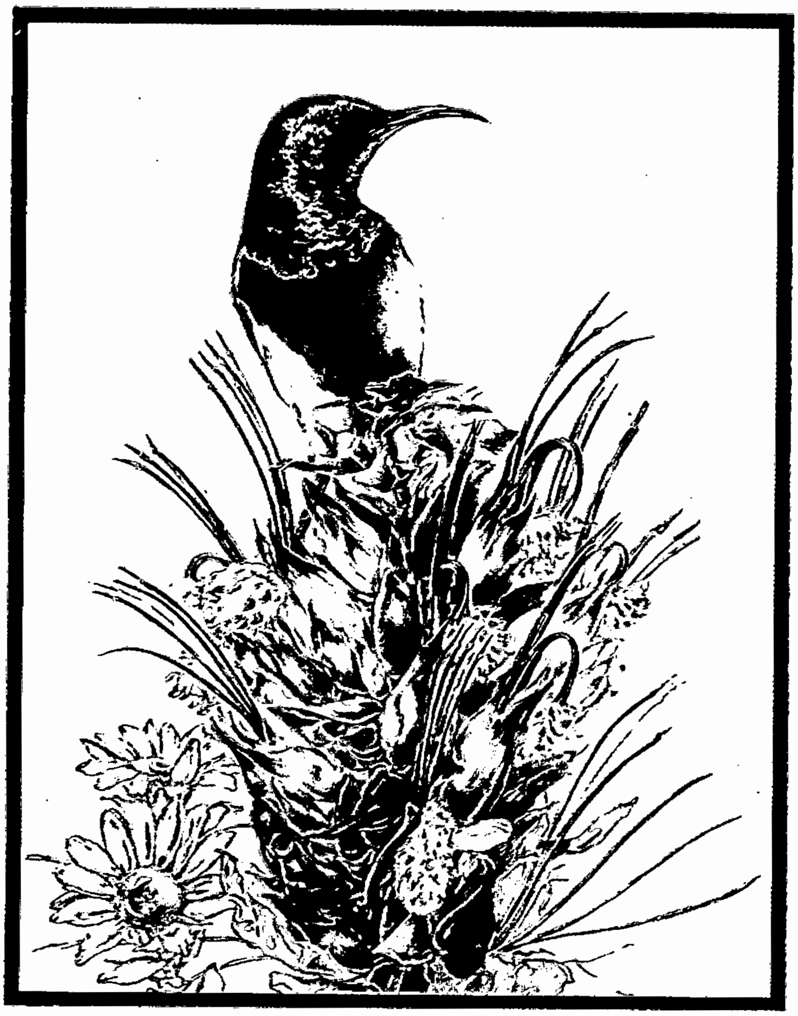

FRONTISPIECE

An adult male Orangebreasted Sunbird
<u>Nectarinia</u> <u>violacea</u> on <u>Mimetes</u> <u>hirtus</u>.
In Mountain Fynbos, the density of
nectarivores, such as this sunbird,
can exceed that of all other birds combined.

Illustration by Liz McMahon from

A Fynbos Year

by Liz McMahon and Michael Fraser
(1988; David Philip, Cape Town)

EFFECTS OF NATURAL VEGETATION, FIRE AND ALIEN PLANT INVASION ON BIRD SPECIES ASSEMBLAGES IN MOUNTAIN FYNBOS OF THE SOUTHWESTERN CAPE PROVINCE, SOUTH AFRICA

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Thesis submitted in the Faculty of Science
(FitzPatrick Institute, Department of Zoology)
University of Cape Town
for the degree of Master of Science
March 1990

To my parents and Liz

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DECLARATION

I hereby certify that this dissertation is the result of my own original research, except for contributions mentioned below and in the Acknowledgements section. This dissertation has not been submitted for a degree at any other university.

Signed by candidate

18 March 1990

Publications emanating from this dissertation:

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ABSTRACT

The effects on birds of fine-scale differences in plant species assemblage and vegetation structure, and of two major disturbance factors (woody alien plant infestation and fire), were investigated in Mountain Fynbos at two sites in the southwestern Cape Province, South Africa. Three associated processes were also studied. These were the relative importance of three animal taxa as seed predators following fire, the extent to which an indigenous bird species ate alien Acacia cyclops fruits, and potentially dispersed its seeds, and the number of nectarivorous birds which visited an isolated nectar resource.

Avian responses to fire in Mountain Fynbos varied according to season, locality and burning regime. Recently and cleanly burnt fynbos at a flat, low altitude, coastal site supported a distinctly non-fynbos avifauna, characterized by relatively large-bodied, ground-feeding, opportunistic species. Bird species similarities were low between young (1,5 year-old) and old (>15 years) vegetation. At a steeper, high-altitude inland site, where much of the vegetation survived a slow, cool burn, the fire had less impact on birds and overall species composition was virtually unchanged.

Post-fire avian successional trends varied according to floristic composition and the rate of vegetation recovery. A putatively climax avifauna occupied 5,5 year-old marsh vegetation dominated by restionaceous species, but took longer to occupy plant species assemblages characterized by proteaceous shrubs. Vegetation structure was a poor indicator of bird species composition or species richness at all ages of recovery. By contrast,

floristics were an important determinant of avian assemblages in old vegetation.

A successional shift from an insectivore- to nectarivore-dominated avifauna was apparent in plant species assemblages where proteaceous food plants occur. The nectar feeding guild (Cape Sugarbird Promerops cafer and three sunbird species (Nectarinidae)), dominated (in terms of density) old Mountain Fynbos. This guild was most severely impacted by habitat modification (specifically, elimination of food plants), through burning or alien plant infestation. It also displayed the greatest seasonal variation in density, as a response to the flowering phenology of food plants. Burning of reseeding Protea species had greater short term detrimental effects on nectarivores than the burning of resprouting species.

Responses of birds to alien woody plant infestation varied according to the fynbos plant species assemblage which was infested, and the species of alien. The relative densities of frugivorous and granivorous birds tended to increase, and nectarivores to decrease, with increasing infestation. Unchecked alien infestation has the long term potential to disrupt the bird/plant pollination relationship in Mountain Fynbos. However, a minimum study period of one year is required to provide representative data of the dynamics of avian assemblages in Mountain Fynbos.

Low levels of removal of Phalaris canariensis seeds from experimental dishes were recorded in recently burnt fynbos. Small mammals accounted for the majority of visits to dishes on which seeds was removed. No removal of seeds by birds was recorded in burnt vegetation although granivorous species were present at the study site. Cinnamon Dove Aplopelia larvata took seed from dishes in unburnt forest. Ants were recorded within seed dishes but not removing seed.

Redwinged Starlings Onychognathus morio consumed fruits of alien Acacia cyclops apparently in preference to those of indigenous plants. A. cyclops may act as a pivotal food source during times of general fruit scarcity, a role traditionally filled by Rhus spp. A. cyclops seeds are eaten throughout the year, and by concurrently feeding on nectar from isolated stands of proteaceous shrubs, the birds potentially disperse alien seeds into previously uninfested fynbos.

The number of Malachite Sunbirds Nectarinia famosa utilizing an isolated patch of Leonotis oxymifolia at the Cape of Good Hope Nature Reserve was estimated from recaptures of ringed birds using a Bayesian method. The statistical technique was described and an illustrative example of its application presented. This approach to estimating utilization may be particularly useful when the population of animals is small. The estimated number of Malachite Sunbirds feeding at the Leonotis patch probably greatly exceeded the reserve population. Such food sources in protected areas are likely to become increasingly important following the fragmentation of natural vegetation in the Fynbos Biome.

In addition to identifying the abovementioned bird-plant interactions this research supplements and extends the previously small database for fynbos avifauna.

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Fynbos is sclerophyllous shrub vegetation confined to areas in the southern and southwestern Cape, South Africa, a region classified as a Mediterranean-type ecosystem (Day et al. 1979). Fynbos is dominated floristically by plants which characterize the Cape Floristic Kingdom (Takhtajan 1969), including proteoid, ericoid and restioid components (Moll & Jarman 1984; Taylor, 1978). These components are largely, but not exclusively, represented by members of the families Proteaceae, Ericaceae and Restionaceae. Fynbos is renowned for its diversity of plant species (ca 8 500), and high level of plant endemism (68%) (Bond & Goldblatt 1984). It is also characteristically heterogeneous and incorporates more than 20 major vegetation types (Moll et al. 1984), which vary greatly in plant species composition on both the macro- and micro-geographic scales (Kruger 1979). Fine-scale studies have further split these vegetation types into many individual plant species assemblages (Campbell 1985; McDonald 1985; Taylor 1977, 1983, 1984).

In marked contrast to its flora, the avifauna of fynbos is relatively poor, with only six endemic species (Winterbottom 1968a). Two of these, the Cape Sugarbird *Promerops cafer* and the Orangebreasted Sunbird *Nectarinia violacea*, are strongly associated with members of the plant families Proteaceae and Ericaceae, feeding on their nectar and associated insects, and synchronizing breeding with their flowering periods (Broekhuysen 1959, 1963; Collins 1983a,b; Mostert et al. 1980; Rebelo 1987 and references therein; Skead 1967; Winterbottom 1962, 1964).

Although birds are regarded as the best known group of animals in fynbos (Bigalke 1979), this is more a reflection of the lack of information on other groups, rather than the depth of knowledge of fynbos birds. Winterbottom (1972) summarized the limited work carried out prior to 1970 on bird community composition in fynbos. This comprised predominantly his own work (Winterbottom 1966) and that of Broekhuysen (1966). These studies largely involved the analysis of lists of bird species recorded on repeated visits to major fynbos vegetation types (Mountain Fynbos, Coastal Fynbos, Renosterveld, Strandveld). From these lists limited deductions were made of the "dominance" of any given bird species in particular vegetation types on the basis of the frequency with which it occurred in the relevant list. Subsequent research on fynbos birds concentrated on comparing the avian diversities and densities along fynbos habitat gradients which were defined largely in structural terms (e.g. Cody 1975, 1983; Cody & Mooney 1978). A second approach investigated differences in the bird species richness, densities and trophic structure of the major vegetation types in fynbos based on physical and floristic characteristics (Siegfried 1983; Siegfried & Crowe 1983).

Despite differences in approach, much of this work was largely complementary in terms of the conclusions reached. For example, the rapid replacement of species with increasing habitat structural complexity (Cody 1975) and the marked changes in avian species composition between major vegetation types (Siegfried & Crowe 1983), both imply that fynbos birds tend to occupy narrow niches and are stereotyped to narrow habitat ranges. However, interpretation of existing databases must be exercised with caution, particularly where non-comparable sampling strategies are involved (Siegfried 1983; Wiens 1981). The results of Siegfried & Crowe's (1983) 3 ha plot censuses, for example, indicate that bird species richness is 2-3 times lower in Mountain Fynbos than in lowland vegetation types, whereas the larger sample areas of Winterbottom (1966, 1968a) suggested that species richness in Mountain Fynbos and lowland vegetation types are very similar. The difficulty of comparing these results is also illustrated by the finding of Winterbottom (1968b) that "Coastal Macchia" supports 2-4 times the bird population which occur in "Coastal Renosterbosveld". Siegfried (1983), in contrast, records a bird density in "Coastal Renosterveld" of nearly five times that in "Coastal Fynbos". An added complication is that this work was carried out before the emergence of a generally acceptable classification of the major fynbos vegetation types (Moll _et_ _al_. 1984). The absence of this classification and the ambiguous use of terminology complicates subsequent comparisons between the birds of the various vegetation types. Furthermore, the heterogeneity of fynbos vegetation may result in differences in the avifaunas of the constituent plant species assemblages **within** the major vegetation types which are as marked as those **between** these vegetation types.

The present study assesses the effects on birds of two major disturbance factors (fire and invasion by alien woody plants) in Mountain Fynbos. It also represents a first attempt at assessing differences between the avian assemblages of plant species assemblages within a major fynbos vegetation type (Mountain Fynbos).

Fire

Fire is a natural phenomenon to which fynbos vegetation is pre-adapted and upon which it is dependent (Bond 1980, 1983; van Wilgen 1982, 1987; van Wilgen et al. 1985). The fire interval under natural conditions is irregular and can vary from six to 40 years (Kruger & Bigalke 1984). Only rarely does the vegetation reach the oldest stage, however, and many fynbos plants appear to be adapted to a fire interval of between 10 and 30 years (van Wilgen 1987). Under the present managerial regime, fynbos is usually burnt at between 12 and 15 years of age.

Fire is considered to be the single most important factor influencing Mediterranean-type ecosystems (Keeley 1986). In fynbos, its effects on plants (Cowling et al. 1987 and references therein) and, to a lesser extent, on small mammals (Breytenbach 1987; Fox et al. 1985; Frost 1984; Willan & Bigalke 1982), are relatively well documented, but little is known of its effects on birds. A fynbos bibliography (Jarman et al. 1981) contains no references keyworded for both "fire" and "avifauna". Cody et al. (1983) state that "Fire affects bird communities...and is particularly important in South Africa", but do not supply supporting details. Siegfried & Crowe (1983) note that old Mountain Fynbos communities apparently support a lower avian species richness than younger ones, and that a distinctly non-fynbos avifauna may typify the youngest communities.

Studies of avian succession in regenerating fynbos are further complicated by the fact that the existing heterogeneity of the vegetation is increased by burning. Furthermore, low nutrient levels retard plant growth rates so that fynbos vegetation may take many years to regain its previous structure, density and species composition. Certain fynbos plants do not reproduce for many years after burning. In other southern African biomes, notably savanna, the effect of fire is short-lived and the next rainy season restores the status quo (Cowling et al. 1987; Kruger 1977; Winterbottom 1972). In savanna, where fires may occur annually, the short term effects on birds of vegetation burning are relatively well documented (Dean 1987). Here, and in grasslands, fire attendance and post-fire utilization by birds are pronounced (Dean 1987; Manry 1983, 1985).

Avian responses to fire can take a number of forms (Kruger & Bigalke 1984). Birds may leave an area immediately and recolonize only when conditions resemble those pre-fire; other birds may linger after the fire but leave if they are unable to adapt to new circumstances; opportunistic species may immigrate and briefly but heavily exploit temporarily available post-fire resources. Such changes in bird species composition and feeding guilds may, in turn effect the nature of the regenerating vegetation. For example, anecdotal reports describe large influxes of granivorous birds to freshly burnt fynbos. Removal of seeds may thus influence the composition of the post-fire flora, particularly as many plants flower and seed within a few weeks of a fire (Kruger 1981). The density of granivorous birds in post-fire fynbos may allow some prediction of their impact on vegetation recovery.

The destruction of flowering proteaceous and ericaceous species may deprive nectarivores of a food source. Does this cause mortality or do the birds move elsewhere to utilize other feeding sites? Large congregations of nectarivorous birds may occur at nectar sources, and preliminary results from bird ringing indicate that such birds move extensively within the fynbos biome (Fraser & McMahon 1989; Fraser et al. 1989; McMahon & Fraser 1988), and may go some way to predicting the responses of such birds to fire in fynbos and how they react to the sudden loss of feeding resources.

Alien vegetation

Fynbos is more severely infested with alien vegetation than any other biome in South Africa (Macdonald 1984). The most important alien plants (in terms of the extent of invasion) are *Pinus* spp. and Australian *Acacia* spp. and *Eucalyptus* spp. (Stirton 1978). Such aliens may occur in dense stands which completely exclude the indigenous flora (Macdonald et al. 1987; Richardson & van Wilgen 1985). Indeed, alien invasion is the greatest threat facing 50% of the plant species presently in danger of extinction in the fynbos biome (Hall et al. 1984). Since some fynbos birds, notably nectarivores, appear to be intimately associated with certain fynbos plants (in this instance, the Ericaceae and Proteaceae (Rebelo 1987; Rebelo et al. 1984, 1985)), the loss of indigenous vegetation has important negative implications for the fynbos avifauna. On the other hand, the recent colonization of fynbos by at least two species of birds has been attributed to the spread of alien vegetation (Macdonald 1986; Macdonald et al. 1986).

Little work has been done on the fine-scale effects of alien plant species on birds, however. Pines appear to provide a generally inimical habitat for birds, with the result that dense stands are almost devoid of bird life (Cody 1975). The *Acacias*, Hakeas and Eucalyptus species, however, are utilized more extensively by birds (Breytenbach 1986; Fourie 1968; Fraser 1987; Glyphis et al. 1981; Middlemiss 1963). Dense stands of Acacia spp. contain bird assemblages distinct from the indigenous fynbos vegetation (where trees are scarce (Moll et al. 1980)), comprising a mixture of species from fynbos and scrub-forest (Winterbottom 1970).

A number of bird species have been recorded eating the fruits of alien plants (Broekhuysen 1960; Glyphis et al. 1981; Hofmeyer 1989; Middlemiss 1963; Winterbottom 1970). Frugivorous birds are naturally scarce in Mountain Fynbos (Siegfried 1983) and seed dispersal by birds in such vegetation is virtually non-existent (Cody 1975). If the numbers of frugivorous birds increase in response to increasing Acacia infestation, the birds themselves may contribute to the rate and extent of alien seed dispersal.

The project is aimed to broaden the fynbos avian database, particularly with respect to fine-scale distributions of birds. The results are intended to help managers predict the effects on fynbos birds of burning and clearance of alien plants, and of the latter's uncontrolled spread.

CHAPTER 1

EFFECTS OF VEGETATION AGE AND PLANT-SPECIES ASSEMBLAGE ON THE BIRDS OF MOUNTAIN FYNBOS IN THE CAPE OF GOOD HOPE NATURE RESERVE

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EFFECTS OF VEGETATION AGE AND PLANT SPECIES ASSEMBLAGE ON THE BIRDS OF MOUNTAIN FYNBOS IN THE CAPE OF GOOD HOPE NATURE RESERVE

1.1 INTRODUCTION

The Fynbos Biome (which occupies Mediterranean-climate zone South Africa and approximates the area of the Cape Floral Kingdom), is floristically exceptionally diverse and characteristically heterogeneous (Bond & Goldblatt 1984; Day et al. 1979; Gibbs Russell 1985; Taylor 1978). The biome's sclerophyllous vegetation comprises numerous structural formations and plant species assemblages. These vary greatly on both macro- and microgeographic scales (Campbell et al. 1981; Moll et al. 1984; Kruger 1979; McDonald 1985; Taylor 1977, 1978, 1984).

Floristic and structural diversity in fynbos, the most extensive and floristically rich vegetation type in the biome, are modified by fire, the most important factor influencing Mediterranean-type communities (Keeley 1986). Fynbos vegetation is fire-adapted and fire-dependent, although natural fires (ignited mainly by lightning and rock falls), occur irregularly and the inter-fire period may be long (Manry & Knight 1986; van Wilgen 1982, 1987). Prescribed rotational burning is now carried out as part of water catchment and nature reserve management. The recovery rate of fynbos vegetation varies, but generally is slow in comparison with that of other fire prone biomes in southern Africa (Kruger & Bigalke 1984).

The avifauna of Fynbos Biome in general, and fynbos in particular, does not reflect the floral richness or diversity of the vegetation, and is species poor relative to other southern African biomes (Siegfried & Crowe 1983; Winterbottom 1968a). Avifaunal attributes differ markedly between at least four of the major vegetation types (Coastal Renosterveld, Coastal Fynbos, Mountain Fynbos, Strandveld) of the biome (Siegfried 1983; Siegfried & Crowe 1983; Winterbottom 1968b, 1972). In addition, fine-scale differences in the bird species composition, density and biomass of discrete components <u>within</u> these vegetation types are considered to exceed those between them, although there is no quantitative basis for this observation (Siegfried 1983).

Avian responses to fire in fynbos are largely undocumented, but appear to vary according to locality, season and vegetation assemblage (Chapter 3; Dean 1989). Recently burnt fynbos may support a distinctly non-fynbos avifauna (Siegfried & Crowe 1983), and fire may disrupt animal-plant interactions, notably ornithophily which has a relatively high incidence in fynbos (Rebelo 1987). Nothing is known of successional trends in fynbos birds. Indeed, although birds are probably the most well-studied animals in fynbos (Bigalke 1979), this reflects mainly a lack of knowledge of other groups. The present study is a first attempt at investigating the combined effects on birds of fine-scale differences in vegetation composition and of successional stage within one vegetation type (Mountain Fynbos) in the Fynbos Biome.

1.2 STUDY AREA

The study was conducted at the Cape of Good Hope Nature Reserve (CGHNR) (34 15S, 18 25E), at the southern tip of the Cape

Peninsula, South Africa. A history of land use and the establishment of the reserve is given by Taylor (1983, 1984). Geologically, the reserve is composed predominantly of level or gently inclined Table Mountain Sandstone. The climate is Mediterranean-type, with warm, dry summers and cool, wet winters (70% of the annual rainfall, which ranges from 355 mm per annum in the south of the reserve to 698 mm per annum in the north, occurs in April-September). Six Mountain Fynbos plant species assemblages are recognized (Taylor 1984), three of which account for more than 90% of the reserve's land area. These are Upland Mixed Fynbos, Restionaceous Plateau Fynbos and Restionaceous Tussock Marsh (hereinafter referred to as Upland, Plateau and Marsh, respectively). They occur in the approximate ratio of 5:3:2 by area. Burning of <u>ca</u> 1 000 ha blocks as part of reserve management has taken place since 1975; accidental and undocumented fires have occurred before and since (D. L. Clark pers comm., pers obs). A mosaic of plant species assemblages within Mountain Fynbos of different ages is thus present in the reserve.

1.3 **METHODS**

1.3.1 <u>Study plots</u>

A 4 ha plot was marked with flagged poles in representative homogeneous areas of each of 1,5-, 5,5- and >15-year old post-fire Upland, Plateau and Marsh at between 60 m and 140 m a.s.l. Upland is essentially a three-layer assemblage of emergent, seasonally flowering Proteaceae up to 3 m tall, fine-leaved canopy shrubs and a ground layer of Cyperaceae. Plateau comprises primarily a low-growing closed layer of Restionaceae and low or sprawling shrubs with emergent <u>Leucadendron</u> spp. It contains no distinctive plant species but resembles a mosaic of Upland and Marsh. The latter comprises almost exclusively dense stands of *Elegia* spp. and occurs on shallow soils where standing water is present in winter. Marsh is the most sharply demarcated plant-species assemblage considered here.

1.3.2 Vegetation

The vegetation in each plot was categorized structurally after Campbell *et al*. (1981). Foliage profiles (a plot of vegetation density against height (Cody 1975, 1983a)), were constructed from measurements taken at 10 random points within each plot. A habitat index (*H*) was calculated from these, where $H = \log_{10}$ (half-height + height). "Half-height" is that height at which the area under the foliage profile is divided equally in two; "height" is the height of the vegetation. *H* is a function of vegetation height and density which allows habitats to be ranked. The more structurally complex the vegetation, the higher the *H* value (Cody 1975). Point data collected at 500 spots along five random 10 m transects in each plot provided a physical description of the habitat.

1.3.3 Resource availability

1.3.3.1 Nectar

Mature *Leucospermum conocarpodendron* and *Mimetes fimbriifolius* (both Proteaceae) bushes, whose inflorescences are exploited by nectarivorous birds, were counted in each plot. Flowering phenology and the number of ripe inflorescences were recorded for up to five bushes of each species in each plot throughout the study period.

1.3.3.2 Invertebrates

Aerial invertebrates were sampled using sticky traps (Cody 1983a; Koen & Crowe 1987). These comprised 20 cm x 30 cm perspex plaques suspended from ground to canopy level between two poles. The plaques were coated with Formex, a commercial resinous ant-guard to which invertebrates adhere. Ground surface invertebrates were sampled using a 500 ml glass jar containing 250 ml glycerol in alcohol solution and sunk into the ground, the lip flush with the ground surface. Three apparatus were operated in each plot for three to seven days per month in 1985. Invertebrate availability is expressed as the mean number of invertebrates per plaque or pitfall trap day^{-1}.

1.3.4 Birds

Bird counts were undertaken in the nine plots on fine, calm mornings between three and 11 times per month from July 1984 to April 1986. Birds were recorded on slow walks through each plot, following a different route on each visit. Birds entering the plot after the commencement of a count, obligate aerial foragers and roosting nocturnal birds were excluded. The standard units of analysis were mean avian density (birds ha^{-1}), and standing crop biomass (live weight of birds in g ha^{-1}). Bird masses were obtained from Maclean (1985) and birds mistnetted for ringing in the reserve (M.W. Fraser, unpubl. data). An assignment of birds to feeding guilds was based on Maclean (1985), Richardson & Fraser (in press) and Siegfried (1983). Energy requirements were calculated as follows:

Basal Metabolic Rate (BMR) after Lasiewski & Dawson (1967), where for passerines: BMR = 541,8 mass in $g^{0,724}$

and for non-passerines: BMR = 328,9 mass in $g^{0,723}$

and Field Metabolic Rate (FMR) after Nagy (1987), where for passerines: $\log_{10}$ FMR (kJ day^{-1}) = 0,949 + 0,749 $\log_{10}$ mass in g and for non-passerines:

$\log_{10}$ FMR (kJ day^{-1})= 0,681 + 0,749 $\log_{10}$ mass in g

FMR is an estimate of the energy metabolism of free-living animals and includes, in addition to BMR, activities such as locomotion, feeding and predator avoidance. It is likely to give more representative values for energetic requirements in the field than BMR, which is included here for comparative purposes.

1.3.5 Statistical analysis

Correspondence analysis (Greenacre 1984; Underhill & Peisach 1985; Underhill 1989), was employed to illustrate patterns of avian density and associations between bird species and plant species assemblages. Sorensen's Coefficients of Community (Smith 1986) were calculated to compare similarities between the bird species compositions of the various plots.

1.4 RESULTS

1.4.1 Vegetation

The structure and characteristic plants of each plot are given in Table 1.1. Foliage profiles and $\underline{H}$ values of the vegetation in each of the plots are presented in Fig. 1.1.

Structurally simple vegetation characterized all the youngest plant species assemblages. The vegetation became more complex with age and $\underline{H}$ values increased across vegetation gradients within same-age vegetation at 5,5 and >15 years old. Plateau was structurally the simplest of the three vegetation assemblages at all ages. Old Upland was structurally the most complex.

Point data histograms describing the physical composition of the plots are given in Fig. 1.2. Predictably, the extent of bare soil was high in all the recently burnt assemblages. Marsh displayed the greatest proportion of photosynthetic material at this early stage, probably a result of wetter conditions favouring vegetation recovery. This component dropped gradually with age in Marsh, where the contribution of litter remained low and standing dead material increased. This had the effect of maintaining vegetation structure despite widespread senescence (H values were almost identical in the 5,5- and >15-year-old). Marsh, therefore had reached a putatively climactic state by 5,5 years, a trend also reflected in its avifauna (see below).

There was no significant correlation between increasing vegetation complexity (H) and avian species richness (Spearman rank correlation $r_s = 0,037$; NS), density ($r_s = 0,237$; NS), biomass $r_s = -0,166$; NS) or FMR ($r_s = 0,083$; NS).

1.4.2 **Resources**

1.4.2.1 Nectar

Mature Leucospermum conocarpodendron and Mimetes fimbriifolius shrubs grew only in Upland at 5,5 and >15 years. In the former assemblage the bushes were scattered and stunted (maximum height 1 m), but higher densities of taller (up to 3,0 m) bushes occurred in the latter (Table 1.2). Potentially more nectar was thus available in the oldest than in the 5,5 year-old Upland plot. The flowering phenology and productivity (as reflected in the number of inflorescences during the flowering season) of these is illustrated in Fig. 1.3. Although flowering was prolonged, a spring peak was evident.

TABLE 1.1

STRUCTURAL FORMATIONS (CAMPBELL *ET AL*. 1981) AND CHARACTERISTIC PLANT SPECIES OF THREE PLANT SPECIES ASSEMBLAGES IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

Age (years)	Plant species assemblage	Formation	Characteristics
1,5	Upland	Sparse graminoid shrubland	5%-25% canopy cover; height 25-75cm; *Tertraria thermalis*, Restionaceae
5,5	Upland	Low open shrubland with emergent proteiod shrubs	25%-50% canopy cover; 25-100cm; Restionaceae, *Mimetes fimbriifolius*, *Leucospermum conocarpodendron*, ericaceous shrubs
>15	Upland	Low mid-dense shrubland with tall emergent proteoid shrubs	50%-75% canopy cover; height 25cm-300cm; *Leucospermum conocarpodendron*, *Mimetes fimbriifolius*, Cyperaceae, Restionaceae, ericaceous shrubs
1,5	Plateau	Sparse restioland	0,1%-5% canopy cover; height 15cm.; Restionaceae
5,5	Plateau	Open graminoidland with low emergent shrubs	25%-50% canopy cover; height 40cm.; *Leucadendron laureolum*, *Elegia* spp.
>15	Plateau	Mid-dense restiod shrubland	50%-75% canopy cover; height 50cm-100cm; *Leucadendron laureolum*, *Elegia* spp.
1,5	Marsh	Sparse restioland	0,1%-5% canopy cover; height 15cm.; Restionaceae
5,5	Marsh	Tall closed restioland	75%-100% canopy cover; height 100cm; *Elegia cuspidata*,*E. parviflora*
>15	Marsh	Tall closed restioland	75%-100% canopy cover; height 100cm; *Elegia cuspidata*, *E. parviflora*

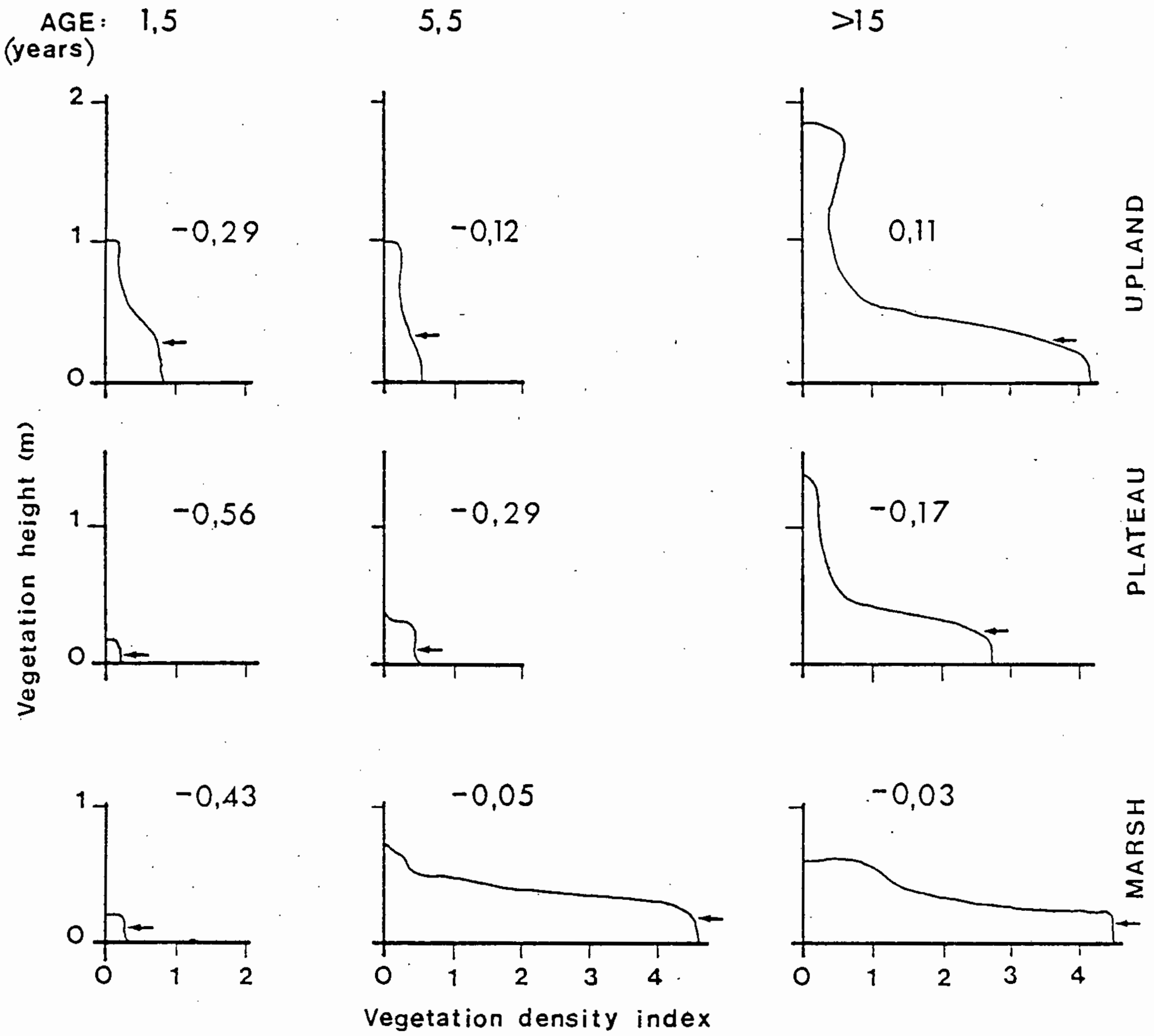

FIGURE 1.1

FOLIAGE PROFILES OF THREE PLANT SPECIES ASSEMBLAGES IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE. THE FIGURE ABOVE EACH PROFILE IS THE HABITAT INDEX (H). THE ARROW INDICATES THE HALF-HEIGHT

