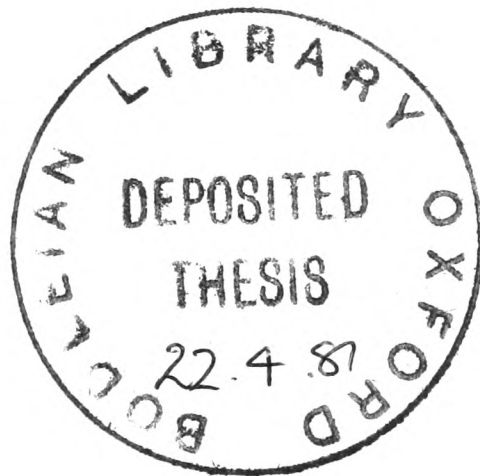


THE HABITATS AND FEEDING STATIONS OF
BIRDS IN TSAVO NATIONAL PARK, KENYA

A thesis submitted for the degree of
Doctor of Philosophy

by

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ABSTRACT

The land-bird community of Tsavo East National Park was studied for two years. There are two wet seasons each year: November-December and April-May, but the latter were very poor in both study years. Six habitat types were designated on the basis of canopy cover of woody vegetation. Riverine vegetation was also studied. Most of the open habitats extant are derived from woodland by destruction of trees, a process largely caused by elephants.

Food supplies are seasonally variable. Insects and grass seeds are most abundant in December and January. In the open habitats the few fruits also peak then, but Commiphora spp., which is only in woodland and is the most abundant fruit in Tsavo, peaks July to September.

The ecology of each species of land-bird is described and most are found to be ecologically separate from each other.

The annual cycle of numbers of birds in each habitat is closely correlated with the food supplies. In the open habitats birds are almost all insectivorous, granivorous or both, and peak numbers (about five times the dry season density) occur in December and January. In woodland, numbers remain fairly constant through the year and frugivores are more prominent, especially around August. The wet season peaks in all habitats are caused by immigrations of different species, both from elsewhere in Africa most of which come in to breed, and species which breed in the Palaearctic. The August peak in Woodland consists mainly of species which have resident populations.

The results are particularly related to the recent habitat changes in the Park. They are compared with other bird studies in African savannas and other components of the Tsavo ecosystem. Finally, the means by which birds are able to survive in the harsh and unpredictable conditions of Tsavo are discussed.

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CHAPTER 1 General Introduction

1.1. Aims and Scope

This study was carried out in Tsavo East National Park, Kenya from November 1974 till January 1977. The main aims of the project were:

1. to complete an annotated list/^{of} all the birds that occur in Tsavo East National Park (N.P.) and its immediate surrounds
2. to determine the habitat distribution of each bird species
3. to determine the numbers of each species in each habitat
4. to determine any seasonal changes in species and numbers in each habitat
5. to determine an outline of the feeding ecology of each species
6. from a knowledge of the available food types to try to determine the reasons for any patterns of distribution and abundance found.

An annotated list has been prepared in conjunction with Drs. W. Leuthold and C. Smeenk (Lack, Leuthold & Smeenk 1980). The remaining aims are the concern of this thesis. The emphasis is on the effects that the elephant-induced habitat changes in the Park, since it was gazetted in 1948, have had on the bird populations. The study is restricted to land-birds since these are the species more likely to be affected by such changes. Water-birds were not studied in detail because their habitats are very localised in Tsavo East N.P. and they can be studied more comprehensively elsewhere. Birds of prey too are omitted. They have been the subject of a separate study by Smeenk (1974), and because they are mostly large and wide-ranging species, they would have required different methods of study.

In this chapter I present a brief summary of relevant bird research in the savannas of Africa south of the Sahara and of previous research in Tsavo N.P. The environment of the Park, especially the climate and the vegetation types is described in Chapter 2. In Chapter 3 I describe the main methods of bird censusing that I used. The food supplies and their

seasonal variation are discussed in Chapter 4. In Chapter 5 the bird species found are treated family by family with respect to their habitat selection and feeding ecology, emphasising the means by which they are separated ecologically from each other. The bird community, as a whole, in each habitat at each season is described in Chapter 6, and is compared to other savanna bird communities that have been studied in Africa. Finally, in Chapter 7, the life cycles of the birds are discussed, especially the breeding seasons and movements.

