

**ANIMAL-HABITAT RELATIONSHIPS IN THE KNYSNA FOREST:  
DISCRIMINATION BETWEEN FOREST TYPES BY BIRDS AND INVERTEBRATES**

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**DECLARATION**

I hereby certify that this is the result of my own original investigation, except where acknowledged herein, and has not been submitted for a degree at any other university.

Signed by candidate

J.H. Koen

**ABSTRACT**

Some silvicultural practices in the Knysna Forest are aimed at the sustained-yield production of valuable timber tree species, albeit on limited areas only. This study investigates effects of forest plant species composition and physiognomy on bird and invertebrate communities in three discrete, relatively undisturbed forest types along a dry-wet soil moisture gradient. Using discriminant functions analysis, a 100% floristic and a 78% vegetation structural discrimination was obtained between the three forest types. However, the bird communities of these floristically and structurally different forest types were very similar in species composition and had much lower densities than normally encountered in other superficially similar forests. It was only possible to discriminate between the wet and the moist/dry forest types by using the two best bird discriminators, the blackheaded oriole (Oriolus larvatus) and the sombre bulbul (Andropadus importunus). A separation of the moist and dry forest types was not possible. Although an 81% discrimination between forest types was attained through analysis of ground surface invertebrates, measures of litter and aerial invertebrate abundance were of limited use as discriminators. Historical and biogeographic factors and the low nutritional levels in the soil and vegetation may be the cause of low bird and invertebrate density and diversity. It is concluded therefore, that floristics and vegetation structure have, at best, a minor influence on bird community structure, and possibly also on the invertebrate community in the Knysna Forest and that management practices need

not cater for variation in forest vegetation composition and physiognomy.

## INTRODUCTION

In the southern Cape Province of South Africa there are still large tracts of state-owned indigenous evergreen forest or private forests under state control. The primary goal of indigenous forest management in this area is the conservation of biotic diversity. One of the secondary goals is the production of high-quality furniture timber on a sustained-yield basis. Some management practices employed in these forests include removal or in situ killing of trees (Seydack et al. 1982). The effects of these treatments on the forest biota are not known, although some may play important roles in the long-term survival of the forest. For example, the disruption of plant-animal links, such as seed dispersal, may have major effects on the reproductive capability of the system. Therefore, to ensure that the objective of maintaining biotic diversity is met, it is important to investigate the quantitative and qualitative effects of habitat alteration on their faunas. It was decided not to study Knysna Forest mammals because most forest mammals are solitary and nocturnal and censusing techniques used in studying them are costly and/or time-consuming (Odendaal et al. 1980; Schmidt 1983; Seydack 1984). However, due to the relative ease of sampling birds and invertebrates, as well as the well-documented relationships between terrestrial bird and invertebrate community structure and density and vegetation (MacArthur et al. 1966; Willson 1974; Roth 1976; Terborgh 1977; Beedy 1981; Folse 1982; James and Wamer 1982; Kikkawa 1982; Rice et al. 1983; Sutton



et al 1983; Erdelen 1984), it was decided to investigate their possible use as indicators of variation in the floristics and structure of the different forest types.

Relatively little is known about the community structure of South African forest birds and invertebrates. Apart from some descriptive work on birds (Skead 1964; Clancey 1975), limited detailed quantitative research has been done (e.g. Oatley 1966, 1970, 1978 and Earlé 1983). This preliminary, baseline study is aimed at determining relationships between Knysna Forest bird and invertebrate communities and vegetation structure and composition. If any relationships are discovered, effects of management practices will be investigated in the light of these results. The bird and invertebrate communities of three forest types along a dry-wet moisture gradient were investigated with the following questions in mind:

- 1) Are the forest types floristically and structurally distinct?
- 2) Are the bird communities of the forest types distinct?
- 3) Are the invertebrate communities of the forest types distinct?
- 4) Is there seasonal variation in the populations of birds or invertebrates in the forest types?

## STUDY AREA

This study was conducted in the indigenous high forests north of Knysna in the southern Cape Province of South Africa (Fig. 1). In this area, indigenous forest forms a nearly continuous belt along the Outeniqua and Tsitsikamma Mountains from Mossel Bay to Humansdorp and is widest (18 km) east of Knysna. This forest is classified by Acocks (1975) as Knysna Forest (Veld Type no. 4), although White (1983) sees it as an extension of his Afromontane Forest vegetation type. Moreover, it also contains elements of the Indian Ocean Coastal Belt Forest e.g. Burchellia bubalina (wild pomegranate), Canthium spp and Cassine (C.J. Geldenhuys, pers. comm.). Zoogeographically (based on birds), the area falls within Winterbottom's (1974) Southern Sub-district of his East African Coastal District.

In general, the forest canopy is 20-25m high with local emergents e.g. Podocarpus falcatus (yellowwood) reaching about 40m. Other common canopy trees include P. latifolius (real yellowwood), Pterocelastrus tricuspidatus (candlewood), Ocotea bullata (stinkwood), Olea capensis macrocarpa (ironwood), Rapanea melanophloeos (cape beech), Apodytes dimidiata (white pear), Gonioma kamassi (kamassi) and Nuxia floribunda (forest elder).

Mean monthly rainfall in the study area tends to be evenly distributed throughout the year (Weather Bureau 1954, 1977), contrasting with the marked seasonal rainfall which predominates in southern Africa (Jackson 1961). At the Diepwalle State Forest (33°57'S, 23°10'E; 519 m a.s.l.) the mean rainfall for a 36 year

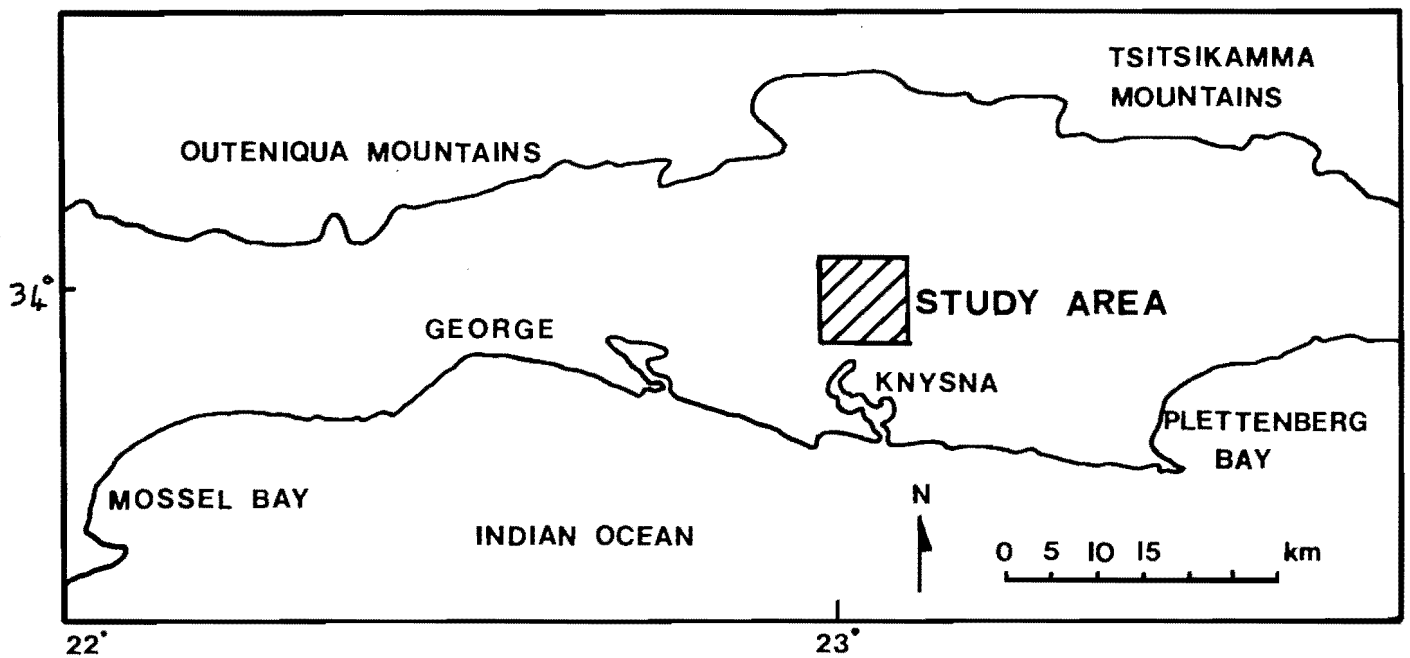
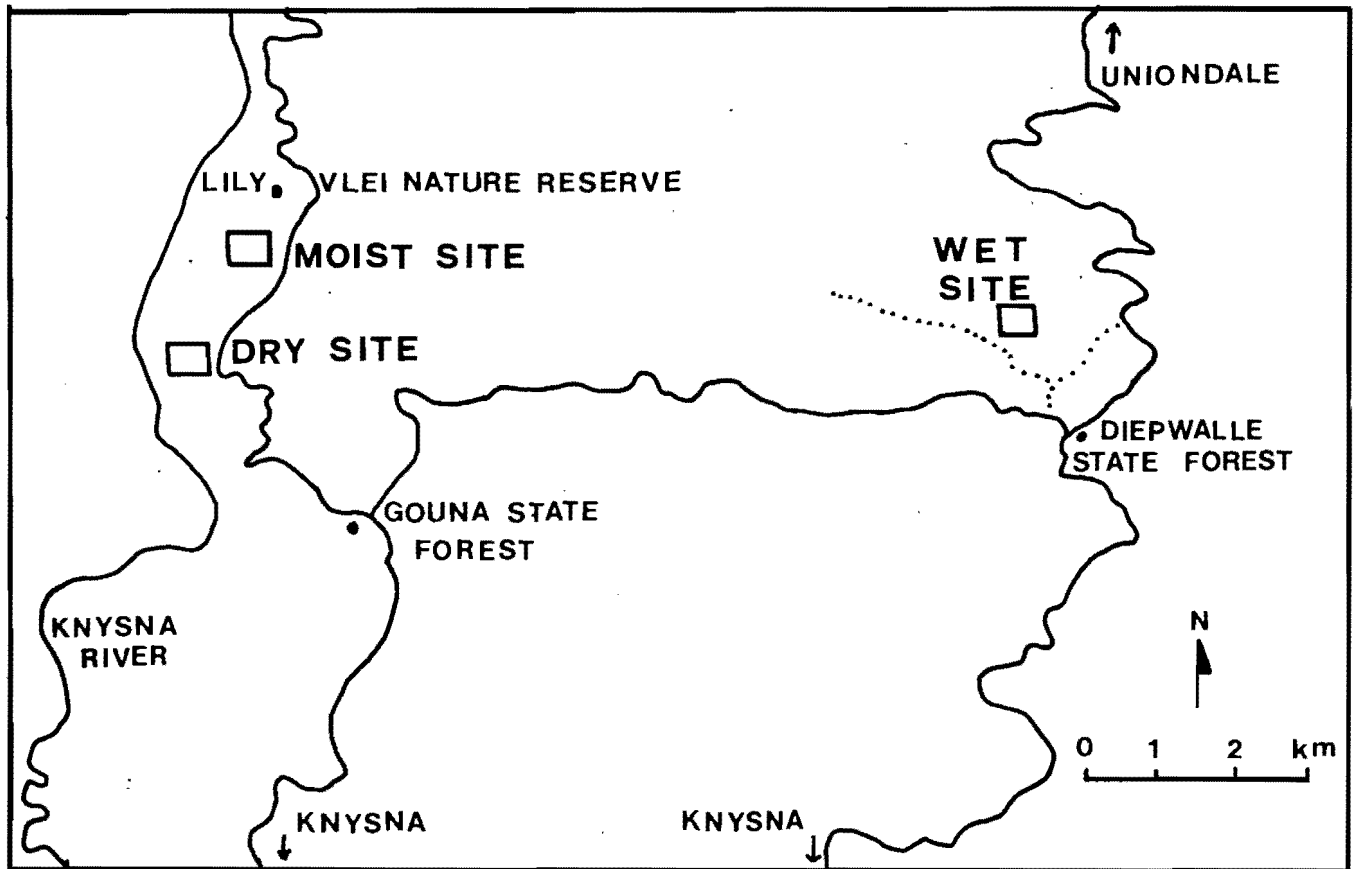


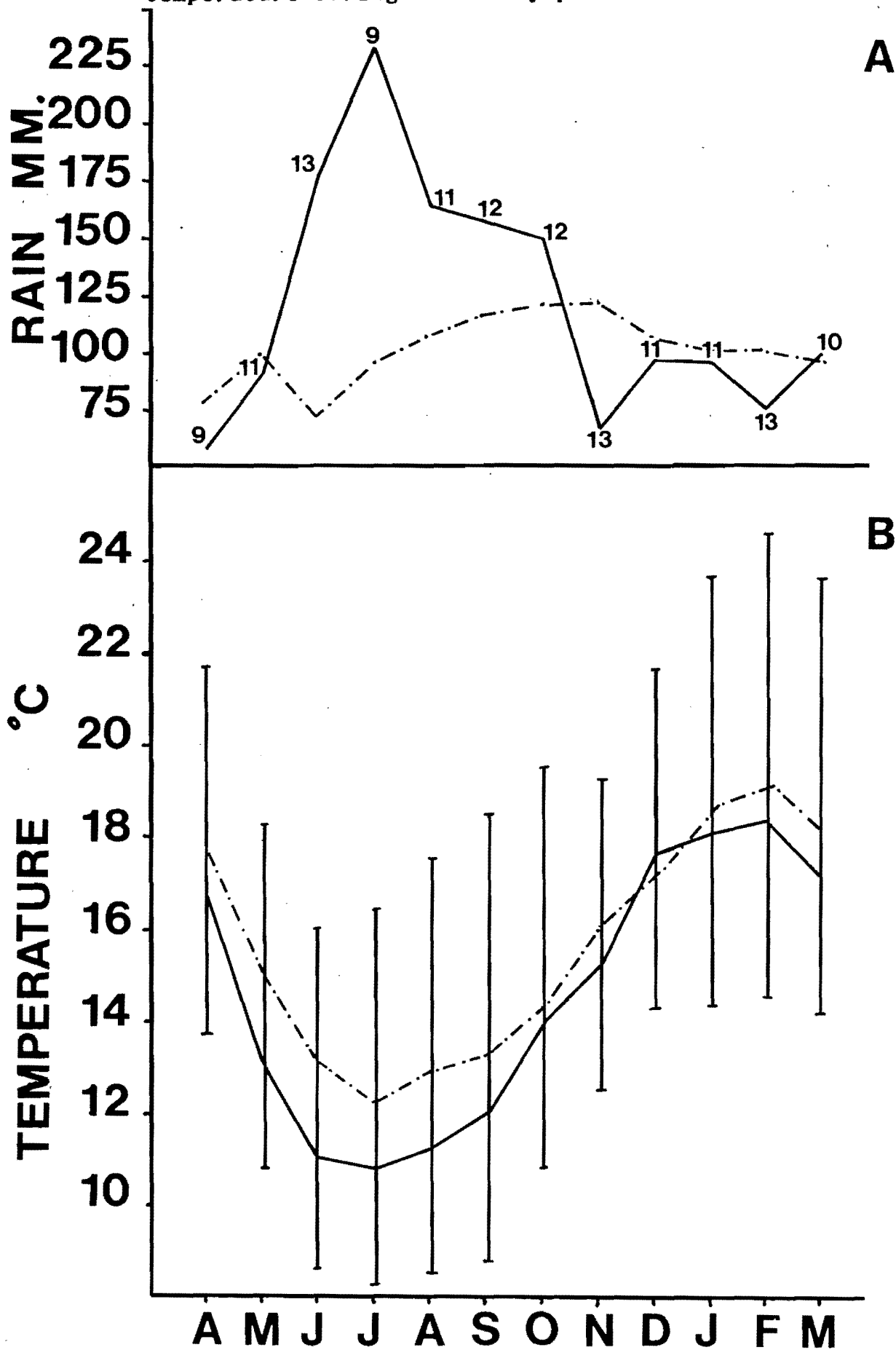
Fig. 1. The study area and the study sites

period was 1192,9 mm with 126 rainy days per annum, and the mean maximum temperature was 20,1°C and the mean minimum temperature 11,0°C (Fig. 2).

Three study sites were selected along a moisture gradient in dry, moist and wet relatively undisturbed forest (Fig. 1). These three forest types are classified according to soil moisture (at a depth of 250 to 400 mm), shrubs and, to a lesser extent, the tree flora (Geldenhuys 1983). Each study site was about 6 ha, and was selected to be as homogeneous as possible according to slope, aspect and vegetation (physiognomy and species composition). The size of the study sites was determined by the time available for censussing (Engstrom and James 1981). The dry and moist forest sites were in the Lily Vlei Nature Reserve of the Gouna State Forest (33°56'S 23°02'E), and the wet forest site was in the Van Huyssteen Bos area of the Diepwalle State Forest (33°56'S 23°09'E).

The overall physiognomy of the forest types is shown in Fig. 3. The forest at the wet study site consists of straight-stemmed and slender-crowned trees with an understorey of ferns, especially Cyathea capensis. At the moist forest site, the trees have more rounded crowns and the understorey is dense, 2-5 m high Trichocladus crinitus (onderbos). The dry forest site has fairly dense vegetation with an understorey of tree regeneration and thorny shrubs.

Fig. 2. Rainfall (A) and temperature (B) in the Knysna Forest. Solid lines indicate data for the study period: broken lines are 36 year means. Numbers on rainfall graph are number of rainy days, and range limits are provided for temperature during the study period



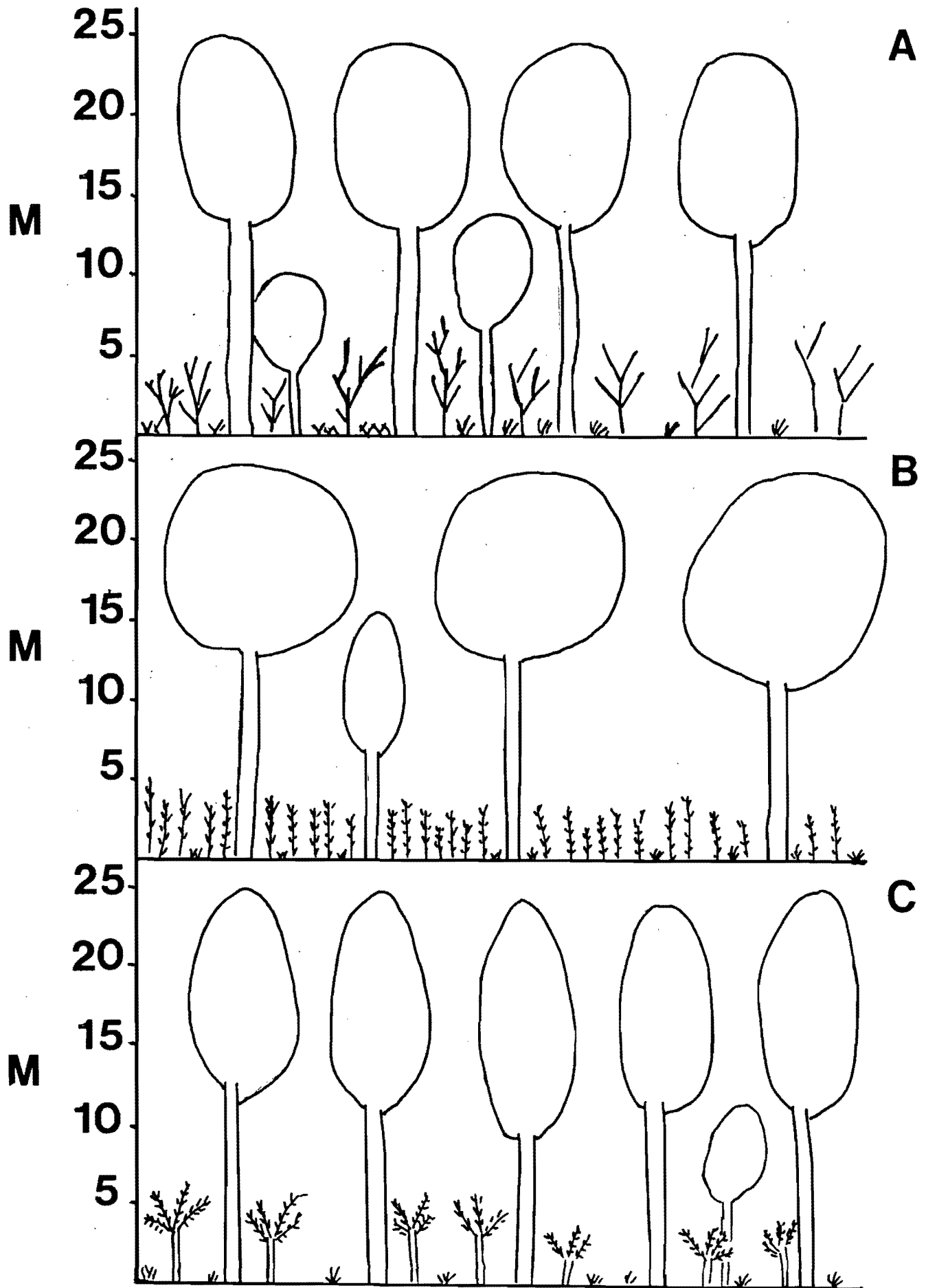


Fig. 3. Schematic representation of the physiognomy of the three study sites. A=dry; B=moist; C=wet