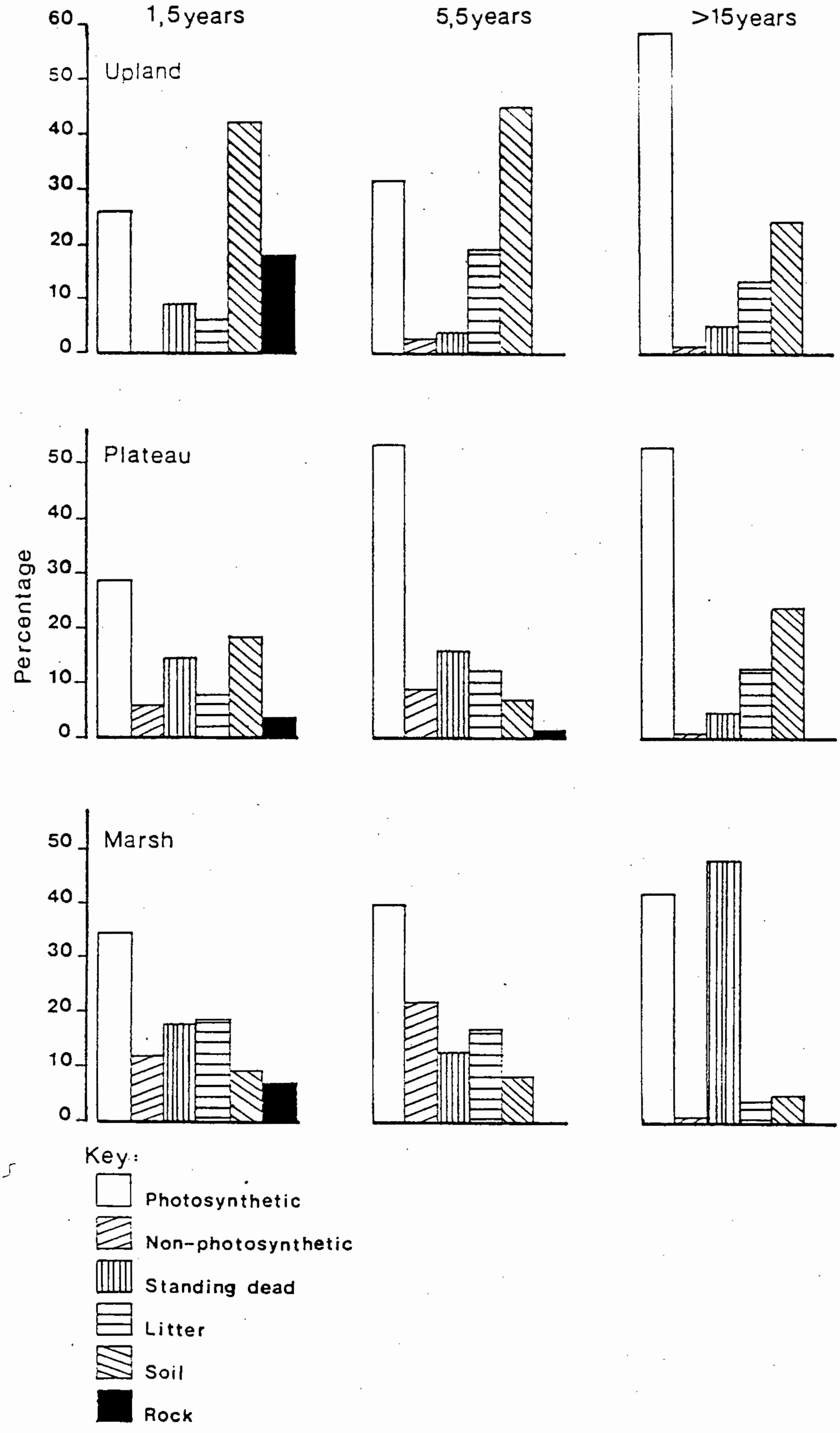

FIGURE 1.2

PHYSICAL CHARACTERISTICS (FROM POINT DATA) OF THREE PLANT-SPECIES ASSEMBLAGES IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

TABLE 1.2

DENSITY AND PRODUCTIVITY OF MATURE PROTEACEOUS SHRUBS IN UPLAND MIXED FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

Proteaceous species	Density of mature bushes (mean per ha ±SD) in flowering season		Ripe inflorescences (mean per bush ±SD)	
	Vegetation age (years)			
	5,5	>15	5,5	>15
Leucospermum conocarpodendron	0,4 ± 0,9	5,5 ± 2,4	4,0 ± 2,8	30,0 ± 30,3
Mimetes fimbriifolius	1,7 ± 1,5	3,7 ± 1,3	8,3 ± 7,5	31,8 ± 34,5

1.4.2.2 Invertebrates

Fig. 1.4 shows the mean monthly number of invertebrates trapped at each level within the vegetation, providing an indication of relative abundance within each plant species assemblage. The number of invertebrates trapped in the lower three vegetation layers (i.e.: those common to all plant species assemblages) tended to increase with increasing vegetation age (Table 1.3), but this was not statistically significant (Spearman rank correlation r_s = 0,41; NS). More invertebrates were potentially available to foliage-gleaning insectivorous birds in >15 year-old Upland as a function of increased vegetation height.

1.4.3 Birds

The overall results indicate that fire dramatically alters species composition and increases biomass, but has little effect on species richness or density.

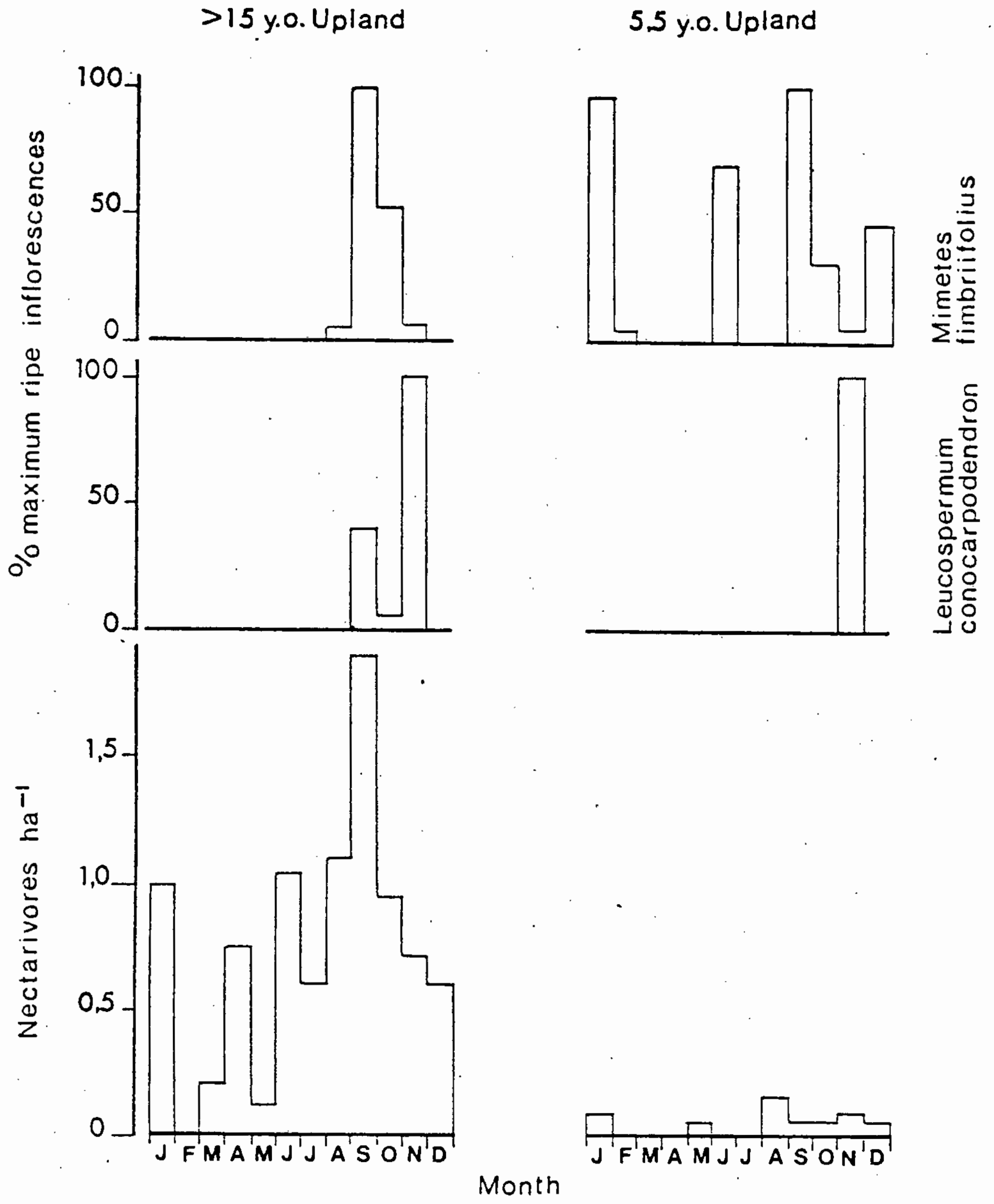

FIGURE 1.3

NECTARIVORE DENSITIES AND FLOWERING PHENOLOGIES OF
MIMETES FIMBRIIFOLIUS AND LEUCOSPERMUM CONOCARPODENDRON
IN 5,5- AND 15 YEAR-OLD UPLAND MIXED FYNBOS
AT THE CAPE OF GOOD HOPE NATURE RESERVE

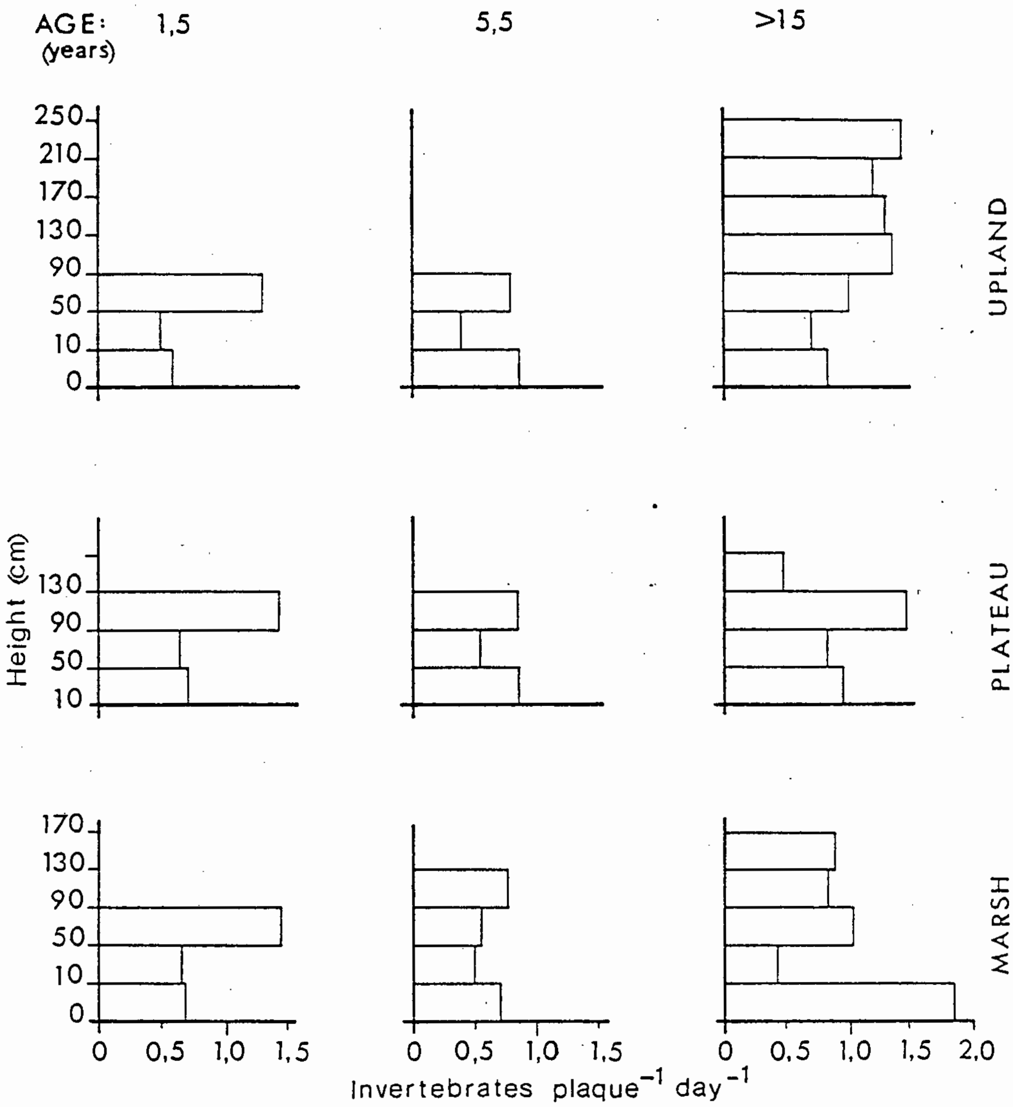

FIGURE 1.4

INVERTEBRATE ABUNDANCE (MEAN NUMBER TRAPPED PER JAR OR PLAQUE PER DAY) IN THREE PLANT SPECIES ASSEMBLAGES IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

TABLE 1.3

MEAN DAILY NUMBER OF INVERTEBRATES TRAPPED IN THE LOWER THREE VEGETATION STRATA OF THREE PLANT SPECIES ASSEMBLAGES IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

Vegetation age (years)	Plant species assemblage	No. of invertebrates (mean per jar or plaque)	Total
1,5	Upland	2,3	
	Plateau	2,8	
	Marsh	2,2	7,3
5,5	Upland	2,0	
	Plateau	2,2	
	Marsh	3,9	8,1
>15	Upland	2,5	
	Plateau	3,2	
	Marsh	3,3	9,0

1.4.3.1 <u>Avian species richness and composition</u>

Twenty-nine bird species were observed in the plots combined (Table 1.4). Avian species richness was highest overall in the 1,5 year-old vegetation and lowest in the 5,5 year-old. Within the individual plant species assemblages, avian species richness was highest in 1,5 year-old Upland. Nine species found in the 1,5 year-old vegetation were absent from the oldest vegetation. The most widespread species, occurring in eight of the nine plots was Yellowrumped Widow (scientific names of birds are given in Table 1.4). The degree of similarity between avian species composition was greatest between 5,5- and >15 year-old in all plant species assemblages (Table 1.5d). Plateau and Marsh displayed the greatest similarity overall.

Twenty per cent of bird species in each of two younger vegetations were found in all plant species assemblages, suggesting that birds discriminate less than in the oldest

TABLE 1.4

MEAN AVIAN SPECIES DENSITY (BIRDS PER HECTARE X 10) IN THREE PLANT SPECIES ASSEMBLAGES (U=UPLAND, P=PLATEAU, M=MARSH), IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

	Vegetation age (years)								
	1,5			5,5			>15		
	Plant-species assemblage								
Species	U	P	M	U	P	M	U	P	M
Yellowbilled Duck *Anas undulata* (M)*	0	0	0	0	0	0	0	0	0,08
Greywing Francolin *Francolinus africanus* (M)	0	0,24	0,14	0,33	0,07	0	0	0	0
Blackrumped Buttonquail *Turnix hottentotta* (I)	0	0	0	0	0	0	0	0,04	0
Crowned Plover *Vanellus coronatus* (I)	1,2	3,6	0,9	0	0	0	0	0	0
Ethiopian Snipe *Gallinago nigripennis* (I)	0	0	0,06	0	0	0	0	0	0
Rock Pigeon *Columba guinea* (G)	0,73	0	0	0	0	0	0	0	0
Cape Turtle Dove *Streptopelia capicola* (M)	0,03	0	0	0	0	0	0,04	0	0
Ground Woodpecker *Geocolaptes olivaceus* (I)	0,03	0	0	0	0	0	0	0	0
Clapper Lark *Mirafra apiata* (I)	0,14	0,03	0	0,07	0	0	0	0	0
Sentinel Rock Thrush *Monticola explorator* (I)	0,21	0	0	0	0	0	0	0	0
Familiar Chat *Cercomela familiaris* (I)	0,28	0	0	0	0	0	0	0	0
Cape Robin *Cossypha caffra* (M)	0	0	0	0	0	0	0,63	0	0
Grassbird *Sphenoeacus afer* (I)	0	0	0,04	0	0,04	1,0	0,20	0,20	0
Cloud Cisticola *Cisticola textrix* (I)	0	0,28	0,20	0	0	0	0	0	0
Greybacked Cisticola (I) *Cisticola subruficapilla*	0,03	0	0	0,40	0,37	0,22	1,3	0,46	0,79
Levaillant's Cisticola *Cisticola tinniens* (I)	0	0	0	0	0	1,3	0	0	2,9
Spotted Prinia *Prinia maculosa* (I)	0	0	0	0	0	0	0	0,04	0

(continued)

TABLE 1.4 (continued)

	Vegetation age (years)								
	1,5			5,5			>15		
	Plant-species assemblage								
Species	U	P	M	U	P	M	U	P	M
Plainbacked Pipit *Anthus leucophrys* (I)	0,35	2,1	0,88	0	0	0	0	0	0
Orangethroated Longclaw *Macronyx capensis* (I)	0,03	1,1	0,54	0	0,37	0,11	0,08	0,12	0
Fiscal Shrike *Lanius collaris* (M)	0	0	0	0,11	0,12	0	0	0	0
Bokmakierie *Telephorus zeylonus* (M)	0	0	0	0	0	0	0,08	0,04	0
Redwinged Starling *Onychognathus morio* (M)	0	0	0	0	0	0	0,12	0	0
Cape Sugarbird *Promerops cafer* (N)	0	0	0	0	0	0	3,7	0	0
Malachite Sunbird *Nectarinia famosa* (N)	0,73	0	0	0,33	0	0	2,3	0,04	0
Orangebreasted Sunbird *N. violacea* (N)	0	0	0	0,15	0	0	3,1	0	0
Yellowrumped Widow *Euplectes capensis* (G)	0,03	0	0,20	0,04	0,11	0,30	0,08	0,12	0,99
Cape Siskin *Serinus totta* (G)	0,17	0	0	0	0	0	0	0	0
Cape Canary *S. capicollis* (G)	0,69	0	0	0	0	0	0,20	0	0
Cape Bunting *Emberiza capensis* (G)	0,24	0	0	0,15	0	0	0,47	0	0
No. species	15	6	8	8	6	5	13	8	4
Plot-specific species	4	0	1	0	0	0	3	1	1

*Feeding guild: I = Insectivore, N = Nectarivore, G = Granivore, M = Mixed feeder

vegetation where 11% of species occurred in all plant species assemblages. Plateau and Marsh vegetations recovered relatively quickly from fire, and at 5,5 years old their avifaunas strongly resembled those at >15 years old (Tables 1.4 and 1.5b,c).

Upland, however, was relatively slow to recover, and the 5,5 year old bore little structural or avifaunal resemblance to the >15 year old. Marsh was the first to regain its putatively climax, as indicated by the relatively high similarity between bird species compositions of the two older plots (Table 1.5c).

TABLE 1.5

SORENSEN'S COEFFICIENT OF COMMUNITY FOR BIRD SPECIES RECORDED IN THREE PLANT SPECIES ASSEMBLAGES IN MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

(a) Upland

	Vegetation age (years)	
	5,5	>15
1,5	43	35
5,5		47

(b) Plateau

	Vegetation age (years)	
	5,5	>15
1,5	33	15
5,5		61

(c) Marsh

	Vegetation age (years)	
	5,5	>15
1,5	46	17
5,5		89

(d) All plant species assemblages

	Vegetation age (years)	
	5,5	>15
1,5	48	19
5,5		52

Seasonal increases in density were exhibited by Yellowbilled Duck and Ethiopian Snipe (visitors to flooded Marsh in winter), and nectarivorous species, notably Cape Sugarbird, which visited spring-flowering Proteaceae (see below).

1.4.3.2 Density and biomass

The densities of individual species recorded in each plot are given in Table 1.4, and the overall densities in Table 1.6. In Upland and Marsh the highest avian densities were found in the oldest vegetation, whereas 1,5 year-old Plateau supported the highest avian density of this plant species assemblage. Mean avian densities decreased at 5,5 years old in all assemblages but, with the exception of Plateau (which was unchanged), increased in >15 year old.

TABLE 1.6

AVIAN DENSITY IN THREE PLANT SPECIES ASSEMBLAGES IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

Plant-species assemblage	Vegetation age (years)	Avian density (birds ha^{-1}±SE)
Upland	1,5	0,43 ±0,08
	5,5	0,16 ±0,04
	>15	1,23 ±0,12
Plateau	1,5	0,74 ±0,08
	5,5	0,11 ±0,03
	>15	0,11 ±0,02
Marsh	1,5	0,30 ±0,06
	5,5	0,29 ±0,04
	>15	0,42 ±0,08

The first two dimensions of a correspondence analysis of avian densities accounted for 59,1% of the inertia of the data matrix. The first axis, which portrayed the most important feature of the data matrix, accounted for 30,4% of the inertia of the data matrix and displayed the contrast between the youngest plots and the others. A large proportion of the inertia of the first axis was attributable to the restriction of certain species to a particular age of vegetation (notably Crowned Plover in the youngest vegetation) or plant species assemblage (Levaillant's Cisticola in Marsh). Axis 2, which accounted for a further 28,7% of the inertia, contrasted those species found only in Plateau and Marsh with those found in Upland at all successional stages (Fig. 1.5). Large contributions were made to the inertia of Axis 3 (not shown), by those species found exclusively in the youngest Upland (Rock Pigeon, Ground Woodpecker, Sentinel Rock Thrush, Familiar Chat and Cape Siskin). The two older Marsh plots lie in the same direction from the origin, illustrating the strong association between their respective avifaunas. By contrast, 1,5 year-old Marsh is more strongly associated with Plateau of the same age. Crowned Plovers appeared to favour Plateau, but their density was not significantly higher than in other assemblages of the same age (X^2_2 = 2,3; NS). The two older Plateau avifaunas do not fit into any of the groups described.

In all plant species assemblages avian biomass was maximal in 1,5 year-old vegetation (Table 1.7). The decrease displayed in the 5,5 year-old vegetation by avian density was matched by biomass. Avian biomass in Plateau, however, decreased still further in >15 year old. High biomass was not necessarily reflected in high density, most notably in the youngest Plateau where a small number of relatively large-bodied birds (Crowned Plover) occurred.

Fig. 1.6 illustrates the mean monthly avian densities for each of the plots (values for these are given in Appendices 1.1 and 1.2). There was no obvious pattern in avian density and no apparent successional trends within the study period (which would be anticipated in the youngest vegetation, at least). High or low density values were irregular and not necessarily matched in the same month the following year.

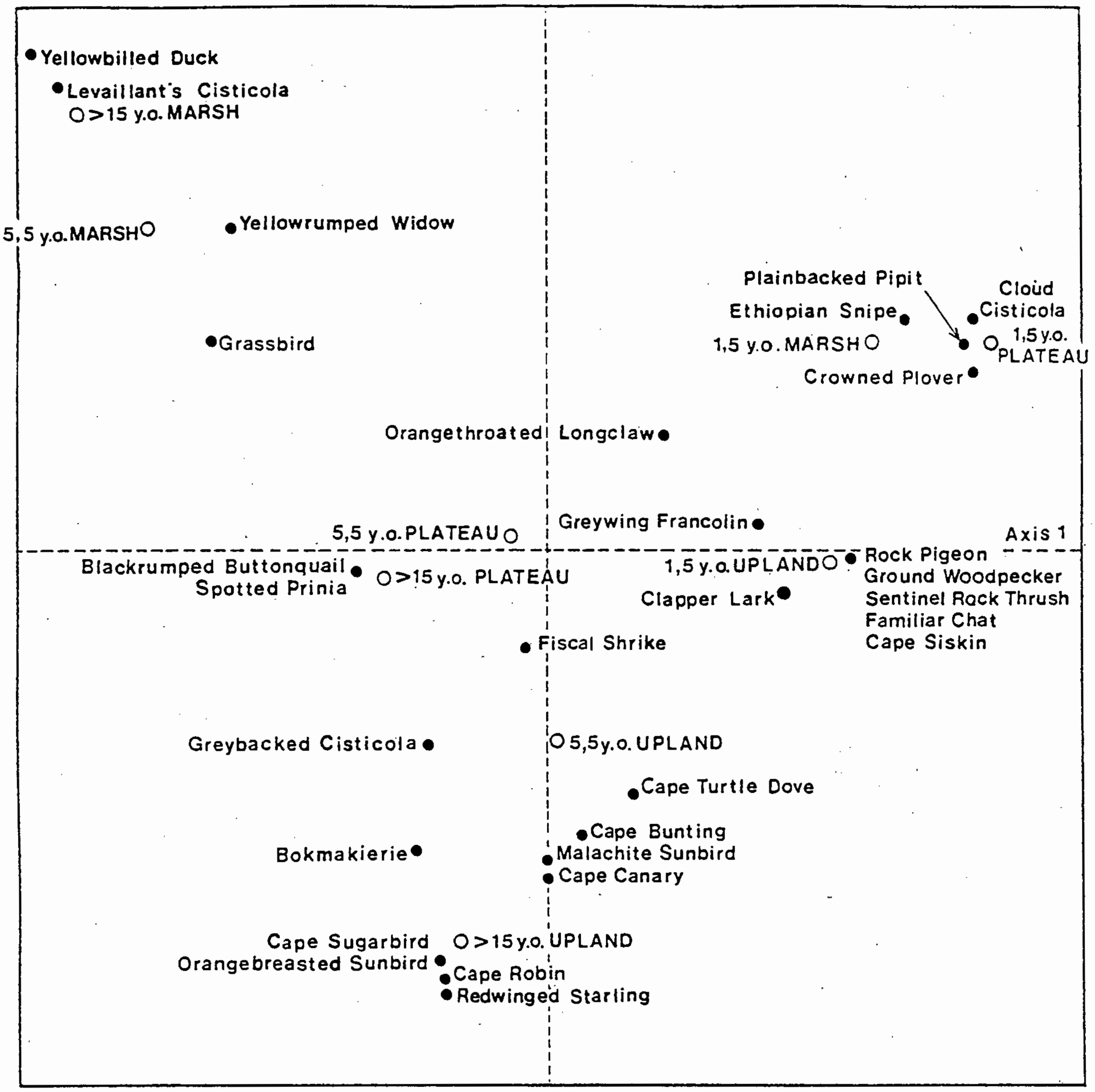

FIGURE 1.5

CORRESPONDENCE ANALYSIS OF AVIAN SPECIES DENSITIES IN THREE PLANT SPECIES ASSEMBLAGES IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

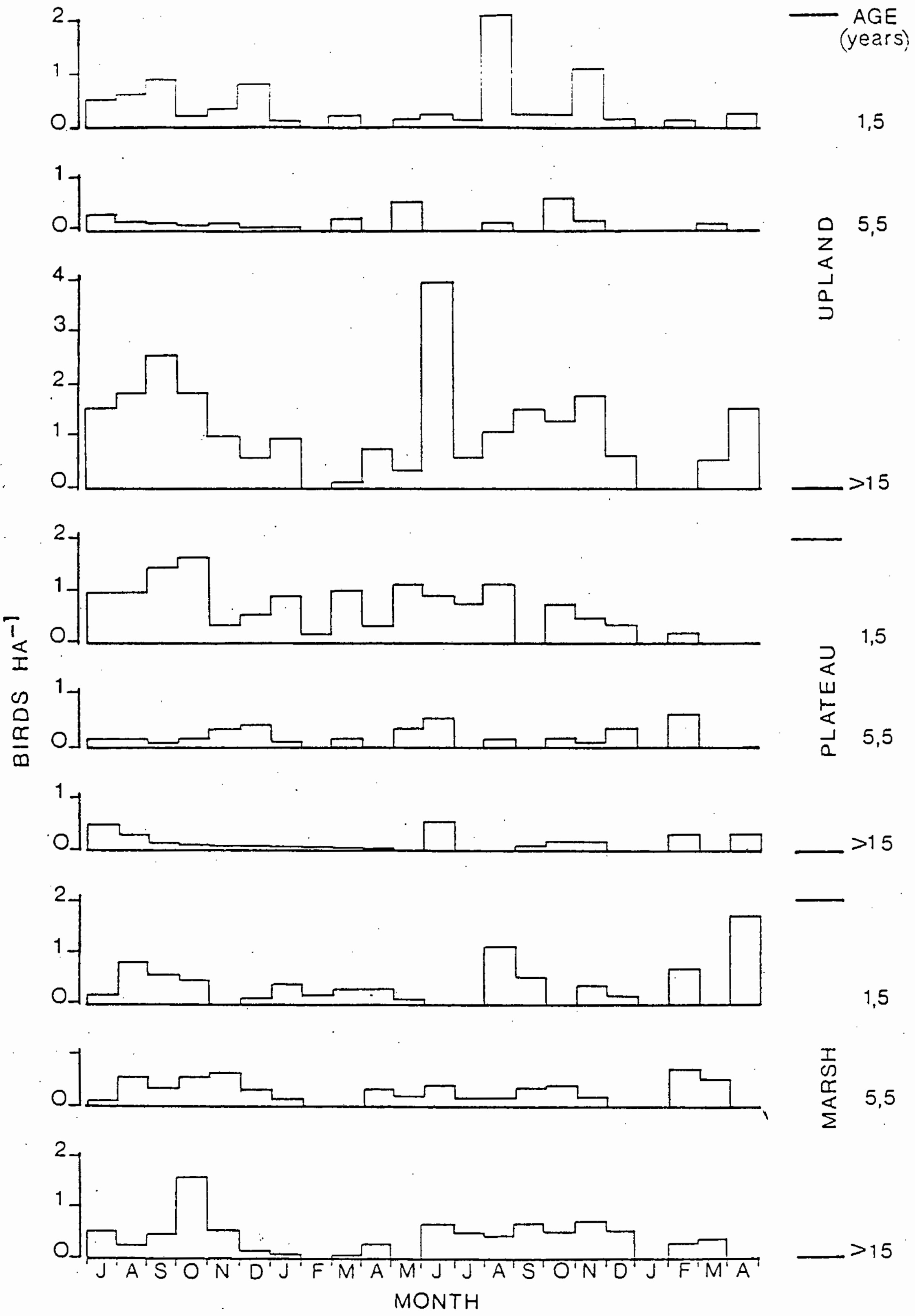

FIGURE 1.6

MEAN MONTHLY AVIAN DENSITIES (BIRDS HA^{-1}) IN THREE PLANT SPECIES ASSEMBLAGES IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

TABLE 1.7

AVIAN BIOMASS IN THREE PLANT SPECIES ASSEMBLAGES
IN THREE AGES OF MOUNTAIN FYNBOS
AT THE CAPE OF GOOD HOPE NATURE RESERVE

Plant species assemblage	Age of vegetation (years)	Avain biomass ($g\ ha^{-1}$±SE)
Upland	1,5	51,3 ±15,7
	5,5	15,1 ± 8,5
	>15	27,8 ± 3,8
Plateau	1,5	80,1 ±13,7
	5,5	6,9 ± 3,1
	>15	2,5 ± 0,6
Marsh	1,5	26,2 ±8,1
	5,5	6,1 ±0,9
	>15	15,0 ±7,3

1.4.3.3 Feeding guilds

The proportional contribution of feeding guilds to avian densities in the plots are illustrated in Fig. 1.7. A notable feature was the successional shift from an insectivore- to a nectarivore-dominated avifauna in Upland. Nectarivores were the most important guild (in terms of density and biomass) in the oldest Upland, reflecting the relatively high density and productivity of their food plants. Seasonal abundance of nectarivores was marked in this plant species assemblage, where their density was positively correlated with the number of ripe inflorescences on proteaceous shrubs (Spearman rank correlation $r_s = 0,60; p<0,01$). Where these plants did not occur, or outside their flowering season, nectarivorous species were virtually or totally absent.