1.2. Previous ornithological work in the savannas of Africa south of the Sahara

There are only two ecological studies of the bird community of savanna in the whole of eastern Africa, and both deal only with very small plots. Angwin (1968) worked on a 2 acre (about 1 ha) plot of riverine Acacia woodland in Nairobi N.P. and Beals (1970) worked on a 2 ha plot of Euphorbia-Acacia woodland in the Rift Valley of Ethiopia. Two groups land-birds have, however, received some more detailed attention: the birds of prey by, for example, Brown (1966) and Smeenk (1974), and the Palaearctic migrants by, for example, Pearson (1972), Britton (1974), Pearson & Backhurst (1976) and Sinclair (1978); but of these latter authors only Britton (1974) did more than discuss the timing of movements, although Sinclair (1978) attempted to relate the movements, and the breeding seasons of the local species, to the seasonal abundance of insects.

This paucity of studies is the more surprising when one considers that much of the general descriptive information is available in two handbooks (Jackson 1938, Mackworth-Praed & Grant 1957-60), and many ecological problems have been raised in two works by Moreau (1966, 1972). Despite this, even now the majority of ornithological work in East Africa is carried out by amateurs, most of the professional ecologists being more concerned with large mammals and their management. National Parks organisations and others

are, however, beginning to realise that birds are important elements in East African ecosystems. This is both from the biological viewpoint - many are easily visible, sensitive indicators of ecological changes, apart from being always a common and conspicuous part of the vertebrate fauna; and from the economic viewpoint - they are increasingly a tourist attraction especially 'special interest' tours. In addition a few species are already, or have the potential for becoming, agricultural pests. Species lists already exist for many areas of tourist importance for example in Williams (1967); and for two National Parks detailed annotated lists are available - Arusha N.P., Tanzania (Beesley 1972), and Kidepo N.P., Uganda (Elliott 1972).

With a few notable exceptions the rest of Africa is in a similar situation. Again, handbooks exist for several countries, the most recent being for South Africa (McLachlan & Liversidge 1977), Malawi (Benson & Benson 1977) and Zambia (Benson et al. 1973). But there are only few quantitative studies of bird communities. In southern Africa, Maclean's (1969, 1970) studies in the Kalahari Desert are the most comprehensive. Winterbottom (1972a) reviewed the data on species composition of many habitat types, and gave bird density estimates for these where they were available. In West Africa there have been four thorough quantitative studies (one containing three sites), but all were based on single small plots none of which was larger than 50 ha. Two of these plots were in Sahel savanna and appear from the descriptions to be very similar to Tsavo N.P., both in climate and vegetation. These are the 25 ha plots studied by the Morels in Senegal, firstly near Richard Toll (Morel & Bourlière 1962, Morel 1968), and secondly the International Biological Programme plot near Fété Olé (Morel & Morel 1972, 1974, in press). The other two studies were both in areas of considerably higher rainfall, and hence lush vegetation. Thiollay (1971 and other papers) worked on a 50 ha plot of a savanna-gallery

forest mosaic in Côte d'Ivoire, and de Greling (1972) worked on three sites in northern Cameroun.

1.3. Previous research in Tsavo National Park

Because of its location on the main route inland from the coast at Mombasa, many of the early missionaries and explorers of the late 19th Century passed through the Tsavo area; but because of its aridity and harshness, it was usually traversed as fast as possible and there are relatively few accounts of it in the journals of these men. Corfield (1974) has extracted the relevant parts of reports by these early travellers but there are only a few notes on the presence (or absence) of mammals, and almost none on the birds. Tsavo National Park was gazetted in 1948, and the story of its establishment and development have been broadly documented by Sheldrick (1973).