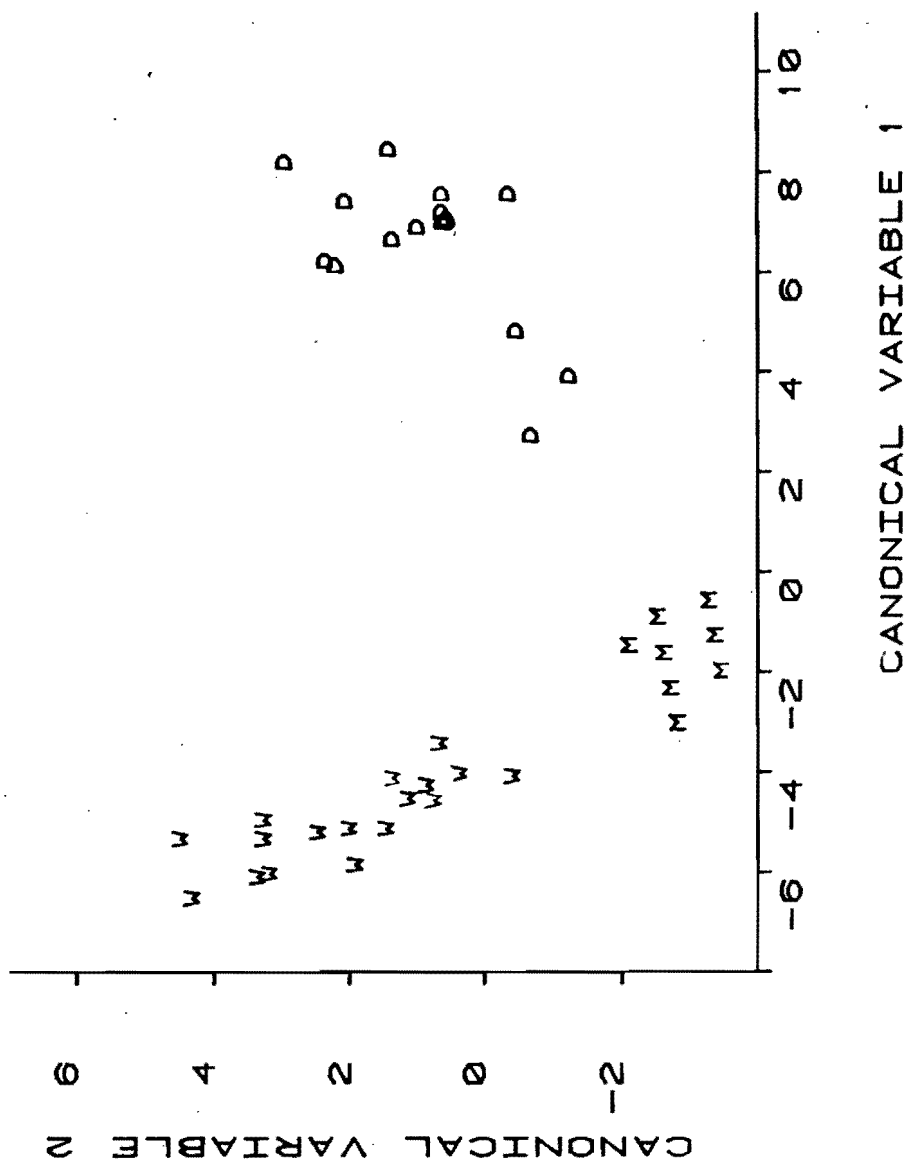


Fig. 4. Floristic discrimination between forest types (100%)

## METHODS

Data on bird communities, vegetation composition and structure, and invertebrate availability were collected between April 1983 and March 1984.

### Vegetation

Vegetation data were collected in five growth form classes: ground flora, seedlings and saplings, trees, tree ferns (*C. capensis*) and onderbos (*T. crinitus*). In each forest type, twenty 0,04 ha circular plots were sampled floristically and the mean species diversity and density calculated for trees, seedlings, saplings, onderbos and tree ferns. A further five 1,0 m diameter sub-plots per plot were sampled for the density and species composition of the ground flora. The total plant density was determined and fitted to density classes.

Vegetation structure is a well-documented correlate of bird community structure. To determine the importance of vegetation structure to the Knysna forest birds, density profiles (MacArthur and MacArthur 1961; Cody 1983) were constructed for eight plots in each study site from the means of four assessments per plot at 14 different strata. At lower strata, the distances to a density board half covered by vegetation were measured directly. At higher strata, this horizontal distance was estimated from ground level. Vegetation density is the reciprocal of the horizontal distance to the density board (Cody 1983). Thus, a high foliage density is represented by a high value.



## Invertebrates

Invertebrate density data were collected from the litter, at the soil surface and at various heights above ground. At each study site, between 4-8 litres of litter were collected monthly, and invertebrates therein extracted using one 200 watt globe as a source of light and heat in a Berlese funnel (Southwood 1978). Invertebrate abundance is represented as abundance per litre of litter. In each study site, for a 4-7 day period, surface invertebrates were collected in 25 15cm wide pitfall traps arranged on a 25 x 25 m grid. Commercial motor vehicle antifreeze was used as preservative in these traps. Abundance is represented as the daily abundance per trap. Aerial insects were sampled at 14 strata (0.5 m intervals to 2 m and then 2 m intervals to the canopy). At each stratum, a plastic plaque (10 x 20 cm) covered with Formex (a sticky substance used as an insect barrier around the stems of trees in orchards) was suspended from a pulley system. Four pulley systems were employed per study site, and sampling was conducted continuously for 4-7 days per month. Density is represented as the daily abundance per plaque.

Except for aerial taxa, all invertebrates were classified to order level and, in some cases, to family level as well as into three size classes: 0-3, 3-5 and greater than 5 mm long. Invertebrates were preserved in alcohol and were later placed on blotting paper to remove excess preservative before wet biomass was determined.

## Birds

Avifaunal data were originally collected using two standard techniques, mist-netting and spot-counts (Anderson and Shugart 1974). Mist-netting was discontinued after six months, since it was time consuming and unrewarding (netting success being as low as 39 net-hours per bird caught). In tropical forest undergrowth only 2.9 hours were required per bird (Karr 1980). See Appendix 1 for mensural data collected from the netted birds.

All bird population census techniques have methodological problems (Dawson 1981; Bull 1981). Most current census techniques were developed in north-temperate latitudes for application to breeding birds. Application of these methods to south-temperate habitats is not straight-forward, since many of the birds in these areas are more secretive and sing less than their northern counterparts. Singing intensity may also vary during different stages of the breeding cycle (Wilson and Bart 1985), and may have a major influence on density estimation. These factors, combined with characteristically denser vegetation than in north-temperate areas, pose special problems.

Due to the dense vegetation in the study area it was decided not to use transect sampling methods (Emlen 1971, 1984) (attention focused on negotiating the way) or the variable circular-plot method (Reynolds et al. 1980). Both of these methods rely on continuous estimation of distances to counted birds, which is effectively impossible in a closed forest, especially when a large percentage of birds are detected by song only. Spot-mapping

in which the territories are mapped (Williams 1936; Kendeigh 1944; Oelke 1966; Williamson 1972; Nillson 1979; Franzreb 1981) was inapplicable as well, since most birds defend territories only during the breeding season.

In this study, the spot-count method was modified to include limited observer movement within a survey area of 50 m radius in order to overcome the effects of dense vegetation. Similar single point surveys have been compared with the more labour-intensive breeding bird spot-mapping by Whitcomb et al. (1981). These authors concluded that three 20-minute point counts were necessary to discover about 90% of the species in an area. Granholm (1983) found that density estimates for 10-minute counts were up to 56% higher than for 5-minute counts. The critical assumption for spot counts is that bird movement during the count period does not affect the density estimate through cumulative estimates. For the local circumstances, 10-minute spot-counts appeared to be the most satisfactory. Between 16 and 26 spot counts were completed each month per study site and were conducted from sunrise to about 12h00. The mean number of birds per hectare was the unit of analysis. Time of censusing was found to be of minor importance (Pomeroy and Muringo 1984), and, during this study, it appeared not to affect the counts. During early morning counts it was difficult to identify the birds in the outer canopy due to the darkness of the foliage. Any effect that time of day might have had on census data was minimized by rotating the sequence of censuses each day. All birds except aerial feeders (swifts and

swallows) were counted. It must be stressed that this is a sampling technique. It yields a quantitative estimate of bird density and diversity in the vicinity of the study site, but not an exhaustive count. However, since data were collected by a single observer, any error in estimation is hopefully constant between and within study sites.

For each direct observation of a bird, its height above ground level and activity were noted, and the following activity classes were used: feeding, singing, flying and feeding chicks.

#### Data analysis

The vegetation, invertebrate and bird data were analysed using the stepwise discriminant functions (D.F.A.) program of the BMDP series (BMDP-7M; Dixon 1981). D.F.A. is a multivariate statistical method used to differentiate pre-determined groups (Crowe et al. 1981; Rice et al. 1983), such as the vegetation, invertebrate and bird community data for the three study sites in the present study. The discrimination is based on quantitative differences in variables used to describe individual members of the groups.

Ecologically, the method is useful in establishing the degree of statistical separation of the groups, and to identify which of the variables differ most consistently, and by the greatest amount, among the groups. BMDP-7M also calculates basic univariate statistics (mean, standard deviation and coefficient of variation) and performs a one-way analysis of variance as step number zero.

Shannon-Weaver diversity indices ( $H'$ ) (Peet 1974; Stocker et al

1985) and Jaccard and Czekanowski similarity coefficients (Southwood 1978) were calculated for the bird data. The Shannon-Weaver index is influenced by both the species richness (number of species) and the distribution of individuals among species, while the similarity coefficients are measures of the extent to which two samples have similar species composition. The formulae for the determination of the similarity coefficients are as follows:

Jaccard  $C = j/(a + b - j)$

Czekanowski  $C = 2j/(a + b)$

where  $j$  is the number of species common to both habitats and  $a$  and  $b$  are the total number of species in the respective habitats.

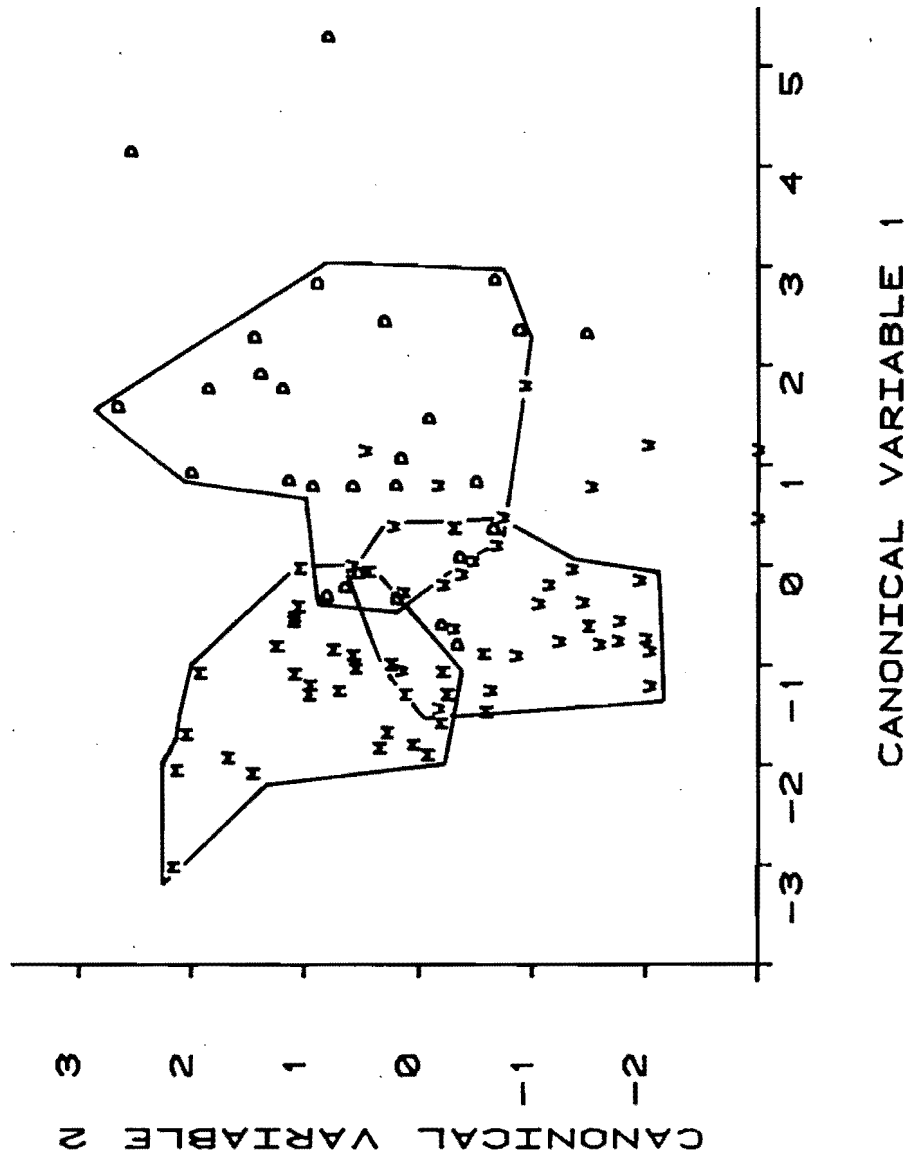


Fig. 5. Structural discrimination between forest types (78%)

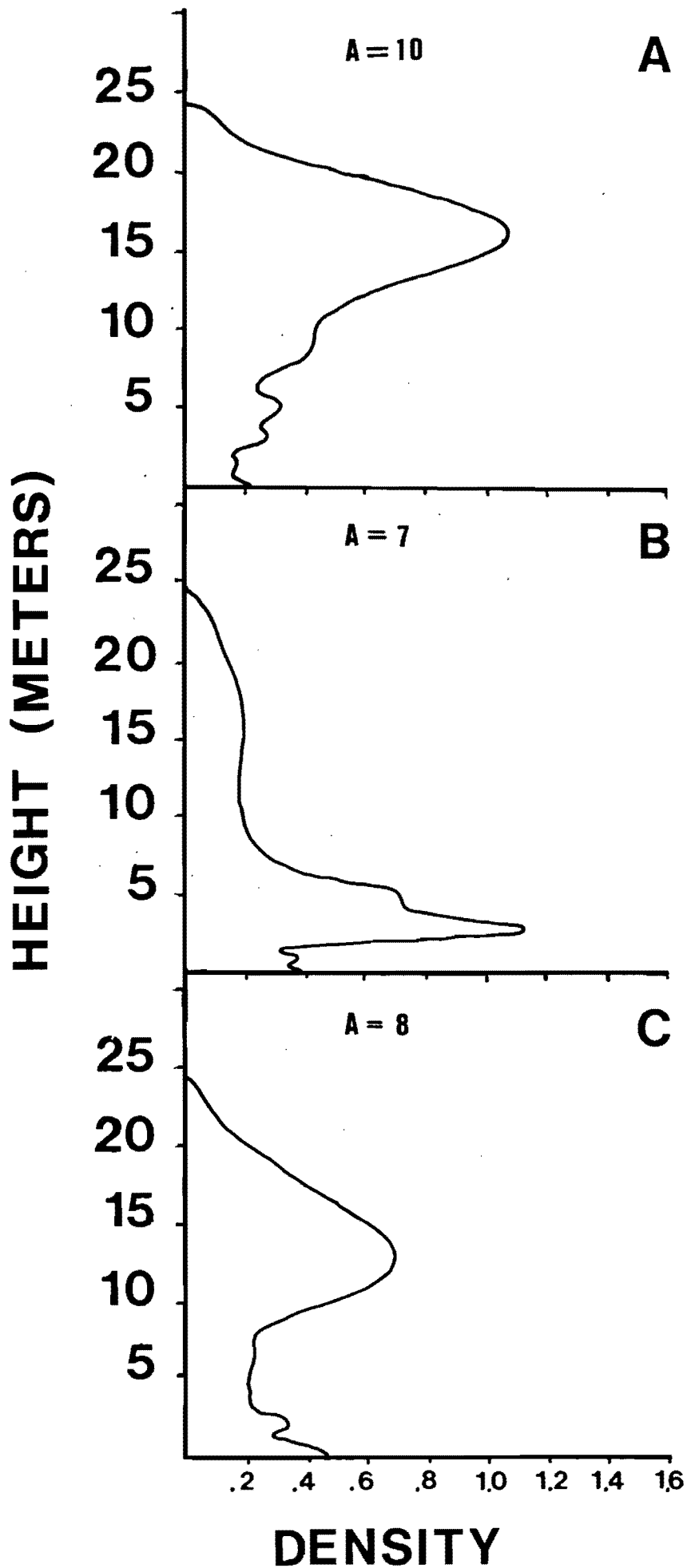


Fig. 6. Vegetation profiles with the area under the curves for the three forest types. A=dry; B=moist; C=wet

## RESULTS

### Vegetation

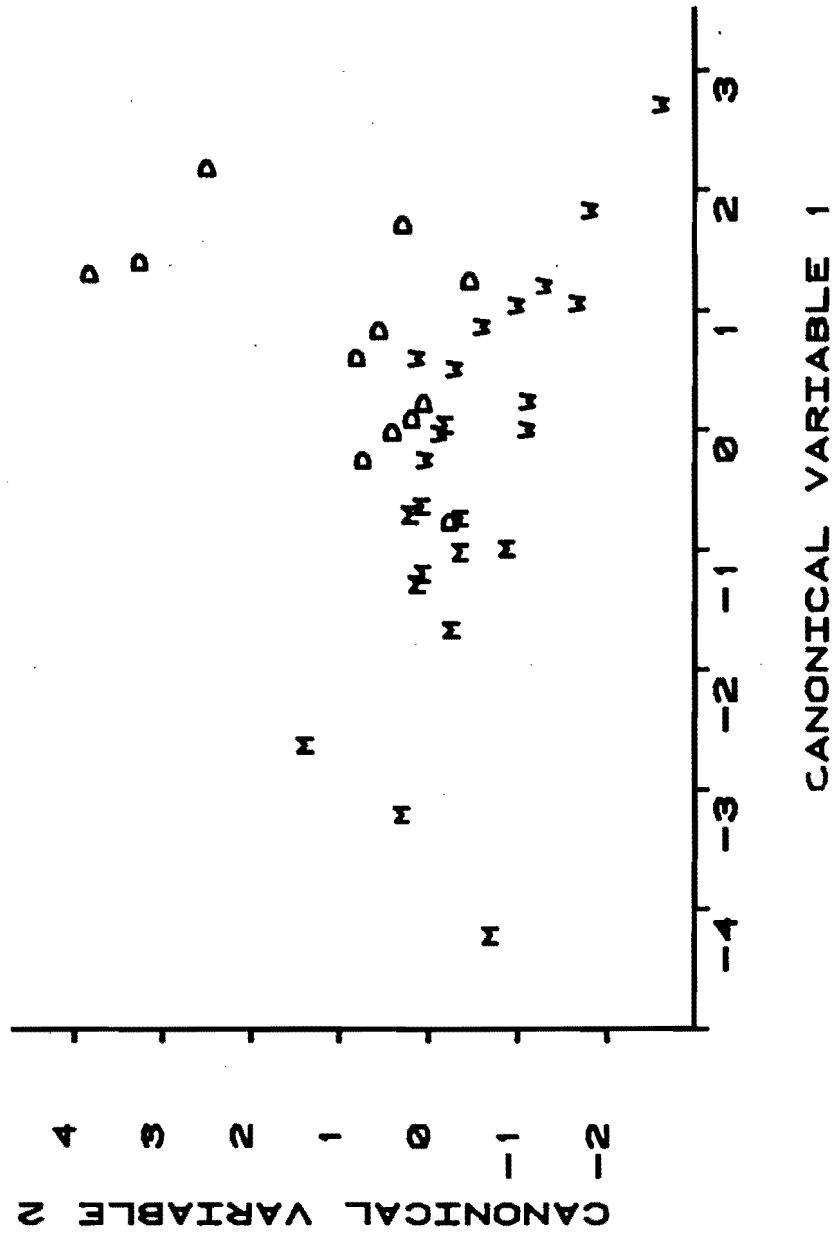
The mean plant density values used in the D.F.A. are given in Appendix 2. The D.F.A. of the vegetation species composition and density produced a 100% discrimination of the three study sites (Fig. 4). In the analysis of vegetation structure, the discrimination was somewhat lower (78%) but was still effective. The moist plots were the most successfully classified (91% correct discrimination), and both the dry and wet plots lower (72% discrimination) (Fig. 5). Figure 6 represents the vegetation profiles of the three study sites, and the areas under the curves are proportional to the total leaf area per unit ground area.