The proportion of insectivores was relatively high in Plateau and Marsh at all ages (Fig 1.7). The overall density of insectivorous birds (i.e. those in the three plant species assemblages combined), did not increase with age. The density of insectivorous birds in each plot showed no relationship to invertebrate abundance (Spearman rank correlation $r_s = 0{,}39$; NS), in contrast to the tendency displayed by invertebrate abundance. Nor did insectivores increase with increasing vegetation complexity (Spearman rank correlation $r_s = 0{,}177$; NS). Granivores were most abundant (in absolute and proportional terms), in the youngest Upland (doves Columbidae, and canaries Fringillidae), and the oldest Marsh (Yellowrumped Widow). Mixed feeders made a small contribution throughout.

The contributions of each guild to avian biomass are shown in Fig. 1.8. The shift from an insectivore- to a nectarivore-dominated avifauna is again apparent in Upland. Insectivores dominated in the youngest and oldest Plateau and the two younger Marsh assemblages. The high contribution to avian biomass made by mixed feeders in 5,5 year-old Upland and >15 year-old Marsh contrasts with the relatively small contribution made by this guild to avian density. This was attributable to the small number of relatively large-bodied birds involved (Greywinged Francolin and Fiscal Shrike in Plateau, Yellowbilled Duck in Marsh).

1.4.3.4 Energetic requirements

Avian energetic requirements are given in Tables 1.8 and 1.9. Non-passerines accounted for most of the energy requirements in young vegetation. In the oldest plots, passerines accounted for between 83% and 99% of energy requirements. The energy requirements of avian feeding guilds paralleled the trend exhibited by guild density and biomass, with a shift to nectarivore dominance in old Upland and insectivores dominating in the younger vegetation (Table 1.9).

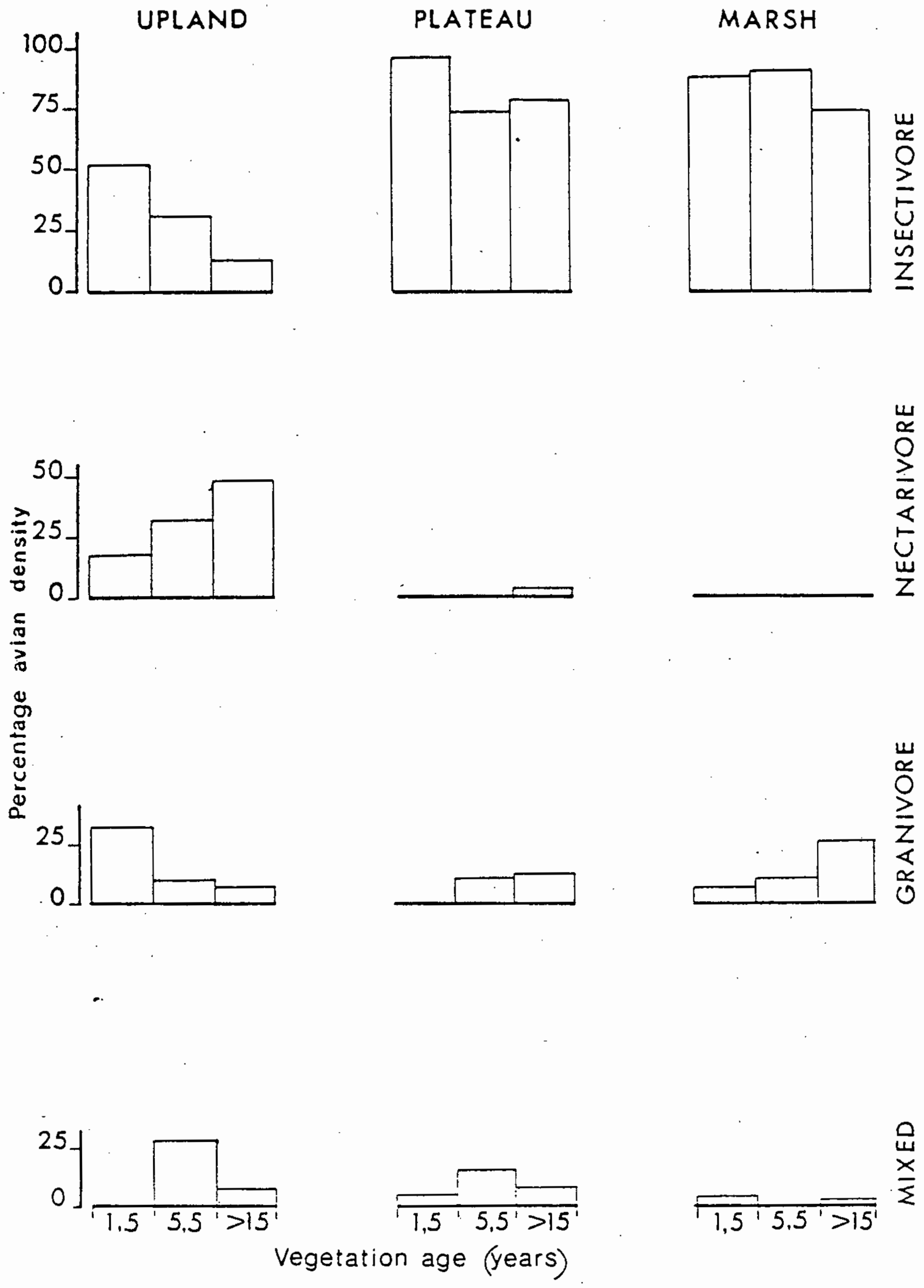

FIGURE 1.7

CONTRIBUTIONS OF AVIAN FEEDING GUILDS TO AVIAN DENSITY IN THREE PLANT SPECIES ASSEMBLAGES IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

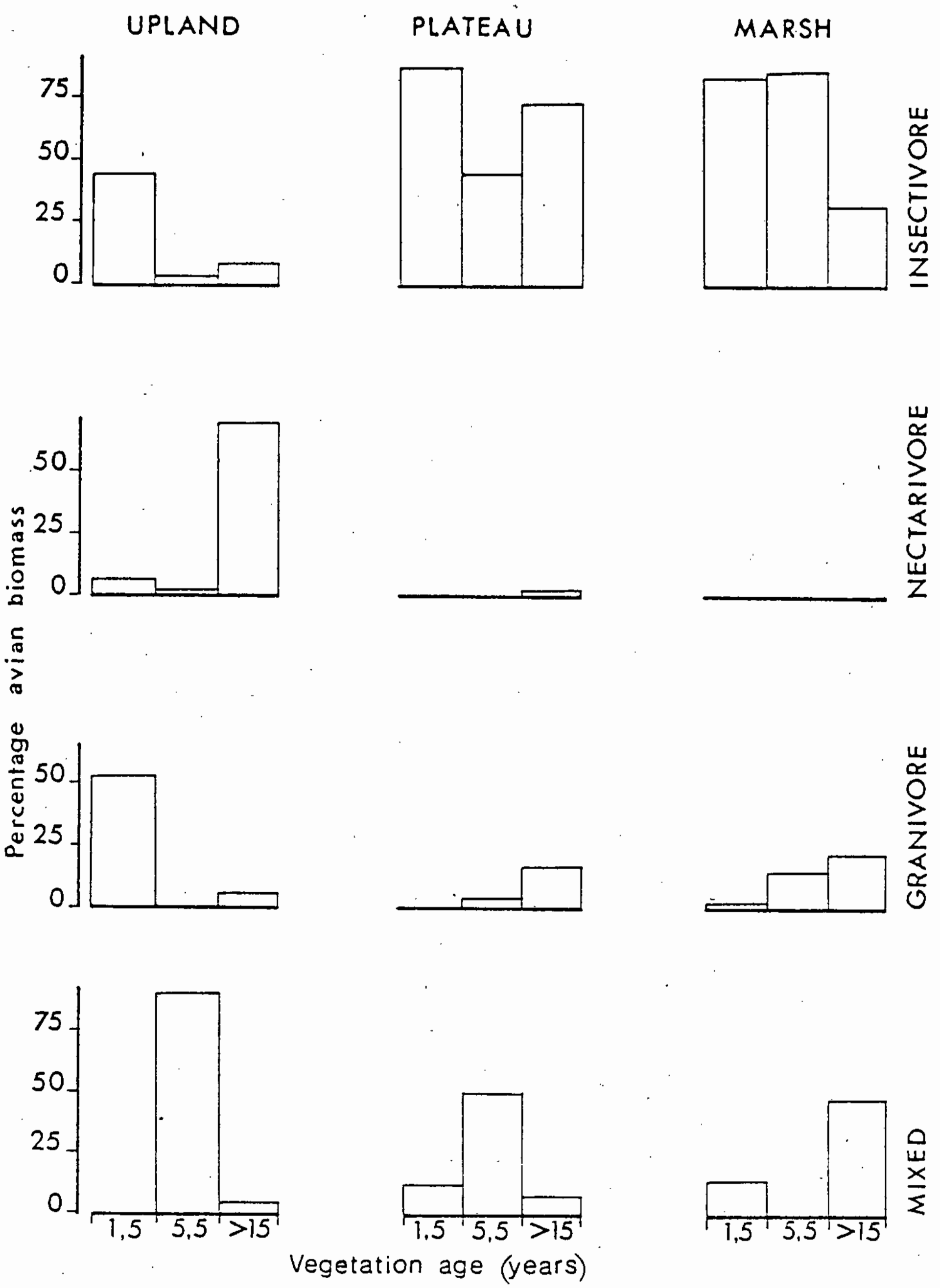

FIGURE 1.8

CONTRIBUTIONS OF FEEDING GUILDS TO AVIAN BIOMASS IN THREE PLANT SPECIES ASSEMBLAGES IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

TABLE 1.8

AVIAN ENERGY REQUIREMENTS (BASAL METABOLIC RATE (BMR) AND FIELD METABOLIC RATE (FMR) IN kJ/DAY HA^{-1}) IN THREE PLANT SPECIES ASSEMBLAGES (U=UPLAND, P=PLATEAU, M=MARSH), IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE. P = PASSERINES; NP = NON-PASSERINES

Age of vegetation	Plant species assemblage	Energy requirements (kJ/day ha^{-1})					
		BMR			FMR		
		P	NP	Total	P	NP	Total
1,5	Upland	9,5	22,4	31,9	25,1	55,7	80,8
5,5	Upland	3,5	5,5	9,0	9,1	13,8	22,9
>15	Upland	40,0	0,3	40,3	106,6	0,8	107,4
1,5	Plateau	14,4	36,4	50,8	38,3	89,9	128,2
5,5	Plateau	3,5	5,5	9,0	11,0	2,9	13,9
>15	Plateau	3,4	0,1	3,6	9,1	0,3	9,4
1,5	Marsh	7,6	10,8	18,4	20,3	26,8	47,1
5,5	Marsh	9,3	0	9,3	24,8	0	24,8
>15	Marsh	11,9	2,4	14,3	31,6	6,3	37,9

TABLE 1.9

ENERGY REQUIREMENTS (FIELD METABOLIC RATE IN kJ/DAY HA^{-1}) OF AVIAN FEEDING GUILDS IN THREE PLANT SPECIES ASSEMBLAGES (U=UPLAND, P=PLATEAU, M=MARSH), IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

Age of vegetation (years)	Plant species assemblage	Energy requirements (kJ/day ha^{-1})				
		Avian diet				
		Nectar	Insects	Seeds	Mixed	Total
1,5	Upland	5,1	38,9	36,8	0	80,8
5,5	Upland	3,0	2,7	1,8	15,4	22,9
>15	Upland	77,2	10,0	7,2	13,0	107,4
1,5	Plateau	0	118,1	0	10,1	128,2
5,5	Plateau	0	7,9	1,3	4,7	13,9
>15	Plateau	0,3	6,6	1,4	1,1	9,4
1,5	Marsh	0	38,9	2,3	5,8	47,1
5,5	Marsh	0	21,3	3,5	0	24,8
>15	Marsh	0	19,8	11,9	6,2	37,9
1,5	All	5,1	195,9	39,1	15,9	256,0
5,5	All	3,0	31,9	6,6	20,1	61,6
>15	All	77,5	36,4	20,5	20,3	154,7

1.5 DISCUSSION

Comparisons between the avifaunas of different Mountain Fynbos localities are complicated by the highly variable effects of fire on fynbos vegetation. The pre-burn ages of the 1,5- and 5,5 year-old plots were not known (but may have exceeded 15 years), and there is no record of the conditions under which they were burnt (D.L. Clark pers. comm.). The composition of the vegetation, fuel loads, season, topography and prevailing weather conditions together influence the intensity of the burn and, in turn, the subsequent recovery of the vegetation (Bond 1980; van Wilgen 1987 and references therein). Post-fire regeneration and succession are also highly variable and probably influenced by grazing and seed predation (Cowling *et al*. 1987; Bond 1984; Kruger 1983). Responses of birds to fire are likely to be similarly diverse and influenced by fire intensity, frequency and the subsequent rate and extent of vegetation recovery. The legitimacy of using different plots to represent successive seral stages is questionable because of the heterogeneity of the vegetation and other microenvironmental variation. Essentially, no two fynbos areas (even ones close to each other) are the same. In addition, Cape Rockjumper *Chaetops frenatus*, Victorin's Warbler *Bradypterus victorini* and Protea Canary *Serinus leucopterus*, which are endemic to the Fynbos Biome and which feature in other fynbos studies (Chapter 2; Cody 1975, 1983b; Siegfried 1983; Siegfried & Crowe 1983), are absent from the Cape Peninsula (Hockey *et al*. 1989; Fraser & Richardson 1989). No long-term avian studies have been undertaken in fynbos and previous research was conducted before a generally acceptable vegetation classification of the Fynbos Biome (Moll *et al*. 1984) was adopted. This further hampers valid comparisons.

Against this background, the extrapolation of results from short-term, single-site studies, their use as predictors of the effects of fire and seral stage on fynbos birds in general, and comparisons with existing data must be exercised with caution.

Using a transect census method (Emlen 1971) for ten months before and from three to 12 months after the fire, R. P. Prys-Jones and D. L. Clark (unpubl. data) found that bird density in Upland showed a 66% reduction and biomass a 19% reduction from pre-burn levels. Density was virtually unchanged in Plateau but biomass increased by 500% (almost entirely due to Crowned Plovers). Density and biomass in Marsh declined by about 50%. Overall species richness declined slightly but composition and abundance changed markedly. Although the density of birds recorded by Prys-Jones and Clark after the fire exceeded those found in this study (commenced nine months later), the general trends recorded, notably the shift from a nectarivore- to an insectivore-dominated avifauna in young vegetation and a dominance of open country species following fire, are complementary.

1.5.1 <u>Bird species richness and composition</u>

Increased structural diversity and high nectar availability (essentially, where the vegetation was dominated by proteaceous shrubs), promoted the highest avian alpha diversity in Mountain Fynbos (Cody 1975, 1983b; Siegfried 1983). At CGHNR, alpha diversity was highest in recently burnt Upland, although some apparently anomalous species contributed to the high species richness here and in the youngest vegetation in general. A number of these species are described by Maclean (1985) as birds of burnt veld and short, dry grasslands. The Crowned Plover, for example, characterizes newly-burnt fynbos at CGHNR, but has not been recorded in studies in this habitat elsewhere in the southern Cape (G.J. Breytenbach, pers. comm.; Chapter 3; Dean 1989; Siegfried & Crowe 1983). It is listed by Winterbottom (1966) as avoiding Mountain Fynbos. Similarly, the Clapper Lark is more typical of Sand Plain Fynbos and the Cloud Cisticola of short grass and Renosterveld (Hockey et al. 1989; Winterbottom 1966). Other species, notably Orangethroated Longclaw, Greybacked Cisticola (which is replaced by the congeneric Neddicky *Cisticola fulvicapilla* in fynbos at higher altitude (Winterbottom 1966)), and Cape Bunting typify lowland vegetation types in the southwestern Cape (Siegfried & Crowe 1983; Winterbottom 1966, 1968a,b). The presence of these "non-fynbos" species in the CGHNR study plots sets the avifauna apart from that of Mountain Fynbos elsewhere. This peculiarity may be the result of a number of features of the reserve. The low altitude of the study site contrasts with the upland setting of most Mountain Fynbos. Its level topography contrasts with the steep ground which characterizes much Mountain Fynbos. The peninsular location and associated salt-laden winds (wind-shear is apparent on much of the vegetation), and relatively low rainfall (nearby mountain slopes may receive double the amount of rainfall recorded at coastal locations (Fuggle & Ashton 1979; Kruger 1981), are also unusual for Mountain Fynbos. Past agricultural land use and subsequent reserve management involved frequent burning and attempts to improve grazing for introduced alien large mammals through ploughing, brushcutting and sowing with alien pasture grasses (Taylor 1984). Large herbivores are not a feature of Mountain Fynbos (Bigalke 1979). Where fynbos shrublands are burnt at short intervals, tall shrubs that regenerate from seed are eliminated. Tall closed shrublands are thus converted to closed graminoid shrublands with a subsequent shift in characteristic bird species (Richardson & Fraser in press). Burning may increase the restionaceous component of the vegetation (Low 1984), and the proteoid element may be eliminated if the inter-fire period in less than ten years (van Wilgen 1981). Management fires tend to be in "safe" seasons (spring and winter), whereas natural fires occur mainly in summer (Horne 1981; van Wilgen 1984). A shift in seasonality may expose Proteaceae seed to predation for long periods before conditions are suitable for germination (Bond 1984). Such past agricultural use and management practices may have contributed to the open growth form of the vegetation and low density of arborescent Proteaceae at CGHNR, resulting in an avian assemblage which is probably unrepresentative of Mountain Fynbos in general.

1.5.2 Bird species richness, density and vegetation structure

Cody (1975) recorded an accumulation of bird species with increasing H values (i.e.: increasing vegetation structural complexity). He argued that bird species were "recognizing and selecting habitats on the basis of many of the same criteria that we use to classify these vegetation types". However, habitat descriptions based on structural characteristics alone are unlikely to predict accurately bird species compositions or densities in Mountain Fynbos. Moreover, it is recognized that the relationship between alpha diversity and vegetation structure breaks down in more open vegetation types and in habitats occupied by more specialized feeders (MacArthur & MacArthur 1961). Mountain Fynbos satisfies both these criteria and the results here support this reservation.

At CGHNR, there was no linear relationship between avian density and species richness and structural attributes of the vegetation. Floristic variation (specifically, the presence of mature proteaceous shrubs), was responsible for high avian densities in old vegetation. In younger vegetation, there was no apparent relationship between floristics and bird density or species richness. Levaillant's Cisticola was restricted to Marsh dominated by Elegia spp., and may be dependent on this taxa in Mountain Fynbos. Elsewhere it occurs in a variety of wetland vegetation types (Hockey et al. 1989; Maclean 1985).

In Californian coastal sage scrub, Stanton (1986) found that fire decreased bird species richness and avian density was significantly higher in old than in recently burnt vegetation. Floristic variation accounted for over half the variation in bird community structure in North American grasslands, whereas physiognomy was responsible for only one third (Rotenberry 1985). In a Mediterranean habitat in Israel, Rankevich & Warburg (1983) found no direct relationship between vegetation type or structure and bird species diversity. Bird species dropped out of the community as architecture and composition became more simple along an Arizonan vegetation gradient (Vander Wall & MacMahon 1984). Most species distributions were determined by requirements for specific vegetation components for nesting and foraging. Bird species diversity was significantly associated with foliage height diversity and new species were added with increasing vegetation complexity, but none was lost. This was roughly the situation at CGHNR if one progressed only from 5,5 year-old to >15 year-old vegetation. The youngest vegetation did not fit into this pattern, and, as has been discussed, supported an atypical Mountain Fynbos avifauna.

Cody (1975) found that species widely distributed along the vegetation gradient displayed similar densities or declined with decreasing vegetation complexity. Whereas this was the general pattern for Orangethroated Longclaw and Yellowrumped Bishop, the opposite was true for Greybacked Cisticola. This species increased with increasing $\underline{H}$ values (Spearman rank correlation $r_s = 0{,}87$; $p<0{,}01$). None of these three species can be claimed to typify Mountain Fynbos, however, and their distribution and densities might again have been a product of the anomalous plant communities and other atypical attributes (as far as Mountain Fynbos is concerned), of the study site. Certainly in fynbos it is not possible to interpret bird species richness in simple terms of vegetation structure, as noted by Bigalke (1979).

There were few similarities between CGHNR and other Mountain Fynbos sites. Seven species (58%) of pre-fire inland Mountain Fynbos at Jonkershoek were also present at CGHNR (Chapter 2).

Of 12 dominant Mountain Fynbos bird species recorded by Cody (1983b), eight were recorded in the present study, four of them at very low densities only. Of the five species characterizing "pre-fire Mountain Fynbos" at a site on the northern Cape Peninsula (Siegfried & Crowe 1983), only one (Yellowrumped Bishop) was recorded in old Mountain Fynbos in study plots at

CGHNR. Indeed, the species listed from their study site by Siegfried & Crowe (1983) are more characteristic of kloof forest or alien vegetation than Mountain Fynbos (Chapter 4; Winterbottom 1970; Richardson & Fraser in press; Hockey et al. 1989), underlining the difficulties inherent in categorizing vegetation types.

Avian densities recorded here all were lower than (in some cases less than 1% of), those previously reported for Mountain Fynbos in general (Cody 1983b; Siegfried 1983; Siegfried & Crowe 1983; Winterbottom 1978), or discrete vegetation structural formations within Mountain Fynbos (Chapter 2). The densities in the 1,5 year-old vegetation were also lower than the average figure obtained in immediate post-burn Mountain Fynbos at an inland site (Chapter 2).

Siegfried (1983) reports an avian biomass of between 31 g and 141 g ha^{-1} for "Mountain Fynbos". His lowest value is exceeded in the present study only by 1,5 year-old Upland and Plateau.

1.5.3 Feeding guilds

Nectarivorous birds are important primary consumers in Mountain Fynbos (Siegfried 1983), but not in shrublands of other Mediterranean-type regions (Cody 1973). Large numbers aggregate at flowering food plants in a variety of vegetation types in the Fynbos Biome (Chapter 6; Fraser et al. 1989; Skead 1967), in which at least 300 plant species are considered to be bird-pollinated (Rebelo 1987; Rebelo et al. 1984, 1985).

The absence of nectarivores from Plateau and Marsh is clearly a result of the absence of suitable food plants. Leucadendron spp.

are the only proteaceous shrubs in these two plant species assemblages, but these do not bear flowers attractive to birds. This contrasts with the extensively bird-visited *Mimetes fimbriifolius* and *Leucospermum conocarpodendron* in Upland. The density and productivity of proteaceous shrubs in the 5,5 year-old Upland was presumably too low to attract Cape Sugarbirds. The small number of nectarivores recorded in the youngest Upland comprised Malachite Sunbirds attracted to flowering geophytes, particularly *Watsonia tabularis* (Iridaceae).

Cape Sugarbirds and sunbirds also feed on arthropods, particularly those associated with their food plants (Skead 1967; Maclean 1985; Mostert *et al*. 1980). Outside the flowering season of food plants, however, there was no indication of a shift to an insectivorous diet, nor were the birds recorded in other plant species assemblages where food plants were absent. It is likely that the majority of birds left the area entirely, therefore. Little is known of the migration patterns of nectarivores, but ringing has shown that at least some birds (including ones marked at CGHNR), undertake extensive movements, presumably in response to food availability (Fraser *et al*. 1989; Oschadleus & Fraser 1988).

This study demonstrates that the frequency with and density in which nectarivores occur are strongly linked to the spatial and temporal distribution of the flowers from which they feed. Avian visitors to Californian coastal sage scrub were found by Stanton (1986) to use seasonal and patchy food sources not exploited by residents. This is also found in Mountain Fynbos, where nectarivores may be considered seasonal visitors. Fynbos and sage scrub both, therefore, differ from Mediterranean scrub communities in Spain where non-residents were generalist feeders able to exploit spatially unpredictable resources (Herrera 1978).

Since the density of nectarivores can exceed that of all other species combined (Chapter 2; Siegfried 1983), studies which fail to cover periods when these birds are likely to occur will produce misleading and unrepresentative results. Moreover, many other bird species are known to feed on nectar (Oatley & Skead 1972; Richardson & Fraser in press). In Mountain Fynbos at CGHNR proteaceous inflorescences were visited by Cape Bulbul Pycnonotus capensis, Redwinged Starling, Cape White-eye Zosterops pallidus and Cape Weaver Ploceus capensis (Chapter 5; M.W. Fraser unpubl. data). At certain times of the year these birds potentially could make a large contribution to avian density, again emphasizing the importance of long-term studies. Indeed, even these are at best indicative, for Diehl (1986), found that although the abundance of nesting passerines in North American shrubby meadows increased with increasing habitat complexity as the vegetation aged, a regular annual pattern of alternating increasing and decreasing numbers was superimposed on the overall increase. In addition, the densities of many species could not be predicted from habitat changes.

Almost 50% of the bird species recorded in the study plots combined were insectivores, supporting Siegfried's (1983) findings. These tended to be larger bodied, ground-foragers in the youngest vegetation and smaller, leaf-gleaners in the older. Virtually nothing is known of arthropod dynamics in fynbos (Jarvis 1979). However, high concentrations of secondary defensive compounds (phenolics and terpenes), occur in fynbos plants (Morrow et al. 1983). Coupled with the low nutrient status and summer drought, these could limit the abundance of herbivorous insects and, consequently, insectivorous birds. This phenomenon was also held responsible for low invertebrate levels in southern Cape forest (Koen & Crowe 1987). Nevertheless, expressed in terms of daily captures m^{-2} of sticky trap, aerial invertebrates were about 45 times more abundant there than in CGHNR Mountain Fynbos. The absence of a relationship between insectivorous birds and invertebrate numbers was proposed by Cody (1983a) for southern African forests. In Australian heathland, insectivores made up only 8% of bird density and there was little correspondence between the biomass of flying insects and that of insectivorous birds (Pyke 1985).

Granivores were most abundant in the youngest Upland, presumably a response to seed availability. In the immediate post-fire phase, seed germination occurs for all or most species within twelve months (Kruger 1981). Granivores were probably exploiting the seeds of fast-growing annuals and early successional species, therefore. However, the density of granivores was never high, and no flocks of traditionally itinerant and opportunistic seed eaters (doves or canaries) were recorded. This parallels other findings (Chapter 2; Dean 1989), and supports my contention (Chapter 3), that birds are probably not important seed predators in post-fire Mountain Fynbos.

The absence of frugivores from Mountain Fynbos reflects the virtual absence of plants producing fleshy fruits in this vegetation type. The paucity of such plants and, therefore, ornithochory has been attributed to the low nutrient levels in fynbos (Cody _et_ _al_. 1983; Milewski 1982; Siegfried 1983).

Vale _et_ _al_. (1982) found that in America ground seedeaters were the most important guild in grasslands, and foliage insectivores in "scrub" (including chaparral, the vegetation of Mediterranean-climate zone North America). Nectarivores were relatively unimportant, but featured most prominently in "woodland". This pattern was not paralleled in Mountain Fynbos, if it is accepted that Plateau at all stages resembles "grassland". Vale _et_ _al_. (1982) also noted that the impact of land management practices, such as burning and scrub clearance, favoured an array of birds resembling that of a naturally more open environment, a logical progression that was also evident at CGHNR, but not necessarily at other Mountain Fynbos sites (Chapter 2; Dean 1989; Siegfried 1983; Siegfried & Crowe 1983).

1.5.4 Comparison with other biomes

In comparison with other vegetation types, avian parameters are low in fynbos. Cody (1975) found that as _H_ increased along a gradient from grassland to forest, bird diversity increases. Fynbos vegetation is relatively low and structurally less diverse than woodland and would be expected to support fewer bird species than steppe or woodland communities. The trends found across vegetation types (_i.e_. moving from fynbos to woodland), were apparent at the study site between the constituent plant species assemblages in the oldest vegetation. The least complex (youngest) vegetation supported the most species overall, thus contradicting previous attempts to interpret bird species richness in terms of vegetation structure alone.

Siegfried (1983) listed bird densities from a number of vegetation types in southern Africa, all of which exceeded the densities recorded at CGHNR. Even the highest densities obtained here were an order of magnitude lower than those for Mopane Woodland, for example (Milewski & Campbell 1976). Inter- and intra-African migrants are virtually absent from fynbos. Seasonal influxes of passerines, in particular, which typify African and other biomes are not a feature of fynbos (Winterbottom 1971; Hockey et al. 1989). Lack (1987) found that two-thirds of insectivorous species recorded in Kenyan savanna-woodland were Palaearctic migrants. The reason why Mountain Fynbos fails to attract such birds is not clear (Winterbottom 1971), but may be a consequence of low productivity which, in turn, is a reflection of low nutrient availability.

Certain species of African birds have clear associations with fire, notably in savanna woodland (Dean 1987). Although fynbos is a fire-prone environment, the absence of such an association is likely to be due to the unpredictability of fires in the biome and the long inter-fire interval (Chapter 2; Dean 1989). Birds are thus unlikely to provide much insight into the fire regimes in which fynbos animals and plants have evolved. The inconsistency of fire regime and associated plant responses together with the heterogeneity of the vegetation make it unrealistic to construct anything but the most general predictive models concerning the effects of fire on fynbos birds.

APPENDIX 1.1

MEAN MONTHLY AVIAN DENSITY (BIRDS PER HECTARE) IN THREE PLANT SPECIES ASSEMBLAGES (U=UPLAND, P=PLATEAU, M=MARSH) IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

		Vegetation age (years)								
		1,5			5,5			>15		
		Plant-species assemblage								
Year	Month	U	P	M	U	P	M	U	P	M
1984	July	0,6	1,0	0,2	0,3	0,1	0,1	1,6	0,5	0,5
	August	0,6	1,0	0,7	0,2	0,2	0,5	1,9	0,2	0,2
	September	0,9	1,4	0,5	0,1	0,1	0,3	2,7	0,1	0,4
	October	0,2	1,5	0,4	0,1	0,2	0,5	1,7	0,1	1,6
	November	0,4	0,4	0	0,2	0,2	0,6	1,0	0,6	0,6
	December	0,8	0,5	0,1	0,1	0,3	0,3	0,7	0,1	0,2
1985	January	0,6	0,9	0,3	0,1	0,1	0,1	1,0	0,1	0,1
	February	0,1	0,2	0,2	0	0	0	-	-	-
	March	0	1,0	0,2	0,2	0,2	0	0,1	0,1	0,1
	April	0,3	0,3	0,3	0	0	0,2	0,7	0,1	0,3
	May	0	1,2	0,1	0,6	0,4	0,2	0,4	0	0
	June	0,2	0,8	0	0	0,5	0,3	4,0	0,5	0,7
	July	0,2	0,8	0	0	0	0,1	0,7	0	0,5
	August	0,1	1,1	1,1	0,1	0,1	0,1	1,1	0	0,4
	September	2,1	0	0,5	0	0	0,2	1,5	0,6	0,6
	October	0,2	0,7	0	0,6	0,1	0,4	1,3	0,1	0,5
	November	0,2	0,4	0,4	0,2	0,1	0,1	1,1	0,4	0,7
	December	1,1	0,4	0,1	0	0,2	0	0,6	0	0,5
1986	January	-	-	-	-	-	-	-	-	-
	February	0,1	0,1	0,6	0	0,1	0,7	0	0,2	0,2
	March	0	0	0	0,1	0	0,5	0,5	0	0,3
	April	0,2	0	1,7	0	0	0	1,5	0,2	0

APPENDIX 1.2

MEAN MONTHLY AVIAN BIOMASS (GRAMS PER HECTARE) IN THREE PLANT SPECIES ASSEMBLAGES (U=UPLAND, P=PLATEAU, M=MARSH), IN THREE AGES OF MOUNTAIN FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

		Vegetation age (years)								
		1,5			5,5			>15		
		Plant-species assemblage								
Year	Month	U	P	M	U	P	M	U	P	M
1984	July	10,4	158,1	5,4	79,9	5,9	1,7	23,9	16,0	5,4
	August	28,3	131,2	32,3	2,6	7,3	12,7	47,7	5,9	32,3
	September	75,5	195,8	72,6	4,4	0,7	4,0	63,9	1,2	79,1
	October	6,2	228,5	27,8	1,9	34,3	10,0	39,6	2,0	36,8
	November	53,5	26,8	0	2,2	8,7	11,5	16,2	0,6	8,7
	December	160,7	40,5	1,2	0,8	10,4	6,4	10,5	2,6	1,9
1985	January	0,6	52,6	49,9	0,5	2,2	1,5	28,1	1,5	0,6
	February	41,7	7,3	7,3	0	0	0	-	-	-
	March	0	20,1	11,0	5,8	4,5	0	0,8	2,5	0,9
	April	3,4	11,0	2,3	0	0	7,6	10,2	0,8	7,1
	May	0	127,2	3,7	125,3	10,5	3,4	7,0	0	0
	June	3,8	42,3	0	0	15,2	10,3	72,3	11,7	13,4
	July	2,0	95,5	0	0	0	1,4	15,0	0	8,8
	August	260,4	180,9	157,6	2,0	3,8	3,8	45,5	0	9,1
	September	20,5	0	12,6	0	0	7,6	30,1	4,1	9,5
	October	4,1	41,1	0	9,5	3,8	9,0	23,3	1,2	10,4
	November	307,1	12,0	45,1	3,5	0,6	2,6	40,0	1,2	10,9
	December	3,0	13,9	3,0	0	2,5	0	21,7	0	5,6
1986	January	-	-	-	-	-	-	-	-	-
	February	1,9	3,3	2,7	0	2,7	15,6	0	6,3	5,2
	March	0	0	0	0,8	0	10,4	9,4	0	3,6
	April	6,2	0	37,4	0	0	0	17,5	7,6	0

CHAPTER 2

SHORT-TERM RESPONSES OF BIRDS TO FIRE IN OLD MOUNTAIN FYNBOS

CHAPTER 2

SHORT-TERM RESPONSES OF BIRDS TO FIRE IN OLD MOUNTAIN FYNBOS

2.1 INTRODUCTION

Fire is the most important factor influencing Mediterranean-type plant and animal communities (Keeley 1986; van Wilgen 1987). The influence of fire on fynbos plant communities is relatively well studied (Cowling et al. 1987), but little is known of its effects on birds (Dean 1989). For example, Cody et al. (1983) state that "Fire affects bird communities...and is particularly important in South Africa", but do not supply supporting references. Siegfried & Crowe (1983) noted only that "Old Mountain Fynbos communities apparently support a lower avian species richness than younger ones, and very young communities can embrace a distinctly non-fynbos avifauna". Anecdotal reports have described influxes of granivorous birds into recently-burnt fynbos vegetation. As some plant species may flower and seed within a few weeks of a fire (Kruger 1981), and many species display fire-stimulated seed release (le Maitre 1987), influxes of granivorous birds and their post-fire predation of seeds could potentially influence the extent and rate of recovery of certain components of the vegetation.

