Hypothesis 4: The relative density of nectarivorous species will decrease as the extent of alien infestation increases

Results here support this hypothesis. The correspondence display of the *Acacia cyclops* infested Tall Mixed Fynbos plots (Figure 1), shows that three out of the four species of nectarivore are strongly associated with low levels of infestation. Given the positive correlation in this study between nectarivore density and the number of flowering Proteaceae, this reduction is presumably due to suppression of flowering food plants by the alien vegetation. Breytenbach (1986) recorded that nectarivorous birds disappeared completely from fynbos vegetation heavily infested with alien *Hakea sericea.*

Members of the Proteaceae and Ericaceae flower at different times of year and together provide a year-round food source for nectarivorous birds. If these birds do play an important role in the pollination of some fynbos plant species, notably Proteaceae and Ericacae (Collins 1983; Rebelo 1987), the potential exists for the breakdown of this bird/plant pollination relationship with increasing levels of alien infestation. As indigenous plant densities decrease with increasing alien infestation, elements of the year-round resource will be removed leading to a collapse of the bird/plant relationship. Similarily, low pollination levels of relict Proteaceae and Ericaceae would result in low seed set which would itself exacerbate the decrease in indigenous plant density initiated by the alien infestation.

Cody (1983) considers that vegetation structure is a major determinant of bird community organization. However, the distribution and abundance of nectarivores in the CGHNR study plots apparently were determined by the presence of food-plant species, rather than vegetation structure, since nectarivorous bird species are scarce in the uninfested plot where there are few food plants. This result parallels the findings of Rotenberry (1985), who showed that North American shrubsteppe bird community composition is more closely associated with floristic variation than with vegetation physiognomy. From the management aspect, therefore, maintenance of structural configuration of the vegetation is inappropriate if food plants (proteoid and ericoid shrubs) are replaced by alien species which may exibit similar physiognomy but are unsuitable food plants.

Hypothesis 5: Increasing alien infestation will provide more resting and feeding substratum for phytophagous and other insects which will result in an increase in the relative density of insectivorous birds

Results from the *Acacia cyclops* infestations do not support this hypothesis consistently. In Mountain Fynbos infested with *Hakea sericea,* Breytenbach (1986) found that the densities of some insectivorous bird species (e.g. spotted prinia), increased with increasing alien infestation. This was attributed to an increase in flying insects. The densities of spotted prinia and other insectivores in the present study, however, were highest in the 42% *A. cyclops* infested plot, where the abundance of aerial insect taxa was, if anything, marginally lower than in the 10- or 72%-infested plots (Figure 4).

More insects were potentially available to birds in the 100% infested mixed alien plot than in the densest *Acacia cyclops*-infested plot, as the vegetation was taller in the former. The only sallying insectivore (dusky flycatcher) occurred in the 100% infestation. The Cape white-eye, a foliage gleaner, occurred at its highest density in the 100%-infested plot, however. Pyke (1985) found only a weak relationship between the abundances of insectivorous birds and flying insects in Australian *Eucalyptus* forest. Indeed, in the 100%-infested plot three out of five avian insectivores were largely ground-foraging species, reflecting the high levels of ground invertebrates.

Hypothesis 6: Increasing alien infestation will lead to an increase in the relative density of granivorous birds

This hypothesis was supported by results from the mixed-alien infestations, but not from the *Acacia cyclops* infestations. Granivores in *A. cyclops* infested Tall Mixed Fynbos occurred in lower densities and, with the exception of Cape turtle dove *Streptopelia capicola,* comprised smaller bodied species than those of the mixed-alien infestation. Such species (Cape siskin and Cape bunting) are, however, unlikely to be able to process the large, hard seeds of the alien. These bird species are common elsewhere in the reserve in uninfested Mountain Fynbos (M. W. Fraser, personal observation). There is no apparent reason for failure of large-bodied granivores, notably Cape francolin and helmeted guineafowl, to utilize *A. cyclops* seeds. The relatively high proportion of these granivores in the 100% infested mixed alien plot contrasts strongly with the observation of Siegfried (1983) that fynbos avifauna is characterized as one of relatively small-bodied birds. Siegfried (1983) also found that granivores made the lowest contribution to avian biomass in Mountain Fynbos. In the present study this guild made by far the greatest contribution in the densest mixed alien infestation. These data indicate the disruptive effect on fynbos bird assemblages of the alien invasives, presumably, in this instance, through seed availability.

Conclusions

Avian species richness, density and biomass in Mountain Fynbos at the Cape of Good Hope Nature Reserve are affected by increasing infestation by alien woody plants, but differ according to the plant-species assemblage which has been infested, the species of invasive alien woody plant and the time of year. It can be concluded that mixed-alien infestation increases bird density and species richness in Restionaceous Tussock Marsh but that *Acacia cyclops* infestation of Tall Mixed Fynbos does not do so. However, nectarivorous species decrease in density with increasing infestation by *A. cyclops* of Tall Mixed Fynbos since their food plants are eliminated. Thus, removal of alien vegetation from this and other plant-species assemblages supporting high proteaceous shrub density might be given high priority from the reserve authorities where the aim is to maintain populations of nectarivorous birds.

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