### Invertebrates

Both the composition and biomass of the invertebrates are very similar (Appendices 3-7) among the study sites. In the D.F.A.'s, the discrimination varies from 50% for litter invertebrates, to 62% for aerial insects and 81% for ground invertebrates. Thus, ground invertebrates appear to be the only class that could possibly be used successfully as a discriminator (Fig. 7).

Seasonally, invertebrate abundance follows the expected pattern of higher numbers and biomass in summer (November-March) and a decline from autumn to winter (April-August) (Fig. 8-12). Similar fluctuations have been found in rainforests elsewhere (Greenberg 1981; Woinarski and Cullen 1984). The occurrence of invertebrates





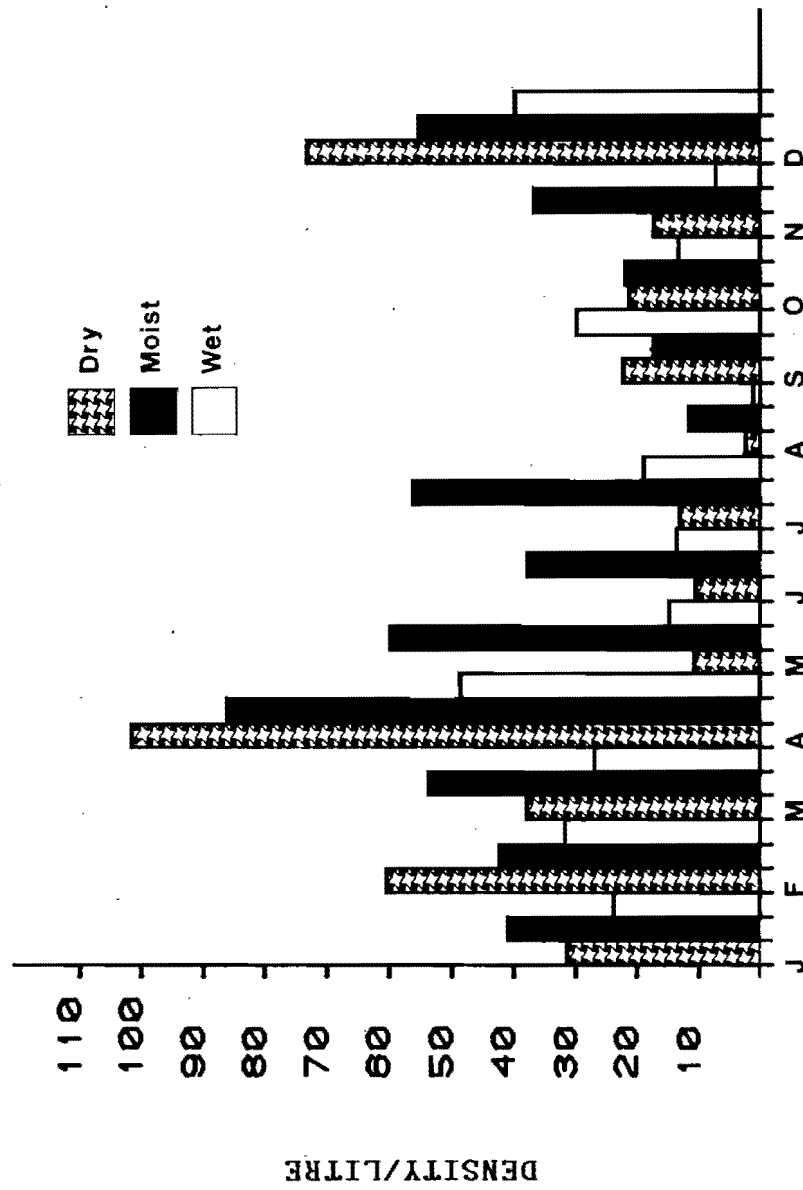


Fig. 8. Seasonal variation of litter invertebrate density

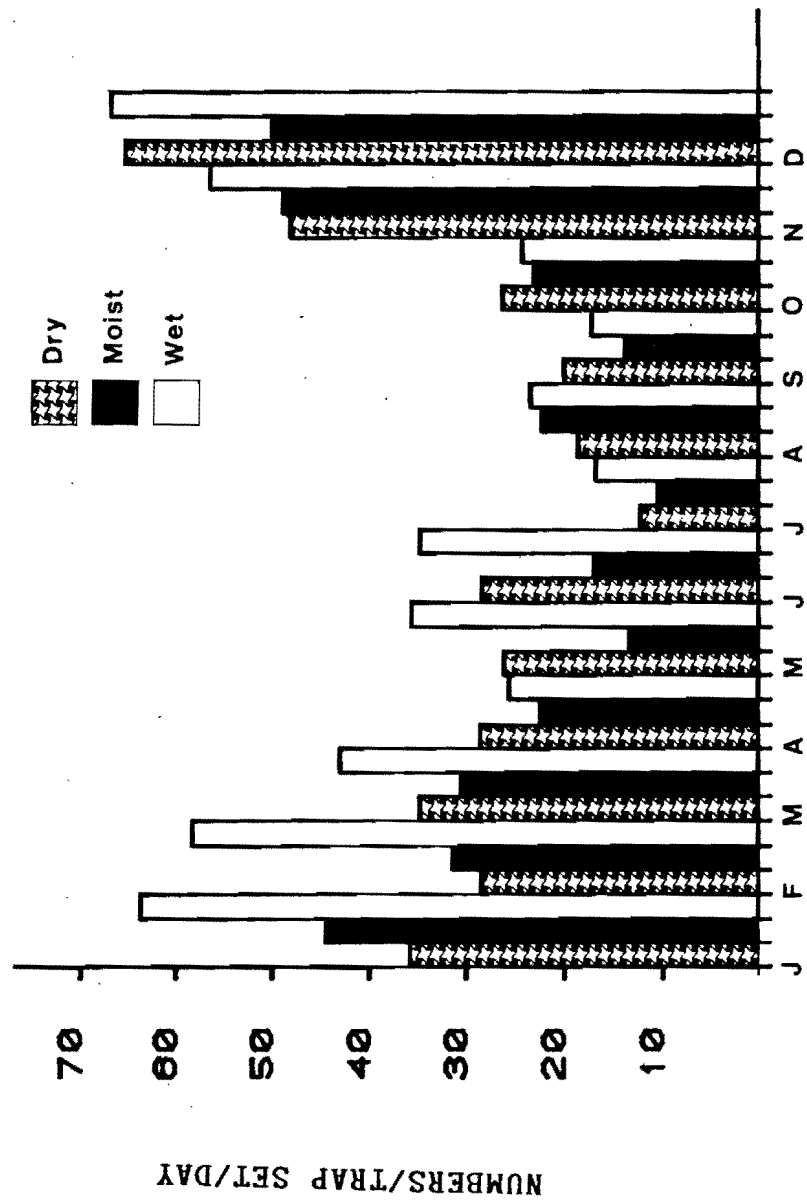


Fig. 9. Seasonal variation of aerial invertebrate density

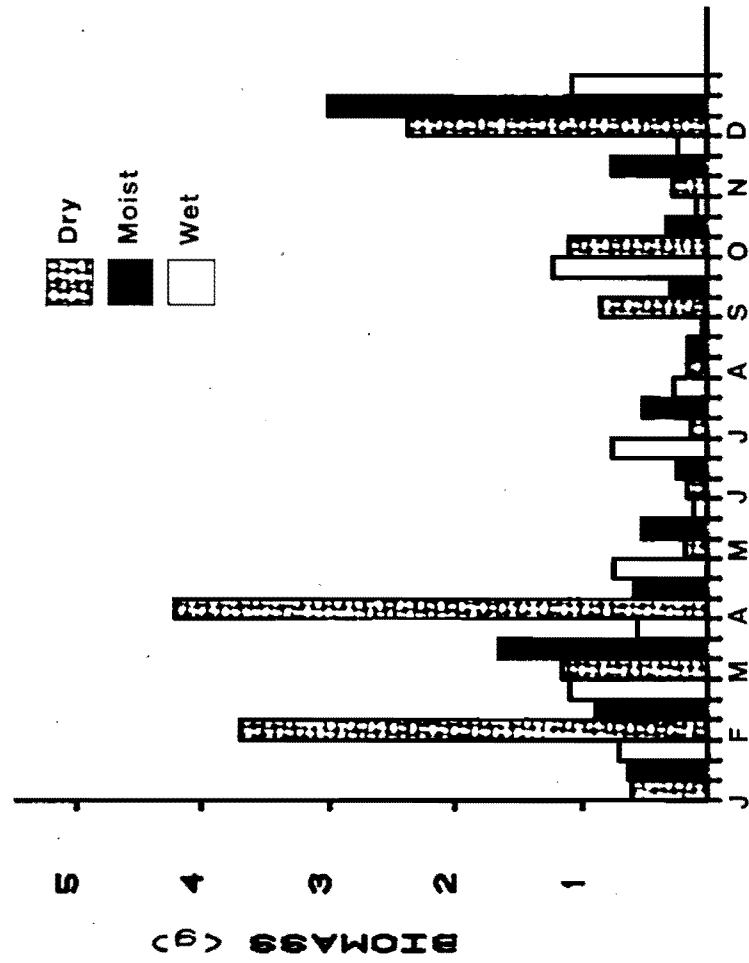


Fig. 10. Monthly biomass of the litter invertebrates/litre



Fig. 11. Monthly biomass of ground invertebrates/25 traps

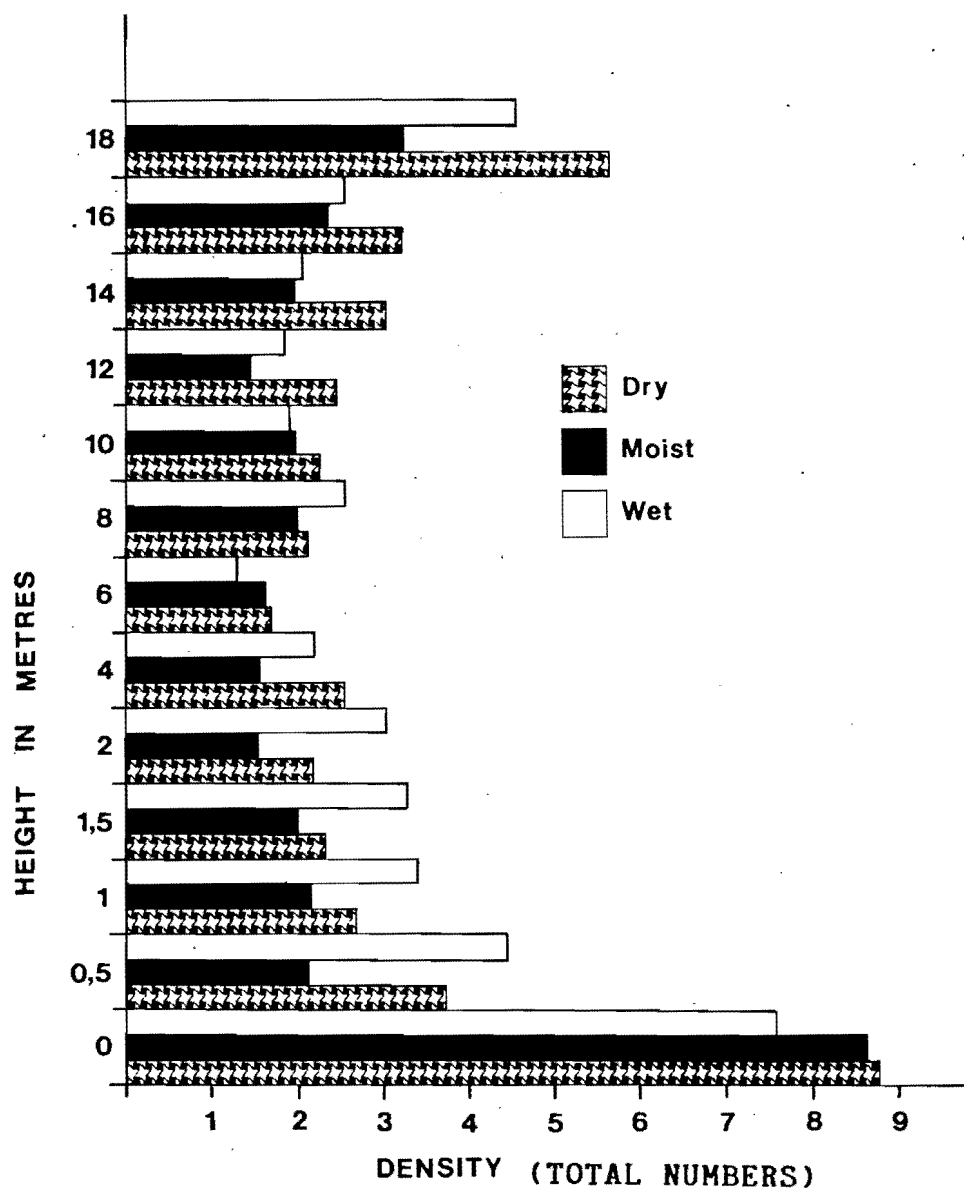


Fig. 12. Mean invertebrate abundance at different strata

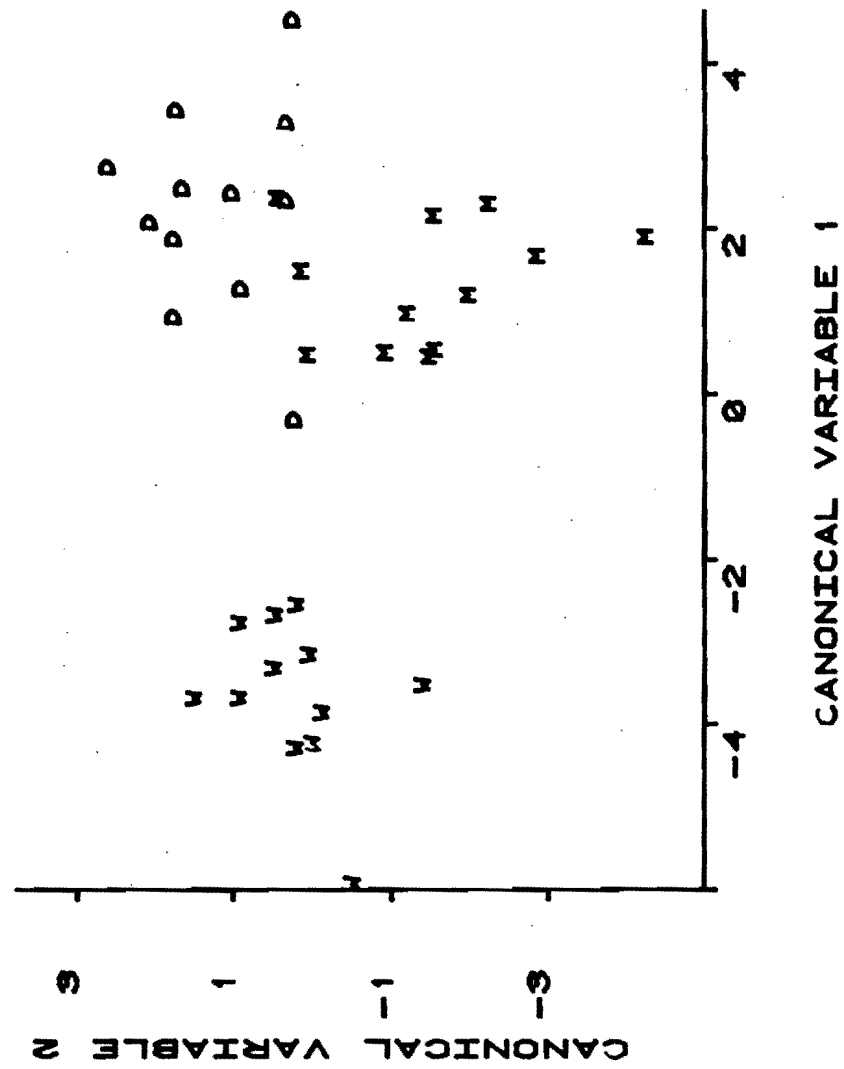
in the different height strata was also positively related to the amount of vegetation in a specific layer, i.e. with higher numbers in the denser lower layers as well as in the canopy (Sutton et al. 1983). This pattern was also observed in all three forest types (Fig. 12).

### Birds

The scientific names and monthly mean densities of birds at the three study sites are given in Appendices 8-10. Total monthly bird densities and species richness values are presented in Table 1. A total of 63,2% of the observations were of birds singing, 20,8% feeding and 16% flying.

As with the invertebrate data, the D.F.A. results for birds did not yield high discrimination between the three study sites. The correct classification of wet forest study site samples to forest type was very high (92%), but it was not possible to separate counts made in the two remaining forest types (Fig. 13). Two species feature prominently in the discrimination between the wet and moist/dry study sites. The blackheaded oriole (Oriolus larvatus) was more abundant at the wet site, and the sombre bulbul (Andropadus importunus) was equally common at the moist and dry sites, but much less common in the wet site (Fig. 14).