I report here the effects of fire on bird density, species richness and feeding guild composition in 28-year-old Mountain Fynbos vegetation in the southwestern Cape. The study forms part of a multi-disciplinary project investigating Mountain Fynbos ecosystems (van Wilgen 1986).

2.2 STUDY AREA

The study was carried out at the Swartboskloof subcatchment (34 00S, 18 57E), in the Jonkershoek Valley, 15 km southeast of Stellenbosch, Cape Province, South Africa. The vegetation is largely Mesic Mountain Fynbos (Moll *et al*. 1984), dominated by Tall proteoid shrublands comprising *Protea neriifolia*, *P*. *repens* and *P*. *nitida*. Patches of Afromontane Forest occur on higher scree slopes and in sheltered ravines; riparian woodland (mainly *Brabejum stellatifolium* and *Cunonia capensis*) fringes the kloof's perennial streams (McDonald 1985). The 28 year-old vegetation was burnt in a prescribed fire in March 1987 as part of catchment management undertaken by the Forestry Branch of the Department of Environment Affairs.

2.3 METHODS

Avian density was assessed using the fixed-radius plot count method of Hutto *et al*. (1986). Counts were made from February 1987 to March 1988 (*i.e*. from six weeks before until one year after the fire), in 25 m radius plots in six vegetation structural formations, viz: Mid-high Mid-dense Shrubland, Tall Sparse Shrubland, Tall Open Shrubland, Tall Closed Shrubland, Closed Woodland and Tall Forest (Campbell *et al*. 1981; see Table 2.1 for definitions). The plots lay between 380 m and 540 m a.s.l. Avian species richness and density (birds ha^{-1}) were calculated for each count. Correspondence analysis (Greenacre 1984; Underhill & Peisach 1985; Underhill 1989) was used to assess relationships between bird species densities and vegetation structural formations before and after the fire. Sorensen's coefficient of community (Smith 1986) was used to assess similarities between the bird species compositions of the six plots. This coefficient (CC) is derived from the formula

$$CC = 2c/s1 + s2$$

where c is the number of species common to both plots, and s1 and s2 are the number of species in the two plots respectively.

TABLE 2.1

CHARACTERISTICS OF PRE-FIRE STRUCTURAL VEGETATION FORMATIONS OF STUDY PLOTS AT SWARTBOSKLOOF

Formation	Characteristics
Mid-high Mid-dense Shrubland	Crowns not interlocking; 50%-75% projected canopy cover; characteristic species: Protea neriifolia, Cliffortia spp.
Tall Sparse Shrubland	Crowns not interlocking; 5%-25% projected canopy cover; characteristic species: Protea nitida
Tall Open Shrubland	Crowns not interlocking; 25%-50% projected canopy cover; characteristic species: Protea nitida, Protea neriifolia
Tall Closed Shrubland	Interlocking crowns; 75%-100% projected canopy cover; characteristic species: Protea neriifolia
Closed Woodland	Crowns not interlocking; 25%-50% projected canopy cover; characteristic species: Brabejum stellatifolium, Cunonia capensis
Tall Forest	Interlocking crowns; 75%-100% projected canopy cover; characteristic species: Cunonia capensis, Ilex mitis, Rapanea melanophloeos.

All species encountered on each visit to the study site as a whole were recorded to assess changes in overall richness and composition following the fire. Observations were made at the flame front and in freshly burnt vegetation to assess the immediate reactions of birds to the passage of the fire. Post-fire recaptures and sightings of birds mistnetted and uniquely colour-ringed before the fire allowed an assessment to be made of the survival of individual birds.

2.4 RESULTS

2.4.1 The fire and its effects on the vegetation

Swartboskloof was burnt under calm and warm conditions with high relative humidity (61-74%) on 17 and 18 March 1987. The fire was cool and slow and flares fired from a helicopter and the ground were employed to ignite unburnt vegetation. Nevertheless, much fynbos vegetation remained largely unburnt because of topography, wind direction and increasing humidity (Anon 1987). The Mid-high Mid-dense Shrubland plot was clear-burnt, but much standing vegetation remained in the other fynbos shrubland plots. The vegetation in the Tall Forest and Closed Woodland plots was unmodified by the fire and was thus available as potential refugia for birds displaced from burnt areas.

2.4.2 Reaction of birds to the passage of the fire

There was little apparent response by birds to the passage of the fire. Cape Sugarbirds (scientific names of birds are given in Tables 2.2 and 2.3) fed from *Protea nitida* inflorescences and Lesser Doublecollared Sunbirds and Cape White-eyes from *Cunonia capensis* inflorescences within 2 m of the flame front. Rameron Pigeons flew through thick smoke to reach fruiting trees in Tall Forest. No opportunistic feeding by birds on displaced animals (small mammals, reptiles or arthropods) was recorded either at or behind the flame front. Similarly, there was no evidence of scavenging in burnt vegetation after the fire. A pair of Whitenecked Ravens *Corvus albicollis* present on the day of the fire were not seen to utilize the area, and had been present before the fire. Following an accidental burn in nearby Mountain Fynbos vegetation the previous spring, Rock Kestrel *Falco tinnunculus* and Redwinged Starling *Onychognathus morio* were observed catching insects in clear-burnt ground. A Sentinel Rock Thrush _Monticola explorator_ foraging in the same area was probably taking scorched insects. After a further accidental fynbos fire in the Jonkershoek Valley in October 1987, Nicholson's Pipits _Anthus similis_ colonized a clear-burnt area at _ca_ 1 100 m a.s.l. (M.W. Fraser, unpubl. data; R. Martin pers. comm.).

2.4.3 _Bird species compositions and densities in study plots before and after the fire_

The bird species recorded within the six study plots before and after the fire are listed in Tables 2.2 and 2.3. In the correspondence analysis of pre-fire bird densities, the first axis accounted for 42% of the inertia and groups those bird species closely associated with or exclusive to Tall Forest (_e.g_. Rameron Pigeon) and Closed Woodland (_e.g_. Lesser Doublecollared Sunbird), and contrasts them with those species found in fynbos shrublands (Fig. 2.1). Cape Robin, Olive Thrush and Cape Batis are positioned in the centre of the display reflecting their relatively wider habitat tolerance.

In the correspondence analysis of bird densities in the six-week post-fire period, 54% of the inertia was accounted for by the first axis. This again contrasted those species characteristic of forest/woodland with those of fynbos shrublands (Fig. 2.2). In this respect, six species were found only in Tall Forest, and Cape White-eye, although found elsewhere, occurred at its greatest density here. No birds were recorded in the Tall Closed Shrubland or Mid-high Mid-dense shrublands in the six week post-fire period.

TABLE 2.2

BIRD DENSITIES (MEAN HA^{-1}) IN SIX VEGETATION STRUCTURAL FORMATIONS SIX WEEKS PRE-FIRE AT SWARTBOSKLOOF

Species	Vegetation structural formation**					
	1	2	3	4	5	6
	Birds ha^{-1}					
Rameron Pigeon (F)* *Columba arquatrix*	0	0	0	0	0	1,0
Redeyed Dove (G) *Streptopelia semitorquata*	0	2,0	0	0	0	0,5
Cape Bulbul (M) *Pycnonotus capensis*	0	0,5	0	0	0	0
Olive Thrush (M) *Turdus olivaceus*	0	0	0	0,5	0	1,0
Cape Robin (M) *Cossypha caffra*	0	0	0,5	0,5	0,5	1,0
Barthroated Apalis (I) *Apalis thoracica*	0	2,0	0	1,0	0	0
Grassbird (I) *Sphenoeacus afer*	0	1,0	0,5	0	0	0
Neddicky (I) *Cisticola fulvicapilla*	0	0	0	0	1,0	0
Spotted Prinia (I) *Prinia maculosa*	1,0	1,0	0	0	0,2	0
Dusky Flycatcher (I) *Muscicapa adusta*	0	0	0	0	0	1,0
Cape Batis (I) *Batis capensis*	0	0	0,5	0,5	0	0
Paradise Flycatcher (I) *Terpsiphone viridis*	0	0	0	0	0	0,5
Southern Boubou (M) *Laniarius ferrugineus*	0	0	0,5	0,5	0	0
Cape Sugarbird (N) *Promerops cafer*	0	4,1	2,0	0,5	0	0
Malachite Sunbird (N) *Nectarinia famosa*	0	0,5	0	0	0	0
Orangebreasted Sunbird (N) *N. violacea*	6,6	2,0	7,1	2,0,	0,5	0
Lesser Doublecollared Sunbird (N) *N. chalybea*	0	0	0	0	1,0	0
Cape White-eye (M) *Zosterops pallidus*	0	0	0	0	9,7	6,4
Protea Canary (G) *Serinus leucopterus*	0	0	0,5	0	0	0
TOTAL	7,6	13,1	11,6	5,5	12,9	11,4

*Feeding guilds: I = Insectivore; F = Frugivore; G = Granivore; N = Nectarivore; M = Mixed feeder

Vegetation structural formation

** 1: Mid-high Mid-dense Shrubland
2: Tall Sparse Shrubland
3: Tall Open Shrubland
4: Tall Closed Shrubland
5: Closed Woodland
6: Tall Forest

TABLE 2.3

BIRD DENSITIES (MEAN HA^{-1}) IN SIX VEGETATION STRUCTURAL FORMATIONS (AS IN TABLE 2.2), SIX WEEKS POST-FIRE AT SWARTBOSKLOOF

Species	Vegetation structural formation					
	1	2	3	4	5	6
	Birds ha^{-1}					
Cape Turtle Dove (M)* _Streptopelia capicola_	0	0,5	0	0	0	0
Klaas's Cuckoo (I) _Chrysococcyx klaas_	0	0	0	0	0	0,5
Olive Woodpecker (I) _Mesopicos griseocephalus_	0	0	0	0	0	1,0
Cape Bulbul (M)	0	0	0,5	0	0	0
Sombre Bulbul (M) _Andropadus importunus_	0	0	0	0	0	0,5
Olive Thrush (M)	0	0	0	0	0	0,5
Cape Robin (M)	0	1,0	0	0	0,5	0,5
Barthroated Apalis (I)	0	0,5	0,5	0	0	0
Neddicky (I)	0	1,0	0,5	0	0	0
Victorin's Warbler (I) _Bradypterus victorini_	0	0,5	0	0	0	0
Spotted Prinia (I)	0	0,5	1,5	0	0	0
Dusky Flycatcher (I)	0	0	0	0	0	1,0
Cape Batis (I)	0	0	0,5	0	0	1,0
Orangebreasted Sunbird (N)	0	0	0,5	0	0	0
Lesser Dc Sunbird (N)	0	0	0,5	0	1,0	0
Cape White-eye (M)	0	0,5	2,0	0	3,1	14,8
TOTAL	0	4,5	6,5	0	4,6	19,8

*Feeding guilds: I = Insectivore; F = Frugivore; G = Granivore; N = Nectarivore; M = Mixed feeder

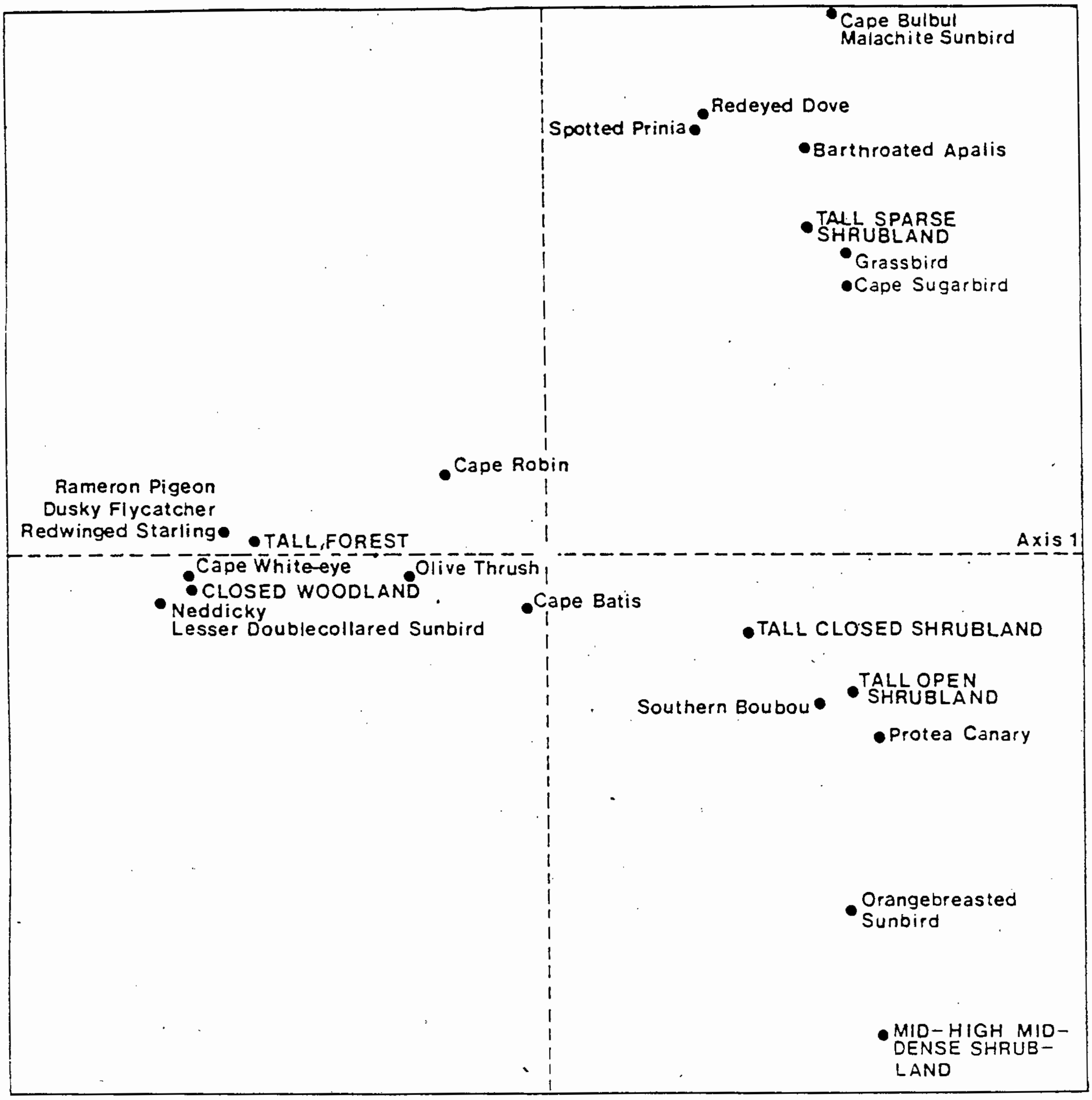

FIGURE 2.1

CORRESPONDENCE ANALYSIS OF PRE-FIRE AVIAN SPECIES DENSITIES IN SIX VEGETATION STRUCTURAL FORMATIONS AT SWARTBOSKLOOF

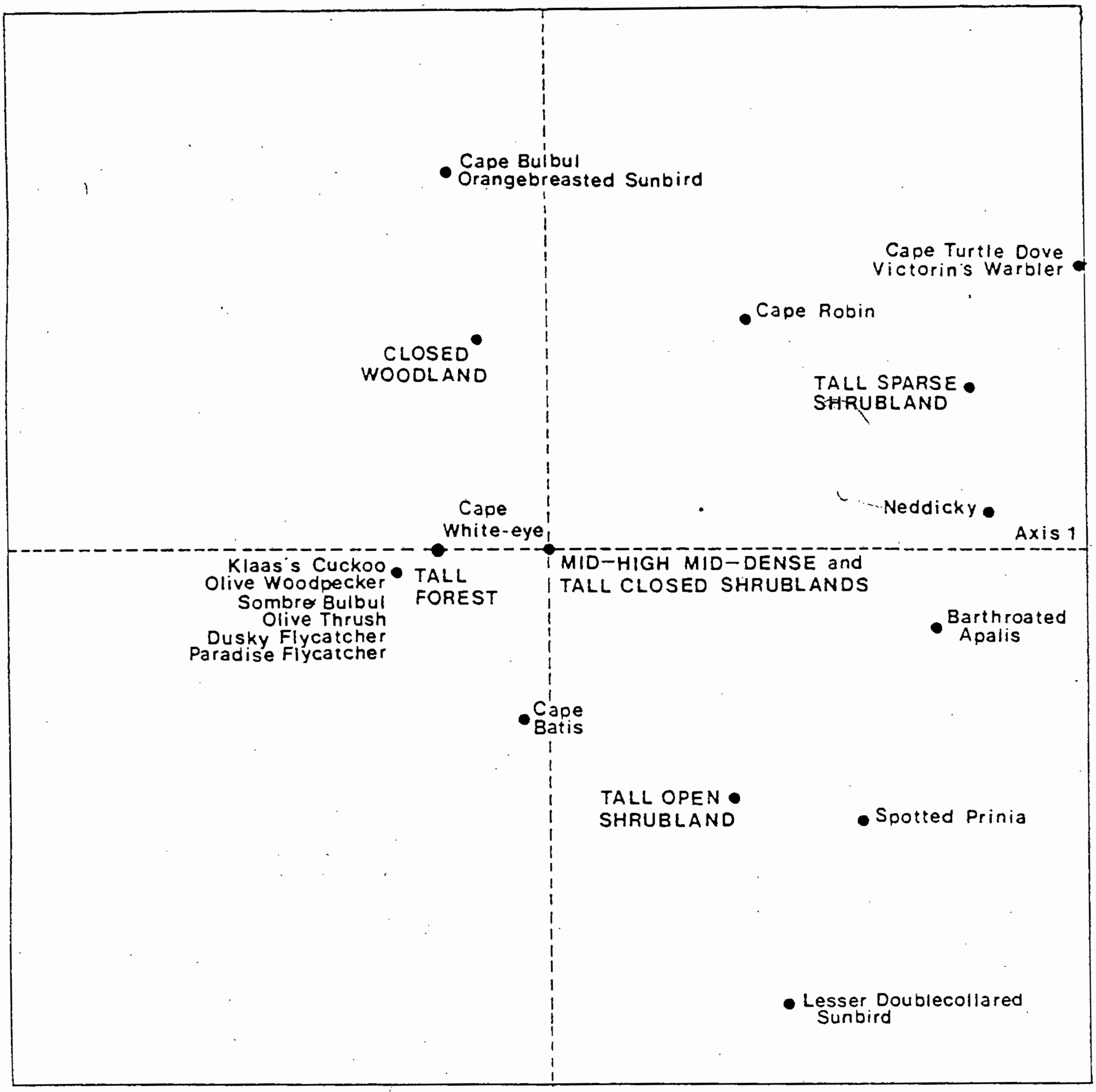

FIGURE 2.2

CORRESPONDENCE ANALYSIS OF AVIAN SPECIES DENSITIES 0-6 WEEKS AFTER FIRE IN SIX VEGETATION STRUCTURAL FORMATIONS AT SWARTBOSKLOOF

Bird species composition and densities in each of the six vegetation structural formations are given in Table 2.2 (pre-fire) and Table 2.3 (six weeks post-fire, the same duration as the pre-fire study period). Mean bird densities over the six-week post-fire period dropped by 48%-100% in all plots with the exception of the Tall Forest plot which saw a 42% increase.

Mean monthly bird densities in the six vegetation structural formations for the whole study period are given in Fig. 2.3. Although there was a tendency for bird densities to decrease after the fire, a comparison of median bird densities in the pre- and six-week post-fire periods (to minimize seasonal variability), showed significantly lower values only in the unburnt Closed Woodland (U=20; P<0,05, Mann-Whitney U test), and the clear-burnt Mid-high Mid-dense Shrubland (U=20; P<0,05, Mann-Whitney U test). The increase in median post-fire bird density in the other potential refuge, Tall Forest, following fire was not significant (U=59,5; NS, Mann-Whitney U test).

Avian recolonization of the burnt area was only discernible in the Mid-high Mid-dense Shrubland. No birds were recorded for six months after the fire until a pair of Neddickys established a territory there. The similarity between bird species compositions in the pre- and post-fire study plots was low, particularly between forest or woodland and fynbos (Tables 2.4a,b). Pre- and post-fire species similarities within the individual plots were relatively high in the forest and woodland, but low in fynbos (Table 2.5). Avian species composition in the study site as a whole was virtually unchanged by the fire. No species were lost and two new species (Klaas's Cuckoo and African Sedge Warbler Bradypterus baboecala) were recorded only in the year after the fire.

TABLE 2.4

COMPARISON OF AVIAN SPECIES COMPOSITION BETWEEN SIX VEGETATION STRUCTURAL FORMATIONS (AS IN TABLE 2.2), AT SWARTBOSKLOOF USING SORENSEN'S COEFFICIENTS OF COMMUNITY

Vegetation structural formation

(a) **Pre-fire**

	2	3	4	5	6
1	40	22	22	50	0
2		40	40	28	13
3			71	31	14
4				31	28
5					31

(b) **0-6 weeks post-fire**

	2	3	4	5	6
1	0	0	0	0	0
2		27	0	36	27
3			0	36	27
4				0	0
5					33

TABLE 2.5

COMPARISON OF PRE- AND SIX WEEKS POST-FIRE AVIAN SPECIES COMPOSITION WITHIN SIX VEGETATION STRUCTURAL FORMATIONS (AS IN TABLE 2.2), AT SWARTBOSKLOOF USING SORENSEN'S COEFFICIENTS OF COMMUNITY

Vegetation structural formation

	1	2	3	4	5	6
1	0					
2		27				
3			28			
4				0		
5					60	
6						53

Mean avian species richness (for each visit) before and for six weeks after the fire (to minimize seasonal variability) was not significantly different (18,3 and 18,6 species respectively; _U_ = 44,5; NS, Mann-Whitney _U_ test). Of the bird species recorded at Swartboskloof over the study period 26,6% were present in all months after the fire and may be classified as resident.

2.4.4 Avian feeding guilds

The relative contributions made by avian nectarivores, insectivores and mixed-feeders (after Maclean 1985; Richardson & Fraser in press) to avian density in the six study plots are shown in Figs. 2.4-2.6. Nectarivorous species displayed the most marked decrease in fynbos shrublands following the fire. 33,5% of all birds recorded in the study plots combined before the fire were members of this guild, compared to 2,8% in the six weeks after the fire.

Birds with a mixed diet dominated in almost all months in the Closed Woodland and Tall Forest plots. Their relative monthly density in the fynbos plots was variable, however, and they were absent only from the Mid-high Mid-dense Shrubland plot (Fig. 2.4c). Predominant in this feeding guild was Cape White-eye which was absent from the Tall Forest and Closed Woodland plots only in the summer months (although recorded in these vegetation structural formations elsewhere in the study site throughout the year).

The scarcity of granivorous birds was a notable feature of both the pre- and post-fire plots. Only Redeyed Dove and Protea Canary were recorded in the pre- and six-weeks post fire period from the study plots, both in low densities (Table 2.2). Elsewhere in the study area up to 65 Cape Siskins were observed extracting seeds directly from the split, burnt cones of standing Widdringtonia nodiflora trees from a month after the fire. No flocks of ground-foraging granivorous birds were recorded in the study site after the fire.

2.4.5 Survival of ringed birds

34% of pre-fire ringed birds are known to have survived the fire (Table 2.6). Twelve birds were relocated where they were originally ringed, despite the vegetation having been burnt. A Cape Batis moved 100 m into unburnt riparian vegetation within a day of the fire, but returned the following day to the burnt vegetation at its original ringing site. Three Cape Sugarbirds and an Orangebreasted Sunbird were found in adjacent unburnt vegetation feeding from Protea neriifolia inflorescences two months after the fire. Two of these Cape Sugarbirds were also retrapped there in May 1988. A single pre-fire ringed Malachite Sunbird was found feeding from P. neriifolia inflorescences 1 km from Swartboskloof in August 1988, 17 months after the fire.

TABLE 2.6

PRE-FIRE RINGED BIRDS RECORDED AFTER THE FIRE AT SWARTBOSKLOOF

Species	Number ringed pre-fire	Number and % recorded post fire
Olive Woodpecker	1	0 (0)
Cape Bulbul	10	3 (30)
Olive Thrush	4	1 (25)
Cape Robin	5	1 (20)
Barthroated Apalis	1	1 (100)
Grassbird	1	1 (100)
Spotted Prinia	2	1 (50)
Dusky Flycatcher	1	0 (0)
Fiscal Flycatcher Sigelus silens	1	0 (0)
Cape Batis	6	1 (17)
Southern Boubou	1	1 (100)
Cape Sugarbird	9	3 (33)
Malachite Sunbird	3	1 (33)
Orangebreasted Sunbird	11	1 (9)
Lesser Dc Sunbird	7	0 (0)
Cape White-eye	9	4 (44)
Protea Canary	4	1 (25)
TOTAL	76	20 (mean = 34)

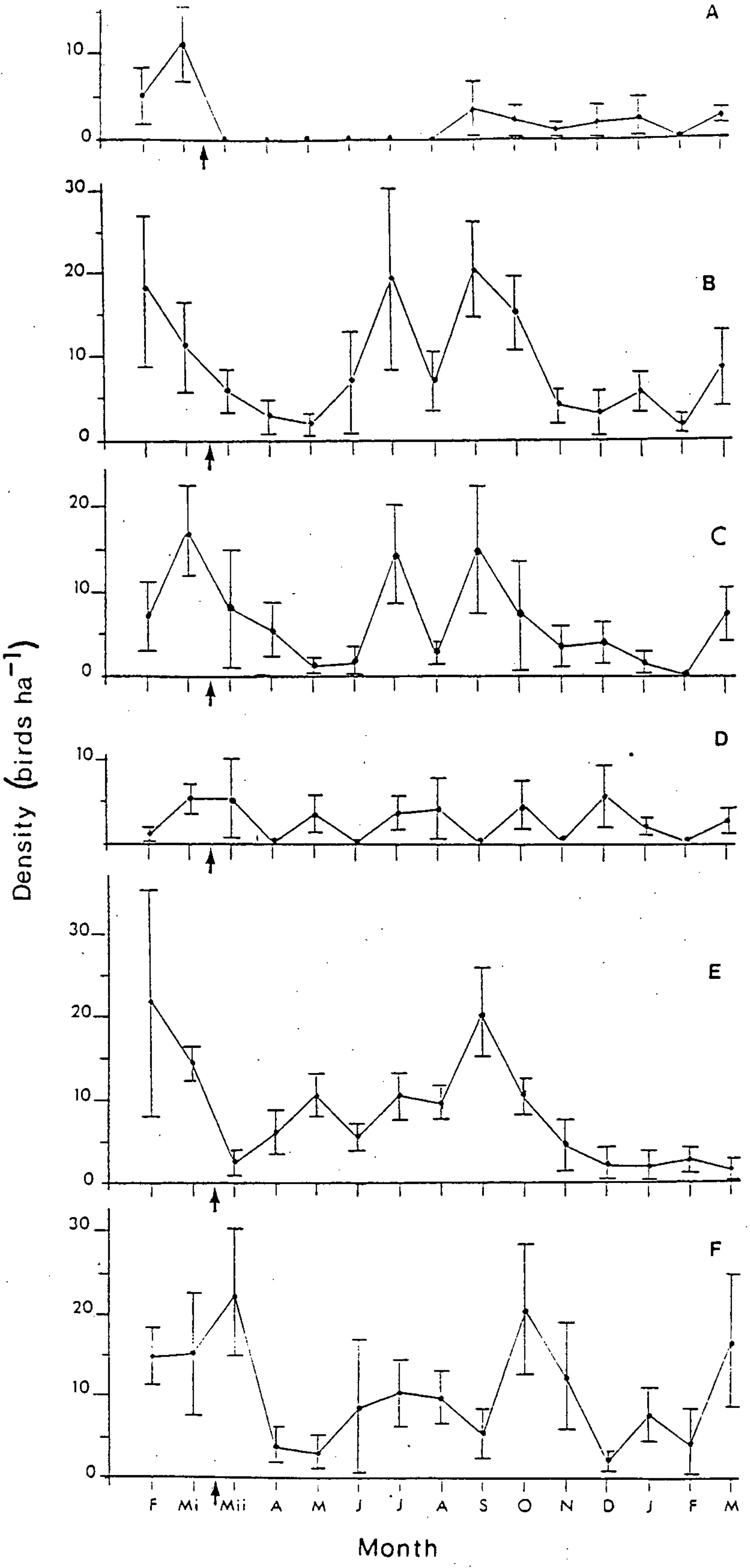

FIGURE 2.3

MEAN MONTHLY AVIAN DENSITIES (BIRDS HA^{-1} ± SE) IN SIX VEGETATION STRUCTURAL FORMATIONS AT SWARTBOSKLOOF. (A) MID-HIGH MID-DENSE SHRUBLAND; (B) TALL SPARSE SHRUBLAND; (C) TALL OPEN SHRUBLAND; (D) TALL CLOSED SHRUBLAND; (E) CLOSED WOODLAND; (F) TALL FOREST. THE ARROW INDICATES THE TIME OF THE FIRE; MARCH IS SPLIT INTO PRE- AND POST-FIRE PERIODS

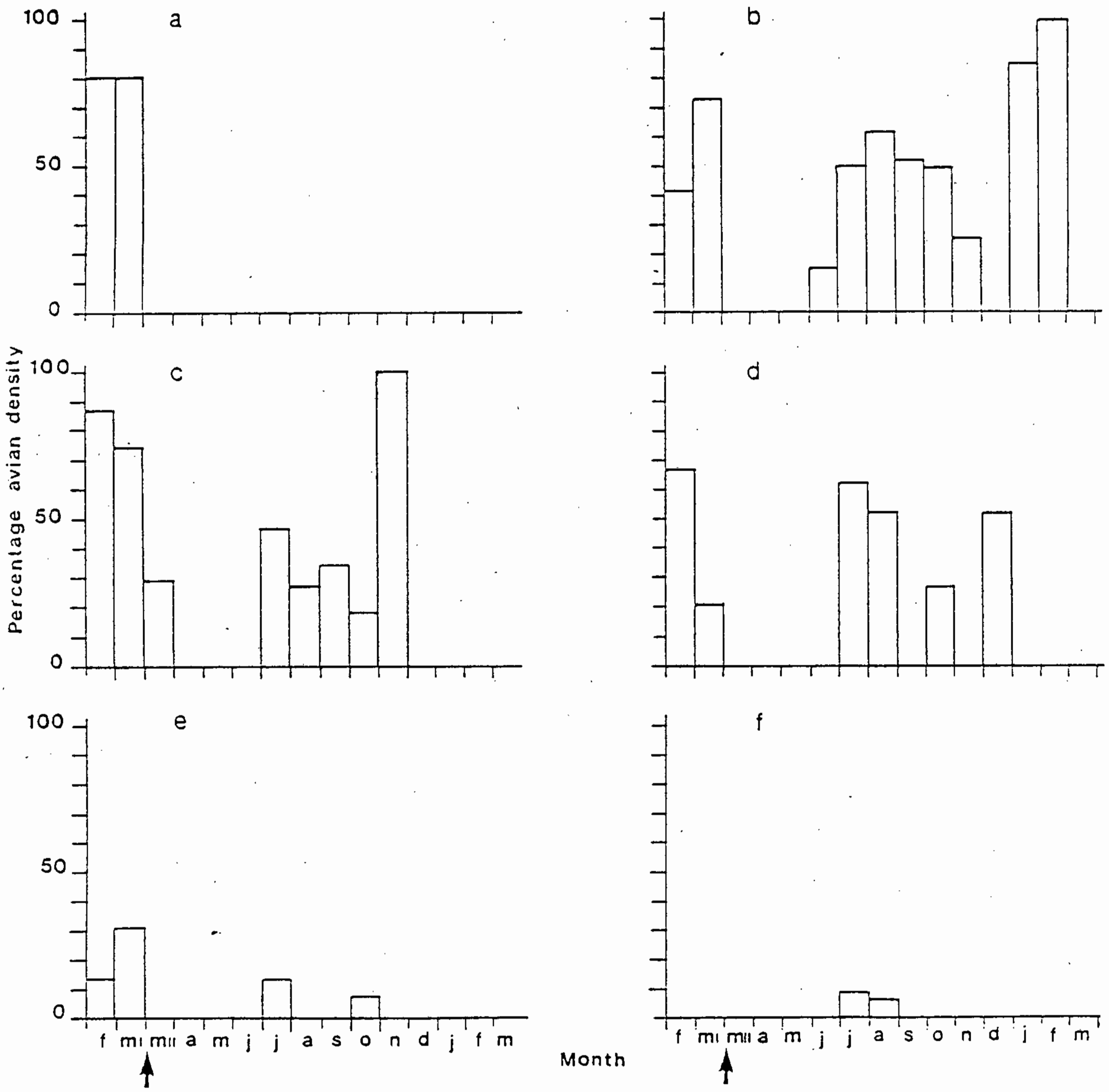

FIGURE 2.4

PROPORTION OF NECTARIVOROUS BIRDS RECORDED EACH MONTH IN SIX VEGETATION STRUCTURAL FORMATIONS (AS IN FIG. 2.3) AT SWARTBOSKLOOF

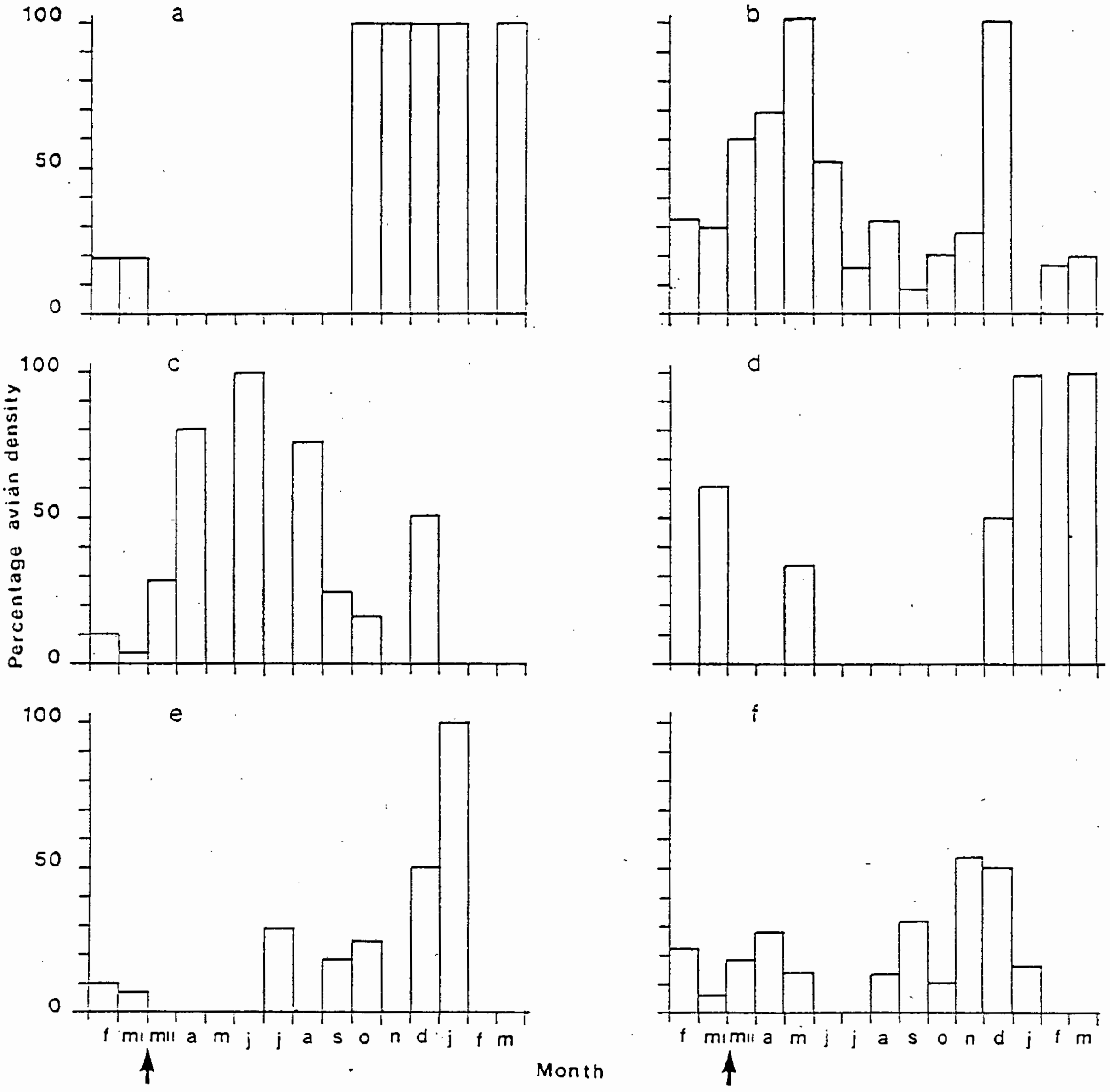

FIGURE 2.5

PROPORTION OF INSECTIVOROUS BIRDS RECORDED EACH MONTH IN SIX VEGETATION STRUCTURAL FORMATIONS (AS IN FIG. 2.3) AT SWARTBOSKLOOF

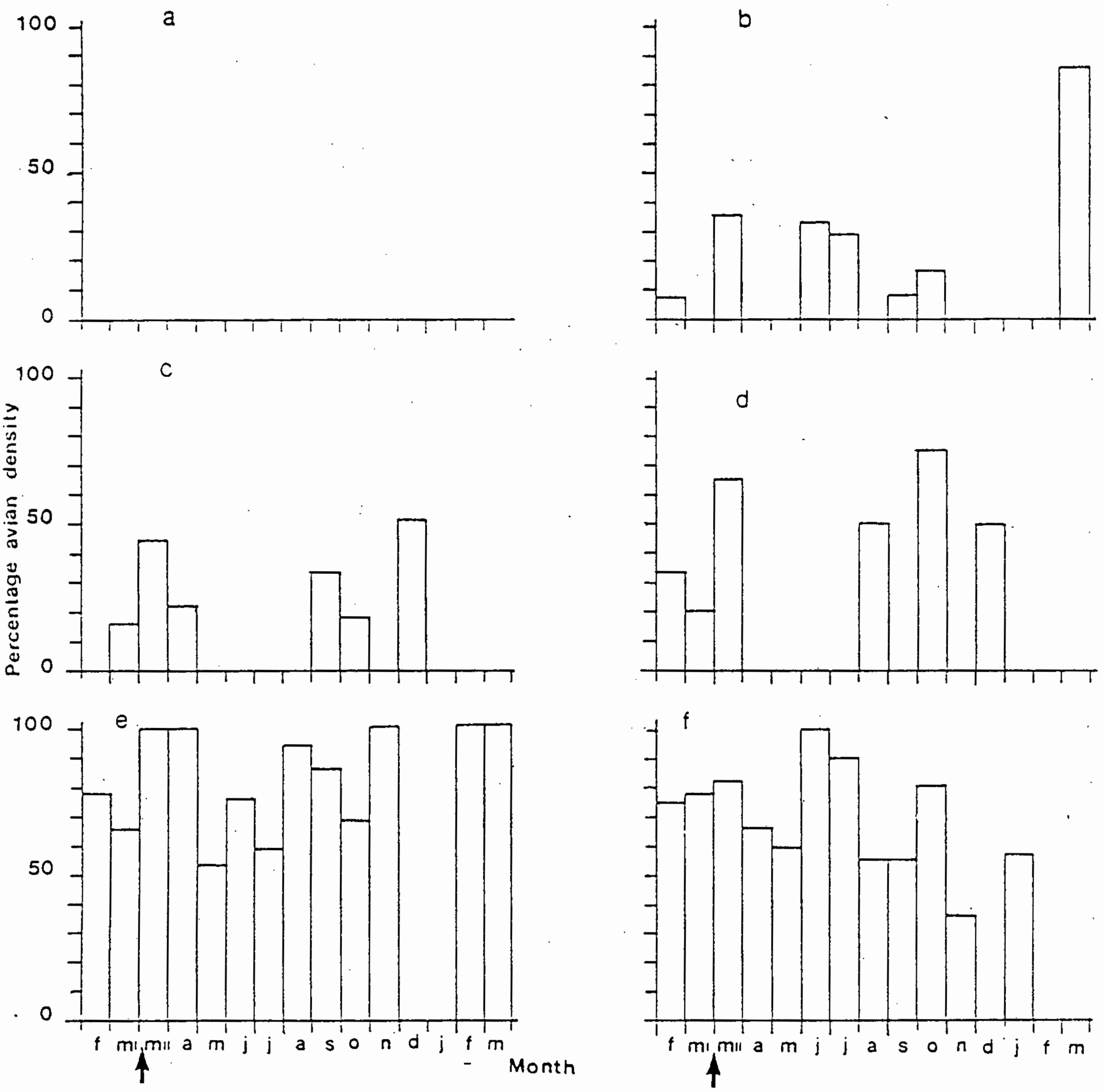

FIGURE 2.6

PROPORTION OF MIXED FEEDERS RECORDED EACH MONTH IN SIX VEGETATION STRUCTURAL FORMATIONS (AS IN FIG. 2.3) AT SWARTBOSKLOOF

2.5 DISCUSSION

Faunal responses to fire in fynbos can take a number of forms. Some animals may emigrate immediately and return only when conditions resemble those prevailing before the fire. Others may linger after the fire but emigrate if they cannot adapt to changes in habitat and resources. Alternatively, fire may prompt immigration and the utilization of new feeding resources or habitat (Kruger & Bigalke 1984).

2.5.1 Reaction of birds to the passage of the fire

Few birds exploited freshly-burnt fynbos in the southern Cape and only Forktailed Drongo *Dicrurus adsimilis* (which does not occur at Swartboskloof), hawked prey during the fire but not at the flame front (Dean 1989). The lack of immediate responses by birds to fire in fynbos contrast strongly with observations in other southern African vegetation types. Dean (1987) reports 76 species of bird associating with fire in savanna woodland where birds fed on flushed or killed prey items. Territorial behaviour of some bird species broke down in the presence of abundant food, and diurnal species even fed at night at the flame fronts. Six of the species noted by Dean (1987) as associating with fire also occur in Swartboskloof (Fraser & Richardson in press); a further 10 occur locally in the Jonkershoek Valley (Siegfried 1962; M.W. Fraser & D.M. Richardson, unpubl. data). Fire in fynbos is a natural phenomenon and fynbos vegetation is fire-adapted and fire-dependent (van Wilgen 1982). The apparent lack of fire-related responses by fynbos birds may be attributed to the unpredictability of such fires. Fynbos vegetation is adapted to fire intervals of between 10 and 30 years but the frequency, intensity and size of fires are highly variable (van Wilgen 1987). Such inconsistencies and the relatively long inter-fire period (grasslands, in contrast, may burn annually) may preclude adaptive responses by birds, as suggested by Dean (1989). In addition, the Swartboskloof burn was slow and cool, much of the vegetation was unburnt and there were few wide, clear areas to attract traditionally open-country birds. Fynbos fires under natural circumstances occur mainly in the hottest and driest months, and tend to be more intense and consume more standing vegetation than management fires. The results from Swartboskloof are, therefore, not necessarily representative of natural conditions.

2.5.2 Bird species compositions and densities in study plots before and after the fire

Of the 45 bird species recorded in Swartboskloof over the study period, 12 (26,6%) were present in all months. A mean of 26,8 species (59,5%) (range: 22-32 (48,9%-71,1%)) occurred in any one month. The presence or absence of any bird species in any one month is therefore not necessarily the result of fire. The two species recorded subsequent to the fire were vagrants to the study area (Richardson & Fraser in press). Dean (1989) recorded three species in burnt fynbos which had not been present before the fire.

The variation in avian density over the whole study period (Fig. 2.2) could be seasonal rather than fire-related. Relatively high bird densities in winter in Tall Sparse Shrubland and Tall Open Shrubland, for example, had dropped to immediate post-fire levels by the following summer.

Wiens & Rotenberry (1985) found no evidence of an immediate response by a breeding bird population to habitat changes in

North American sagebrush. This they attributed to time lags produced by the site tenacity of breeding individuals. Although few bird species at Swartboskloof are known to be resident, attempts to formulate management policies on the basis of short-term "before and after" surveys are complicated by such time lags. Short-term studies are of limited value in fynbos where the vegetation takes a number of years to regain its pre-fire height and density. Fire is more frequent and regular in other southern African biomes (notably grassland), its effects are temporary and the next rainy season restores the status quo (Manry & Knight 1986; Winterbottom 1972).

The Swartboskloof results contrast with findings following fire in Mountain Fynbos at the Cape of Good Hope Nature Reserve. At the latter site much of the study area was clear-burnt, although some tall proteoid shrubs and pockets of vegetation amongst rocks did survive. Overall avian species richness dropped slightly here, but avian density went down sharply and species composition changed markedly. There was also a tendency for recently burnt fynbos vegetation to support smaller numbers of larger birds than the old vegetation (R.P. Prys-Jones and D.L. Clark, unpubl. data). This trend was not apparent at Swartboskloof. The two sites shared few species either before or after fire (Sorensen's coefficient of community, pre-fire = 11; post-fire = 40). A number of open-country bird species (e.g. Crowned Plover Vanellus coronatus and Orangethroated Longclaw Macronyx capensis) recorded after fire in the Cape of Good Hope Nature Reserve (Chapter 1) were not recorded in post-fire fynbos in the present study or in mountains elsewhere in the southern Cape (G.J. Breytenbach, pers. comm.). Thus, results from the Cape of Good Hope are not applicable to

Mountain Fynbos vegetation at Swartboskloof and vice versa; neither sets of results may be applicable to sites elsewhere in the Fynbos Biome.

The bird density figures for pre-fire fynbos plots at Swartboskloof exceed those given by Winterbottom (1968) for "Fynbos", Siegfried (1983) for "Mountain Fynbos" and R.P. Prys-Jones and D.L. Clark's unpublished data for Taylor's (1984) "Upland Mixed Fynbos" at the Cape of Good Hope Nature Reserve. The post-fire densities also exceed those found by Prys-Jones and Clark in their post-fire transects.

2.5.3 Avian feeding guilds

In fynbos the marked seasonal change in plant growth and flowering affects the composition of bird communities, and complicates comparative studies (Siegfried 1983). Seasonal changes are most marked in the case of nectarivorous birds and their relationships with certain plants (notably Cape Sugarbird and *Protea* spp., and Orangebreasted Sunbird and *Erica* spp). Nectarivorous birds in the southwestern Cape are known to be itinerant (Fraser *et al*. 1989), presumably in response to the spatial and temporal availability of flowering food plants. Nectarivores may comprise a high proportion of bird density at certain times of year (Siegfried 1983), and, as reported here (Table 2.1; Figure 2.4), may exceed the density of all other bird species combined. Thus, the minimum period for such studies should be one year.

The effects of a fire, if outside the flowering season of a particular food plant (notably, at Swartboskloof, *Protea neriifolia* which flowers in late autumn and winter) are likely to be masked by normal seasonal movements of the nectarivorous birds, and will only be manifested in the following year when returning birds are unable to find food in the burnt area. Such effects may be less marked where the food plant concerned is a resprouter (such as P. nitida) which is able to flower relatively soon after the fire. P. neriifolia is a reseeder, and does not mature for three or more years (van Wilgen 1981), thus depriving nectarivores of a food source for a longer period than P. nitida.

If the fire had occurred during the flowering period of Protea neriifolia, the immediate effects on nectarivores could have been considerable where this plant species dominates (notably, at Swartboskloof, Tall Closed Shrubland). P. neriifolia, when in flower, is heavily utilized by nectarivorous species, particularly Orangebreasted Sunbirds (e.g. 114 of 186 (61%) birds caught in mistnets in a flowering patch of P. neriifolia adjacent to Swartboskloof in May 1987 and May 1988 were Orangebreasted Sunbirds (M.W. Fraser, unpubl. data)). The Cape Canary Serinus canicollis and Protea Canary were recorded in small numbers in the Tall Open and Tall Sparse Shrubland plots. There was no increase in their numbers after the fire, although Milewski (1976) found that the largest flocks of Protea Canaries were associated with the loosened seeds of P. neriifolia 18 days after a fire. The small numbers of Cape Canaries present at the study site in September-November may have been fire-related, but similar numbers were recorded most frequently between August and November 1986 (Richardson & Fraser in press). Milewski (1978) recorded that flocks of 10 or more Cape Siskins comprised less than 10% of his observations of the species in Mountain Fynbos, but much larger flocks were recorded at Swartboskloof.

In conclusion, this study demonstrates that avian species richness, composition and density in Mountain Fynbos may not be drastically altered by fire. No increase in bird density or species richness was noted in potential refugia. Burning of reseeding <u>Protea</u> species has potentially more detrimental effects on nectarivorous birds, in the short term, than burning of resprouting <u>Protea</u> species. The influx of Cape Siskins to <u>Widdringtonia</u> <u>nodiflora</u>, together with the virtual disappearance of nectarivores, were the only avian community responses which could be exclusively attributed to the fire rather than season.

CHAPTER 3

SMALL MAMMALS, BIRDS AND ANTS AS SEED PREDATORS IN EARLY POST-FIRE MOUNTAIN FYNBOS

CHAPTER 3

SMALL MAMMALS, BIRDS AND ANTS AS SEED PREDATORS IN EARLY POST-FIRE MOUNTAIN FYNBOS

3.1 INTRODUCTION

Fire is the most important disturbance factor in Mediterranean ecosystems such as fynbos (Keeley 1986; van Wilgen 1987). Seasonally arid fynbos shrublands contain plant species which regenerate only from seed in a short post-fire period. Over 300 species of fynbos plant have serotinous (canopy-stored) seed and lack persistent soil seed reserves (le Maitre 1987). About 1 300 (20%) fynbos plant species, including members of 30 families, are myrmecochorous (Bond & Slingsby 1983). Such seeds display an elaiosome (food body) which attracts and is eaten by ants once the seed has been transported to their underground nests. The seeds are thereby dispersed and protected from fire (Bond & Slingsby 1983, 1984; Slingsby & Bond 1981, 1982). Adaptations for long-distance seed dispersal are rare in fynbos plants and dispersal distances generally short (Breytenbach et al. 1986; Manders & Cunliffe 1987; Siegfried 1983; Slingsby & Bond 1985).

The rocky terrain characteristic of much mountain fynbos precludes "rolling" dispersal by Protea fruits (Bond 1988). Seed input from outside burnt areas is probably low, therefore. The survival rates of seeds between seed release and germination are thus critical, and may influence the composition of the plant community for many subsequent years (Cowling et al. 1987).

Small mammal density generally decreases after fire (Breytenbach

1987), and granivorous birds are scarce in fynbos (Chapters 1 & 2; Siegfried 1983; Siegfried & Crowe 1983). Neither taxa may occur in densities high enough, nor be able to increase their numbers sufficiently to consume all the serotinous seed before it germinates following its fire-stimulated release. Nevertheless, small mammals, birds and ants do feed on seeds in fynbos (Bond 1984; Bond & Breytenbach 1985; Bond & Slingsby 1984; Breytenbach et al. 1986) and serotiny and myrmecochory in fynbos could be adaptive responses to high seed predation pressures (Breytenbach 1984). The present study was designed to assess the relative importance of small mammals, birds and ants in imposing these pressures in post-fire Mountain Fynbos.

3.2 STUDY AREA AND METHODS

The study was carried out at the Swartboskloof subcatchment (34 00S, 18 57E), in the Jonkershoek Valley, 15 km southeast of Stellenbosch, Cape Province, South Africa. The Mountain Fynbos vegetation at Swartboskloof is dominated by tall proteoid shrublands comprising largely Protea neriifolia, P. repens and P. nitida. Patches of afromontane forest occur on higher scree slopes and in sheltered ravines; riparian woodland dominated by Brabejum stellatifolium and Cunonia capensis fringes the kloof's perennial streams (McDonald 1985). About 33% of fynbos plant species at Swartboskloof are obligate reseeders (van der Merwe 1966). The 28 year-old vegetation was burnt in a prescribed fire in March 1987 as part of a catchment management programme (Anon 1987).

3.2.1 Seed dish experiment

The relative importance of small mammals, birds and ants as seed predators was assessed using a seed dish technique (Mares &

Rosenzweig 1978; Parmenter et al. 1984). Petri dishes filled with 10 g of commercial brand Phalaris canariensis seeds were used in the following treatments:

1) Accessible to ants only. Dishes sunk into the ground until the lip was flush with the soil surface. Twigs and leaves were positioned to serve as access ramps into the dishes for ants. Small mesh wire cages were secured over each dish to exclude small mammals and birds.
2) Accessible to small mammals and birds only. Dishes glued onto inverted, thin-stemmed wine glasses. The stems were coated with Formex (a sticky resin used to protect fruit trees from insect attack) and the glasses placed ca 30 mm into the ground.
3) Accessible to all taxa (control). Procedure as for treatment 1 (above), but without the wire exclosures.

Three replicates of the three treatments were set out on three or four consecutive days and nights each month from August 1987 to January 1988 inclusive at seven stations at Swartboskloof. Four stations were sited in burnt fynbos shrublands and one each in unburnt fynbos shrubland, forest and riparian woodland. The terminology and pre-fire characteristics of the vegetation at the stations are detailed in Table 3.1.

The seed dishes were checked at dawn and dusk each day and seeds renewed where necessary. Amounts of seed removed were determined by weighing. The experiment was carried out under dry conditions because rain inhibits the foraging activities of ants (Bond & Breytenbach 1985). This technique assumes that Phalaris canariensis seeds are equally attractive to all taxa and that all taxa have an equal probability of finding and using seed dishes. The unit of analysis in this study is termed a "treatment", i.e. one seed dish per day or per night.

TABLE 3.1

STRUCTURAL FORMATION (CAMPBELL ET AL. 1981) AND CHARACTERISTIC PLANT SPECIES (RICHARDSON & FRASER IN PRESS) OF VEGETATION AT SEED DISH STATIONS IN SWARTBOSKLOOF

Formation	Description and characteristic plants
Tall Forest	Interlocking crowns; 75%-100% projected canopy cover. Cunonia capensis, Ilex mitis, Rapanea melanophloeos
Closed Woodland	Crowns not interlocking; 25%-50% projected canopy cover. Brabejum stellatifolium, Cunonia capensis
Tall Closed Shrubland	Interlocking crowns; 75%-100% projected canopy cover. Protea neriifolia
Tall Open Shrubland	Crowns not interlocking; 25%-50% projected canopy cover. Protea nitida, P. neriifolia
Tall Sparse Shrubland	Crowns not interlocking; 5%-25% projected canopy cover. Protea nitida
Mid-high Mid-dense Shrubland	Crowns not interlocking; 50%-75% projected canopy cover. Protea neriifolia, Cliffortia

3.3 **RESULTS**

Visits to seed dishes, as indicated by the removal of seed, were recorded for only 99 (4%) of 2 583 treatments (Table 3.2). Of these visits, 17% were attributable to birds (a Cinnamon Dove Aplopelia larvata was observed feeding from seed dishes in Tall Forest), 50% to nocturnal small mammals and 33% to diurnal small mammals and/or birds.

TABLE 3.2

PERCENTAGE OF VISITS (N = 99) TO SEED DISHES IN BURNT AND UNBURNT VEGETATION AT SWARTBOSKLOOF

Vegetation structural formation	**% visits**
Burnt vegetation	
Tall Sparse Shrubland	21,2
Tall Open Shrubland	5,1
Tall Closed Shrubland	0
Mid-high Mid-dense Shrubland	12,1
Unburnt vegetation	
Tall Sparse Shrubland	27,3
Closed Woodland	21,2
Tall Forest	13,1

No seeds were removed from dishes accessible only to ants. *Myrmicaria nigra*, *Anoplolepis custodiens* and the alien *Iridomyrmex humilis* were observed within seed dishes, and although manipulating seeds, did not remove any. No evidence (direct observations or chewed seed) of predation by other invertebrates was recorded. As no seeds were removed from the dishes accessible to ants (or other invertebrates) only, it is assumed that control dishes (open to all taxa), were also not visited by invertebrates. Thus, these treatments are analyzed and discussed accordingly (viz: the dishes were visited only by small mammals and/or birds).

Seed dishes in burnt Tall Sparse Shrubland received significantly more visits than those in other burnt fynbos vegetation ($\chi^2 = 32{,}41$; df = 6; $P<0{,}05$). A greater proportion of seed dishes were visited in unburnt fynbos and in forest/woodland than in burnt fynbos (Table 3.3). The number of seed dishes visited overall did not increase significantly with time since the fire (Spearman rank correlation $r^{s}_{4} = 0,43$; NS). The amount of seed removed by nocturnal small mammals ranged from 6,4 g to 10 g, and that by diurnal small mammals and/or birds 8,9 g to 10 g. This method does not allow determination of the rates of seed removal by the various taxa, however, since the experiment is truncated by the removal of all seed (as occurred on 32 visits).

TABLE 3.3

PERCENTAGE OF SEED DISHES VISITED MONTHLY BY NOCTURNAL MAMMALS (NM), OR DIURNAL MAMMALS/BIRDS (DM/B) IN BURNT AND UNBURNT VEGETATION AT SWARTBOSKLOOF (N = TREATMENTS)

	Burnt fynbos				unburnt fynbos				unburnt forest/woodland			
Taxa	NM	(n)	DM/B	(n)	NM	(n)	DM/B	(n)	NM	(n)	DM/B	(n)
<u>Month</u>												
August	3	(96)	0	(72)	4	(24)	0	(18)	0	(48)	0	(36)
Sept.	0	(96)	0	(96)	0	(24)	0	(24)	0	(48)	0	(48)
October	12	(72)	0	(72)	5	(18)	0	(18)	0	(36)	0	(36)
Nov.	7	(72)	0	(72)	5	(18)	5	(18)	28	(36)	33	(36)
Dec.	1	(72)	0	(72)	11	(18)	0	(18)	0	(36)	0	(36)
January	22	(96)	0	(96)	46	(24)	0	(24)	25	(48)	0	(48)
Total	8	(504)	0	(504)	20	(126)	1	(120)	9	(252)	5	(240)

3.4 **DISCUSSION**

3.4.1 Small mammals

The level of seed predation by small mammals recorded in this study was perhaps surprisingly low, since they appear to be important seed predators in fynbos. Mice have been attributed with the ability to consume the entire annual seed production of Widdringtonia cedarbergensis within a few weeks (Bigalke 1979). In laboratory trials, mice are capable of consuming all unburied myrmecochorous seed within 48 h, and of detecting elaiosome-bearing seed at depths of 150 mm (Bond & Breytenbach 1985). That the seeds used in this study were alien and lacked an elaiosome may account for this low level of predation. However, Phalaris canariensis seeds were eaten by individual captive Grey Climbing Mouse Dendromus melanotis, Striped Mouse Rhabdomys pumilio, Pygmy Mouse Mus minutoides and Namaqua Rock Mouse Aethomys namaquensis with or without alternative food (M.W. Fraser, unpubl. data). In a cafeteria experiment in Dune Fynbos, Pierce (1987) found no significant differences in the rate of removal between intact fynbos seeds and those from which the elaiosome had been removed. The use of alien Phalaris canariensis seeds in the present study was not necessarily responsible for the low level of seed predation by small mammals.

Six species of mouse recorded at Swartboskloof before the fire were seed eaters (Anon 1986; Botha 1988; Smithers 1983). Significant seasonal variation in small mammal community structure was recorded before the fire. Some species were temporarily absent following fire, but the full pre-fire species complement had returned within six months of the fire, although their density (as indicated by trapping success), was low (van Hensbergen & van Wilgen 1987). Low post-fire small mammal densities enhance the predator satiation escape mechanism adopted by fynbos plants (Bond 1984). Results here suggest that, even in unburnt vegetation, small mammal densities were too low either to locate or consume all the seed provided. However, the relatively high number of visits in unburnt fynbos may support Breytenbach's (1984) single-agedness hypothesis that predation is the major factor controlling the survival of seeds (and seedlings) in mature fynbos. Results from this study suggest that small mammals were the most important seed predators in recently burnt mountain fynbos at Swartboskloof.

3.4.2 Birds

Granivorous birds were scarce at Swartboskloof before and after the fire (Chapter 2; Richardson & Fraser in press). This agreed with observations made at other Mountain Fynbos sites (Chapter 1; Siegfried 1983; Siegfried & Crowe 1983). There was no increase in the density of ground-foraging granivorous birds in study plots at Swartboskloof after the fire, nor was any additional granivorous species observed in the study site as a whole at this time (Chapter 2). Up to 65 Cape Siskins *Serinus totta* arrived after the fire, but were recorded exclusively feeding on *Widdringtonia nodiflora* seeds which they extracted directly from split cones on the standing trees. Other birds whose diet comprises exclusively or partly seeds and present at the study site at the time of the seed dish experiment were Cape Turtle Dove *Streptopelia capicola*, Yellowrumped Widow *Euplectes capensis*, Cape Canary *Serinus canicollis*, Bully Canary *S. sulphuratus*, Protea Canary *S. leucopterus* and Cape Bunting

Emberiza capensis. None of these is known to have visited the seed dishes. The failure of these birds to eat the seed provided is considered to be a result of their overall low density in the study site rather than an aversion to the seeds. This is supported by the direct observations of a Cinnamon Dove eating seeds from the dishes in Tall Forest. Conversely, of the granivorous birds recorded at Swartboskloof, only the Protea Canary is known habitually to eat the large, hairy seeds of Protea which it extracts directly from the inflorescences (Milewski 1978; Maclean 1985; Fraser & Richardson 1989). Bond (1984) recorded no significant removal by birds of indigenous seed (Protea repens) from open-topped exclosures in fynbos. My results suggest that birds were probably not important consumers of seed, at least from the ground, in recently burnt fynbos at Swartboskloof.

3.4.3 Ants

Although ants are important dispersers of seeds in fynbos, their role is probably restricted to elaiosome-bearing species. Location and removal of elaiosome-bearing seeds by ants is rapid (Bond & Breytenbach 1985; Bond & Slingsby 1984). Removal rates were significantly reduced, however, when the elaiosomes were removed (Bond & Slingsby 1984). Although not all indigenous ants are successful dispersers of such seed (Bond & Breytenbach 1985), elaiosomes are a functional adaptation for attracting ants and minimizing seed mortality through fire and predation. Bond & Slingsby (1984) found that where the alien Argentine Ant Iridomyrmex humilis had infested fynbos, seed removal distances and rates were depressed. Argentine Ants are slow at finding seeds and do not transport them to underground nests. Seeds were thus exposed to potentially higher levels of predation.

Pre-fire studies indicated a lower ant species richness at Swartboskloof than at other sites in the Jonkershoek Valley; this was attributed to the presence of Argentine Ants at Swartboskloof (Donnelly & Gillomee 1985), which are known to oust native species (Skaife 1961). A suppression of native ant species richness may be a contributory factor to the absence of seed removal by ants. However, the nature of the seeds (hard, shiny seed coats and no elaiosomes) used in this study is perhaps a more likely explanation of the absence of seed removal by ants.