Shannon-Weaver diversity indices and the Jaccard and Czekanowski similarity coefficients for the avifauna of the three study sites (Table 2) also indicate strong similarities between the three study sites, although there was a slightly higher affinity between





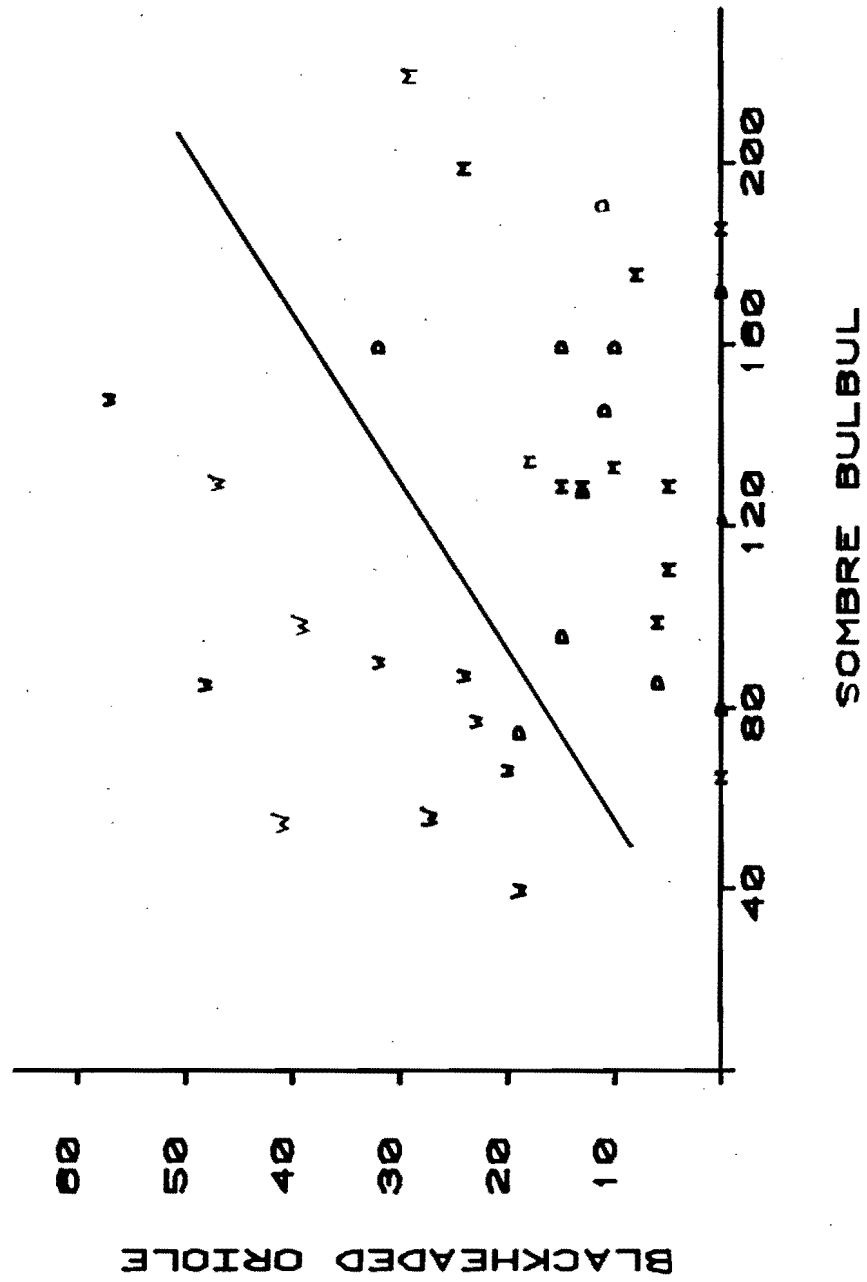


Fig. 14. Forest type separation by using the two most important bird discriminators (densities/10 ha)

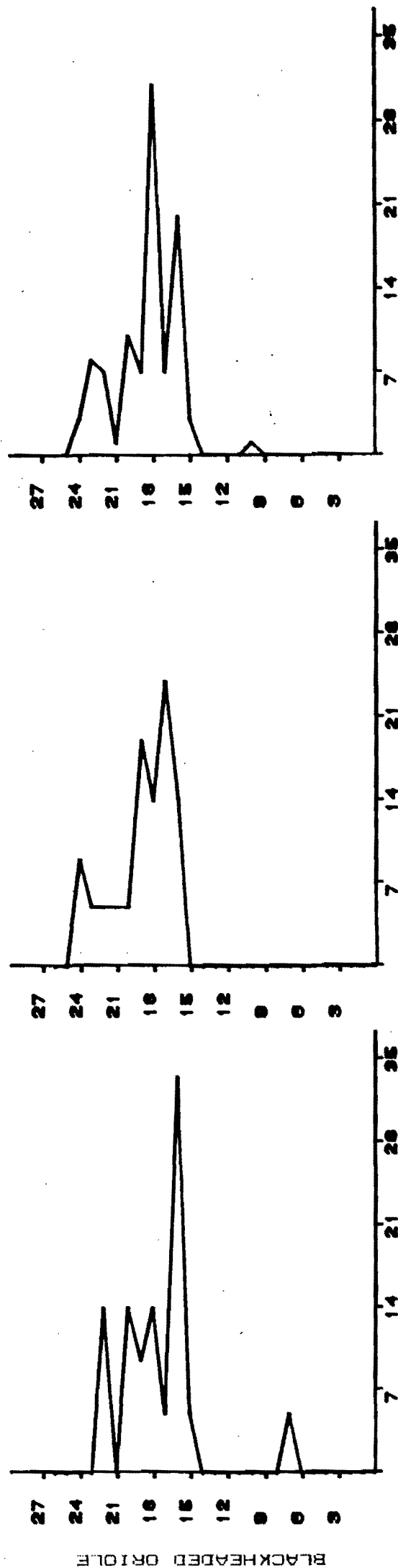
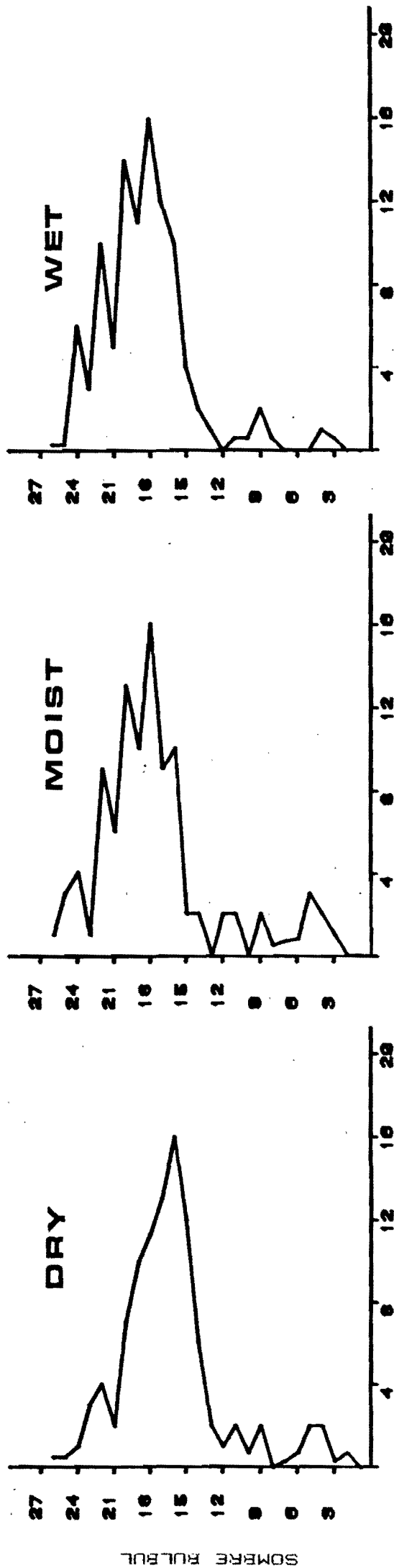


Fig. 15 a). Percentage occurrence of birds at different strata (expressed in metres)

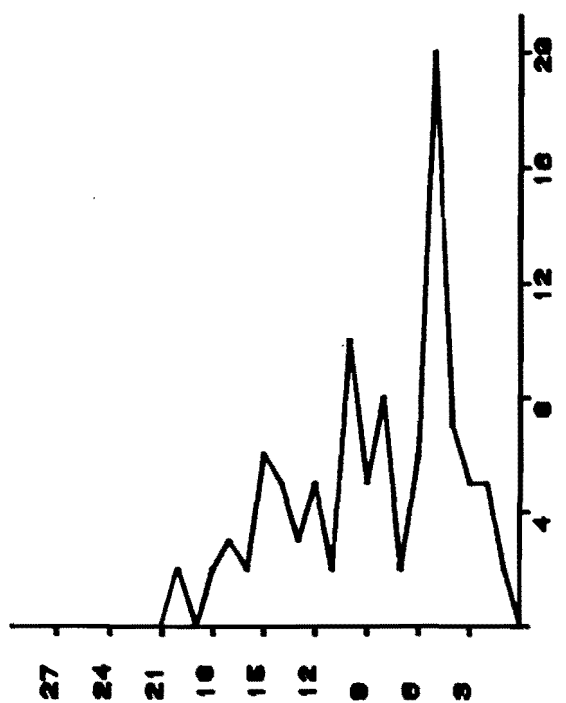
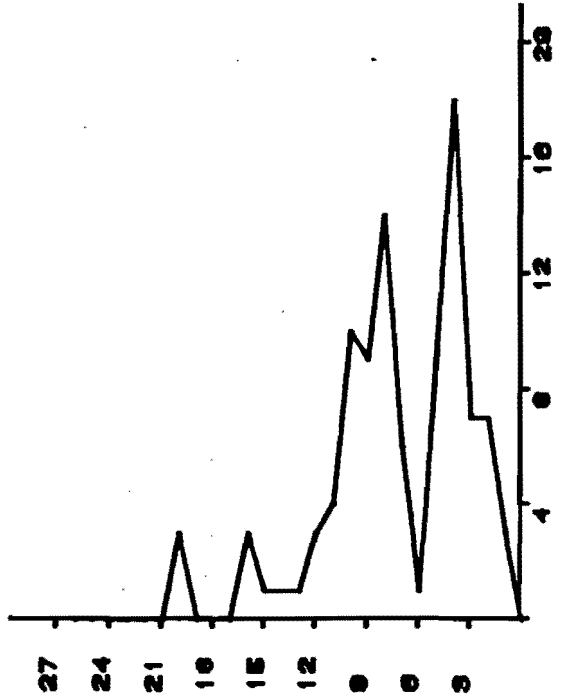
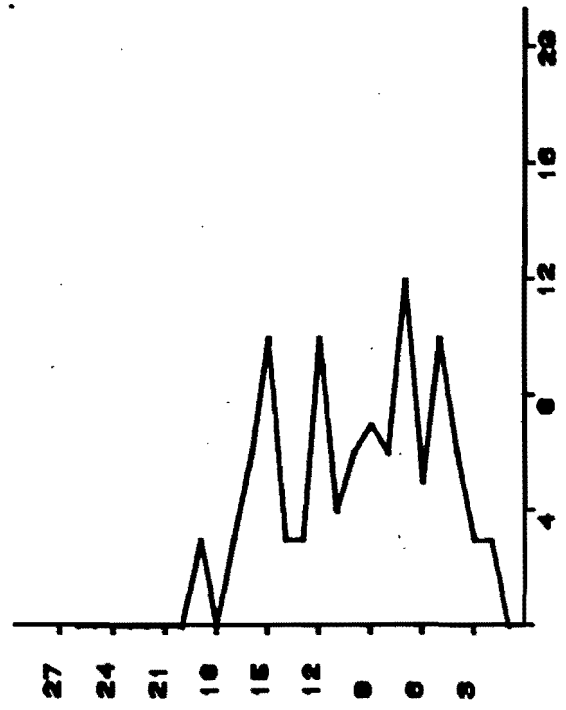
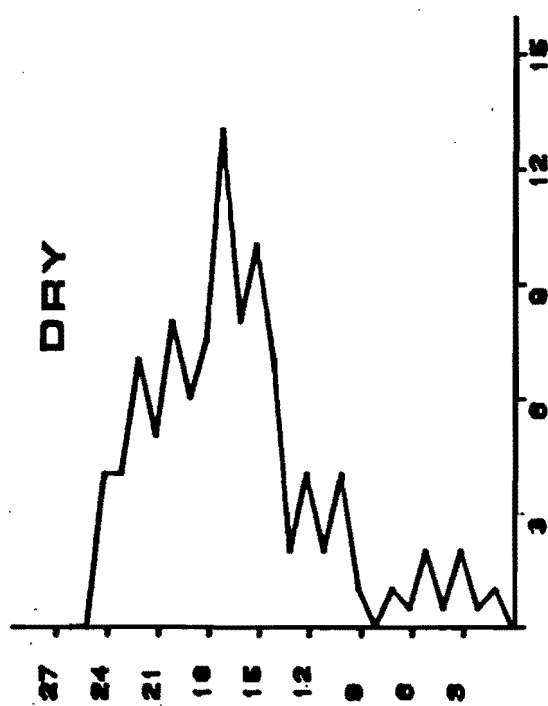
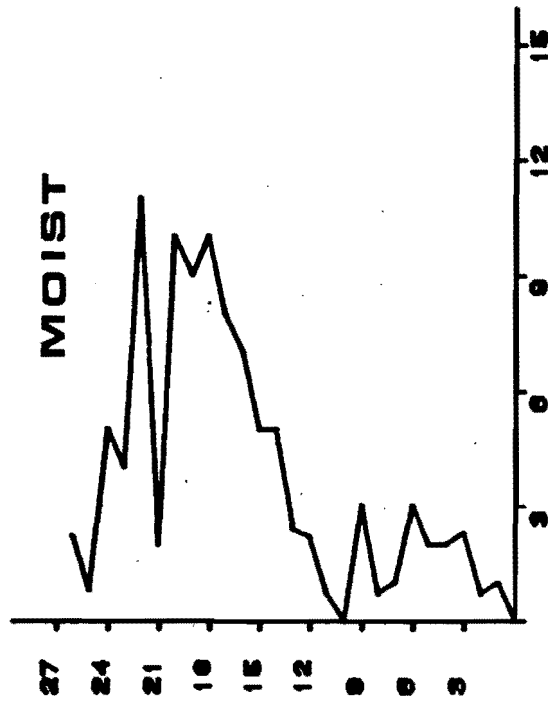
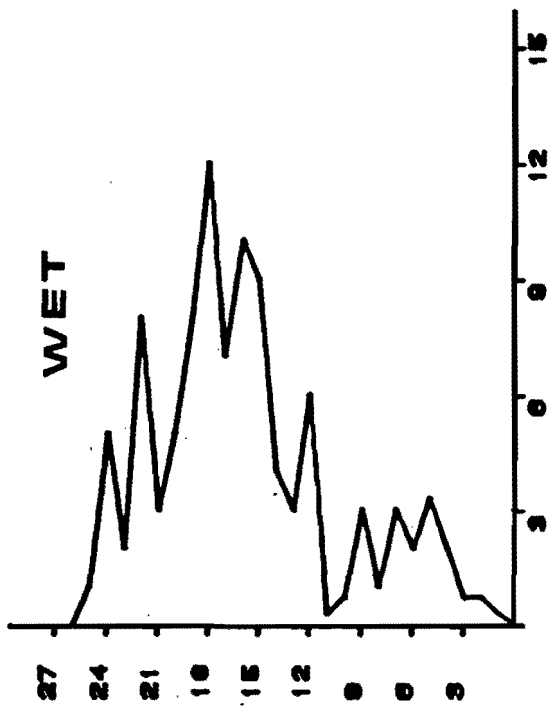


Fig. 15 b). Percentage occurrence of birds at different strata (expressed in metres)

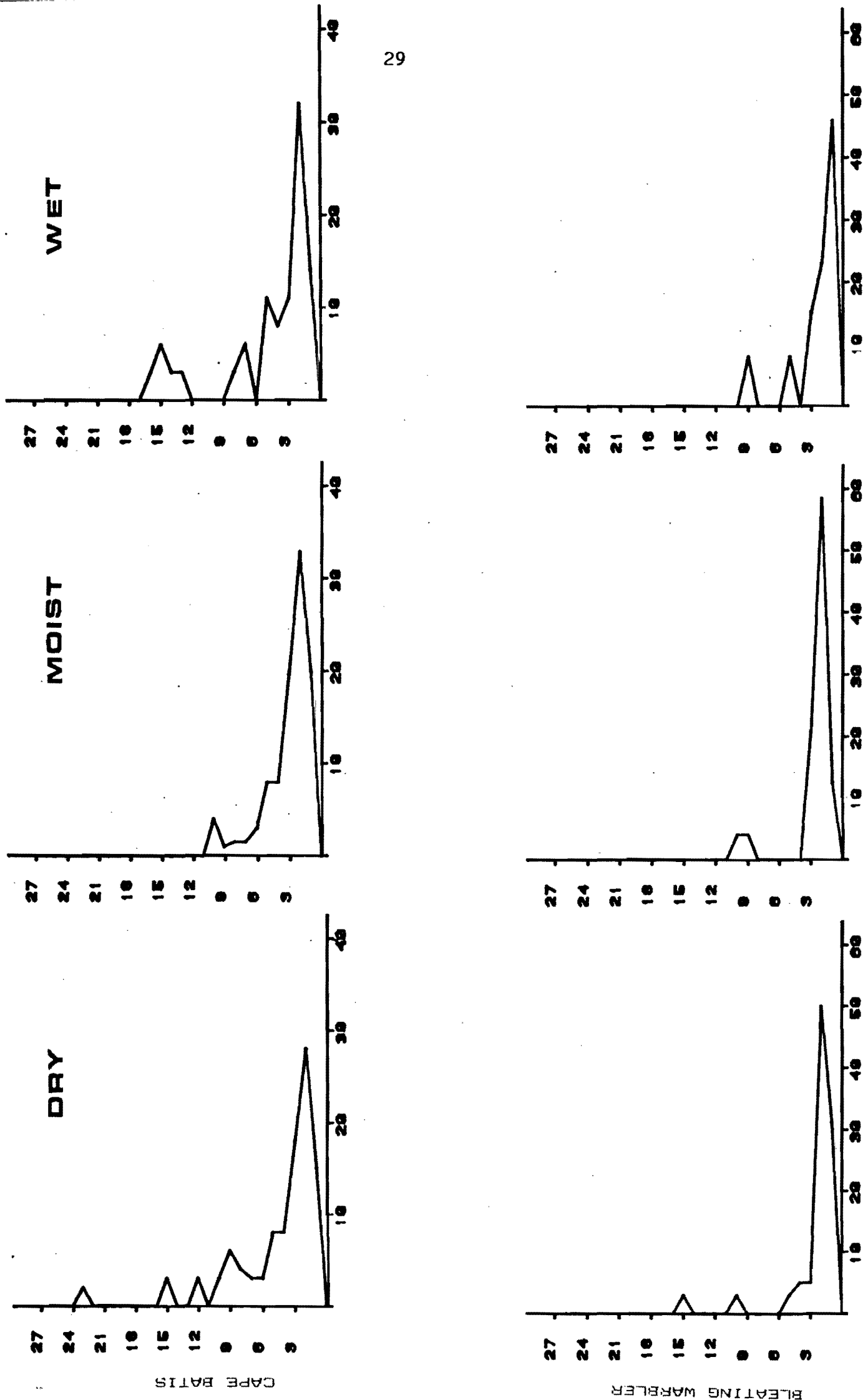


Fig. 15 c). Percentage occurrence of birds at different strata (expressed in metres)

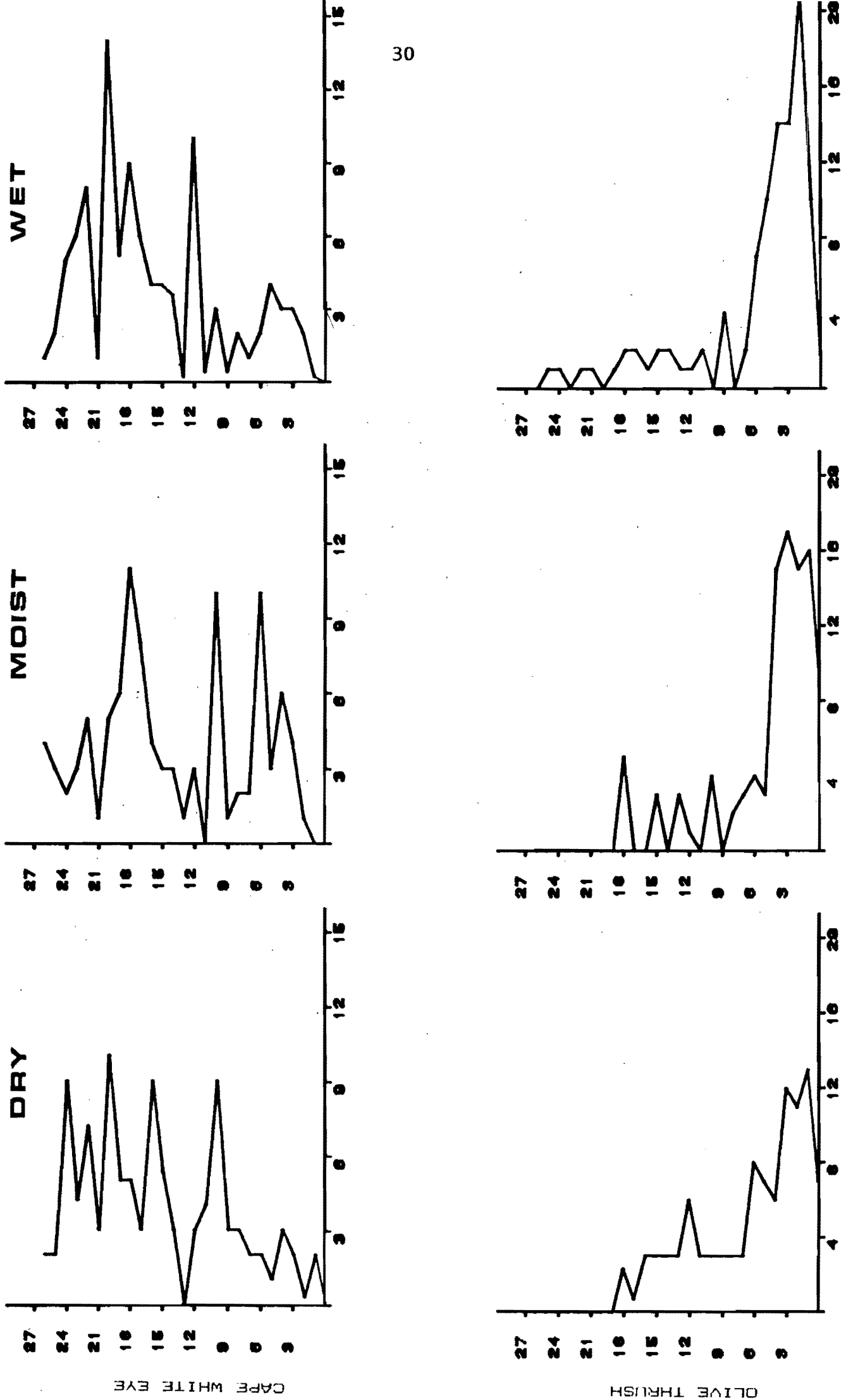


Fig. 15 d). Percentage occurrence of birds at different strata (expressed in metres)