CHAPTER 4

EFFECTS OF ALIEN WOODY-PLANT INVASION ON THE BIRDS OF MOUNTAIN FYNBOS IN THE CAPE OF GOOD HOPE NATURE RESERVE

CHAPTER 4

EFFECTS OF ALIEN WOODY PLANT INVASION ON THE BIRDS OF MOUNTAIN FYNBOS IN THE CAPE OF GOOD HOPE NATURE RESERVE

4.1 INTRODUCTION

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; McMahon & Fraser 1988). 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).

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 southwestern 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". Furthermore, alien woody vegetation forms dense stands which exclude indigenous vegetation (Taylor et al. 1985; Richardson & van Wilgen 1985) and potentially can alter fire behaviour in fynbos vegetation (van Wilgen & Richardson 1985). 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 heterogeneous fynbos vegetation is increasingly infested by alien woody plants.

Bird species richness and density 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 (Nectarinidae), 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 (Collins 1983a; Collins & Rebelo 1987; Rebelo et al. 1984; Rebelo 1987). 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. However, since the spread of alien A. cyclops has been enhanced by dispersal of the seeds by frugivorous birds (Glyphis et al. 1981; Middlemiss 1963), and since there are few ornithochorous plants and frugivorous birds in uninfested Mountain Fynbos (Chapters 1 & 2; Siegfried 1983), an increase in frugivorous bird abundance and/or species richness might be an expected response to A. cyclops infestation.

The factors controlling the density and diversity of fynbos invertebrates are poorly understood (Jarvis 1979). However, positive correlations between insect abundance and foliage density have been reported in other vegetation types (e.g. Murdoch et al. 1972; Koen & Crowe 1987). Thus, if vegetation density is increased by alien infestation, a rise in insect numbers 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 et al.

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 are 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.

4.2 STUDY AREA

Fieldwork was carried out at the Cape of Good Hope Nature Reserve (CGHNR), (34 15S, 18 25E), in the southwestern Cape Province, South Africa. The CGHNR is bounded by the cold

Atlantic on the west and the relatively warmer waters of False Bay on the east. The soils of the reserve are derived from quartzitic sandstones of the Table Mountain Group of the Cape Supergroup and are shallow, infertile and generally well-drained (Taylor 1984). The climate is Mediterranean-type, *i.e*. with warm, dry summers and cool, wet winters. Persistent winds from the southeast have a cooling effect over the reserve in summer.

The vegetation of the CGHNR comprises Mountain Fynbos (Moll *et al*. 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* spp., *Eucalyptus* spp. and *Pinus* spp. (Taylor *et al*. 1985; Macdonald *et al*. 1988, 1989).

4.3 **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.).

4.3.1 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 excluded. 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% A. 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 unpubl. data), or from Maclean (1985) and Richardson & Fraser (in press). To assess the effects of alien infestation on avian trophic structure, birds were grouped into feeding guilds (nectarivore, insectivore, frugivore, granivore and folivore), after Maclean 1985, Siegfried (1983) and Richardson & Fraser (in press).

4.3.2 Statistical methods

Correspondence analysis (Greenacre 1984; Underhill 1989; Underhill & Peisach 1985), was employed to assess relationships between the densities of individual bird species in each plot. Sorensen's coefficients of community (Smith 1986) were calculated to illustrate the degree of similarity between bird species assemblages and provide an index of species turnover between plots. 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.

4.3.3 Resource availability

Invertebrate abundance was assessed using sticky traps (Cody 1983a). Between seven and 18 (depending on the height of the vegetation) 10 cm x 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% Acacia cyclops-infested plots and one sampling station in the 100% mixed-alien infestation. These were operated for three to eight days a month throughout 1985.

The densities of mature Leucospermum conocarpodendron and Mimetes fimbriifolius bushes (food plants of avian nectarivores) were recorded in each plot, and their flowering phenology and number of ripe inflorescences counted 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 Acacia cyclops pods was recorded each week 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).

4.3.4 Vegetation structure

Since bird community structure may be influenced by vegetation structure (Cody 1975, 1983a,b), foliage profiles and half-heights (Cody 1983a) were constructed using a density board in all the *Acacia 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 to be measured. In these three plots, the pre-fire projected canopy covers of the mixed aliens were estimated to be 0%, 25% and 50% respectively.

4.4 **RESULTS**

4.4.1 Tall Mixed Fynbos infested with Acacia cyclops

4.4.1.1 Birds

Twenty-two bird species were recorded in plots infested with *A. cyclops* (Table 4.1). Eight species (36%) were found at all levels of infestation, and four (18%) (Cape Bulbul (scientific names are given in Table 4.1), Cape Robin, Southern Boubou and Cape Siskin), 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 between all levels of infestation, but lowest between the least (<1%) infested and the other plots (Table 4.2). Avian density was highly variable between plots, but was highest overall in the 10% infested plot (Table 4.1). Mean avian densities were not significantly correlated with increasing infestation (Spearman rank correlation: $r_s = 0,18$; 4 df, NS). Moreover, monthly bird density did not differ significantly between plots (Friedman Test $X_5^2 = 9,0$, N.S.).

In the correspondence analysis of the plots infested with _Acacia cyclops_ (Fig. 4.1), the first axis accounted for 48% of the inertia and contrasted the densities of three nectarivores (Cape Sugarbird, Malachite Sunbird and Orangebreasted Sunbird), which were associated with low levels of _A_. _cyclops_ infestations, against the Cape Bulbul, Cape Robin, Southern Boubou and Cape White-eye which were associated with the 42% and 72% infestations. Along the first axis, the plots were ordered with respect to a decreasing level of infestation, except that the 42%- and 50%-infested plots were interchanged. The second axis, which accounted for a further 21% of the inertia, contrasted the relative abundance of Cape Sugarbirds in the 10% infested plot (where the density of proteaceous shrubs was 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, $r_s = 0,37$; 2 df, NS), but was highest in the 10% infested plot (Table 4.3). Here nectarivores and Redwinged Starlings accounted for much of the overall avian density and biomass. Indeed, the latter made the greatest contribution to avian biomass in all plots.

TABLE 4.1

MEAN AVIAN DENSITY AND SPECIES RICHNESS IN ACACIA CYCLOPS-INFESTED TALL MIXED FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

	Acacia cyclops density (% projected canopy cover)					
	<1	10	18	42	50	72
Species	Birds ha^{-1}					
Cape Turtle Dove Streptopelia capicola (G)*	-	,03	-	,07	,04	,03
Speckled Mousebird Colius striatus (Fo)	-	-	-	,02	-	-
Ground Woodpecker Geocolaptes olivaceus (I).	-	-	,08	-	-	-
Cape Bulbul Pycnonotus capensis (Fr)	-	,06	,23	,27	,25	,53
Olive Thrush Turdus olivaceus (I)	-	,01	-	,02	-	-
Cape Robin Cossypha caffra (I)	-	,14	,08	,38	,15	,45
Grassbird Sphenoeacus afer (I)	,03	,02	-	,03	-	-
Longbilled Crombec Sylvettia rufescens (I)	-	-	-	-	,08	-
Greybacked Cisticola Cisticola subruficapilla (I)	,14	,14	,10	,15	,04	,05
Spotted Prinia Prinia maculosa (I)	,46	,72	,40	1,47	,54	,64
Southern Boubou Laniarius ferrugineus (I)	-	,02	,02	,18	,06	,19
Bokmakierie Telephorus zeylonus (I)	-	,09	-	,02	-	,02
Redwinged Starling Onychognathus morio (Fr)	,16	,51	,12	,07	,61	,17
Cape Sugarbird Promerops cafer (N)	,40	1,10	,22	,13	,23	,13
Malachite Sunbird Nectarinia famosa (N)	,11	,13	,05	,12	,08	,02
Orangebreasted Sunbird N. violacea (N)	1,76	1,50	1,27	,92	1,04	,41
Lesser doublecollared Sunbird N. chalybea (N)	,22	,19	,35	,41	,21	,20
Cape White-eye Zosterops pallidus (I)	-	,12	-	,17	,08	,57
Cape Weaver Ploceus capensis (G)	-	-	-	-	,04	-
Cape Siskin Serinus totta (G)	-	,09	,37	,08	,33	,13
Yellow Canary Serinus flaviventris (G)	-	,01	-	,05	-	-
Cape Bunting Emberiza capensis (G)	,08	,09	,10	,08	,08	,15
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
Species number	9	18	13	19	16	15
Plot-specific species	0	0	0	1	2	0

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

TABLE 4.2

SORENSEN'S COEFFICIENTS OF COMMUNITY FOR AVIAN SPECIES COMPOSITION OF ACACIA CYCLOPS-INFESTED TALL MIXED FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

Percent infestation	10	18	42	50	72
0	67	73	64	64	67
10		77	81	82	91
18			75	83	86
42				80	88
50					90

It is noteworthy that the Redwinged Starling, although classified as a frugivore (Siegfried 1983), was observed feeding in the study plots exclusively from proteaceous inflorescences 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 $X_5^2 = 18,28$; $\underline{P} < 0,01$) with increasing alien infestation. The density of nectarivores (Cape Sugarbird and three sunbird species) was significantly correlated ($r_s = 0,98$ $\underline{P} < 0,05$; 4 df.) with the number of flowering _Leucospermum_ _conocarpodendron_ and _Mimetes_ _fimbriifolius_ shrubs. Thus, the density of these nectarivores decreased significantly (Friedman Test $X_5^2 = 38,3$; $\underline{P} < 0,01$) with increasing infestation by _A. cyclops_ (Fig. 4.2).

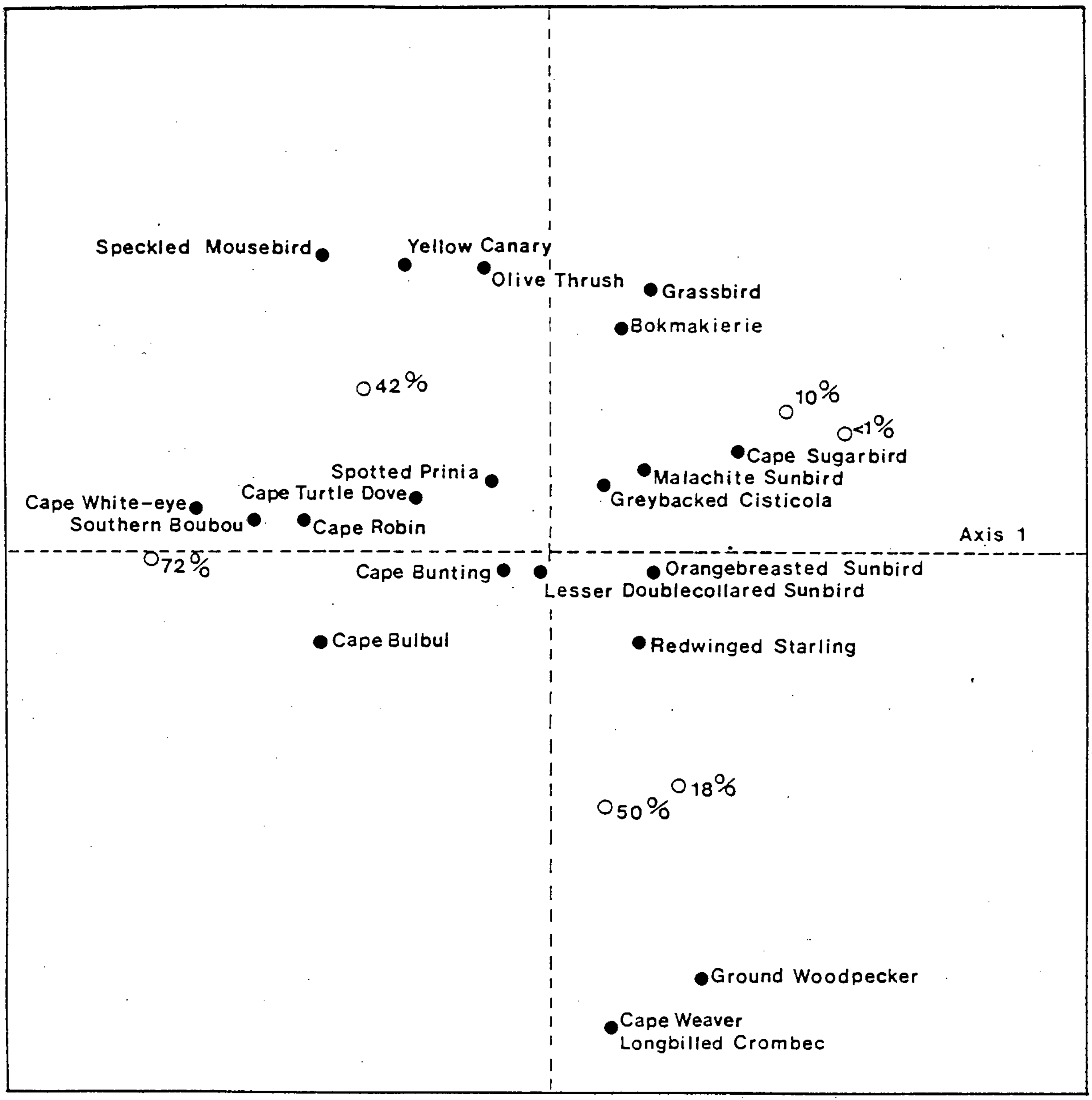

FIGURE 4.1

CORRESPONDENCE ANALYSIS OF BIRD SPECIES DENSITIES IN
<u>ACACIA</u> <u>CYCLOPS</u>-INFESTED TALL MIXED FYNBOS
AT THE CAPE OF GOOD HOPE NATURE RESERVE

TABLE 4.3

AVIAN STANDING CROP BIOMASS IN ACACIA CYCLOPS-INFESTED TALL MIXED FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

Acacia cyclops (% projected canopy cover)	Avian biomass (mean g ha^{-1} ± SE)
<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

Insectivore density varied considerably between plots (Fig. 4.2) and, although not displaying a consistent trend, was significantly higher (Friedman Test $X_5{}^2 = 15,6$; $\underline{P} < 0,01$) 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 (Fig. 4.2) (Friedman Test $X_5{}^2 = 17,38$; $\underline{P} < 0,01$).

In terms of avian density, the dominant species in the <1%, 10%, 18% and 50% infested plots was the Orangebreasted Sunbird. In the 42% and 72% infested plots an insectivore, the Spotted Prinia, occurred at the highest density.

4.4.1.2 Vegetation structure and resource availability

Although the foliage profiles and half-heights of the vegetation differed between the *Acacia cyclops*-infested plots (Fig. 4.3), invertebrate densities were similar (Fig. 4.4). 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

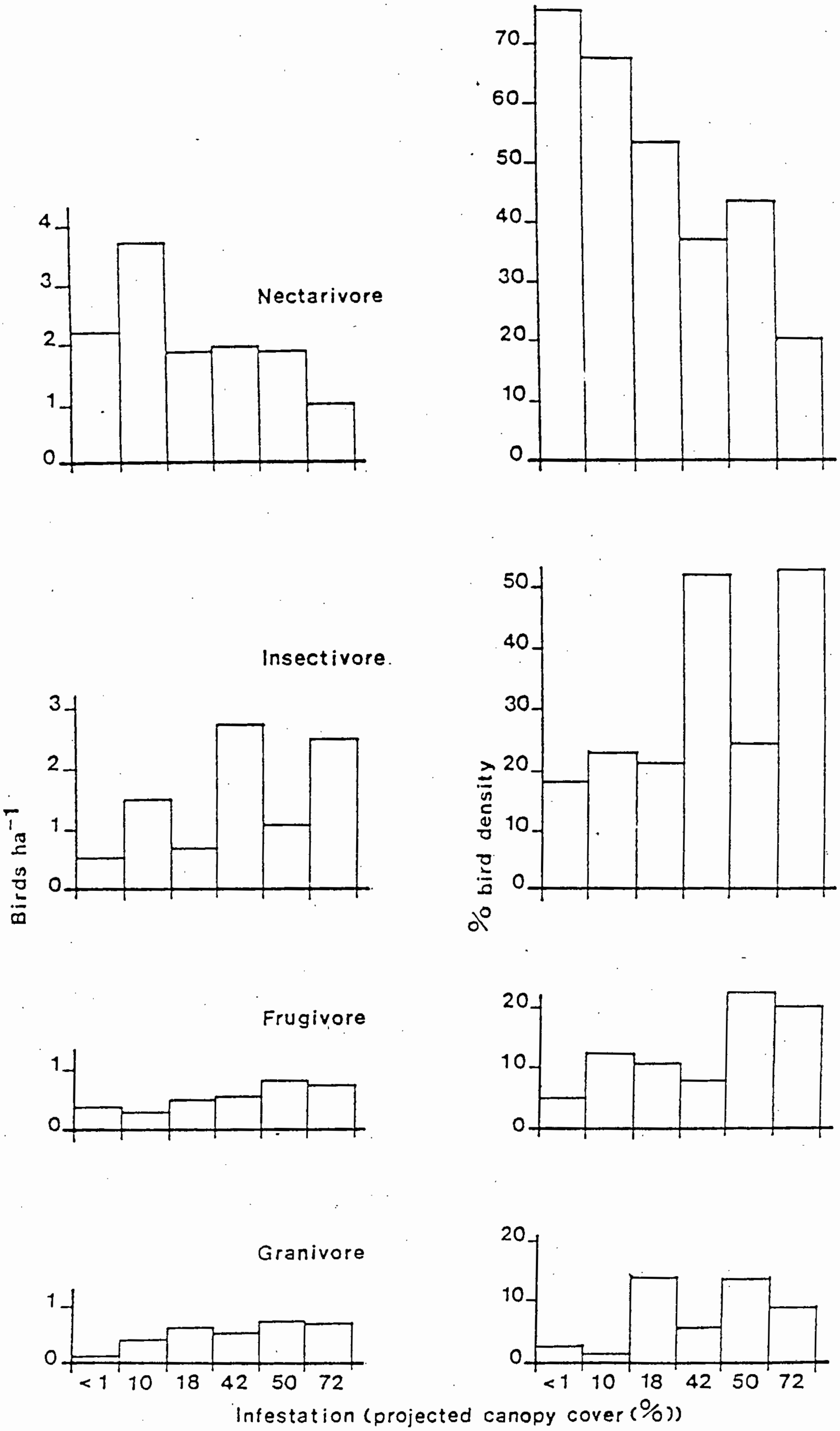

FIGURE 4.2

ABSOLUTE (LEFT) AND RELATIVE (RIGHT) CONTRIBUTIONS OF AVIAN FEEDING GUILDS TO BIRD DENSITY IN <u>ACACIA CYCLOPS</u>- INFESTED TALL MIXED FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE

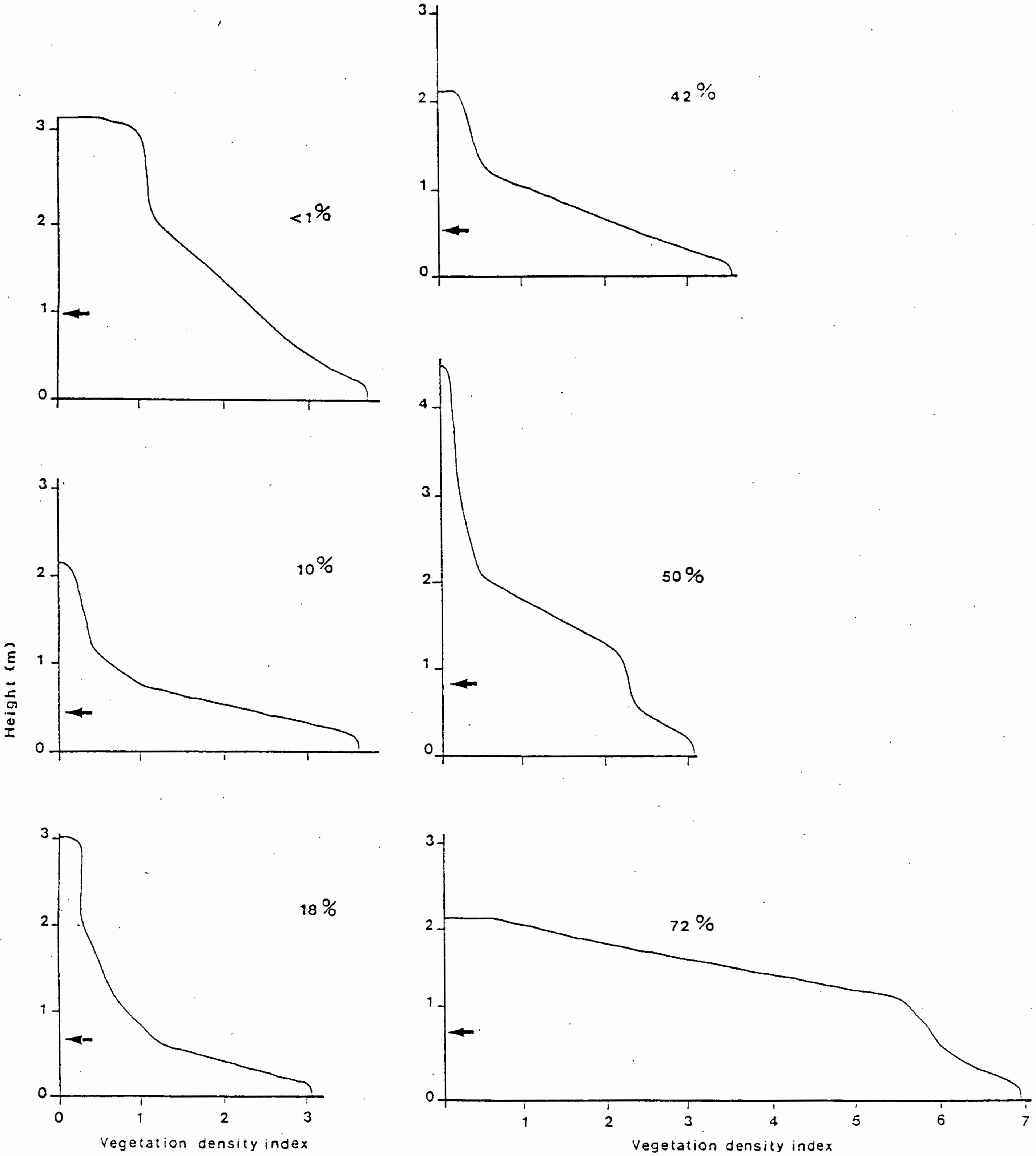

FIGURE 4.3

FOLIAGE PROFILES OF ACACIA CYCLOPS-INFESTED TALL MIXED FYNBOS
AT THE CAPE OF GOOD HOPE NATURE RESERVE.
HALF-HEIGHT VALUES ARE INDICATED BY ARROWS

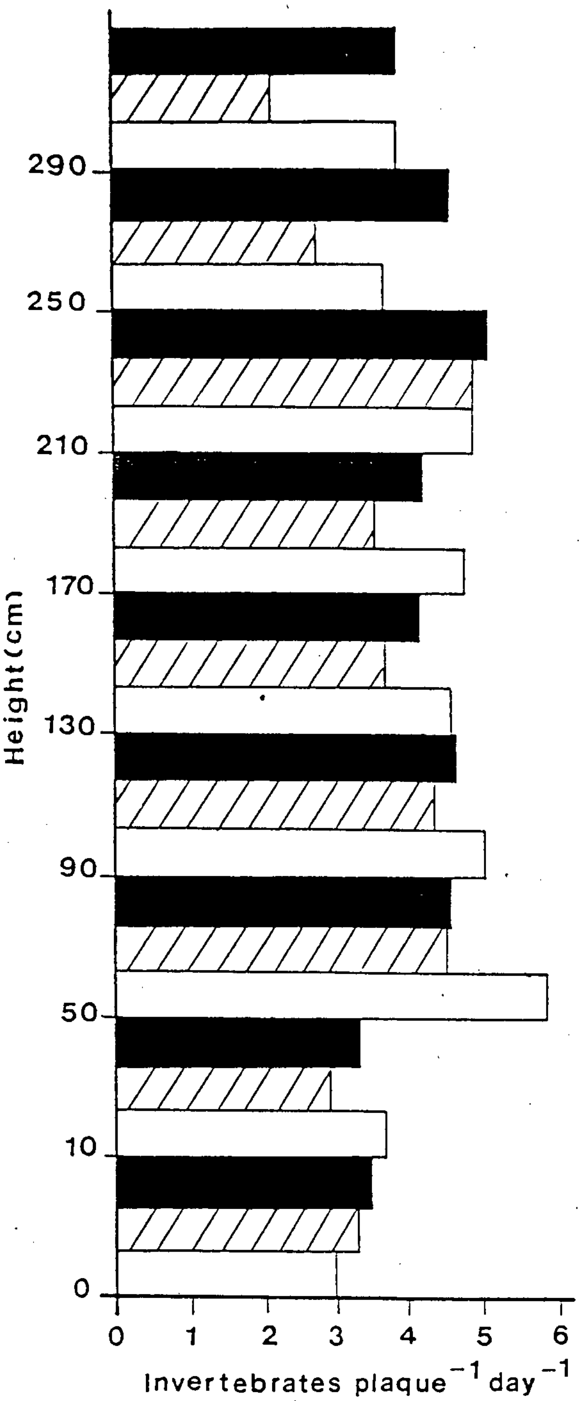

FIGURE 4.4

INVERTEBRATE ABUNDANCE (MEAN PER JAR OR PLAQUE PER DAY) AT DIFFERENT STRATA IN <u>ACACIA</u> <u>CYCLOPS</u>-INFESTED TALL MIXED FYNBOS AT THE CAPE OF GOOD HOPE NATURE RESERVE (OPEN, HATCHED AND SOLID BARS ARE, RESPECTIVELY, 10%, 42% AND 72% PROJECTED CANOPY COVER OF <u>A</u>. <u>CYCLOPS</u>)

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.

4.4.2 Restionaceous Tussock Marsh infested with mixed aliens

4.4.2.1 Birds

Twenty-three bird species were recorded in Restionaceous Tussock Marsh infested with mixed aliens (Table 4.4). Four species (three sunbird species and Cape White-eye) were found at all levels of infestation. Interplot similarity values (Table 4.5) for the bird species assemblages of mixed alien infestations varied markedly, but were lower than those between plots infested by Acacia cyclops (Table 4.2). 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), these were relatively large-bodied, granivorous species. Four of these (Helmeted Guineafowl, Cape Francolin, Redeyed Dove and Laughing Dove), were restricted to the 100% mixed-alien infestation where they were responsible for the high avian biomass recorded in this plot (Table 4.6).

Avian density was highest in the two most densely infested plots (Table 4.4). In a correspondence analysis based on species density (Fig. 4.5), the first two axes accounted for 63% and 37% respectively of the inertia, i.e. the data matrix was well displayed in two dimensions. Along axis 1, the plots were ordered with respect to level of alien infestation, with the largest contributions to the inertia being made by Cape Sugarbird and Orangebreasted Sunbird, which were associated with low infestation levels. The most important feature of the display was the contrast between the 100%-infested plot and the three lesser infestations. This contrast was 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, Olive Thrush and Dusky Flycatcher), to the 100% infestation.

In contrast to the other nectarivores, the Lesser Doublecollared Sunbird made a relatively small contribution to the analysis. The contrast between the 100% infestation and the nectarivore density in the other plots was again borne out in axis 2. Here high densities of Orangebreasted and Malachite Sunbirds in the 50% infestation contrasted with the absence of Cape Sugarbird from this plot and emphasized 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 showed greater similarity to each other than the 0% and 100% infestations. The proximity of Malachite and Orangebreasted Sunbirds demonstrated their similar pattern of occurrence.

TABLE 4.4

MEAN AVIAN DENSITY AND SPECIES RICHNESS IN MIXED-ALIEN INFESTED RESTIONACEOUS TUSSOCK MARSH AT THE CAPE OF GOOD HOPE NATURE RESERVE

	Mixed-alien density (estimated percentage projected canopy cover)			
	0	25	50	100
Species	Density of birds per plot			
Cape Francolin *Francolinus capensis* (G)*	–	–	–	,08
Helmeted Guineafowl *Numida meleagris* (G)	–	–	–	,31
Redeyed Dove *Streptopelia semitorquata* (G)	–	–	–	,01
Cape Turtle Dove (G)	–	–	,20	,97
Laughing Dove *Streptopelia senegalensis* (G)	–	–	–	,04
Speckled Mousebird (Fo)	–	–	–	,01
Cape Bulbul (Fr)	–	,04	,04	,17
Olive Thrush (I)	–	–	–	,12
Cape Robin (I)	–	,04	,12	,56
Grassbird (I)	,12	,12	–	–
Greybacked Cisticola (I)	–	,04	–	–
Spotted Prinia (I)	,28	,24	,20	–
Dusky Flycatcher *Muscicapa adusta* (I)	–	–	–	,01
Southern Boubou (I)	–	–	,08	,47
Bokmakierie (I)	–	–	,04	–
Cape Sugarbird (N)	1,0	,12	–	,06
Malachite Sunbird (N)	,08	,56	1,36	,35
Orangebreasted Sunbird (N)	,36	,88	2,08	,04
Lesser Doublecollared Sunbird (N)	,04	,16	,32	,60
Cape White-eye (I)	,08	,40	1,24	1,29
Cape Weaver (G)	–	–	,04	–
Yellowrumped Widow *Euplectes capensis* (G)	,20	–	–	–
Common Waxbill *Estrilda astrild* (G)	,08	–	–	,05
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	8	13	17
Plot-specific species	1	1	1	7

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

The absolute and relative contributions of feeding guilds to overall bird density in the Restionaceous Tussock Marsh plots are presented in Fig. 4.6. As in Acacia cyclops-infested Tall Mixed Fynbos, the relative density of nectarivores tended to decrease with increasing alien infestation. 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: $r_s = 0,20$; NS, 4 df). Granivores were very scarce or absent in 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 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.

4.4.2.2 Vegetation structure and resource availability

A foliage profile of the 100% mixed-alien infestation is given in Fig. 4.7. 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 (Fig. 4.8).