**Table 1.** Total monthly densities and species richness of the birds in three forest types

| Dry |         |               | Moist   |               | Wet     |               |
|-----|---------|---------------|---------|---------------|---------|---------------|
|     | Species | Density (/ha) | Species | Density (/ha) | Species | Density (/ha) |
| Jan | 21      | 11,9          | 21      | 8,8           | 19      | 6,4           |
| Feb | 15      | 7,0           | 20      | 5,7           | 18      | 5,9           |
| Mar | 19      | 6,4           | 20      | 5,7           | 21      | 10,5          |
| Apr | 16      | 6,0           | 18      | 8,1           | 9       | 4,5           |
| May | 18      | 7,3           | 15      | 5,9           | 12      | 10,1          |
| Jun | 18      | 7,7           | 13      | 4,4           | 15      | 4,4           |
| Jul | 16      | 7,6           | 16      | 8,1           | 16      | 7,7           |
| Aug | 14      | 10,3          | 19      | 8,5           | 18      | 9,0           |
| Sep | 11      | 8,1           | 15      | 8,4           | 16      | 15,2          |
| Oct | 21      | 10,9          | 16      | 11,1          | 20      | 11,2          |
| Nov | 18      | 5,8           | 18      | 7,6           | 26      | 12,9          |
| Dec | 18      | 7,2           | 20      | 7,2           | 19      | 8,1           |

**Table 2.** Bird diversity and similarity between forest types

| Date    | Species richness |       |     | Diversity $\bar{H}$ |       |      |
|---------|------------------|-------|-----|---------------------|-------|------|
|         | Dry              | Moist | Wet | Dry                 | Moist | Wet  |
| 01/1984 | 21               | 21    | 21  | 3,30                | 3,72  | 3,73 |
| 02/1984 | 15               | 20    | 20  | 3,46                | 3,74  | 3,74 |
| 03/1984 | 19               | 20    | 20  | 3,41                | 3,63  | 3,64 |
| 04/1983 | 16               | 18    | 18  | 3,59                | 3,53  | 3,54 |
| 05/1983 | 18               | 14    | 15  | 3,48                | 3,06  | 3,05 |
| 06/1983 | 18               | 13    | 13  | 3,40                | 2,88  | 2,88 |
| 07/1983 | 16               | 16    | 16  | 3,24                | 3,21  | 3,22 |
| 08/1983 | 14               | 19    | 19  | 3,23                | 3,24  | 3,25 |
| 09/1983 | 11               | 15    | 15  | 2,76                | 2,68  | 2,68 |
| 10/1983 | 21               | 16    | 16  | 3,39                | 3,18  | 3,18 |
| 11/1983 | 18               | 18    | 18  | 3,55                | 2,98  | 2,98 |
| 12/1983 | 18               | 20    | 20  | 3,53                | 3,59  | 3,61 |

**SIMILARITY COEFFICIENTS****JACCARD**

|       | DRY  | MOIST |
|-------|------|-------|
| DRY   |      |       |
| MOIST | 0,66 |       |
| WET   | 0,70 | 0,76  |

**CZEKANOWSKI**

|       | DRY  | MOIST |
|-------|------|-------|
| DRY   |      |       |
| MOIST | 0,79 |       |
| WET   | 0,82 | 0,87  |

the moist and the wet sites than between the others.

Bird height class usage results are summarized in Fig. 15, and monthly counts for the three most abundant species (lesser doublecollared sunbird, Cape white eye, sombre bulbul) are summarized in Figs. 16-18.



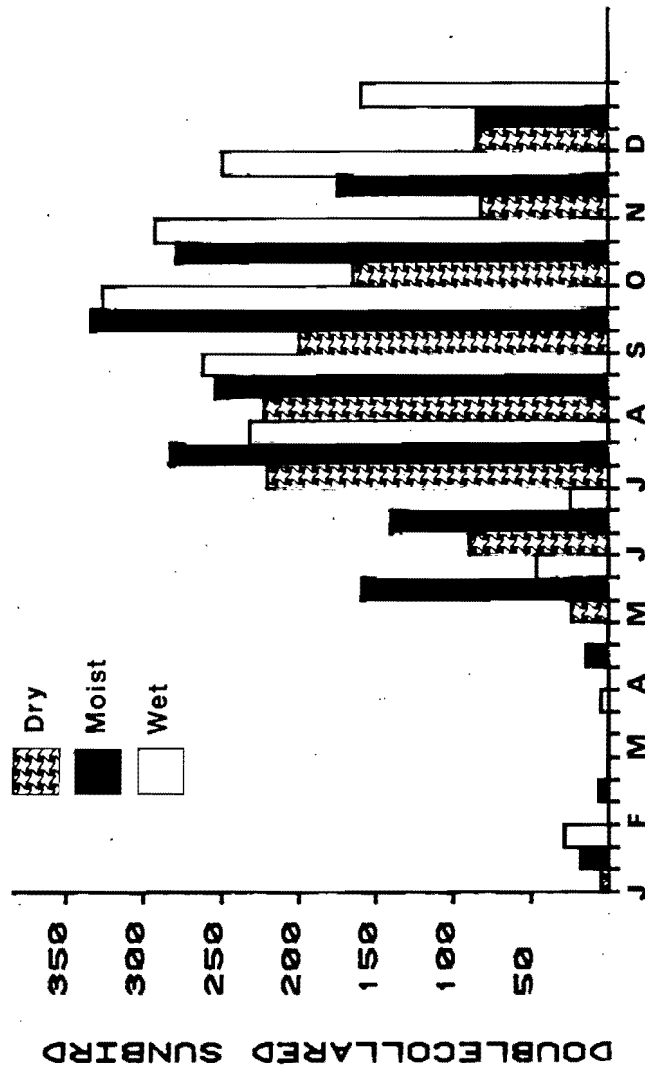


Fig. 16. Seasonal occurrence of the lesser doublecollared sunbird in the three forest types (densities/100ha)

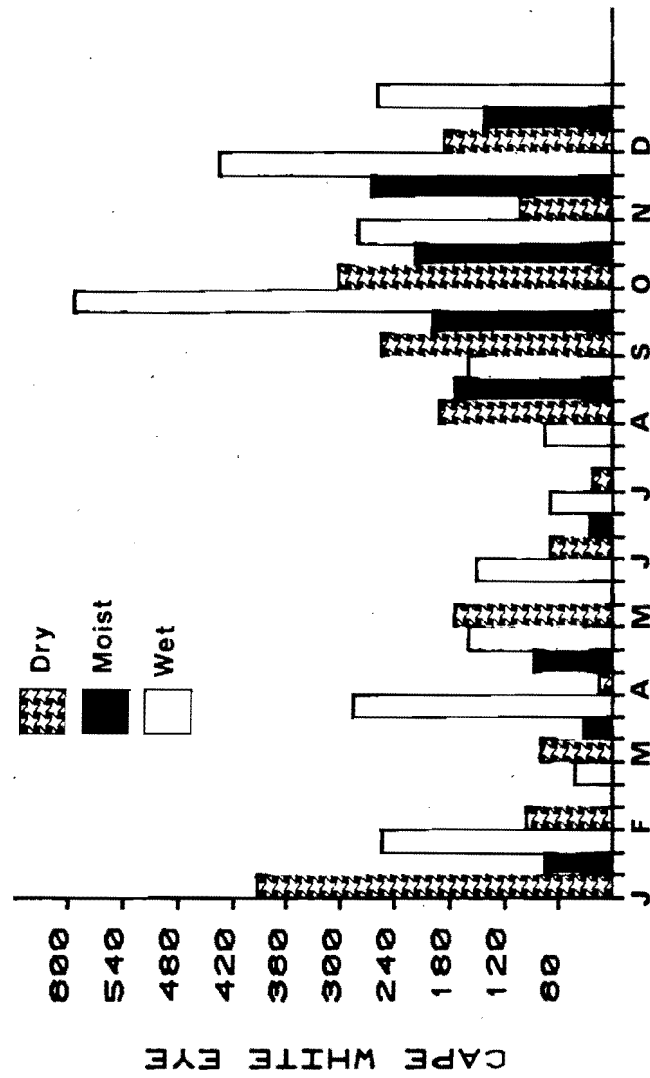


Fig. 17. Seasonal occurrence of the Cape white eye in the three forest types (densities/100ha)

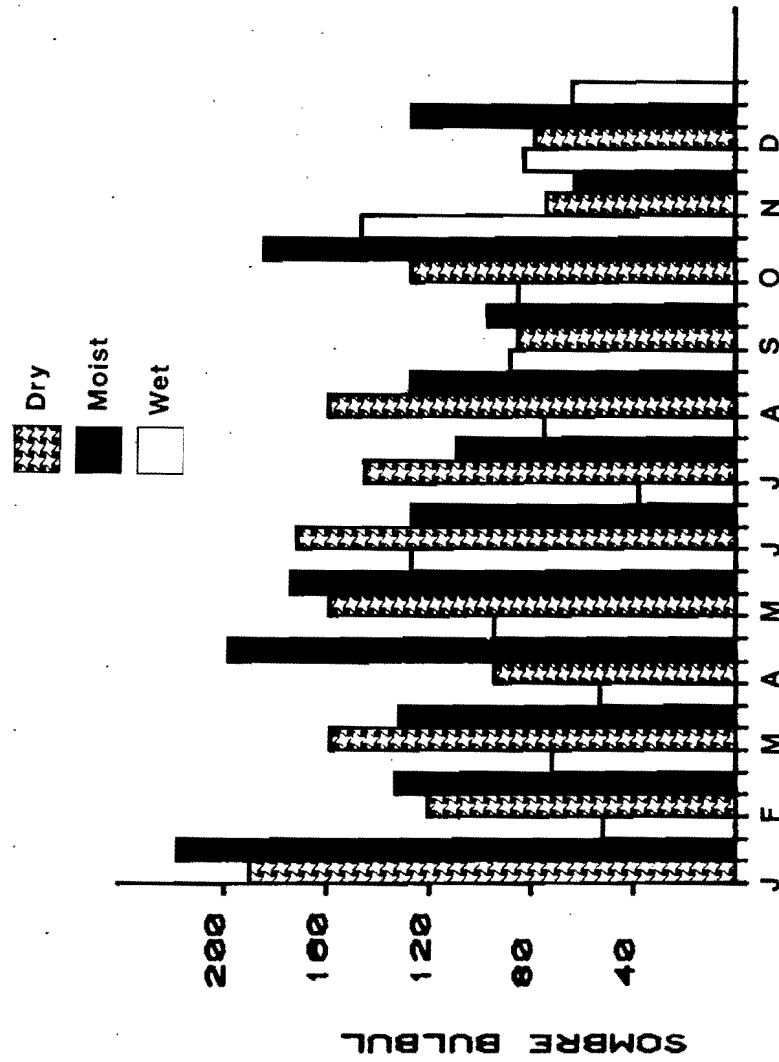


Fig. 18. Seasonal occurrence of the sombre bulbul in the three forest types (densities/100ha)

## DISCUSSION

### Factors affecting low bird species diversity and densities

#### Low local density

Despite striking inter-site differences in vegetation composition and structure (Figs. 3-6), invertebrate density and biomass varied little between sites, and bird community compositions were similar and bird densities uniformly very low (annual mean 7-9 birds/ha; monthly means, 4-15 birds/ha). These low bird density values are similar to those found in Afromontane forest in the eastern Transvaal (R.A. Earlé, pers. comm.) and at George, about 60 km to the west of the present study area (J.H. Koen, unpublished data). Cody (1983), on the other hand, found a threefold greater density (22,48 birds/ha) during a short (6-10 day) study conducted in the Knysna Forest near the wet forest study site during October-November 1979. Some of the species included in his estimates tend to occur only at the forest edge, e.g. redwinged starling (Onychognathus morio), greater doublecollared sunbird (Nectarinia afra), cardinal woodpecker (Dendropicos fuscescens) and the black cuckooshrike (Campephaga flava), and may account, in part, for these higher total density values. Cody also excluded some of the summer migrants, such as the cuckoos, while including others such as the paradise flycatcher (Terpsiphone viridis). He also used a mapping census technique in which all individuals are added on a gridded map until no new birds are encountered. This census technique differs from the one used during the present

study. All migrants (three species) were included during the present study, and the highest density found was 15,2 birds/ha during September on the wet forest study site. It must be stressed that bird densities may fluctuate over a longer period than the length of this study. However, this type of fluctuation should be in parallel between plots during successive years, which would make contemporaneously collected data comparable. On the other hand, tree species compositions in the different forest types are not the same, and, because of the even rainfall, the different species flower and fruit at different seasons. This, in turn, may affect the long-term fluctuation in bird densities.

Bird species numbers (35 species overall: dry 28, moist 31, wet 29) and densities (overall 8,1/ha: dry 8,0, moist 7,5, wet 8,8) at Knysna differ significantly from those for lowland rainforest in New Guinea (Bell 1980). In a 2,5 ha study area, Bell recorded 165 species with a density of 69 birds per ha. Zimmerman (1972) also found 69 birds per ha in primary forest in Kenya, and Karr (1976) 24 in the understorey of Malaysian rainforest. The much higher densities for birds in these tropical forests are probably due to higher resource levels and less fluctuation in the annual temperature range (Janzen 1974). Resource levels in the Knysna Forest are discussed below. Because of the higher above-ground vegetation biomass and plant species diversity in tropical lowland rainforests, more nutrients and foraging substrates will be available to support the invertebrate fauna with its associated birds (Sutton et al. 1983). Moreover, in tropical forests, a high

diversity and abundance of fruits is also available throughout the year to frugivorous birds (Orians 1969).

### **Biogeography**

Biogeographic theory suggests that a species tends to be less abundant, even in its preferred habitat, towards the edge of its distribution (Brown and Gibson 1983). This gives rise to species depauperate areas where many species' range limits coincide, and could be responsible, in part, for the low number of bird species in the study area. Both the Afromontane and Indian Ocean Coastal Belt forest elements that join in the eastern Cape become depleted in the southern Cape, resulting in a more impoverished and fragmented habitat towards the west (McKenzie 1978; Scriba 1984). Of the 122 woody species that reach the area from the east, 21% have dropped out at George and 29% at Swellendam (C.J. Geldenhuys, pers. comm.). Most of the tropical bird species also reach their distributional limits in the eastern and southern Cape (Winterbottom 1974). Moreover, Cody (1983) found a decline in species numbers from 43 at Alexandria (east of Port Elizabeth) to 15 in the most isolated and fragmented forests at Cape Town. According to Maclean (1985), 29% of the species recorded at Knysna reach the end of their distribution at George and 50% at Swellendam.

As species drop out due to this east-to-west 'subtraction effect', Cody (1983) suggests that those which persist exhibit a density compensation which operates independently from any

increase in foliage density and insect abundance. This compensation is most readily observed in dominant insectivores (e.g. Cape white eye Zosterops pallidus, dusky flycatcher Muscicapa adusta). In the present study, variation in total invertebrate numbers (Figs. 8-9) and biomass (Figs. 11-12) did not correlate with variation in bird numbers. This supports Cody's speculation that bird and insect density are not correlated. Thus, in the study area, it appears that birds might depend on some minimum invertebrate resource level, and do not closely track fluctuations to higher levels. However, owing to the large discrepancies between Cody's bird density values and those found in the present study, further data, collected throughout the year at several sites along the east-west gradient are necessary to test for any density compensation factor.

#### **Endemism and niche breadth**

Other factors contributing to the low bird species numbers in the study areas are the lack of endemism and the broad habitats of most forest bird species in the southern Cape. Many of these species are widespread in Africa (e.g. the sombre bulbul and blackheaded oriole), even over various biomes. Some, such as the lesser doublecollared sunbird, appear to utilize the forest mainly for breeding purposes during winter (Fig. 16).

This wide ecological tolerance and lack of endemism could be explained by the nature and history of the vegetation. The isolation of the forest patches in the southern Cape may not have

been complete enough and the floristic and structural differences not great enough for the development of endemic bird species. Afromontane forest patches may also have been much less patchy until fairly recently in geological time (Cody 1983), with a resultant high rate of species interchange. Alternatively, forest patches in the area may not have been of sufficient size for the evolution and persistence of endemics (Soulé 1980). Some plant species (e.g. Rapanea, Ilex, Apodytes and Podocarpus) have a wide Afromontane distribution (Coates Palgrave 1977), resulting in the local vegetation not being completely distinct, and not providing the necessary opportunity for speciation or specialisation.

### **Resources**

Soil fertility can have dramatic effects on vegetation and associated herbivores (Janzen 1974; Strong et al. 1984). The forests in the southern Cape grow on notoriously nutrient poor soils (van Daalen 1980). Moreover, most of the nutrients available in the system are locked up in the aboveground biomass and have a fast recycling rate, to such an extent that roots penetrate decomposing logs from below the soil surface (J.H. Koen unpublished data). Feeding roots are also concentrated in the upper 30 cm of the substratum (van Daalen 1980). Under such conditions, trees tend to develop nutrient-saving strategies such as evergreenness, sclerophylly or chemical defence mechanisms against herbivores (van Daalen 1984; Tuomi et al. 1984; Vitousek 1984). The rivers



in the area are typical 'blackwater' systems (Janzen 1974), the dark colour being supplied by humic acids (tannins and phenols) leached from the vegetation. These chemicals are used by plants to discourage grazers, but effectively lower their secondary productivity (Janzen 1974). Seasonal foliar nutrient analysis of several local tree species reflects the low soil nutrient status, especially that of phosphorous (Koen 1984). Low nutrient status in the vegetation, combined with possible chemical defence mechanisms, could negatively affect the invertebrate herbivore population (Harborne 1977; Rhoades 1979; Janzen and Waterman 1984). This may, in turn, have a negative influence on populations of insectivorous birds and of species which rely on invertebrate food as a high protein source for nestlings. Therefore, as Nilsson (1979) found in Sweden, low food availability may be the ultimate determinant of low bird species richness and density in the Knysna Forest. Other evidence also suggests that food resources may be the ultimate limiting factors (Karr 1976; Terborgh 1980), and that vegetation structure merely affects the foraging strategies of birds (Smith 1974; Power 1980; Robinson and Holmes 1984). Robinson and Holmes (1982, 1984) maintain that the primary role of vegetation structure is to provide a set of opportunities and constraints that influence how and where birds perceive and obtain their food.

Another important factor which affects food abundance, and hence availability in the study area is the mast-fruiting phenomenon of most of the important fruiting trees, e.g.

P. latifolius, P. falcatus, R. melanophloeos, O. capensis and Curtisia dentata (C.J. Geldenhuys, pers. comm.). Low soil nutrient status and low rainfall favour mast-fruiting (Geldenhuys 1983). Mast-fruiting is considered to be an adaptive strategy to increase a species' reproductive success via predator satiation or to store nutrients for seed crops at longer intervals (Janzen 1974). Moreover, in the Knysna Forest, the fruiting cycles of trees are not synchronized, and, although fruit is available for much of the year, it is only in relatively small quantities. Some bird species, such as the rameron pigeon (Columba arquatrix) move over long distances and closely track fruit availability inside the forest and in adjacent habitats. Therefore, their abundance fluctuates dramatically within and between seasons, for example when O. capensis is fruiting during late summer and autumn (February-April). The abundance of more sedentary species, such as the Knysna lourie (Tauraco corythaix) may be much more closely controlled by fruit availability within the forest.

#### Discrimination between forest types

The bird, and probably invertebrate, communities in all three forest types are very similar (Figs. 8-13), despite clear differences in vegetation species composition and structure (Figs. 3-6). Rice et al. (1984) suggested that absolute tree species densities, and not only structure in the habitat determine bird abundance and diversity. However, the inclusion of these characters in the D.F.A. only influenced the forest type

classification and not the birds. Another possible explanation of the absence of discrete bird community structure in the three forest types is that the birds are distributed independently along habitat gradients (Wiens and Rotenberry 1981). They may also be selecting for past, or present, elements within the three forest types that were not detected by the present sampling. These elements may be associated with the forest as a unit, making it acceptable to all species.