TABLE 4.5

SORENSEN'S COEFFICIENTS OF COMMUNITY FOR AVIAN SPECIES COMPOSITION OF MIXED-ALIEN INFESTED RESTIONACEOUS TUSSOCK MARSH AT THE CAPE OF GOOD HOPE NATURE RESERVE

Projected alien canopy cover (estimated %)	25	50	100
0	82	45	46
25		67	56
50			53

TABLE 4.6

AVIAN STANDING CROP BIOMASS IN MIXED-ALIEN INFESTED RESTIONACEOUS TUSSOCK MARSH AT THE CAPE OF GOOD HOPE NATURE RESERVE

Level of infestation (estimated projected canopy cover)	Avian 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

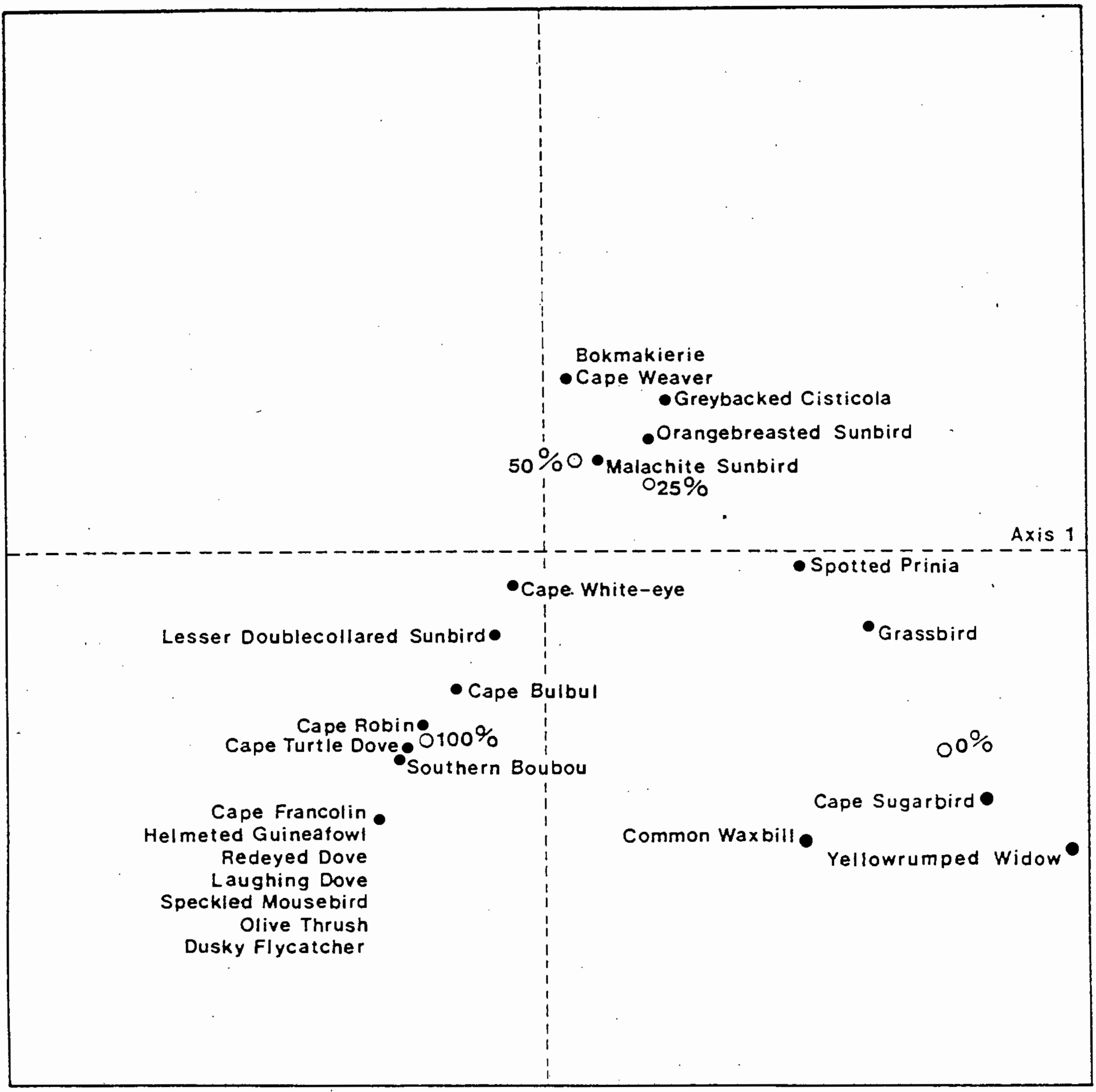

FIGURE 4.5

CORRESPONDENCE ANALYSIS OF BIRD SPECIES DENSITIES IN MIXED-ALIEN INFESTED RESTIONACEOUS TUSSOCK MARSH AT THE CAPE OF GOOD HOPE NATURE RESERVE

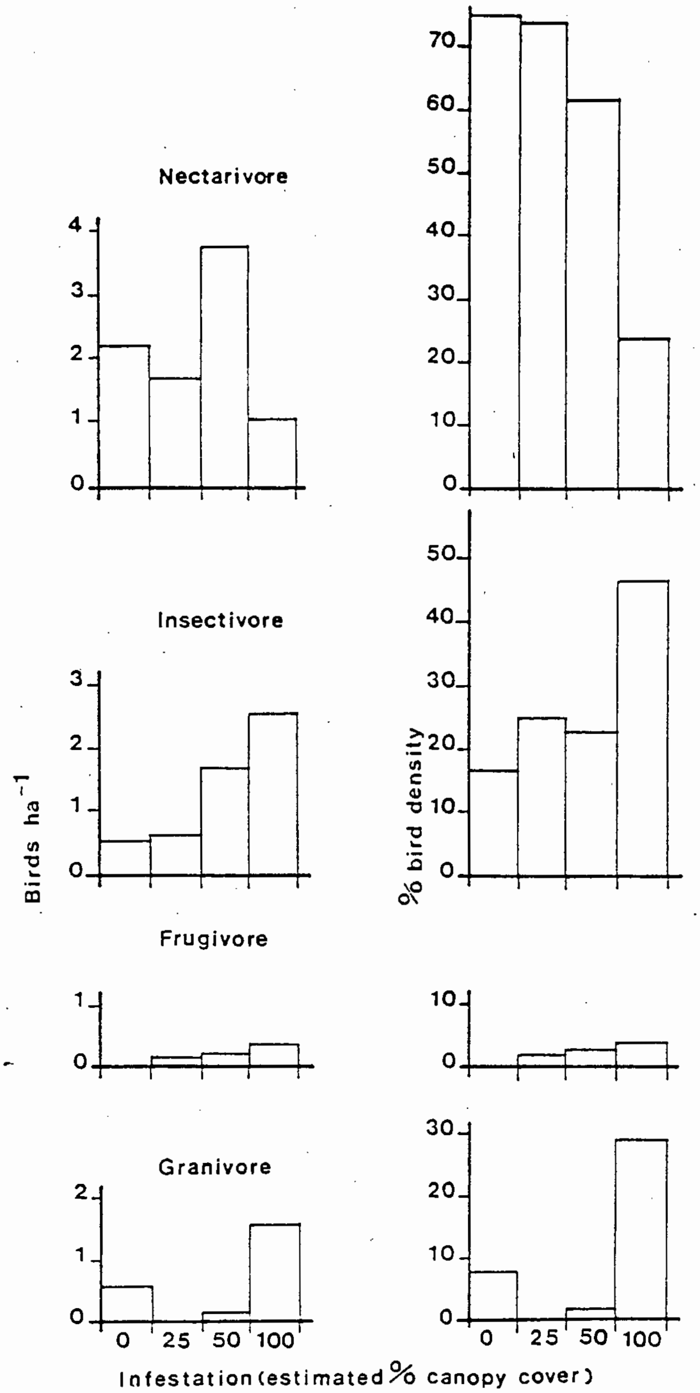

FIGURE 4.6

ABSOLUTE (LEFT) AND RELATIVE (RIGHT) CONTRIBUTIONS OF AVIAN FEEDING GUILDS TO BIRD DENSITY IN MIXED-ALIEN INFESTED RESTIONACEOUS TUSSOCK MARSH AT THE CAPE OF GOOD HOPE NATURE RESERVE

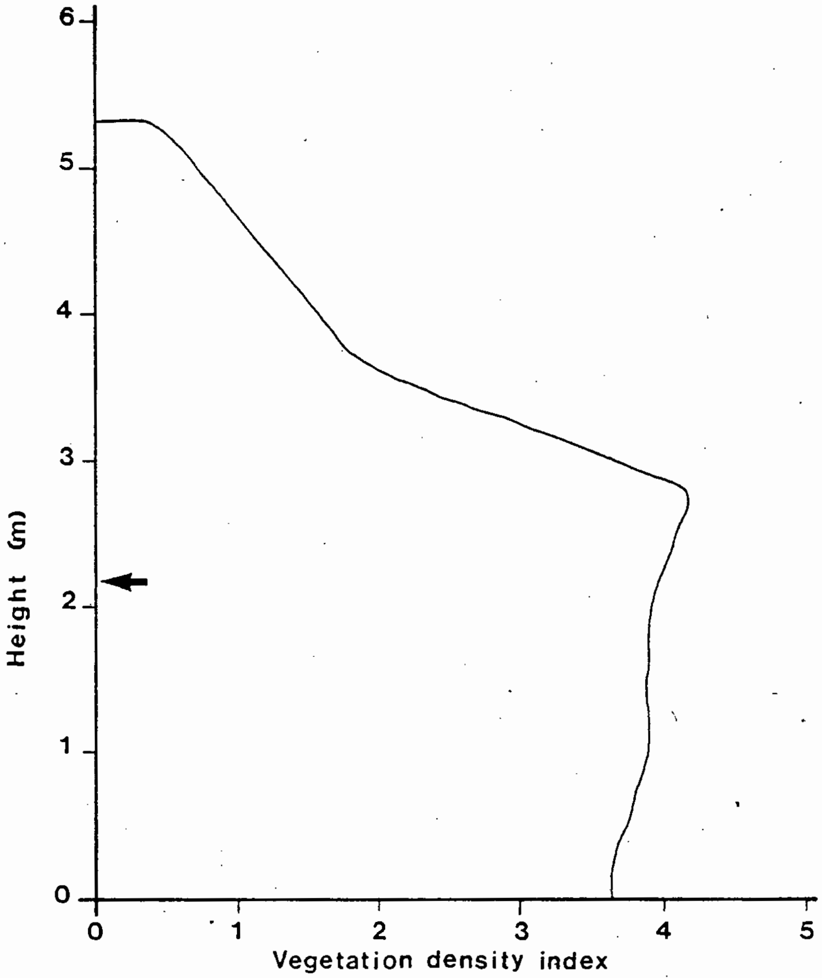

FIGURE 4.7

FOLIAGE PROFILE OF 100% PROJECTED CANOPY COVER
INFESTATION OF MIXED ALIENS IN RESTIONACEOUS TUSSOCK MARSH
AT THE CAPE OF GOOD HOPE NATURE RESERVE

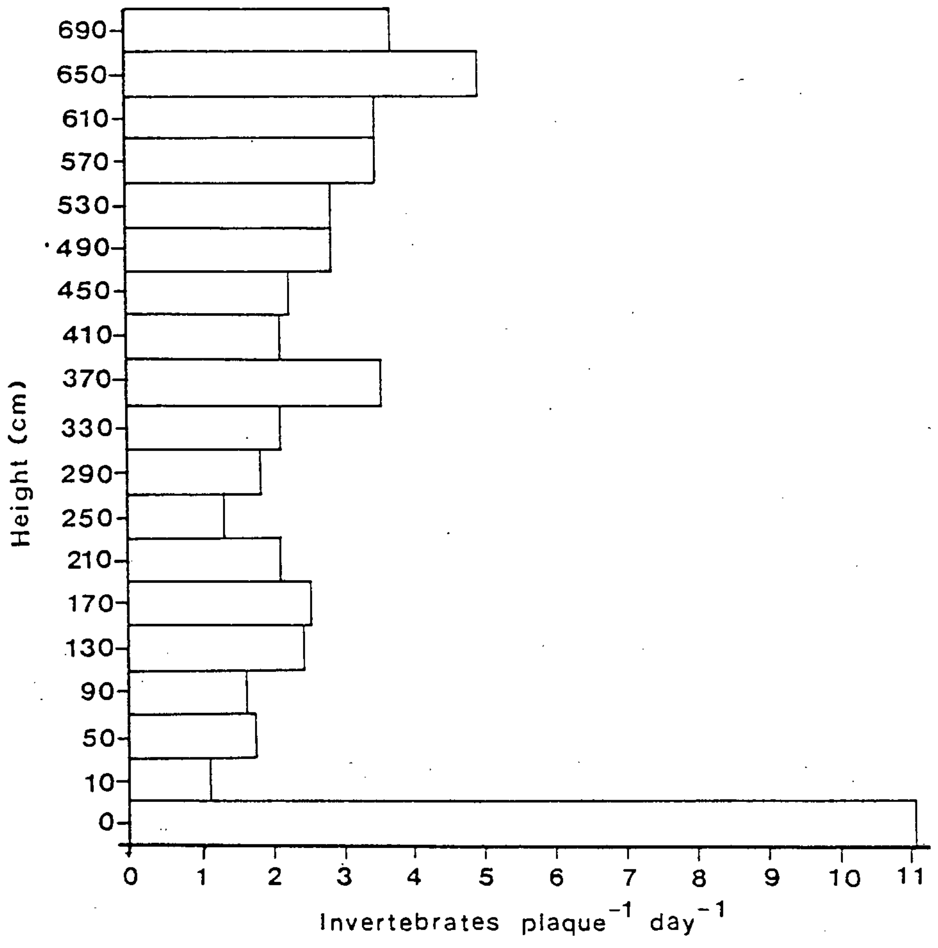

FIGURE 4.8

INVERTEBRATE ABUNDANCE (MEAN PER JAR OR PLAQUE PER DAY)
AT DIFFERENT STRATA IN 100% PROJECTED CANOPY COVER
MIXED-ALIEN INFESTED RESTIONACEOUS TUSSOCK MARSH
AT THE CAPE OF GOOD HOPE NATURE RESERVE

4.6 DISCUSSION

4.6.1 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 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 infested mixed-alien plot was twice that in uninfested Restionaceous Tussock Marsh. This implies that resource availability is increased by alien woody plant infestation of this plant species assemblage. Although invertebrate data are available only from the 100% mixed-alien infestation, comparison with invertebrate data from the Acacia cyclops plots indicates that increased invertebrate availability in this plot may be attributed to taller vegetation and greater invertebrate abundance at ground level (Fig. 4.8). 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.

4.6.2 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, as indicated by the high similarity coefficients between plots (Table 4.3). However, results from the mixed-alien-infested Restionaceous Tussock Marsh support the hypothesis that fynbos species will give way to woodland/thicket species as alien infestation increases.

Winterbottom (1970) described the birds of alien 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. This would tend to contradict Cody's (1975) findings that species replacement is relatively rapid between scrub communities in fynbos. This assumes that increasing levels of infestation are equivalent to moving from one scrub community to another. The results from the A. cyclops-infested Tall Mixed Fynbos support Siegfried & Crowe's (1983) suggestion that there is a relaxation of niche breadth of species in Mountain Fynbos and that, despite its heterogeneity, the same characteristic species occur generally throughout the vegetation. While it may be noted that four bird species which are more typical of thicket or woodland than fynbos, do tend to be more numerous in denser A. cyclops infestations, their density is never high and the same trend is exhibited by two distinctly non-woodland granivores (Cape Siskin and Cape Bunting). The relatively high species richness in even the most densely infested plots, and the low level of bird species turnover tend not to support the widely-held belief that monocultures notoriously restrict the number and variety of species that can be supported (Winterbottom 1970).

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 low-foraging insectivores (Grassbird and Greybacked Cisticola) 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 canopy-foraging Cape White-eyes in the 50%- and 100%-infested plots is to be expected. The Helmeted Guineafowl and Redeyed Dove recently have expanded their ranges into the Fynbos Biome, a trend which has been attributed to agricultural practices and alien woody plant invasion (Brooke 1984, 1986).

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

Results from this study do not support the hypothesis that frugivorous birds will increase in Acacia cyclops infestations. The virtual absence of a response by frugivorous birds to an increased food supply (the arillate seeds of A. cyclops), was unexpected, as a number of species feed on the fruits of this plant (Glyphis et al. 1981; Middlemiss 1963; Winterbottom 1970). In its native Australia, A. cyclops seeds are bird-dispersed (Gill 1985). Analysis of regurgitated and faecal pellets of the Redwinged Starling collected nearby, however, demonstrated that A. cyclops seeds were taken by this species throughout the year at the study site (Chapter 5). The expected large-scale eating of fresh, ripe fruits as they were displayed in open pods in midsummer did not materialize. The reasons for this are unclear, but may include the abundance of A. cyclops fruits elsewhere (this species is widespread on the Cape Peninsula and elsewhere in the southwestern Cape (Stirton (1987)), or the "peninsula" effect of the study site which limits bird immigration. The densities of Cape Bulbuls (similar in the 18%, 42% and 72% infestations and highest in the 100% infestation), perhaps suggest increased utilization by frugivorous birds, but this is not supported by the Redwinged Starling, the only other frugivore recorded. Nor are additional frugivorous species recorded with increasing alien infestation. As the Redwinged Starling is, 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.

4.6.4 <u>Hypothesis 4: The relative density of nectarivorous species will decrease as the extent of alien infestation increases.</u>

Results here support this hypothesis. In the correspondence display of the <u>Acacia cyclops</u>-infested Tall Mixed Fynbos plots (Fig. 4.1) the position of three out of the four species of nectarivores demonstrate a strong association with low levels of infestation. Thus, nectarivores are the species most adversely affected by <u>A</u>. <u>cyclops</u> infestation. Breytenbach (1986) recorded the complete disappearance of nectarivores from fynbos vegetation heavily infested with alien <u>Hakea</u> <u>sericea</u>. Given the positive correlation between nectarivore density and the number of flowering Proteaceae in the present study, this reduction is presumably due to suppression of flowering food plants by the alien vegetation. Nevertheless, the Orangebreasted Sunbird is still the most consistently recorded species in the Tall Mixed Fynbos plots.

Although Cape Sugarbirds have been reported feeding on the nectar of Eucalyptus lehmanni (Fourie 1968), the flowering period of this alien is short and seasonally restricted. Since members of the Proteaceae and Ericaceae flower at different times of year, these together provide a year-round food source. E. lehmanni is not, therefore, a reliable and consistent source of nectar for nectarivorous birds. Moreover, if these birds do play an important role in the pollination of some fynbos plant species, notably Proteaceae and Ericaceae (Rebelo 1987 and references therein), 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. Similarly, 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.

This negative feedback system potentially is the most damaging effect of alien invasion on the avifauna of those Mountain Fynbos plant species assemblages supporting food plants of avian nectarivores. Thus, once the density or absolute number of ericas and/or proteas falls below a certain level, nectarivorous birds may abandon a site totally. However, the relative importance of birds compared to other vectors (notably insects) as pollinators of Proteaceae has not been established, and may have been over-emphasized in the past (Coetzee & Gillomee 1985).

Cody (1975) considers that vegetation structure is a major determinant on the bird community organization. However, the distribution and abundance of nectarivores in CGHNR study plots apparently was 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 other species (e.g. Acacia cyclops) which may exhibit similar physiognomy but are unsuitable food plants.

4.6.5 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. Although the 42%-infested plot supported slightly higher absolute and relative densities of insectivores than the other plots, this was due to the presence of a pair of Spotted Prinias which were consistently recorded on counts. Without these birds, insectivore density would have been generally similar throughout all plots. The apparent failure of invertebrate density to rise in response to the increased vegetation substratum may be an indication of the inability of indigenous arthropods (especially phytophagous insects) to utilize alien plant species. Breytenbach (1986) considers this to be the case with Hakea sericea. In Mountain Fynbos vegetation infested with H. sericea, however, he found that 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 (Fig. 4.4).

More insects were potentially available to birds in the 100%-infested mixed-alien plot than in the densest A. 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. It is noteworthy that in the 100%-infested plot three out of five avian insectivores were largely ground-foraging species, reflecting the high levels of ground invertebrates recorded in this plot (Fig. 4.8).

4.6.6 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 Acacia cyclops-infested Tall Mixed Fynbos occurred in lower densities and, with the exception of Cape Turtle Dove, 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 alien seeds. These bird species are common elsewhere in the reserve in uninfested fynbos vegetation (M.W. Fraser, unpubl. data).

There is no apparent reason for the absence of a response by large-bodied granivores, notably Cape Francolin and Helmeted Guineafowl, to the availability of A. cyclops seeds. The dense understorey might have precluded efficient foraging, however. The relatively high proportion of large-bodied 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. Similarly, whereas Siegfried (1983) 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 of the alien invasives on fynbos bird assemblages, presumably, in this instance, through seed availability.

4.7 **CONCLUSIONS**

Avifaunal responses to increasing infestation of Mountain Fynbos by alien woody plants differ according to the plant species assemblage which has been infested, the species of invasive alien woody plant and the time of year. Bird density increases in Mixed-alien infested in Restionaceous Tussock Marsh, but not in Acacia cyclops-infested Tall Mixed Fynbos. Nectarivorous species decrease in density with increasing infestation by A. cyclops of Tall Mixed Fynbos since their food plants are eliminated. Removal of alien vegetation from this and other plant species assemblages supporting high densities of proteaceous shrubs should receive high priority from the reserve authorities where the aim is maintain populations of nectarivorous birds.

CHAPTER 5

ACACIA CYCLOPS FRUITS AND OTHER FOODS OF REDWINGED STARLINGS AT THE CAPE OF GOOD HOPE NATURE RESERVE

CHAPTER 5

ACACIA CYCLOPS FRUITS AND OTHER FOODS OF REDWINGED STARLINGS AT THE CAPE OF GOOD HOPE NATURE RESERVE

5.1 INTRODUCTION

The Redwinged Starling Onychognathus morio has a broad dietary range of fruits, nectar, invertebrates and small vertebrates (Craig et al. 1989; Maclean 1985; Richardson & Fraser in press). It also feeds on the arillate fruits of Acacia cyclops, which are bird-dispersed in the plant's native Australia (Gill 1985). The Redwinged Starling has thus been implicated in the spread of this invasive alien in the southwestern Cape (Glyphis et al. 1981; Middlemiss 1963). Knight (1986) has suggested that Redwinged Starlings eat A. cyclops fruits in preference to those of indigenous species, notably Rhus spp. (which fruit during periods of general fruit scarcity and act as a "pivotal" food source for frugivorous birds). This feeding shift by the Redwinged Starling (and, possibly, other frugivores), has important implications for the successful dispersal of the A. cyclops and the lessened dispersal of seeds and consequent decrease in recruitment of indigenous plants.

5.2 STUDY SITE AND METHODS

To assess the relative extent to which Redwinged Starlings fed on Acacia cyclops fruits and, therefore, potentially disperse their seeds, I collected fresh faecal and regurgitated pellets from a Redwinged Starling roost at the Cape of Good Hope Nature Reserve (34 15S, 18 25E), between August 1985 and June 1986. The roost was in a disused building 3 km northwest of Cape

Point, the southern tip of the reserve. The vegetation of the reserve is predominantly Mountain Fynbos with a narrow, broken fringe of Strandveld (*sensu* Moll *et al*. 1984). The reserve is infested to various degrees by *A. cyclops* (Macdonald *et al*. 1989; Taylor *et al*. 1985). The vegetation in the vicinity of the roost comprised Taylor's (1984) "Tall Mixed Fynbos" with sparse to dense infestations of *A. cyclops*. The Redwinged Starling is widespread and common in the reserve (Middlemiss & Langley 1975; M.W. Fraser, unpubl. data). Observations were also made on foraging Redwinged Starlings elsewhere in the reserve.

5.3 RESULTS AND DISCUSSION

The composition of 1 087 fresh faecal and regurgitated pellets collected at the roost are given in Table 5.1. The roost was unused in November and May. Analysis of faecal and regurgitated pellets only permits an assessment of food items with indigestible remains. Nectar, for example, appeared to be an important food, but would not be represented in such pellets.

5.3.1 Fruits

Figure 5.1 shows the relative proportions of seeds of alien and indigenous fruits recovered from Redwinged Starling faecal and regurgitated pellets. *Acacia cyclops* seeds ($\bar{x} = 4,01 \pm 2,48$ pellet^{-1}, n = 944) and arils occurred exclusively in 86,8% of pellets. Seeds of indigenous taxa were recorded exclusively from only 67 (6,2%) pellets and present with *A. cyclops* in 70 (6,4%) others. The prolonged display of *A. cyclops* fruits is reflected in their virtual year-round utilization by Redwinged Starlings. *Rhus* spp. were the most extensively utilized indigenous species, but were exceeded by *A. cyclops* both in frequency with which and the number of months in which they were eaten (Table 5.1). This may be a function of either the Redwinged Starling's preference for, or the relatively high availability of, the alien fruits. Plants with fleshy fruits and, consequently, frugivorous birds are scarce in Mountain Fynbos, and seed dispersal by birds is virtually absent in this vegetation type (Cody et al. 1983; Siegfried 1983). Thus, A. cyclops may broaden this feeding niche in Mountain Fynbos. The detrimental effects on fynbos vegetation of A. cyclops infestation may be exacerbated by increased utilization of the alien in preference to indigenous species. The shift from indigenous- to alien-seed dispersal parallels that recorded for the Rameron Pigeon Columba arquatrix and Solanum mauritianum in Natal (Oatley 1984), discussed by Knight (1986).

In Strandveld at the Cape of Good Hope Nature Reserve, Redwinged Starlings were observed taking fruits of the indigenous species Myrica cordifolia (February and March), Rhus lucida (December) and Sideroxylon inerme (December). With the exception of M. cordifolia, which was quickly stripped of its fruits, indigenous fruits appeared to be largely ignored and many berries of Strandveld species, notably S. inerme and Maurocaenia frangularia, rotted on the bushes (M.W. Fraser, unpubl. data).

During January-April, when Acacia cyclops was most heavily utilized by Redwinged Starlings (Table 5.1), there were few or no flowering proteaceous shrubs in the area. Only 4,4% of pellets collected in these months contained indigenous seeds. The alien fruits may, therefore, provide a stop-gap or represent the "pivotal" food source normally provided by Rhus spp. (Knight 1986).

TABLE 5.1

CONTENTS OF REDWINGED STARLING FAECAL AND REGURGITATED PELLETS COLLECTED AT A ROOST IN THE CAPE OF GOOD HOPE NATURE RESERVE

Month	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	TOTAL
Number of pellets containing:												
Fruits only												
Acacia cyclops	114	45	10	0	70	107	85	404	80	0	29	944
(Percentage)	(84,4)	(100)	(47,6)	-	(46,9)	(89,9)	(97,7)	(97,3)	(93,0)	-	(96,7)	(86,8)
A. cyclops and *Pterocelastris tricuspidata*	1	0	0	0	0	0	0	0	0	0	0	1
(Percentage)	(0,7)	-	-	-	-	-	-	-	-	-	-	(0,1)
A. cyclops and *Cassytha ciliolata*	1	0	3	0	0	0	0	0	0	0	0	4
(Percentage)	(0,7)	-	(14,3)	-	-	-	-	-	-	-	-	(0,4)
A. cyclops and *Colpoon compressum*	1	0	0	0	0	0	0	0	0	0	0	1
(Percentage)	(0,7)	-	-	-	-	-	-	-	-	-	-	(0,1)
A. cyclops and *Rhus* sp.	0	0	0	0	31	11	2	11	6	0	0	61
(Percentage)	-	-	-	-	(20,8)	(9,2)	(2,3)	(2,6)	(7,0)	-	-	(5,6)
A. cyclops and unidentified fruits	3	0	0	0	0	0	0	0	0	0	0	3
(Percentage)	(2,2)	-	-	-	-	-	-	-	-	-	-	(0,3)
Cassytha ciliolata	9	0	3	0	0	0	0	0	0	0	1	13
(Percentage)	(6,7)	-	(14,3)	-	-	-	-	-	-	-	(3,3)	(1,2)
Colpoon compressum	0	0	1	0	0	0	0	0	0	0	0	1
(Percentage)	-	-	(4,8)	-	-	-	-	-	-	-	-	(0,1)
Rhus sp.	0	0	0	0	48	1	0	0	0	0	0	49
(Percentage)	-	-	-	-	(32,2)	(0,8)	-	-	-	-	-	(4,5)
Lycium sp.	0	0	4	0	0	0	0	0	0	0	0	4
(Percentage)	-	-	(19,0)	-	-	-	-	-	-	-	-	(0,4)
Fruits and invertebrates												
A. cyclops and *Palystes natalius* (Araneae)	1	0	0	0	0	0	0	0	0	0	0	1
(Percentage)	(0,7)	-	-	-	-	-	-	-	-	-	-	(0,1)
A. cyclops and beetle (Coleoptera)	2	0	0	0	0	0	0	0	0	0	0	2
(Percentage)	(1,5)	-	-	-	-	-	-	-	-	-	-	(0,2)
Invertebrates only												
Cetoniid beetle	3	0	0	0	0	0	0	0	0	0	0	3
(Percentage)	(2,2)	-	-	-	-	-	-	-	-	-	-	(0,3)
Total	135	45	21	0	149	119	87	415	86	0	30	1087

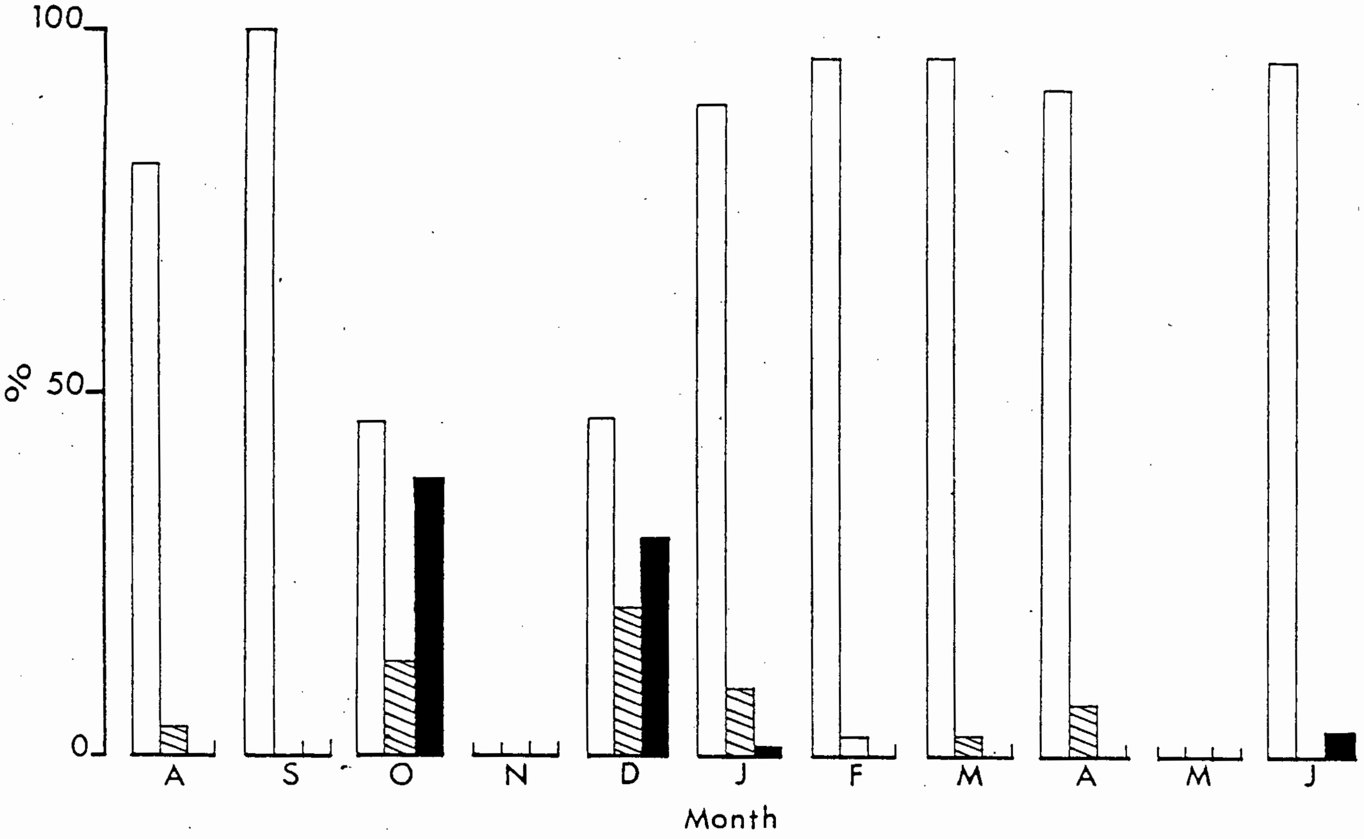

FIGURE 5.1

PROPORTION OF REDWINGED STARLING FAECAL AND REGURGITATED PELLETS CONTAINING SEEDS OF <u>ACACIA</u> <u>CYCLOPS</u> ONLY (OPEN COLUMN), <u>A.</u> <u>CYCLOPS</u> AND INDIGENOUS FRUITS (HATCHED COLUMN) AND INDIGENOUS FRUITS ONLY (SOLID COLUMN)

No large-scale influxes of Redwinged Starlings to exploit indigenous or alien fruits were recorded. Densities of Redwinged Starlings in study plots did not increase with increasing Acacia cyclops infestation (Chapter 4). Birds feeding on Myrica cordifolia included two individuals ringed, respectively, 12 and 16 months previously at the site. Two ringed birds were resident at another location. Fruiting bushes may, therefore, merely concentrate local populations of Redwinged Starlings at the Cape of Good Hope Nature Reserve.

5.3.2 Nectar

Redwinged Starlings ate nectar of Salvia africana (August-September), Mimetes fimbriifolius (August-October) and Leucospermum conocarpodendron (September-December). The largest feeding aggregation of Redwinged Starlings (240 birds), was recorded taking nectar from M. fimbriifolius in August. The highest densities of Redwinged Starlings in mature Mountain Fynbos study plots coincided with the flowering season of L. conocarpodendron (Chapter 1). Starlings sporting conspicuous bright yellow pollen-dusted heads, the result of feeding from these inflorescences, were commonly seen at this time. Redwinged Starlings took Acacia cyclops fruits at the same time as birds were observed feeding on proteaceous nectar. Movements of birds between A. cyclops thickets and nectar sources potentially will disperse alien seeds widely in the reserve.

5.3.3 Invertebrates

Although poorly represented in pellets (Table 5.1), invertebrates appeared, on occasions, to be taken in preference to other foods. Two Redwinged Starlings foraging in Acacia cyclops bushes ignored the ripe fruits but took invertebrates, including a large green mantid. Craig et al. (1989) reported mantids as common prey items. Two birds gleaned invertebrates from a Solanum hermannii bush and ignored the many conspicuous ripe berries. On warm, calm days (rare on the southern Peninsula), Redwinged Starlings hawked protea beetles (Cetoniinae) around Leucospermum conocarpodendron inflorescences in aerial sallies from elevated natural perches and telegraph poles and wires. Starlings were observed springing up from the ground to remove ectoparasites, presumably ticks (Acari), from the bellies of Eland Taurotragus oryx (L. McMahon, pers. comm.). Cape Mountain Zebras Equus zebra are similarly exploited at the reserve (Mangold 1988). Singletons or pairs of Redwinged Starlings foraged in the rocky intertidal zone on the reserve's west coast throughout the study period. A small Littorina sp. was eaten whole, larger ones were beaten on rocks before swallowing. Unidentified prey, possibly Ligia dilatata (which are extremely numerous on the upper rocky shore), were also taken.

CHAPTER 6

BAYESIAN ESTIMATE OF THE NUMBER OF MALACHITE SUNBIRDS FEEDING AT AN ISOLATED AND TRANSIENT NECTAR RESOURCE

CHAPTER 6

BAYESIAN ESTIMATE OF THE NUMBER OF MALACHITE SUNBIRDS FEEDING AT AN ISOLATED AND TRANSIENT NECTAR RESOURCE

6.1 INTRODUCTION

Gazey & Staley (1986) and Zucchini and Channing (1986) independently introduced a Bayesian analog of the Schnabel (1938) census model for estimating the size of a closed population from capture-recapture information. The special case of the Schnabel census model in which animals are trapped, marked and released one at a time was developed by Craig (1956). Du Feu et al. 1983 showed how Craig's method could be used to estimate (the du Feu estimate) the number of birds present in an area during a short period. In the present study, the Bayesian analog of the du Feu estimate is developed and used to estimate the number of Malachite Sunbirds *Nectarinia famosa* utilizing an isolated food resource at which they were mistnetted and ringed.

The Malachite Sunbird occurs widely in southern Africa in a variety of vegetation types (Maclean 1985; Skead 1967). It is predominantly a nectar feeder, often gathering at isolated food sources. Skead (1967) recorded foraging parties of 30-40 birds (without mentioning a specific food plant), and Niven (1968) recorded an aggregation of about 100 Malachite Sunbirds attracted to a flowering patch of *Cotyledon macrantha*. Breeding of Malachite Sunbirds on the Cape Peninsula occurs from late May to November (Skead 1967).

6.2 STUDY SITE AND METHODS

From 06h00 on 5 Dec to 13h00 on 7 Dec 1987, 180 m of mistnets were operated in and around a ca 400 m^2 stand of flowering Minaret Flowers Leonotis oxymifolia about 400 m^2 in Strandveld (dune thicket vegetation (Cowling 1984)), at Olifantsbos (34 16S, 18 03E), Cape of Good Hope Nature Reserve, Cape Peninsula. These plants flower at all times of year, but peak in mid-summer and early autumn. The numbers of Malachite Sunbirds attracted to the flowers varied from season to season and year to year (M.W. Fraser, unpubl. data). There were no other stands of Leonotis within the reserve.

Malachite Sunbirds were trapped, ringed and released within 30 min of capture at a distance of 900 m from the netting site. The order in which the retrapped birds were caught in relation to unringed birds was recorded.

The assumptions that underlie the proposed estimate method are identical those of du Feu et al. (1983), Gazey & Staley (1986) and Zucchini and Channing (1986): the population is closed, so that there is no mortality, natality, emigration or immigration during the sampling period; all individuals have the same probability of being captured, regardless of whether they are marked or not; the captured individuals are all marked and released immediately.

Let N_{max} be a guess at the maximum possible number of birds in the area. Let $p_i(N)$ be the estimate that the population is size N after the ith bird has been handled. The population was set initially as:

$$p_0(n) = \frac{1}{N_{max}},\ n = 1 \ldots N_{max}.$$

Suppose that, when the ith bird is captured, the number of birds already ringed is m. Given that the population size is N, the probabilities that this bird is ringed or unringed are then m/N and $(N - m)/n$, respectively. If the ith bird is unringed, it follows from Bayes' Theorem that

$$p_i(N) = k\,\frac{N - m}{N}\,p_{i-1}(N)$$

where

$$k = \left(\sum_{N=m}^{N_{max}} \frac{N - m}{N}\,p_{i-1}(N)\right)^{-1}$$

Similarly, if the ith bird is ringed,

$$p_i(N) = k\,\frac{m}{N}\,p_{i-1}(N)$$

where

$$k = \left(\sum_{N=m}^{N_{max}} \frac{m}{\mathrm{N}}\,p_{i-1}(N)\right)^{-1}$$

In this way, the probability distribution of the population size is iteratively refined. Useful estimates of the population size are given by the mean, median and mode of this probability distribution. A 95% confidence interval can be obtained from the 2,5% and 97,5% percentiles of the probability distribution. Each unringed bird captured shifts the distribution to the right, increasing the population size; each retrapped bird shifts the distribution to the left, leading to a decrease in the estimated population size. As the number of birds handled, i, increases, and provided the assumptions are met, the probability distribution becomes more concentrated and the successive estimates of population size more stable. If the initial estimate of N_{max} is set too small, the estimated population size converges on this limit. For reasonably large numbers of birds handled, the initial choice of N_{max} has very little influence on the final estimates; thus no harm is done if

N_{max} is overestimated (Zucchini & Channing 1986).

The calculations for a simplified example are shown in Table 6.1. This shows how the probability distribution ($p_i(n)$) becomes more concentrated after each capture (given in the columns); *e.g.* after the eighth capture, the probability that the population has size four is 0,292. The initial estimate of the maximum population size, N_{max}, was ten.

TABLE 6.1

ILLUSTRATIVE EXAMPLE OF THE BAYESIAN METHOD (SEE TEXT).
THE LAST ROWS PROVIDE SUMMARY STATISTICS OF
THE SUCCESSIVE PROBABILITY DISTRIBUTIONS

Iteration or capture number i	0	1	2	3	4	5	6	7	8
Unringed (U) or ringed (R)		U	U	R	U	U	R	R	R
$p_i(1)$	0,100	0,100	0,000	0,000	0,000	0,000	0,000	0,000	0,000
$p_i(2)$	0,100	0,100	0,071	0,181	0,000	0,000	0,000	0,000	0,000
$p_i(3)$	0,100	0,100	0,094	0,161	0,110	0,000	0,000	0,000	0,000
$p_i(4)$	0,100	0,100	0,106	0,136	0,139	0,075	0,129	0,202	0,292
$p_i(5)$	0,100	0,100	0,133	0,116	0,142	0,123	0,169	0,212	0,245
$p_i(6)$	0,100	0,100	0,118	0,101	0,137	0,149	0,169	0,178	0,171
$p_i(7)$	0,100	0,100	0,121	0,089	0,130	0,161	0,157	0,141	0,116
$p_i(8)$	0,100	0,100	0,124	0,079	0,122	0,165	0,141	0,111	0,080
$p_i(9)$	0,100	0,100	0,126	0,072	0,114	0,165	0,125	0,087	0,056
$p_i(10)$	0,100	0,100	0,127	0,065	0,107	0,162	0,111	0,070	0,040
Mean	5,500	5,500	6,364	5,127	6,392	7,358	6,830	6,286	5,776
Median	5	5	6	5	6	7	7	6	5
Mode	-	-	10	2	5	8	6	5	4

6.3 RESULTS

Over the 2,5 d of mistnetting, 255 captures of 202 different Malachite Sunbirds were made. Eight birds were retrapped more than once. From the handling sequence, the number of unringed birds caught between each retrapped bird was derived (Table 6.2).

TABLE 6.2

THE NUMBER OF UNRINGED MALACHITE SUNBIRDS TRAPPED BETWEEN EACH RETRAP OF A RINGED BIRD AT OLIFANTSBOS CAPE OF GOOD HOPE NATURE RESERVE, 5-7 DECEMBER 1987

41*, 5, 20, 12, 4, 1, 5, 6, 5, 0, 12, 1, 1, 9, 2, 1, 5, 11, 6,
5, 6, 3, 0, 2, 3, 0, 4, 4, 2, 2, 1, 0, 0, 0, 4, 4, 1, 1, 6, 1,
0, 1, 0, 0, 4, 0, 0, 0, 0, 0, 0, 1**

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* The number of birds caught before the first retrap.

**The last bird caught was a retrap.

From these data, the Bayesian estimates of the mean, median and mode from the final (255th) probability distribution were 540, 534 and 523 respectively. The 95% confidence interval of the population size was 429 to 684 birds. The same results were obtained when the initial estimates of $\underline{N}_{max}$ were 800 and 1500. The du Feu estimate of the population size was 525 and the 95% confidence interval was 405 to 645.

6.4 DISCUSSION

As du Feu _et_ _al_. (1983) pointed out, all the assumptions of statistical models are rarely completely satisfied. The trapping period was short relative to the flowering period of the _Leonotis_ stand. Immigration, emigration and mortality during the trapping period were probably sufficiently small that the assumption of a closed population is, at least, plausible.

Because 80% of all the birds caught were first-year birds (having fledged between one and five months earlier), most birds were equally inexperienced and equally catchable. One way to examine the assumption of trap-shyness or trap-proneness is to consider the retraps as new birds and apply the same method to the retraps of the retraps. If the estimate obtained from this subset of the data is larger than the estimate from the full data set it would indicate trap-shyness; a smaller estimate would indicate trap-proneness. Unfortunately, the number of birds retrapped more than once (eight), was too small to produce a reliable estimate of this population size, and it is not possible, therefore, to check this assumption. In this, as in other capture-recapture methods, the overall effect of trap-shyness is to inflate the estimates of the population size; trap-proneness has the opposite effect.

The period between capture and release was sufficiently short in relation to the whole trapping period for it not to be a source of serious bias. The fact that the birds were released 900 m from the netting site overcame the potential problem of birds flying directly back into the nets on release. Retraps of some birds were made within 30 minutes of their first capture, indicating that the distance moved was not excessive.

The Bayesian method has advantages over the du Feu estimate. It is computationally and conceptually simpler. More importantly, the confidence intervals are based on an exact probability distribution and not on a Normal approximation to this distribution, the standard distribution of which has also been estimated. For a large sample size, such as that obtained here, the final result does not depend on the initial guess at the maximum population size, provided that this exceeds the actual population size (Zucchini & Channing 1986). The exact distribution of population size is skewed to the right (Gazey & Staley 1986), indicating that there is more uncertainty about the upper limit of the population size than the lower limit (Raftery et al. 1987); consequently the confidence interval should be asymmetric about the mean. Gazey & Staley (1986) also show that the population estimates derived from the traditional Schnabel model are biased and are consistently smaller than the Bayesian estimates. This property is demonstrated by this example.

A further advantage of the Bayesian methods of Gazey & Staley (1986), Zucchini & Channing (1986) and this paper over the Schnabel census and the du Feu estimate occurs when the total population size is small (less than about 100 individuals). The asymptotic approximations to the normal distribution used to find confidence intervals are then increasingly unreliable. One fault is that the lower limit of confidence intervals can be less than the known minimum number of individuals of animals in the closed population: Seber (1973) gives an example relating to Cricket Frogs Acris gryllus in which the total number of frogs trapped and marked was 93, but the 95% confidence interval, based on the asymptotic normality was (90, 100). The illustrative example (Table 6.1) demonstrates an extreme situation. The captures (four unringed and four ringed), were simulated from a population size five: after only eight captures the Bayesian estimate of the probability distribution suggests that four or five is the most likely population size (Table 6.1); the 95% confidence interval for the du Feu estimate is an absurd (2,8). For these very small population sizes, for which the Bayesian procedure provides meaningful results, the asymptotic properties upon which the confidence intervals for the du Feu (and Schnabel) estimates are based break down completely.

The estimated 540 Malachite Sunbirds at Olifantsbos represents the size of the "pool" of birds for which this food resource was within their home range, and the number of birds that would be caught if trapping was continued indefinitely (and the assumptions remained correct). Further discussion of the concept of a pool of birds utilizing a resource is given in Summers et al. (1985).

The average December density of Malachite Sunbirds in a study plot in dune thicket vegetation at Olifantsbos was 0,38 ha^{-1} (M.W. Fraser, unpubl. data). However, by far the dominant vegetation type at the Cape of Good Hope Nature Reserve (7 750 ha) is Mountain Fynbos. Within this, the densities of Malachite Sunbirds vary according to fine-scale differences in plant species assemblage, ranging from 0 to 0,042 ha^{-1} in December (M.W. Fraser, unpubl. data). The Leonotis patch at Olifantsbos clearly attracts more than just the local population of Malachite Sunbirds.

Recoveries of Olifantsbos-ringed Malachite Sunbirds indicate that they undertake extensive movements, presumably in response to seasonal and spatial fluctuation in their food supply (Fraser et al. 1989). The results here show that large numbers of birds may utilize particular food plants at certain times of year. Further ringing is required to provide an insight into the seasonal movements of such birds and how far they are prepared to travel to exploit food resources. Increasing fragmentation of natural habitat in the Fynbos Biome, particularly in lowland areas (Jarman 1986), will result in increased isolation of food sources, placing more importance on the natural vegetation remaining within protected areas.

SYNTHESIS AND GENERAL CONCLUSIONS

7. SYNTHESIS AND GENERAL CONCLUSIONS

Although birds are certainly the best known group of animals in the Fynbos Biome, the major objectives of previous research on fynbos birds have been to relate the composition of avian assemblages to that of the biotope in which they are found (e.g. Cody 1975, 1983b), and major vegetation type (e.g. Siegfried 1983; Siegfried & Crowe 1983), and to determine the ecological role of birds as pollinators of indigenous taxa (e.g. Collins 1983a; Collins & Rebelo 1987; Rebelo 1987 and references therein). Finer-scale analysis of the patterning of avian assemblages within the major biotopes was undocumented, as were the effects on birds of two anthropogenic disturbance factors (woody alien plant infestation and management by burning).

This project was thus designed to supply a database and technical and conceptual framework within which information might be gathered. From this information, predictions could be made of the effects on birds of contemporary fynbos management practices, notably alien-plant clearance and burning regime. The opportunity was also taken to investigate three associated processes in fynbos: utilization of alien fruits by birds, post-fire seed predation by birds and other animals, and the importance of an isolated food source to nectarivorous birds. Such processes are an integral part of fynbos functioning and have important implications for its conservation.

7.1 Counting birds in Mountain Fynbos

Census techniques are as numerous as they are diverse (e.g. Ralph & Scott 1981 and references therein; Taylor et al. 1985 and references therein). Which technique to adopt in Mountain

Fynbos depended very much on the structure (height, density etc.), of the vegetation. In open, low-growing vegetation, such as recently burnt and early successional fynbos, the walk-through-plot method (Chapter 1), was probably satisfactory since it allowed full coverage of the study plot and did not rely exclusively on the activities of the birds to make their presence known. Following a different route, and one which incorporated the whole plot on each count, precluded the risk of consistently missing site-tenacious species, and flushed skulkers such as Grassbirds Sphenoeacus afer and cisticolas Cisticola spp. A line transect method (e.g. Emlen 1971), a popular choice in open habitats, would have been less appropriate because it may have failed to detect skulking species (even those close to the transect may have sat tight rather than be flushed). In addition, the technique often demands some estimation of the distance between observer and bird, introducing a source of error and thus potentially reducing the accuracy of density values. Other difficulties inherent in this technique are discussed by Burnham & Anderson (1984). On balance, the walk-through plot census method was considered most appropriate in Mountain Fynbos at the Cape of Good Hope Nature Reserve (CGHNR). Here the vegetation was generally low-growing and open and the topography level.

This census method was less suitable for the dense, tall vegetation characteristic of pre-fire Swartboskloof (Chapter 2). Initial trials exposed the problems of walking amongst thick bushes. It was suspected that the reduced visibility resulted in disturbed birds moving off without the observer detecting them. Also, the movement of the observer often elicited alarm calls from Spotted Prinias Prinia maculosa and similarly vociferous species. Other birds were attracted to these calls, and in the thick vegetation I was unable to determine if they had come from outside the study plot or were already in it when the count commenced. In dense vegetation, "spishing" (Campbell & Lack 1985) was employed in preliminary trials to locate birds. Despite rendering birds more conspicuous, this had the disadvantage of attracting birds from outside the plot to give nonrepresentative high densities. Also, fynbos birds differed in their response to spishing. Sunbirds (Nectarinidae) reacted very positively and moved conspicuously towards the source of the noise. Canaries (Fringillidae) tended to ignore it and others, notably that arch skulker Victorin's Warbler Bradypterus victorini, often came very close to the spisher, but were not necessarily made any more conspicuous by doing so (M.W. Fraser, unpubl. data).

The method which, on balance, avoided these problems and was best suited to conditions at Swartboskloof in general, was the fixed-radius point count (Chapter 2; Hutto et al. 1986). This method did not involve observer movement through the vegetation, and the small area under observation in each plot gave a higher likelihood of a bird being detected from a central observation point. This technique was continued in the post-burn period for the sake of consistency and because much of the vegetation was unmodified by the fire (and visibility thus remained low). One complication, which reduces the value of spot counts, is that nectarivores are most active under sunny conditions (M.W. Fraser unpubl. data; Goldstein et al. 1987). On dull days, these birds may thus be under-represented in sedentary counts. They are, in contrast, less likely to be overlooked by the plot count method (in which they are flushed), in more open vegetation. It was unrealistic, however, to confine bird counts to sunny days in the limited study period (14 months) at Swartboskloof.

At Swartboskloof, the time spent in each plot (20 minutes), was considered sufficient to detect all birds present, although it was not always possible to determine if a bird had entered the plot after commencement of a count. Fuller & Langslow (1984) considered that counts in British habitats exceeding 10 minutes were "wasteful of field effort". In Mountain Fynbos it was felt that the longer time was necessary since many of the species were silent and/or inconspicuous.

In northern temperate regions, historically the area in which most avian community studies have been undertaken, censuses are traditionally confined to the breeding season. At this time, territorial male birds are relatively easily to locate when they advertise their presence from song posts or in display flights. In the Fynbos Biome, although a distinct spring peak in breeding is apparent (Winterbottom 1963), birds may breed at any time of year. Indeed, the nectarivores, which make such a large contribution to avian density in old protea-dominated fynbos, breed essentially throughout the year (Broekhuysen 1963; Skead 1967). Similarly, birds responding to the creation of new habitat may breed within a week of a fire regardless of season. For example, at CGHNR, Blacksmith Plovers _Vanellus armatus_ nested on a firebreak within a week of a late autumn burn (M.W. Fraser, unpubl. data).

In summary, the variability of the timing of nesting and utilization of transient resources (notably nectar; see Chapter

1), render single-season counts and, indeed, any study period of less than one year, totally inappropriate in Mountain Fynbos.

7.2 Measuring environmental variables in Mountain Fynbos

There is a tradition of relating bird species richness or diversity, composition and density to certain environmental parameters (e.g. Karr & Roth 1971; Rotenberry 1985). The most appropriate of these in terrestrial habitats are representations of vegetation structure and plant-species composition. However, since few ornithologists are also botanists, a simple index of vegetation structure is widely employed. The "foliage profile" and various indices derived from it have been used extensively in quantifying vegetation complexity and providing habitat gradients. This must assume that the birds are discriminating between habitats or vegetation types purely on the basis of the "density" or volume of vegetation at different levels within the canopy. This may be a legitimate assumption in woodland or forest and where bird species are clearly not dependent for food on a particular plant, but, as demonstrated in this study, it cannot be applied in Mountain Fynbos. Here, the Cape Sugarbird <u>Promerops cafer</u> and sunbirds respond specifically to the floristics (<u>i.e</u>. food plants), and not necessarily the structure of the vegetation (although the presence of mature food plants is generally positively correlated with high structural complexity). In addition to these obligate nectarivores, a wide range of other bird species also feed on nectar from proteaceous inflorescences (Chapter 1; Oatley & Skead 1971; Richardson & Fraser in press). A very large proportion of birds may thus be responding to floristics and not structure in Mountain Fynbos, and this must be borne in mind when considering the role of vegetation in shaping fynbos bird communities. Furthermore, until more is known about the diets of fynbos birds, it is unwise to place too much emphasis on interpreting avian community structure on the basis of feeding guilds. For example, often classified as a frugivore, the Redwinged Starling actually has a catholic diet (Chapter 5). At least two swallows (Hirundinidae) eat _Acacia cyclops_ fruits in fynbos (Broekhuysen 1960; Hofmeyer 1989), and the "insectivorous" Spotted Prinia can shatter illusions by catching reptiles as long as itself (Fraser 1988)!

In common with bird censusing techniques, techniques of habitat description have been developed primarily in the northern hemisphere. Examples of these, and discussions of the roles of physiognomy and floristics in determining avian community composition are given by Erdelen (1984), Karr & Roth (1971), Rotenberry 1985 and Vale _et al_. (1982), amongst others. Few of these techniques have been tested in southern Africa (Cody 1983a; Crowe _et al_. 1981; Koen & Crowe 1987), and fewer still in Mountain Fynbos (Cody 1975, 1983b; Siegfried 1983; Siegfried & Crowe 1984). Bond _et al_. (1980) found that the only habitat variable with which Mountain Fynbos rodent species diversity was correlated was foliage density at low heights. Floristic differences were of little value in differentiating rodent niches.

Although the present study has elucidated to some extent the mechanisms underlying habitat selection in birds in Mountain Fynbos, it has not exposed any relationship between birds and vegetation structure. It has, however, demonstrated that some bird species display further refinement of their distributions within Mountain Fynbos according to a number of factors, including plant taxonomic composition and vegetation age. Other birds, however, show less discrimination and occur virtually or completely "across the board". The physical and biotic factors of the habitat and adaptations of the birds which permit such wide tolerance (particularly where, in contrast, plant species have characteristically small natural ranges), are unknown.

7.3 Birds, burns and aliens in Mountain Fynbos

The failure of fynbos birds to respond dramatically to fire was considered to be a reflection of the unpredictability and variability of the burning regime. The results contrast strongly with those from other southern African biomes. However, a more intense fire at Swartboskloof and greater destruction of the vegetation could likely have resulted in a more marked response by birds, notably increased post-fire exploitation by open-country forms. The study did demonstrate that nectarivores were most severely impacted by fire, a consequence that was also applicable to the effects of alien infestation.

In their broad-scale studies of fynbos birds, Siegfried & Crowe (1983) found that different suites of bird species tended to occur in lowland and montane vegetation formations. The present study indicates that such partitioning can also occur within a particular vegetation formation. The species compositions of the various suites are influenced by the age of the vegetation, its structure and floristics. Alien infestation altered the species composition and structure of the vegetation, and this further influenced the composition of the bird assemblages. However, in common with Siegfried & Crowe's (1983) findings, and contrary to MacArthur's (1965) predictions, neither vegetation structure nor floristic composition alone are satisfactory predictors of bird species richness. Certain birds were, however, found to be intimately associated with certain plant species, successional stage or vegetation formation in Mountain Fynbos.

The Fynbos Biome is more severely infested with alien plants than any other southern African biome (Macdonald 1984). Because the eradication of these invasives is generally a difficult and costly task, their effects are likely to increase and persist in the long term (Macdonald et al. 1985). It is thus important that assessments be made of the responses of indigenous taxa to predict the results of increased invasion or a reduction in clearance efforts.

Results of bird counts in alien-infested plots at CGHNR (Chapter 4) were not as clear-cut as anticipated. Birds either persisted in surviving pockets of indigenous vegetation within the alien thickets, or were able to move successfully between vegetation types. The responses depended very much on which plant species assemblage was infested (cf. Chapter 1).

The bird-vegetation relationship at CGHNR was summarized in a dendrogram formed by the Bray & Curtis (1957) similarity coefficient (Fig. 7.1). This compared the bird species densities of all the study plots (including one in Strandveld (coastal thicket (Cowling 1984)), not otherwise considered here. Noteworthy is the grouping of the >15 year-old Upland plot with the Acacia cyclops-infested plots rather than the remaining uninfested fynbos plots. This may be interpreted as a reflection of the birds response to similar vegetation structure. However, the determining factor, as discussed in Chapters 1 and 4, is the presence of mature proteaceous shrubs which provide food for nectarivores. Members of this feeding guild make a major contribution to avian density in mature fynbos and as long as one flowering Leucospermum conocarpodendron, for example, is present, nectarivores will be recorded at least for some of the year. Theoretically, an uninfested plot from which these plants are absent will contain fewer birds than a densely alien-infested plot in which one L. conocarpodendron persists. Taken in isolation, the absurd conclusion could be reached that alien infestation increases bird density. Such observations emphasize the need to classify the vegetation floristically rather than relying on vegetation structure alone from which to predict avifaunal responses.

The dendrogram (Fig. 7.1) conveniently grouped the two older Marsh plots together and the two older Plateau together (Fig 7.1). This arrangement supports the observations that the vegetation of these two assemblages reaches a climax by 5,5 years, resulting in a close similarity between their respective avifaunas thereafter (Chapter 1). In contrast, the 1,5- and 5,5-year-old Upland were grouped together. The dominant species in the oldest Upland were non-resident nectarivores which clearly selected habitat on the basis of floristics. Nevertheless, the remaining, largely resident, species in this plant species assemblage appeared to choose this vegetation type on the basis of structure, since a number of these characterized the structurally similar and complex alien and coastal thicket vegetation (Chapter 4; M.W. Fraser unpubl. data).

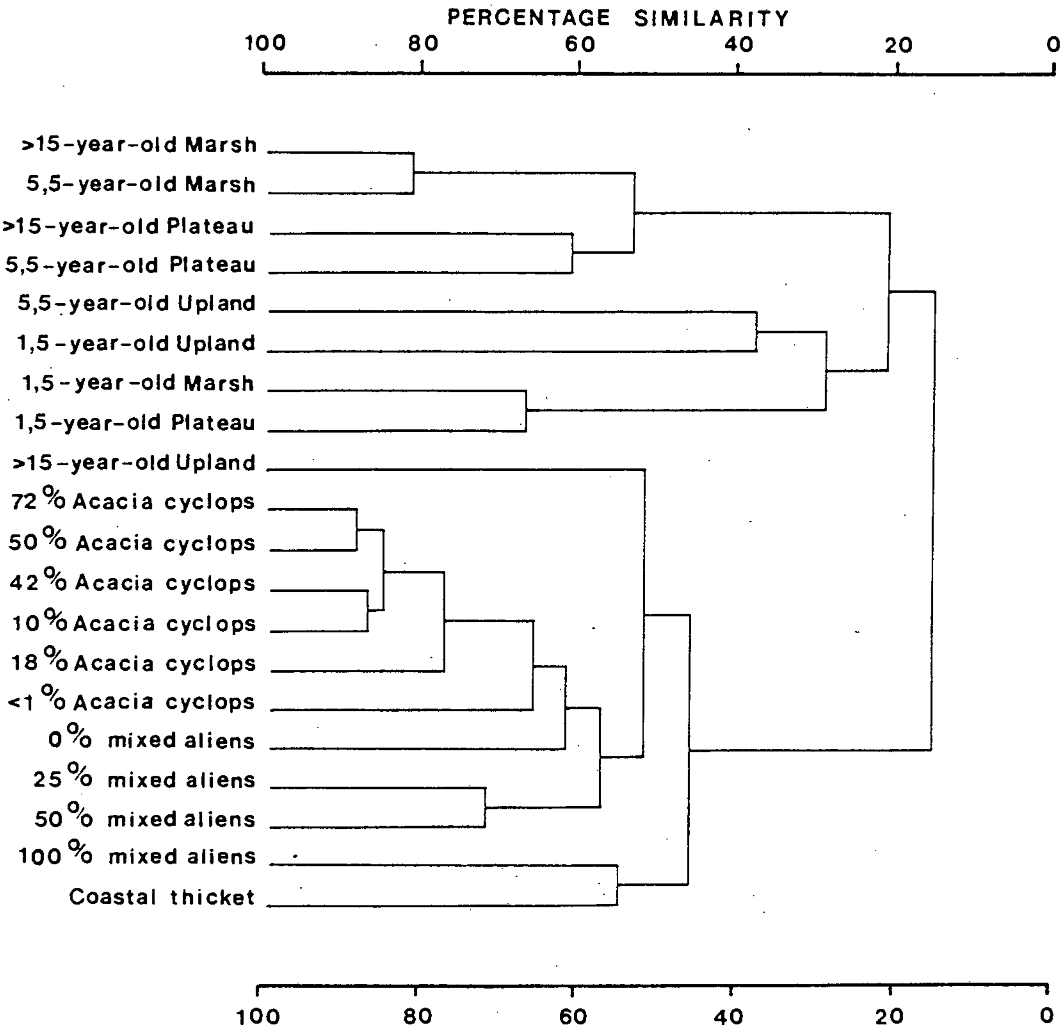

FIGURE 7.1

DENDROGRAM DERIVED FROM THE BRAY-CURTIS (1957) SIMILARITY COEFFICIENT ILLUSRATING THE RELATIONSHIPS BETWEEN BIRD-SPECIES DENSITIES IN DIFFERENT VEGETATION TYPES AT THE CAPE OF GOOD HOPE NATURE RESERVE

Alien fruits are eaten by a number of bird species (Middlemiss 1963; Winterbottom 1970). In Mountain Fynbos, where frugivorous birds were scarce (Chapters 1 and 2), *Acacia cyclops* may broaden their feeding niche. The apparent failure of one fruit-eating bird, the Redwinged Starling *Onychognathus morio*, to exploit an additional food resource (there was little increase in their numbers with increasing *A. cyclops* infestation (Chapter 4)), was not supported by the analysis of its faecal and regurgitated pellets (Chapter 5). Perhaps some aspect of the data collection/census technique or the small size of the study plots (relative to the area infested with *A. cyclops*), failed to detect visits by frugivores. Certainly the area infested at CGHNR was large enough to absorb the few frugivorous birds that were recorded, without them having to visit the small areas (5 ha) included in study plots. Only an integrated approach allowed for a more realistic assessment of the utilization of the alien fruits. The results indicated that bird dispersal of alien seeds exacerbates the problem of alien infestation, particularly where Redwinged Starlings attracted to flowering Proteaceae may concurrently feed on alien fruits. These birds thus have the potential to disperse the seeds into previously uninfested fynbos. This increases the difficulties faced by managers in clearing the weeds efficiently and maintaining alien-free fynbos.

Attempts at estimating the number of nectarivores visiting a nectar source have generally been restricted to individual spot counts or offering estimates which have been impossible to test (Frost & Frost 1980; Fraser *et al*. 1989; McMahon & Fraser 1988; Niven 1968; Skead 1967). Chapter 6 combines standard field (mistnetting) and statistical (Bayesian estimates) techniques to quantify bird visitation of an isolated food resource at CGHNR. The large number (540) of birds estimated to have visited the flowers over 2,5 days provided an indication of the importance of such resources. The number of birds exceeded the estimated local population size, implying that the flowers attracted birds from outside the reserve. Subsequent ringing recoveries have shown that Malachite Sunbirds move up to at least 170 km (Fraser et al. 1989), presumably in response to temporal and spatial fluctuations in food availability.

Other nectarivorous birds common in Mountain Fynbos, the Cape Sugarbird and Orangebreasted Sunbird Nectarinia violacea, also occur in large numbers at favoured food plants. The application of the techniques described in Chapter 6 allows the quantitative assessment of the importance of such food plants and provides the results necessary to predict the impact of the removal of such resources on birds. Once the distance between patches of natural vegetation becomes too great for the bird to cross, the plant loses its pollinator and the bird its food supply.

The seed-dish experiment conducted at Swartboskloof indicated that granivory was low in recently burnt Mountain Fynbos (Chapter 3). Further studies are required to assess if this was attributable to characteristics of the seeds used in the experiment or local factors such as low post-fire densities of potential predators and consequent predator satiation. Nevertheless, the finding that seed predation pressures are low has important implications for the assessment of survival rates of soil-stored and serotinous seed and the subsequent regeneration in burnt areas. If seed removal by granivores is low, the effects of unseasonal fires, for example, may be less damaging (i.e. less seed is eaten between release and conditions favourable for germination; see Bond et al. 1984)

Finally, I believe that the results and conclusions presented here are not necessarily applicable to Mountain Fynbos in general. The heterogeneity of the vegetation and local variation in edaphic and climatic factors limit the value of comparisons between any future studies at other localities and those from the two study sites here. Furthermore, too few data exist regarding the basic natural histories of fynbos (and other southern African) birds to make broad generalizations about their basic needs, habitat requirements and lifestyles and, consequently, their responses to major disturbances. The breeding biologies of many of even the commonest species remain largely or completely unknown, as the sections headed "Breeding" in Maclean (1985) testify. Longevity, migrations and social organization presently are similarly obscure. Few discrete areas of Mountain Fynbos (including nature reserves and mountain catchments), can boast even the most rudimentary bird checklists. Avifaunal responses to the disturbances of fire or alien infestation, are, therefore, virtually impossible to assess even at the most basic level in most areas of Mountain Fynbos.

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8. REFERENCES

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