By using his vegetation height and half height relationship (Cody 1975), Cody (1983) predicted that the bird species richness in southern African forest birds should remain effectively constant at 24-25 species. After finding a nearly three-fold difference (15-45 species) along a west to east gradient, he concluded that structural dissimilarities among southern African forests play a very minor role in structuring their bird communities. In the present study, the areas under the vegetation profile curves differ substantially (five to ninefold) from those Cody (1983) found at the Knysna Forest, mostly due to his higher estimate of forest canopy height. Taylor et al. (1984) found that animal discrimination for vegetation structure is much less refined within tall, closed forest, and that sampling strategy influences the importance of this discrimination. They suggest that there is a threshold level of vegetation structural complexity or life form above which animals do not readily discriminate. This threshold level may be associated with an overstorey. Such a threshold effect may be in action in the Knysna Forest, limiting

habitat discrimination to a minimum and only allowing birds to select habitat at a gross level.

The major unanswered question in both Cody's and the present study is therefore, to what extent is the community structure of birds in southern African Afromontane forests also determined by the physical properties of the environment? There must be a physical or resource mechanism in operation to afford some stability to the community (Cody 1975). This mechanism can only be determined through a longer term study which should include an in-depth look at avian guilds (Verner 1984), and, indeed, abundance/diversity patterns for other components of the biota.

#### Competition and coexistence

Competition between species may play a key role in structuring bird communities (Roughgarden 1983), but it is very difficult to demonstrate its action in nature (Wiens 1983). Species overlap in their use of resources, and it is difficult to specify how much overlap is needed to promote competition. Resource-based competition for food or space may not be the primary determinant of species' niches. The 'struggle' may rather be for enemy free space (Jeffries and Lawton 1984). In other words, communities are not shaped by competition, but rather by the natural enemies of the component species.

Due to similar species composition and densities found in the dissimilar forest types investigated in the present study, it may be concluded that competitive exclusion plays, at best, a very

minor role in structuring the bird community of the Knysna Forest. As evidence in support of this conclusion, two of the three numerically most important species (Cape white eye and lesser doublecollared sunbird) (Figs. 16-17) played no role in discriminating between the bird communities of the respective forest types. Nevertheless, it is difficult to make definitive statements about competition or habitat selection of individual species from diversity indices or the multivariate statistics used.

Possible evidence of competition is spatial or temporal niche variation. In forest birds, this is often evident in the differential use of height (Robinson and Holmes 1982). However, height class usage by the different species in the three forest types was very similar (Fig. 15). Indeed, one striking feature is the wide height range utilised by most birds, making it difficult to separate the layers according to species groups or to fit the birds to the resource (invertebrate) levels available in the layers. Interpretation of foraging height usage may be complicated by the fact that some species have bimodal foraging distributions (Williamson 1971). The lower 4 m layer, which is floristically and structurally the most dissimilar layer between forest types, do not appear to affect the species usage as the same species were encountered in all three forest types.

The structuring of the Knysna Forest bird niches are therefore primarily influenced by low resource availability, and competition is filtered to allow wide habitat use.

## CONCLUSIONS

Vegetation structure and composition variation do not appear to influence the Knysna Forest bird and invertebrate communities. The answers to questions around which this study was structured are all negative, except for the floristic separation of the forest types. A nutritionally poor habitat and the marginal distribution of the habitat type may be the cause of low species densities. Mast-fruiting may have a density control on the respective frugivores, especially more sedentary species.

The sustained-yield management practices as employed in the forest at present are concentrated in the moist forest types. These practices should not have any significant differential effect on the bird communities as such. It may affect individual species (e.g. woodpeckers) to a certain extent, but, as the practices are aimed at sustaining the floristic composition of the forest, the effects should be similar in the respective forest types. As the moist forest type is silviculturally the most important it will be necessary to investigate annual density fluctuations over an extended period to include at least one mast-fruiting cycle. This will indicate the importance of such cycles in maintaining the faunal communities.

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**Appendix 1.** Mensural data for birds mist-netted in the Knysna Forest

| Species                                                 | n  | Mean<br>Mass<br>g | Length (mm) |        |       |       |
|---------------------------------------------------------|----|-------------------|-------------|--------|-------|-------|
|                                                         |    |                   | Culmen      | Tarsus | Tail  | Wing  |
| <u>Andropadus importunus</u><br>sombre bulbul           | 2  | 44,0              | 14,0        | 22,5   | 87,5  | 87,5  |
| <u>Apalis thoracica</u><br>barthroated apalis           | 2  | 10,5              | 12,5        | 20,0   | 53,0  | 51,0  |
| <u>Apaloderma narina</u><br>narina trogon               | 1  | 66,5              | 14,0        | 15,0   | 131,0 | 121,0 |
| <u>Batis capensis</u><br>Cape batis                     | 13 | 11,0              | 11,2        | 20,7   | 44,8  | 59,3  |
| <u>Camaroptera brachyura</u><br>bleating warbler        | 7  | 12,5              | 10,6        | 20,9   | 40,9  | 53,3  |
| <u>Cossypha caffra</u><br>Cape robin                    | 1  | 24,0              | 13,0        | 31,0   | 74,0  | 80,0  |
| <u>Cossypha dichroa</u><br>chorister robin              | 9  | 38,0              | 14,1        | 28,6   | 83,6  | 100,9 |
| <u>Dryoscopus cubla</u><br>puffback                     | 1  | 29,0              | 16,0        | 33,0   | 70,0  | 80,0  |
| <u>Laniarius ferrugineus</u><br>southern boubou         | 2  | 61,0              | 22,0        | 33,0   | 96,5  | 98,5  |
| <u>Phyllastrephus terrestris</u><br>terrestrial bulbul  | 14 | 36,5              | 17,1        | 24,9   | 87,7  | 87,8  |
| <u>Pogonocichla stellata</u><br>starred robin           | 15 | 19,2              | 12,1        | 25,5   | 63,1  | 80,1  |
| <u>Seicercus ruficapillus</u><br>yellowthroated warbler | 2  | 6,5               | 10,5        | 20,0   | 42,5  | 55,0  |
| <u>Serinus scotops</u><br>forest canary                 | 1  | 15,0              | 10,0        | 16,0   | 52,0  | 66,0  |
| <u>Turdus olivaceus</u><br>olive thrush                 | 13 | 79,5              | 20,2        | 32,2   | 85,4  | 114,0 |
| <u>Zosterops pallidus</u><br>Cape white eye             | 4  | 10,6              | 10,8        | 17,8   | 47,8  | 60,0  |

**Appendix 2.** Vegetation data as entered in the D.F.A. Categories used are:

a) seedlings, trees and ground flora

No./plot      Category

|       |   |
|-------|---|
| 0     | 0 |
| 1-4   | 1 |
| 5-8   | 2 |
| 9-12  | 3 |
| 13-16 | 4 |
| 17-20 | 5 |

b) tree fern stems/plot

|        |   |
|--------|---|
| 0      | 0 |
| 1-10   | 1 |
| 11-20  | 2 |
| 21-30  | 3 |
| 31-50  | 4 |
| 51-100 | 5 |

c) onderbos stems/plot

|       |   |
|-------|---|
| 0     | 0 |
| 1-5   | 1 |
| 6-10  | 2 |
| 11-15 | 3 |
| 16-20 | 4 |
| 21-50 | 5 |

All categories divided by 20 for means per forest type.

| Species                         | Dry       |      | Moist     |      | Wet       |      |
|---------------------------------|-----------|------|-----------|------|-----------|------|
|                                 | $\bar{X}$ | S.D. | $\bar{X}$ | S.D. | $\bar{X}$ | S.D. |
| <b>SEEDLINGS</b>                |           |      |           |      |           |      |
| <u>Apodytes dimidiata</u>       | 0,00      | 0,00 | 0,25      | 0,44 | 0,10      | 0,31 |
| <u>Brachylaena neriifolia</u>   | 0,00      | 0,00 | 0,00      | 0,00 | 0,05      | 0,22 |
| <u>Burchellia bubalina</u>      | 0,05      | 0,22 | 0,00      | 0,00 | 0,20      | 0,41 |
| <u>Canthium inerme</u>          | 0,20      | 0,41 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Canthium mundianum</u>       | 0,20      | 0,41 | 0,10      | 0,31 | 0,15      | 0,37 |
| <u>Canthium obovatum</u>        | 0,10      | 0,31 | 0,10      | 0,31 | 0,15      | 0,49 |
| <u>Cassine papillosa</u>        | 0,40      | 0,60 | 0,40      | 0,50 | 0,20      | 0,52 |
| <u>Curtisia dentata</u>         | 0,10      | 0,31 | 0,15      | 0,37 | 0,20      | 0,52 |
| <u>Diospyros whyteana</u>       | 0,70      | 0,86 | 0,25      | 0,44 | 0,50      | 0,61 |
| <u>Gonioma kamassi</u>          | 0,45      | 0,60 | 0,35      | 0,49 | 0,25      | 0,44 |
| <u>Halleria lucida</u>          | 0,05      | 0,22 | 0,05      | 0,22 | 0,00      | 0,00 |
| <u>Ilex mitis</u>               | 0,00      | 0,00 | 0,00      | 0,00 | 0,15      | 0,37 |
| <u>Maytenus acuminata</u>       | 0,00      | 0,00 | 0,05      | 0,22 | 0,05      | 0,22 |
| <u>Maytenus peduncularis</u>    | 0,00      | 0,00 | 0,00      | 0,00 | 0,15      | 0,37 |
| <u>Ochna arborea</u>            | 0,80      | 0,83 | 0,15      | 0,37 | 0,00      | 0,00 |
| <u>Ocotea bullata</u>           | 0,25      | 0,79 | 0,70      | 0,92 | 0,80      | 0,70 |
| <u>Olea capensis macrocarpa</u> | 0,40      | 0,60 | 0,55      | 0,76 | 0,40      | 0,50 |

## Appendix 2. Continued

| SPECIES                             | DRY       |      | MOIST     |      | WET       |      |
|-------------------------------------|-----------|------|-----------|------|-----------|------|
|                                     | $\bar{X}$ | S.D. | $\bar{X}$ | S.D. | $\bar{X}$ | S.D. |
| <u>Pittosporum viridiflorum</u>     | 0,10      | 0,45 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Platylophus trifoliatus</u>      | 0,00      | 0,00 | 0,00      | 0,00 | 0,15      | 0,49 |
| <u>Podocarpus falcatus</u>          | 0,20      | 0,52 | 0,10      | 0,31 | 0,05      | 0,22 |
| <u>Podocarpus latifolius</u>        | 0,70      | 0,92 | 1,50      | 1,00 | 1,30      | 0,86 |
| <u>Pterocelastrus tricuspidatus</u> | 0,10      | 0,31 | 0,05      | 0,22 | 0,00      | 0,00 |
| <u>Rapanea melanophloeos</u>        | 0,15      | 0,37 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Rhamnus prinoides</u>            | 0,00      | 0,00 | 0,05      | 0,22 | 0,00      | 0,00 |
| <u>Rhus chirindensis</u>            | 0,00      | 0,00 | 0,00      | 0,00 | 0,05      | 0,22 |
| <u>Rothmannia capensis</u>          | 0,00      | 0,00 | 0,10      | 0,31 | 0,00      | 0,00 |
| <u>Virgilia oroboides</u>           | 0,00      | 0,00 | 0,05      | 0,22 | 0,00      | 0,00 |
| <b>TREES</b>                        |           |      |           |      |           |      |
| <u>Acacia melanoxylon</u>           | 0,00      | 0,00 | 0,00      | 0,00 | 0,05      | 0,22 |
| <u>Cyathea capensis</u> #2 *2       | 0,00      | 0,00 | 0,05      | 0,22 | 2,25      | 1,83 |
| <u>Apodytes dimidiata</u>           | 0,45      | 0,51 | 0,65      | 0,49 | 0,85      | 0,49 |
| <u>Brachylaena neriifolia</u>       | 0,00      | 0,00 | 0,00      | 0,00 | 0,05      | 0,22 |
| <u>Burchellia bubalina</u>          | 0,35      | 0,49 | 0,10      | 0,31 | 0,40      | 0,50 |
| <u>Canthium inerme</u> *4           | 0,40      | 0,50 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Canthium mundianum</u>           | 0,20      | 0,41 | 0,20      | 0,41 | 0,30      | 0,47 |
| <u>Canthium obovatum</u>            | 0,60      | 0,68 | 0,55      | 0,51 | 0,45      | 0,51 |
| <u>Cassine papillosa</u>            | 0,55      | 0,51 | 0,50      | 0,51 | 0,40      | 0,50 |
| <u>Cassine peragua</u>              | 0,10      | 0,31 | 0,05      | 0,22 | 0,00      | 0,00 |
| <u>Chionanthus foveolatus</u>       | 0,10      | 0,31 | 0,00      | 0,00 | 0,05      | 0,22 |
| <u>Cunonia capensis</u>             | 0,05      | 0,22 | 0,00      | 0,00 | 0,05      | 0,22 |
| <u>Curtisia dentata</u>             | 0,45      | 0,60 | 1,05      | 0,69 | 1,05      | 0,76 |
| <u>Diospyros whyteana</u>           | 0,40      | 0,50 | 0,20      | 0,41 | 0,50      | 0,51 |
| <u>Faurea macnaughtonii</u>         | 0,05      | 0,22 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Gonioma kamassi</u>              | 1,35      | 0,81 | 1,25      | 0,79 | 0,55      | 0,76 |
| <u>Halleria lucida</u> #3           | 0,00      | 0,00 | 0,30      | 0,47 | 0,95      | 0,69 |
| <u>Ilex mitis</u>                   | 0,05      | 0,22 | 0,05      | 0,22 | 0,45      | 0,51 |
| <u>Maytenus acuminata</u>           | 0,50      | 0,51 | 0,20      | 0,41 | 0,25      | 0,44 |
| <u>Maytenus peduncularis</u>        | 0,30      | 0,47 | 0,15      | 0,37 | 0,45      | 0,51 |
| <u>Ochna arborea</u> *3             | 0,35      | 0,49 | 0,15      | 0,37 | 0,00      | 0,00 |
| <u>Ocotea bullata</u>               | 0,25      | 0,55 | 0,30      | 0,47 | 0,30      | 0,47 |
| <u>Olea capensis capensis</u>       | 0,05      | 0,22 | 0,00      | 0,00 | 0,50      | 0,51 |
| <u>Olea capensis macrocarpa</u>     | 2,10      | 1,34 | 1,85      | 0,59 | 0,90      | 0,72 |
| <u>Olinia ventosa</u>               | 0,05      | 0,22 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Pittosporum viridiflorum</u>     | 0,05      | 0,22 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Platylophus trifoliatus</u> #6*6 | 0,00      | 0,00 | 0,00      | 0,00 | 1,00      | 1,12 |
| <u>Podocarpus falcatus</u>          | 0,30      | 0,47 | 0,25      | 0,44 | 0,15      | 0,37 |
| <u>Podocarpus latifolius</u>        | 1,20      | 1,28 | 1,60      | 0,75 | 0,80      | 0,83 |
| <u>Pterocelastrus tricuspidatus</u> | 1,10      | 0,97 | 0,20      | 0,41 | 0,10      | 0,31 |
| <u>Rapanea melanophloeos</u>        | 0,25      | 0,44 | 0,00      | 0,00 | 0,05      | 0,22 |
| <u>Rhus chirindensis</u>            | 0,10      | 0,31 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Rhus lucida</u>                  | 0,05      | 0,22 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Rothmannia capensis</u>          | 0,20      | 0,41 | 0,00      | 0,00 | 0,00      | 0,00 |

## Appendix 2. Continued

| SPECIES                            | DRY       |      | MOIST     |      | WET       |      |
|------------------------------------|-----------|------|-----------|------|-----------|------|
|                                    | $\bar{X}$ | S.D. | $\bar{X}$ | S.D. | $\bar{X}$ | S.D. |
| <u>Trichocladus crinitus</u>       | 2,05      | 0,22 | 1,70      | 0,47 | 2,90      | 1,65 |
| <u>Vepris lanceolata</u>           | 0,05      | 0,22 | 0,00      | 0,00 | 0,00      | 0,00 |
| <b>GROUND FLORA</b>                |           |      |           |      |           |      |
| <u>Aristea ensifolia</u>           | 0,00      | 0,00 | 0,05      | 0,22 | 0,05      | 0,22 |
| <u>Asplenium rutifolium</u>        | 1,00      | 1,17 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Blechnum australe</u>           | 0,05      | 0,22 | 0,05      | 0,22 | 0,20      | 0,52 |
| <u>Blechnum capense</u>            | 0,00      | 0,00 | 0,15      | 0,67 | 0,80      | 0,83 |
| <u>Blechnum giganteum</u>          | 0,00      | 0,00 | 0,35      | 0,67 | 0,55      | 0,51 |
| <u>Brachypodium flexum</u>         | 0,30      | 0,73 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Carex clavata</u>               | 0,05      | 0,22 | 0,00      | 0,00 | 0,25      | 0,44 |
| <u>Carissa bispinosa</u>           | 0,25      | 0,44 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Centella eriantha</u>           | 0,20      | 0,70 | 0,05      | 0,22 | 0,20      | 0,89 |
| <u>Cheilanthes viridis</u>         | 0,00      | 0,00 | 0,20      | 0,52 | 0,00      | 0,00 |
| <u>Clutia affinis</u>              | 0,40      | 0,50 | 0,15      | 0,37 | 0,45      | 0,51 |
| <u>Clutia pulchella</u>            | 0,10      | 0,31 | 0,40      | 0,60 | 0,25      | 0,44 |
| <u>Dietes iridioides</u>           | 2,10      | 1,68 | 1,30      | 0,86 | 1,90      | 2,13 |
| <u>Galopina circaeoides</u>        | 0,35      | 0,81 | 0,45      | 0,60 | 0,90      | 0,79 |
| <u>Myrsiphyllum scandens</u> #5 *5 | 0,10      | 0,31 | 1,20      | 0,83 | 0,50      | 0,61 |
| <u>Oplismenus hirtellus</u>        | 1,15      | 1,42 | 0,85      | 0,67 | 0,65      | 0,81 |
| <u>Oxalis purpurea</u>             | 1,70      | 1,03 | 1,35      | 1,14 | 0,90      | 0,79 |
| <u>Piloselloides cordata</u> #1 *1 | 0,90      | 0,72 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Plectranthus fruticosus</u>     | 0,00      | 0,00 | 0,00      | 0,00 | 0,05      | 0,22 |
| <u>Polystichum lucidum</u>         | 0,05      | 0,22 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Protasparagus setaceus</u> #4   | 0,55      | 0,60 | 0,00      | 0,00 | 0,00      | 0,00 |
| <u>Rumohra adiantiformis</u>       | 0,10      | 0,31 | 0,05      | 0,22 | 0,20      | 0,70 |
| <u>Schoenoxiphium ecklonii</u>     | 0,00      | 0,00 | 0,20      | 0,41 | 0,00      | 0,00 |
| <u>Schoenoxiphium lanceum</u>      | 2,75      | 1,80 | 2,20      | 1,32 | 0,80      | 1,06 |
| <u>Scirpus costatus</u>            | 0,75      | 1,25 | 0,05      | 0,22 | 0,05      | 0,22 |

# = Ranking according to univariate analysis of variance

\* = Ranking according to discriminant functions analysis

## Appendix 3. Litter invertebrates/litre as entered in the D.F.A.

| Classification class |            | Dry       |       | Moist     |       | Wet       |      |
|----------------------|------------|-----------|-------|-----------|-------|-----------|------|
|                      |            | $\bar{X}$ | S. D. | $\bar{X}$ | S.D.  | $\bar{X}$ | S.D. |
| ACARINA              | SMALL      | 0,64      | 1,03  | 1,73      | 1,99  | 0,74      | 0,67 |
|                      | MEDIUM     | 0,02      | 0,07  | 0,00      | 0,00  | 0,00      | 0,00 |
|                      | LARGE      | 0,00      | 0,00  | 0,00      | 0,00  | 0,00      | 0,00 |
| ANNELIDA             | SMALL      | 0,00      | 0,00  | 0,00      | 0,00  | 0,00      | 0,00 |
|                      | MEDIUM     | 0,00      | 0,00  | 0,00      | 0,00  | 0,00      | 0,00 |
|                      | LARGE      | 0,00      | 0,00  | 0,02      | 0,07  | 0,02      | 0,07 |
| ARACHNIDA            | SMALL      | 1,06      | 1,44  | 1,01      | 1,29  | 0,44      | 0,60 |
|                      | MEDIUM     | 0,31      | 0,49  | 0,35      | 0,43  | 0,36      | 0,45 |
|                      | LARGE      | 0,16      | 0,21  | 0,12      | 0,17  | 0,15      | 0,24 |
| BLATODEA             | SMALL      | 0,00      | 0,00  | 0,03      | 0,08  | 0,02      | 0,07 |
|                      | MEDIUM     | 0,01      | 0,04  | 0,00      | 0,00  | 0,03      | 0,08 |
|                      | LARGE      | 0,07      | 0,16  | 0,16      | 0,36  | 0,03      | 0,08 |
| COLEOPTERA           | SMALL 1#1* | 12,18     | 12,10 | 19,34     | 11,16 | 4,31      | 5,03 |
|                      | MEDIUM     | 6,10      | 6,91  | 10,02     | 5,86  | 5,68      | 7,34 |
|                      | LARGE      | 2,14      | 1,73  | 1,05      | 1,48  | 1,57      | 1,36 |
| COLLEMBOLA           | SMALL      | 0,00      | 0,00  | 0,08      | 0,22  | 0,19      | 0,44 |
|                      | MEDIUM     | 0,12      | 0,33  | 0,14      | 0,31  | 0,40      | 0,98 |
|                      | LARGE      | 1,42      | 2,94  | 0,88      | 2,23  | 1,74      | 4,05 |
| DIPTERA              | SMALL 3#   | 0,57      | 0,59  | 1,39      | 1,01  | 0,85      | 0,83 |
|                      | MEDIUM     | 0,50      | 0,73  | 0,56      | 0,98  | 0,93      | 1,17 |
|                      | LARGE      | 0,08      | 0,14  | 0,01      | 0,04  | 0,07      | 0,22 |
| FORMICIDAE           | SMALL      | 1,44      | 2,68  | 2,09      | 4,59  | 0,19      | 0,42 |
|                      | MEDIUM     | 2,77      | 4,80  | 0,75      | 1,12  | 1,38      | 2,16 |
|                      | LARGE      | 0,12      | 0,16  | 0,05      | 0,15  | 0,34      | 0,93 |
| HEMIPTERA            | SMALL 5#   | 0,01      | 0,04  | 0,00      | 0,00  | 0,09      | 0,19 |
|                      | MEDIUM     | 0,37      | 0,99  | 0,15      | 0,38  | 0,07      | 0,19 |
|                      | LARGE      | 0,12      | 0,25  | 0,17      | 0,43  | 0,14      | 0,36 |
| HYMENOPTERA          | SMALL      | 0,03      | 0,11  | 0,22      | 0,58  | 0,00      | 0,00 |
|                      | MEDIUM     | 0,00      | 0,00  | 0,12      | 0,22  | 0,03      | 0,11 |
|                      | LARGE      | 0,00      | 0,00  | 0,02      | 0,07  | 0,01      | 0,04 |
| LEPIDOPTERA          | SMALL      | 0,62      | 2,13  | 0,01      | 0,04  | 0,00      | 0,00 |
|                      | MEDIUM     | 0,17      | 0,54  | 0,02      | 0,07  | 0,04      | 0,14 |
|                      | LARGE      | 0,20      | 0,24  | 0,42      | 0,79  | 0,36      | 0,47 |
| MOLLUSCA             | SMALL      | 0,00      | 0,00  | 0,00      | 0,00  | 0,02      | 0,07 |
|                      | MEDIUM     | 0,05      | 0,15  | 0,02      | 0,07  | 0,03      | 0,06 |
|                      | LARGE      | 0,09      | 0,19  | 0,09      | 0,16  | 0,09      | 0,16 |
| MYRIAPODA            | SMALL      | 0,00      | 0,00  | 0,08      | 0,19  | 0,06      | 0,18 |
|                      | MEDIUM     | 0,08      | 0,22  | 0,22      | 0,38  | 0,55      | 1,07 |
|                      | LARGE      | 1,41      | 1,84  | 1,51      | 2,61  | 1,49      | 2,09 |
| ORTHOPTERA           | SMALL      | 0,02      | 0,07  | 0,01      | 0,04  | 0,04      | 0,10 |
|                      | MEDIUM 2#  | 0,15      | 0,27  | 0,01      | 0,04  | 0,00      | 0,00 |
|                      | LARGE      | 0,00      | 0,00  | 0,01      | 0,04  | 0,01      | 0,04 |
| SCORPIONIDAE         | SMALL      | 0,22      | 0,39  | 0,31      | 0,58  | 0,06      | 0,16 |
|                      | MEDIUM 4#  | 0,06      | 0,13  | 0,18      | 0,32  | 0,00      | 0,00 |
|                      | LARGE      | 0,00      | 0,00  | 0,00      | 0,00  | 0,00      | 0,00 |
| UNKNOWN              | SMALL      | 0,00      | 0,00  | 0,00      | 0,00  | 0,00      | 0,00 |
|                      | MEDIUM     | 0,00      | 0,00  | 0,00      | 0,00  | 0,00      | 0,00 |
|                      | LARGE      | 0,19      | 0,47  | 0,13      | 0,25  | 0,18      | 0,34 |

Ranking according to: # = univariate analysis of variance; \* = DFA.

## Appendix 4. Ground invertebrates/trap as entered in the D.F.A.

| Classification class |             | Dry       |      | Moist     |      | Wet       |      |
|----------------------|-------------|-----------|------|-----------|------|-----------|------|
|                      |             | $\bar{X}$ | S.D. | $\bar{X}$ | S.D. | $\bar{X}$ | S.D. |
| ANNELIDA             | SMALL       | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | MEDIUM      | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | LARGE       | 0,15      | 0,14 | 0,06      | 0,08 | 0,12      | 0,13 |
| ARACHNIDA            | SMALL       | 0,29      | 0,25 | 0,13      | 0,18 | 0,18      | 0,15 |
|                      | MEDIUM      | 0,21      | 0,12 | 0,16      | 0,19 | 0,40      | 0,72 |
|                      | LARGE       | 0,29      | 0,15 | 0,28      | 0,57 | 0,19      | 0,13 |
| BLATODEA             | SMALL       | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | MEDIUM      | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | LARGE 4#    | 0,10      | 0,10 | 0,02      | 0,04 | 0,05      | 0,06 |
| COLEOPTERA           | SMALL 2#2*  | 0,19      | 0,19 | 0,84      | 0,85 | 0,16      | 0,23 |
|                      | MEDIUM      | 0,14      | 0,14 | 0,25      | 0,20 | 0,28      | 0,18 |
|                      | LARGE 3#4*  | 1,23      | 0,82 | 2,21      | 1,02 | 1,09      | 0,65 |
| COLLEMBOLA           | SMALL       | 0,00      | 0,00 | 0,03      | 0,01 | 0,03      | 0,12 |
|                      | MEDIUM      | 0,21      | 0,22 | 0,20      | 0,23 | 0,45      | 0,61 |
|                      | LARGE 5#3*  | 1,09      | 0,59 | 0,75      | 0,47 | 1,44      | 0,97 |
| DIPTERA              | SMALL       | 1,89      | 1,41 | 1,22      | 0,97 | 1,87      | 1,64 |
|                      | MEDIUM      | 0,38      | 0,36 | 0,60      | 0,62 | 1,49      | 3,08 |
|                      | LARGE       | 0,60      | 0,33 | 0,54      | 0,43 | 0,79      | 0,43 |
| FORMICIDAE           | SMALL       | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | MEDIUM 1#1* | 1,46      | 1,35 | 0,31      | 0,30 | 0,17      | 0,17 |
|                      | LARGE       | 0,07      | 0,06 | 0,16      | 0,33 | 0,05      | 0,07 |
| HEMIPTERA            | SMALL       | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | MEDIUM      | 0,03      | 0,06 | 0,02      | 0,03 | 0,01      | 0,02 |
|                      | LARGE       | 0,02      | 0,05 | 0,01      | 0,02 | 0,03      | 0,07 |
| HYMENOPTERA          | SMALL       | 0,02      | 0,04 | 0,04      | 0,15 | 0,02      | 0,07 |
|                      | MEDIUM      | 0,10      | 0,21 | 0,05      | 0,07 | 0,03      | 0,05 |
|                      | LARGE       | 0,02      | 0,04 | 0,01      | 0,02 | 0,00      | 0,00 |
| LEPIDOPTERA          | SMALL       | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | MEDIUM      | 0,00      | 0,00 | 0,01      | 0,01 | 0,00      | 0,00 |
|                      | LARGE       | 0,03      | 0,04 | 0,02      | 0,04 | 0,03      | 0,05 |
| MOLLUSCA             | SMALL       | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | MEDIUM      | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | LARGE       | 0,02      | 0,03 | 0,01      | 0,01 | 0,03      | 0,03 |
| MYRIAPODA            | SMALL       | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | MEDIUM      | 0,00      | 0,00 | 0,01      | 0,01 | 0,02      | 0,06 |
|                      | LARGE       | 0,27      | 0,21 | 0,12      | 0,15 | 0,20      | 0,21 |
| ORTHOPTERA           | SMALL       | 0,04      | 0,09 | 0,04      | 0,10 | 0,01      | 0,01 |
|                      | MEDIUM      | 0,17      | 0,37 | 0,10      | 0,17 | 0,02      | 0,05 |
|                      | LARGE       | 1,44      | 1,59 | 0,99      | 0,86 | 0,81      | 0,71 |
| PLATYHELMINTHES      | SMALL       | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | MEDIUM      | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | LARGE       | 2,62      | 3,21 | 3,93      | 3,66 | 4,20      | 4,64 |
| SCORPIONIDAE         | SMALL       | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | MEDIUM      | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | LARGE       | 0,00      | 0,00 | 0,01      | 0,01 | 0,00      | 0,00 |
| UNKNOWN              | SMALL       | 0,00      | 0,00 | 0,00      | 0,00 | 0,00      | 0,00 |
|                      | MEDIUM      | 0,00      | 0,00 | 0,01      | 0,02 | 0,00      | 0,00 |
|                      | LARGE       | 0,01      | 0,03 | 0,01      | 0,02 | 0,01      | 0,03 |

Ranking according to: # = univariate analysis of variance; \* = DFA.



## Appendix 5. Aerial invertebrates/plaque as entered in the D.F.A.

| Height class<br>(m) | Size       | Dry       |      | Moist     |      | Wet       |      |
|---------------------|------------|-----------|------|-----------|------|-----------|------|
|                     |            | $\bar{X}$ | S.D. | $\bar{X}$ | S.D. | $\bar{X}$ | S.D. |
| 0                   | SMALL      | 3,08      | 1,72 | 3,31      | 2,72 | 4,70      | 3,74 |
|                     | MEDIUM     | 1,26      | 1,78 | 1,27      | 1,82 | 1,10      | 1,47 |
|                     | LARGE      | 0,76      | 0,80 | 0,61      | 0,71 | 0,69      | 1,08 |
| 0,5                 | SMALL 1#1* | 2,15      | 1,19 | 1,68      | 0,97 | 3,36      | 1,84 |
|                     | MEDIUM     | 0,40      | 0,44 | 0,33      | 0,30 | 0,55      | 0,58 |
|                     | LARGE      | 0,36      | 0,37 | 0,20      | 0,20 | 0,33      | 0,51 |
| 1,0                 | SMALL 5#   | 1,76      | 1,11 | 1,51      | 0,81 | 2,57      | 1,46 |
|                     | MEDIUM     | 0,29      | 0,41 | 0,26      | 0,27 | 0,36      | 0,42 |
|                     | LARGE      | 0,23      | 0,26 | 0,16      | 0,21 | 0,25      | 0,37 |
| 1,5                 | SMALL 4#   | 1,43      | 0,68 | 1,12      | 0,72 | 2,04      | 1,28 |
|                     | MEDIUM     | 0,34      | 0,43 | 0,32      | 0,34 | 0,38      | 0,46 |
|                     | LARGE      | 0,16      | 0,20 | 0,10      | 0,15 | 0,28      | 0,34 |
| 2,0                 | SMALL      | 1,26      | 0,66 | 1,14      | 0,67 | 1,71      | 1,03 |
|                     | MEDIUM     | 0,30      | 0,32 | 0,25      | 0,32 | 0,35      | 0,51 |
|                     | LARGE      | 0,14      | 0,23 | 0,15      | 0,21 | 0,23      | 0,24 |
| 4,0                 | SMALL      | 1,22      | 0,84 | 1,08      | 0,55 | 1,56      | 1,35 |
|                     | MEDIUM     | 0,29      | 0,28 | 0,20      | 0,25 | 0,38      | 0,42 |
|                     | LARGE      | 0,24      | 0,23 | 0,19      | 0,27 | 0,16      | 0,24 |
| 6,0                 | SMALL      | 1,09      | 0,67 | 1,19      | 0,95 | 1,16      | 0,65 |
|                     | MEDIUM     | 0,24      | 0,36 | 0,20      | 0,22 | 0,26      | 0,37 |
|                     | LARGE 5*   | 0,39      | 0,53 | 0,15      | 0,20 | 0,19      | 0,20 |
| 8,0                 | SMALL      | 1,10      | 0,76 | 1,05      | 0,74 | 1,46      | 0,99 |
|                     | MEDIUM     | 0,28      | 0,30 | 0,20      | 0,26 | 0,27      | 0,36 |
|                     | LARGE      | 0,29      | 0,30 | 0,16      | 0,22 | 0,23      | 0,28 |
| 10,0                | SMALL      | 1,35      | 1,23 | 1,37      | 1,04 | 1,39      | 0,89 |
|                     | MEDIUM     | 0,31      | 0,33 | 0,21      | 0,32 | 0,26      | 0,30 |
|                     | LARGE      | 0,27      | 0,33 | 0,14      | 0,16 | 0,23      | 0,29 |
| 12,0                | SMALL      | 1,40      | 0,89 | 1,44      | 1,00 | 1,52      | 1,09 |
|                     | MEDIUM 4*  | 0,42      | 0,41 | 0,19      | 0,23 | 0,26      | 0,28 |
|                     | LARGE      | 0,28      | 0,34 | 0,17      | 0,23 | 0,20      | 0,30 |
| 14,0                | SMALL      | 1,81      | 1,39 | 1,54      | 1,00 | 1,68      | 1,26 |
|                     | MEDIUM     | 0,43      | 0,63 | 0,35      | 0,29 | 0,30      | 0,43 |
|                     | LARGE      | 0,24      | 0,31 | 0,24      | 0,27 | 0,30      | 0,28 |
| 16,0                | SMALL 2*   | 2,32      | 1,23 | 2,06      | 1,16 | 2,06      | 1,41 |
|                     | MEDIUM     | 0,44      | 0,48 | 0,34      | 0,27 | 0,40      | 0,46 |
|                     | LARGE      | 0,34      | 0,42 | 0,36      | 0,36 | 0,42      | 0,47 |
| 18,0                | SMALL 2#   | 1,33      | 1,90 | 0,90      | 1,58 | 2,94      | 1,83 |
|                     | MEDIUM 3#  | 0,19      | 0,27 | 0,11      | 0,22 | 0,54      | 0,57 |
|                     | LARGE      | 0,29      | 0,53 | 0,12      | 0,24 | 0,55      | 0,87 |
| 20,0                | SMALL      | 0,06      | 0,40 | 0,12      | 0,58 | 0,84      | 1,66 |
|                     | MEDIUM     | 0,06      | 0,02 | 0,12      | 0,21 | 0,84      | 0,57 |
|                     | LARGE      | 0,02      | 0,16 | 0,04      | 0,19 | 0,37      | 0,79 |

# = Ranking according to univariate analysis of variance.

\* = Ranking according to D.F.A.

**Appendix 6.** Monthly biomass of the litter invertebrates/litre

| Date    | Size class | Biomass (g) |        |        |
|---------|------------|-------------|--------|--------|
|         |            | Dry         | Moist  | Wet    |
| 1/1984  | SMALL      | 0,2522      | 0,1957 | 0,2173 |
|         | MEDIUM     | 0,1460      | 0,1108 | 0,0408 |
|         | LARGE      | 0,2157      | 0,3277 | 0,4491 |
| 2/1984  | SMALL      | 1,4109      | 0,3356 | 0,3629 |
|         | MEDIUM     | 0,7968      | 0,3323 | 0,1648 |
|         | LARGE      | 1,4899      | 0,2222 | 0,5631 |
| 3/1984  | SMALL      | 0,5440      | 0,3054 | 0,1997 |
|         | MEDIUM     | 0,1296      | 0,3836 | 0,1025 |
|         | LARGE      | 0,4867      | 0,9694 | 0,2676 |
| 4/1983  | SMALL      | 0,0920      | 0,1102 | 0,0256 |
|         | MEDIUM     | 0,3711      | 0,1529 | 0,1064 |
|         | LARGE      | 3,7462      | 0,3186 | 0,6143 |
| 5/1983  | SMALL      | 0,0080      | 0,0530 | 0,0097 |
|         | MEDIUM     | 0,0430      | 0,2160 | 0,0363 |
|         | LARGE      | 0,1360      | 0,2590 | 0,0575 |
| 6/1983  | SMALL      | 0,0070      | 0,0420 | 0,0110 |
|         | MEDIUM     | 0,0730      | 0,1750 | 0,0740 |
|         | LARGE      | 0,0860      | 0,0330 | 0,6770 |
| 7/1983  | SMALL      | 0,0140      | 0,0520 | 0,0070 |
|         | MEDIUM     | 0,0540      | 0,2010 | 0,0910 |
|         | LARGE      | 0,0650      | 0,2660 | 0,1700 |
| 8/1983  | SMALL      | 0,0030      | 0,0210 | 0,0030 |
|         | MEDIUM     | 0,0320      | 0,1260 | 0,0090 |
|         | LARGE      | 0,1170      | 0,0040 | 0,0250 |
| 9/1983  | SMALL      | 0,0660      | 0,0310 | 0,0290 |
|         | MEDIUM     | 0,1320      | 0,2250 | 0,2550 |
|         | LARGE      | 0,6550      | 0,0450 | 0,9480 |
| 10/1983 | SMALL      | 0,1090      | 0,0220 | 0,0120 |
|         | MEDIUM     | 0,3150      | 0,3030 | 0,1310 |
|         | LARGE      | 0,6690      | 0,0010 | 0,7870 |
| 11/1983 | SMALL      | 0,0230      | 0,0990 | 0,0100 |
|         | MEDIUM     | 0,2550      | 0,4670 | 0,0740 |
|         | LARGE      | 0,0020      | 0,2040 | 0,1550 |
| 12/1983 | SMALL      | 0,2620      | 0,2620 | 0,0630 |
|         | MEDIUM     | 0,9910      | 1,4960 | 0,6460 |
|         | LARGE      | 1,1250      | 1,2520 | 0,3620 |

**Appendix 7.** Monthly biomass of the ground invertebrates/25 traps

| Date    | Size class | Biomass (g) |         |         |
|---------|------------|-------------|---------|---------|
|         |            | Dry         | Moist   | Wet     |
| 1/1984  | SMALL      | 00,0390     | 00,0600 | 00,0390 |
|         | MEDIUM     | 00,1440     | 00,0510 | 00,0780 |
|         | LARGE      | 10,8470     | 11,9040 | 13,5950 |
| 2/1984  | SMALL      | 00,0220     | 00,0470 | 00,0340 |
|         | MEDIUM     | 00,1450     | 02,0760 | 00,4620 |
|         | LARGE      | 37,3550     | 33,6510 | 30,0440 |
| 3/1984  | SMALL      | 00,3130     | 00,0340 | 00,0190 |
|         | MEDIUM     | 00,0380     | 00,0560 | 00,0410 |
|         | LARGE      | 17,6660     | 16,1070 | 07,3400 |
| 4/1983  | SMALL      | 00,0284     | 00,0391 | 00,0119 |
|         | MEDIUM     | 00,0952     | 00,1326 | 00,0374 |
|         | LARGE      | 15,7832     | 05,0014 | 12,0326 |
| 5/1983  | SMALL      | 00,0050     | 00,0100 | 00,0117 |
|         | MEDIUM     | 00,0534     | 00,0451 | 00,0534 |
|         | LARGE      | 03,6640     | 04,0631 | 04,0681 |
| 6/1983  | SMALL      | 00,0067     | 00,0234 | 00,0033 |
|         | MEDIUM     | 00,0451     | 00,0167 | 00,0334 |
|         | LARGE      | 04,7345     | 10,4776 | 02,1226 |
| 7/1983  | SMALL      | 00,0100     | 00,0401 | 00,0351 |
|         | MEDIUM     | 00,0919     | 00,0735 | 00,2371 |
|         | LARGE      | 01,7953     | 03,0945 | 04,1700 |
| 8/1983  | SMALL      | 00,0150     | 00,0134 | 00,0084 |
|         | MEDIUM     | 00,0685     | 00,0351 | 00,0251 |
|         | LARGE      | 07,4465     | 05,8266 | 07,4232 |
| 9/1983  | SMALL      | 00,0418     | 00,0551 | 00,0301 |
|         | MEDIUM     | 00,2071     | 00,2221 | 00,1837 |
|         | LARGE      | 16,3493     | 08,3533 | 13,3700 |
| 10/1983 | SMALL      | 00,0170     | 00,0200 | 00,0620 |
|         | MEDIUM     | 00,0340     | 00,0370 | 00,2950 |
|         | LARGE      | 05,2550     | 01,4980 | 03,3220 |
| 11/1983 | SMALL      | 00,1130     | 00,0630 | 00,0120 |
|         | MEDIUM     | 00,2790     | 00,6260 | 00,0800 |
|         | LARGE      | 13,5720     | 02,8360 | 23,0370 |
| 12/1983 | SMALL      | 00,0530     | 00,0190 | 00,0280 |
|         | MEDIUM     | 00,5600     | 00,0200 | 00,1370 |
|         | LARGE      | 05,6780     | 02,4090 | 21,4890 |

Appendix 8. Monthly densities/ha for birds in the dry forest study site

| Species                          | Jan         | Feb        | Mar        | Apr        | May        | Jun        | Jul        | Aug         | Sep        | Oct         | Nov        | Dec        |
|----------------------------------|-------------|------------|------------|------------|------------|------------|------------|-------------|------------|-------------|------------|------------|
| <u>Andropadus importunus</u>     | 1,90        | 1,21       | 1,59       | 0,95       | 1,59       | 1,71       | 1,45       | 1,59        | 0,85       | 1,27        | 0,74       | 0,79       |
| <u>Apalis thoracica</u>          | 0,11        | 0          | 0,10       | 0,07       | 0,07       | 0,06       | 0          | 0           | 0          | 0,06        | 0,19       | 0,05       |
| <u>Apaloderma narina</u>         | 0,23        | 0          | 0,05       | 0          | 0          | 0          | 0          | 0           | 0,06       | 0,06        | 0,29       | 0,32       |
| <u>Aplopelia larvata</u>         | 0,05        | 0,24       | 0,15       | 0,15       | 0,15       | 0,19       | 0,05       | 0           | 0          | 0,13        | 0,29       | 0,22       |
| <u>Batis capensis</u>            | 0,29        | 0,30       | 0,37       | 0,32       | 0,08       | 0,13       | 0,46       | 0,95        | 0,11       | 0,44        | 0,29       | 0,05       |
| <u>Camacroptera brachyura</u>    | 0,57        | 0          | 0,10       | 0,32       | 0,15       | 0          | 0,05       | 0,08        | 0          | 0,25        | 0,19       | 0,53       |
| <u>Campethera notata</u>         | 0           | 0          | 0          | 0          | 0          | 0,06       | 0          | 0           | 0          | 0           | 0          | 0          |
| <u>Chrysococcyx cupreus</u>      | 0           | 0          | 0          | 0          | 0          | 0          | 0          | 0           | 0          | 0,06        | 0,05       | 0          |
| <u>Columba arquatrix</u>         | 0,29        | 0,36       | 0,10       | 0          | 0,24       | 0,13       | 0          | 0           | 0          | 0,06        | 0          | 0          |
| <u>Cossypha dichroa</u>          | 0,11        | 0          | 0,05       | 0          | 0          | 0,13       | 0,05       | 0,08        | 0          | 0           | 0,05       | 0,05       |
| <u>Cuculus solitarius</u>        | 0           | 0          | 0          | 0          | 0          | 0          | 0          | 0           | 0          | 0           | 0,10       | 0          |
| <u>Dicrurus adsimilis</u>        | 0           | 0,06       | 0          | 0          | 0,08       | 0          | 0          | 0           | 0          | 0           | 0          | 0          |
| <u>Dryoscopus cubla</u>          | 0,18        | 0,97       | 0,47       | 0,15       | 0,24       | 0,44       | 0,57       | 0,47        | 0,48       | 0,51        | 0,19       | 0,42       |
| <u>Mesopicos griseocephalus</u>  | 0,18        | 0,11       | 0,05       | 0,08       | 0,24       | 0,06       | 0,18       | 0,08        | 0          | 0,19        | 0          | 0,05       |
| <u>Nectarinia chalybea</u>       | 0,05        | 0          | 0          | 0          | 0,24       | 0,89       | 2,20       | 2,22        | 1,99       | 1,65        | 0,82       | 0,85       |
| <u>Oriolus larvatus</u>          | 0,11        | 0          | 0,10       | 0,15       | 0,15       | 0          | 0,11       | 0,32        | 0,06       | 0,13        | 0,19       | 0          |
| <u>Phoeniculus purpureus</u>     | 0,41        | 0,11       | 0          | 0,64       | 0,47       | 0,06       | 0,34       | 0,47        | 0,36       | 0,32        | 0          | 0          |
| <u>Phyllastrephus terrestris</u> | 0,64        | 0,66       | 0,10       | 0,39       | 0,64       | 1,21       | 0,52       | 1,10        | 0          | 0,38        | 0          | 0,53       |
| <u>Pogonocichla stellata</u>     | 0           | 0,06       | 0,10       | 0          | 0,08       | 0          | 0          | 0           | 0          | 0,06        | 0          | 0,22       |
| <u>Prodotiscus regulus</u>       | 0           | 0          | 0          | 0          | 0          | 0          | 0,05       | 0           | 0          | 0           | 0          | 0          |
| <u>Seicercus ruficapillus</u>    | 0,46        | 0,55       | 0,37       | 0,15       | 0,39       | 0,25       | 0,23       | 0,39        | 0,24       | 0,25        | 0,05       | 0,32       |
| <u>Serinus scotops</u>           | 0           | 0          | 0          | 1,58       | 0          | 0,06       | 0          | 0           | 0          | 0,06        | 0,10       | 0          |
| <u>Streptopelia semitorquata</u> | 0,05        | 0          | 0          | 0          | 0          | 0          | 0          | 0           | 0          | 0,06        | 0,05       | 0,05       |
| <u>Terpsiphone viridis</u>       | 0,23        | 0,11       | 0,05       | 0          | 0          | 0          | 0          | 0           | 0          | 0           | 0          | 0          |
| <u>Touraco corythaix</u>         | 1,68        | 0,48       | 0,58       | 0,71       | 0,47       | 0,70       | 0,41       | 0,32        | 0,79       | 0,57        | 0,19       | 0,47       |
| <u>Turdus olivaceus</u>          | 0,29        | 0,79       | 1,22       | 0,15       | 0,32       | 0,89       | 0,68       | 0,39        | 0,61       | 1,40        | 1,03       | 0,22       |
| <u>Zosterops pallidus</u>        | 3,92        | 0,96       | 0,79       | 0,15       | 1,74       | 0,70       | 0,23       | 1,91        | 2,54       | 3,01        | 1,03       | 1,85       |
| <b>BIRDS / ha</b>                | <b>11,9</b> | <b>7,0</b> | <b>6,4</b> | <b>6,0</b> | <b>7,3</b> | <b>7,7</b> | <b>7,6</b> | <b>10,3</b> | <b>8,1</b> | <b>10,9</b> | <b>5,8</b> | <b>7,2</b> |

Appendix 9. Monthly densities/ha for birds in the moist forest study site

| Species                          | Jan        | Feb        | Mar        | Apr        | May        | Jun        | Jul        | Aug        | Sep        | Oct         | Nov        | Dec        |
|----------------------------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|-------------|------------|------------|
| <u>Accipiter tachiro</u>         | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0,06        | 0          | 0          |
| <u>Andropadus importunus</u>     | 2,18       | 1,33       | 1,32       | 1,98       | 1,74       | 1,27       | 1,09       | 1,27       | 0,97       | 1,84        | 0,63       | 1,27       |
| <u>Apalis thoracica</u>          | 0,23       | 0,06       | 0,05       | 0,08       | 0          | 0          | 0          | 0,32       | 0,11       | 0,19        | 0,05       | 0,10       |
| <u>Apaloderma narina</u>         | 0          | 0          | 0          | 0          | 0,15       | 0          | 0          | 0          | 0          | 0,06        | 0,05       | 0          |
| <u>Aplopelia larvata</u>         | 0,11       | 0,30       | 0,27       | 0,15       | 0,32       | 0,06       | 0,46       | 0,15       | 0,06       | 0           | 0,19       | 0,10       |
| <u>Batis capensis</u>            | 0,57       | 0,30       | 0,15       | 0,47       | 0,32       | 0,25       | 0,11       | 0,15       | 0,24       | 0,76        | 0,14       | 0,64       |
| <u>Bostreychia hagedash</u>      | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0,08       | 0          | 0           | 0          | 0          |
| <u>Camaroptera brachyura</u>     | 0,41       | 0,06       | 0,22       | 0,24       | 0,08       | 0          | 0          | 0,08       | 0          | 0,06        | 0,05       | 0,27       |
| <u>Chrysococcyx cupreus</u>      | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0           | 0,05       | 0          |
| <u>Columba arquatrix</u>         | 0,05       | 0,06       | 0,22       | 0,15       | 0          | 0          | 0,05       | 0,15       | 0,06       | 0           | 0          | 0          |
| <u>Coracina caesia</u>           | 0,11       | 0,24       | 0,05       | 0,32       | 0,08       | 0          | 0          | 0          | 0          | 0,13        | 0          | 0,05       |
| <u>Cossypha caffra</u>           | 0          | 0          | 0,05       | 0          | 0,08       | 0          | 0          | 0          | 0          | 0           | 0          | 0,05       |
| <u>Cossypha dichroa</u>          | 0          | 0,06       | 0          | 0          | 0          | 0,06       | 0,11       | 0          | 0          | 0           | 0,19       | 0,15       |
| <u>Dicrurus adsimilis</u>        | 0          | 0,06       | 0          | 0          | 0          | 0,06       | 0          | 0          | 0          | 0           | 0          | 0          |
| <u>Dryoscopus cubla</u>          | 0,46       | 0,36       | 0,42       | 0,15       | 0,39       | 0,13       | 0,34       | 0,32       | 0,18       | 0,51        | 0,14       | 0,32       |
| <u>Indicator minor</u>           | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0,08       | 0          | 0           | 0          | 0          |
| <u>Laniarius ferrugineus</u>     | 0,05       | 0,18       | 0,10       | 0          | 0,08       | 0          | 0,23       | 0,15       | 0          | 0,13        | 0          | 0,22       |
| <u>Mesopicos griseocephalus</u>  | 0,34       | 0          | 0,10       | 0,15       | 0,15       | 0,19       | 0,23       | 0,08       | 0          | 0,19        | 0,10       | 0,10       |
| <u>Nectarinia amethystina</u>    | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0           | 0,19       | 0          |
| <u>Nectarinia chalybea</u>       | 0,18       | 0,06       | 0          | 0,15       | 1,59       | 1,40       | 2,83       | 2,54       | 3,33       | 2,79        | 1,75       | 0,85       |
| <u>Oriolus larvatus</u>          | 0,29       | 0,18       | 0,10       | 0,24       | 0,08       | 0,13       | 0,05       | 0,15       | 0,06       | 0           | 0          | 0,05       |
| <u>Phoeniculus purpureus</u>     | 0          | 0,61       | 0          | 0          | 0          | 0,32       | 0,46       | 0,32       | 0          | 0           | 0          | 0          |
| <u>Phyllastrephus terrestris</u> | 1,04       | 0,42       | 0,15       | 1,19       | 0,24       | 0          | 0,64       | 0,24       | 0          | 0,25        | 0,64       | 0,32       |
| <u>Pogonochla stellata</u>       | 0,11       | 0          | 0          | 0          | 0          | 0          | 0          | 0          | 0,11       | 0           | 0,05       | 0,05       |
| <u>Seicercus ruficapillus</u>    | 0,52       | 0,55       | 0,47       | 0,56       | 0,47       | 0,13       | 0,29       | 0,24       | 0,36       | 0,70        | 0,05       | 0,10       |
| <u>Streptopelia semitorquata</u> | 0,05       | 0          | 0,10       | 0,08       | 0          | 0          | 0,23       | 0          | 0,06       | 0           | 0          | 0,15       |
| <u>Terpsiphone viridis</u>       | 0,11       | 0,18       | 0,05       | 0          | 0          | 0          | 0          | 0          | 0          | 0           | 0          | 0          |
| <u>Touraco corythaix</u>         | 0,57       | 0,48       | 0,63       | 0,79       | 0          | 0          | 0,29       | 0,08       | 0,30       | 0,76        | 0,14       | 0,27       |
| <u>Trochocercus cyanomelas</u>   | 0,11       | 0,06       | 0,05       | 0,08       | 0          | 0          | 0          | 0          | 0,06       | 0           | 0          | 0          |
| <u>Turdus olivaceus</u>          | 0,52       | 0,18       | 0,85       | 0,47       | 0,15       | 0,19       | 0,64       | 0,32       | 0,48       | 0,51        | 0,53       | 0,74       |
| <u>Zosterops pallidus</u>        | 0,75       | 0          | 0,32       | 0,88       | 0          | 0,25       | 0          | 1,74       | 1,99       | 2,16        | 2,64       | 1,42       |
| <b>BIRDS / ha</b>                | <b>8,8</b> | <b>5,7</b> | <b>5,7</b> | <b>8,1</b> | <b>5,9</b> | <b>4,4</b> | <b>8,1</b> | <b>8,5</b> | <b>8,4</b> | <b>11,1</b> | <b>7,6</b> | <b>7,2</b> |

Appendix 10. Monthly densities/ha for birds in the wet forest study site

| Species                          | Jan        | Feb        | Mar         | Apr        | May         | Jun        | Jul        | Aug        | Sep         | Oct         | Nov         | Dec        |
|----------------------------------|------------|------------|-------------|------------|-------------|------------|------------|------------|-------------|-------------|-------------|------------|
| <u>Accipiter tachiro</u>         | 0          | 0          | 0           | 0,08       | 0           | 0          | 0          | 0,08       | 0           | 0           | 0           | 0,05       |
| <u>Andropadus importunus</u>     | 0,52       | 0,72       | 0,53        | 0,95       | 1,27        | 0,38       | 0,75       | 0,88       | 0,85        | 1,46        | 0,83        | 0,64       |
| <u>Apalis thoracica</u>          | 0          | 0          | 0,05        | 0          | 0           | 0          | 0,05       | 0          | 0,06        | 0           | 0,14        | 0,05       |
| <u>Apaloderma narina</u>         | 0          | 0          | 0           | 0          | 0           | 0          | 0          | 0          | 0           | 0,06        | 0,34        | 0          |
| <u>Aplopelia larvata</u>         | 0,11       | 0,18       | 0,27        | 0,08       | 0,08        | 0,25       | 0,41       | 0          | 0,24        | 0,06        | 0,24        | 0,10       |
| <u>Batis capensis</u>            | 0          | 0,18       | 0,27        | 0          | 0           | 0,13       | 0,05       | 0,32       | 0,55        | 0,32        | 0,34        | 0,05       |
| <u>Camaroptera brachyura</u>     | 0,11       | 0,11       | 0           | 0          | 0           | 0          | 0          | 0          | 0           | 0,13        | 0,19        | 0,15       |
| <u>Chrysococcyx cupreus</u>      | 0          | 0          | 0           | 0          | 0           | 0          | 0          | 0          | 0           | 0           | 0,05        | 0,05       |
| <u>Columba arquatrix</u>         | 0,05       | 0,79       | 0,58        | 0          | 3,10        | 0,06       | 0,05       | 0,47       | 0,24        | 0           | 0           | 0          |
| <u>Coracina caesia</u>           | 0,11       | 0,11       | 0,05        | 0,24       | 0,08        | 0,06       | 0,05       | 0,32       | 0,18        | 0,19        | 0,05        | 0,10       |
| <u>Cossypha caffra</u>           | 0,11       | 0          | 0,22        | 0          | 0,15        | 0,06       | 0,05       | 0,08       | 0           | 0,13        | 0,14        | 0,15       |
| <u>Cossypha dichroa</u>          | 0,18       | 0,18       | 0,22        | 0          | 0,15        | 0,13       | 0,18       | 0,15       | 0,18        | 0,38        | 0,14        | 0          |
| <u>Cuculus solitarius</u>        | 0          | 0          | 0           | 0          | 0           | 0          | 0          | 0          | 0           | 0,06        | 0,10        | 0,05       |
| <u>Dryoscopus cubla</u>          | 0,34       | 0          | 0,47        | 0          | 0           | 0          | 0          | 0,08       | 0,24        | 0,44        | 0,14        | 0,10       |
| <u>Laniarius ferrugineus</u>     | 0,05       | 0,06       | 0           | 0          | 0           | 0          | 0          | 0          | 0           | 0           | 0,05        | 0          |
| <u>Mesopicos griseocephalus</u>  | 0,05       | 0,18       | 0,42        | 0          | 0           | 0,25       | 0,23       | 0,08       | 0,24        | 0,06        | 0,10        | 0          |
| <u>Nectarinia amethystina</u>    | 0          | 0          | 0           | 0          | 0           | 0          | 0          | 0          | 0           | 0           | 0,14        | 0          |
| <u>Nectarinia chalybea</u>       | 0,29       | 0          | 0,05        | 0          | 0,47        | 0,25       | 2,31       | 2,62       | 3,26        | 2,92        | 2,49        | 1,59       |
| <u>Oriolus larvatus</u>          | 0,41       | 0,18       | 0,27        | 0,39       | 0,47        | 0,19       | 0,23       | 0,32       | 0,24        | 0,57        | 0,48        | 0,20       |
| <u>Phoeniculus purpureus</u>     | 0          | 0          | 0           | 0,15       | 0           | 0          | 0          | 0,32       | 0           | 0           | 0,64        | 0          |
| <u>Phyllastrephus terrestris</u> | 0,18       | 0,48       | 1,27        | 0          | 0           | 0,32       | 0,86       | 0,47       | 0,11        | 0           | 0,44        | 0,20       |
| <u>Pogonocichla stellata</u>     | 0          | 0,36       | 0,05        | 0          | 0           | 0,13       | 0,18       | 0,08       | 0           | 0,06        | 0,34        | 0,15       |
| <u>Seicercus ruficapillus</u>    | 0,23       | 0,66       | 0,58        | 0,32       | 0,88        | 0,64       | 0,69       | 0,71       | 0,55        | 0,32        | 0,19        | 0,42       |
| <u>Serinus scotops</u>           | 0          | 0,18       | 0,64        | 0          | 0           | 0          | 0          | 0          | 0           | 0           | 0,10        | 0          |
| <u>Terpsiphone viridis</u>       | 0,05       | 0,18       | 0,10        | 0          | 0           | 0          | 0          | 0          | 0           | 0,06        | 0,05        | 0          |
| <u>Touraco corythaix</u>         | 0,41       | 0,30       | 0,37        | 0          | 0,15        | 0          | 0          | 0,15       | 0,30        | 0,32        | 0,29        | 0,90       |
| <u>Trochocercus cyanomelas</u>   | 0,11       | 0          | 0,15        | 0          | 0           | 0          | 0          | 0          | 0           | 0,19        | 0           | 0          |
| <u>Turdus olivaceus</u>          | 0,57       | 0,61       | 1,05        | 0,71       | 1,83        | 0,89       | 0,81       | 0,32       | 1,99        | 0,64        | 0,53        | 0,53       |
| <u>Zosterops pallidus</u>        | 2,54       | 0,42       | 2,86        | 1,59       | 1,51        | 0,70       | 0,75       | 1,59       | 5,93        | 2,79        | 4,34        | 2,59       |
| <b>BIRDS / ha</b>                | <b>6,4</b> | <b>5,9</b> | <b>10,5</b> | <b>4,5</b> | <b>10,1</b> | <b>4,4</b> | <b>7,7</b> | <b>9,0</b> | <b>15,2</b> | <b>11,2</b> | <b>12,9</b> | <b>8,1</b> |