Although there were a few isolated studies in the early days of the Park, there was very little detailed research until Tsavo Research Project was set up in 1967, mainly to study the so-called 'Elephant Problem' (Laws 1969). Since then, work on elephants and their effects has dominated research in Tsavo although there was a lull after Laws left in 1968. The large die-off in the 1970-71 drought led to a revival of elephant studies (e.g. Corfield 1973, Leuthold 1976a, 1976b, 1977b), but there is still no detailed quantitative study on the effects of elephants on the vegetation, although a few data, resulting from a series of short field-courses from Nairobi University are given by Agnew (1968) and Leuthold (1977a). The only work on the vegetation is a preliminary vegetation map prepared by W. van Wijngaarden in conjunction with his work on the soils, and some more detailed, as yet unpublished, work on the 1976 position by T.F. Corfield.

Previous to his elephant work, W. Leuthold had been carrying out some detailed studies on the behaviour and feeding habits of several ungulate species (e.g. Leuthold 1971, Leuthold & Leuthold 1975a, 1975b), and the

community dynamics of these and the other major herbivorous mammals have been described by Cobb (1976), who also carried out an extensive analysis of the climate. These studies have resulted in a broad knowledge of the ecology and main limiting factors of the major component of the vertebrate biomass in Tsavo N.P..

Invertebrate studies have been directed almost entirely at two groups of insects associated with decomposition; dung beetles (e.g. Kingston 1977, Kingston & Coe 1977, and currently by T. Palmer), and termites (especially Buxton 1979). Termites are, as will be seen later, crucial to the survival of many bird species in the area, and dung-beetles too are seasonally important for some.

Finally, there have been a few studies of the birds in Tsavo N.P.. A.D. Forbes-Watson lived in the Park for about a year 1959-60 and compiled a species list for the Park (Forbes-Watson 1967). C. Smeenk carried out a survey of the birds of prey and made a detailed study of the large eagles (Smeenk 1974) and two goshawk species (Smeenk & Smeenk-Enserink 1976), and it is largely as a result of these works that my study does not include birds of prey.

In Tsavo West N.P., about 30 km to the west of the Tsavo East N.P. boundary, lies Ngulia Safari Lodge. In recent years this has become the focus of bird-ringing in Kenya, because, at certain times of year, the game-viewing lights bring down large numbers of migrant birds. The majority of these are of Palaearctic origin (Pearson & Backhurst 1976; Backhurst & Pearson 1977a, 1979; Britton & Britton 1977; Pearson & Backhurst 1978), but some Ethiopian region species are also attracted, many of which are known intra-African migrants (Backhurst & Pearson 1977b).

My study has not therefore been carried out in complete isolation, and I hope that the results presented here will be of use, both to bird ecologists in Africa, and the Department of Wildlife Conservation and Management of the Kenya Ministry of Tourism and Wildlife in their planning and management of Tsavo East N.P. in the future.

CHAPTER 2 Tsavo East National Park

2.1. Geography

The Tsavo East National Park (approx. $2^{\circ}00'$ - $3^{\circ}45'S$, $38^{\circ}30'$ - $39^{\circ}15'E$) covers an area of about 13000 km^2 lying between about 80 and 150 km from the Indian Ocean coast of Kenya. It is divided into two parts by the Galana River, and it is only the area to the south of this (about a third of the total area) which is open to the general public. Most of my work, and indeed the majority of other scientific work, has been carried out in this southern area, especially the western two-thirds of it. Fig. 2.1 is a map showing the location of Tsavo East N.P. with the main localities marked. Around much of the northern, eastern and southern boundaries of the Park there are cattle ranches and the general aspect of the land and the vegetation remains much as it is in the Park (but see ch 2.5). The western boundary abuts on Tsavo West N.P., but to the north west and especially to the south west, in the Taita Hills, there is extensive agriculture and a high human population.

2.2. Climate

Tsavo East N.P. lies in a southward extension of the Somali arid belt and, as in all arid and semi-arid areas, the most important element of climate is rainfall, both the total amount and the seasonal distribution. The patterns of rainfall both in time and space have been discussed extensively by Cobb (1976), amplified in a few respects by Kingston (1977) and updated by Buxton (1979). The following brief summary is based on these descriptions.

Fig. 2.2 shows the mean monthly rainfall at Voi Station over 67 years. It shows there are two wet seasons of about equal magnitude and two dry seasons each year. As pointed out by Kingston (1977), the monthly means do, however, give a misleading picture of the dry seasons especially the shorter January-February one. The mean of about 30 mm for each of January and

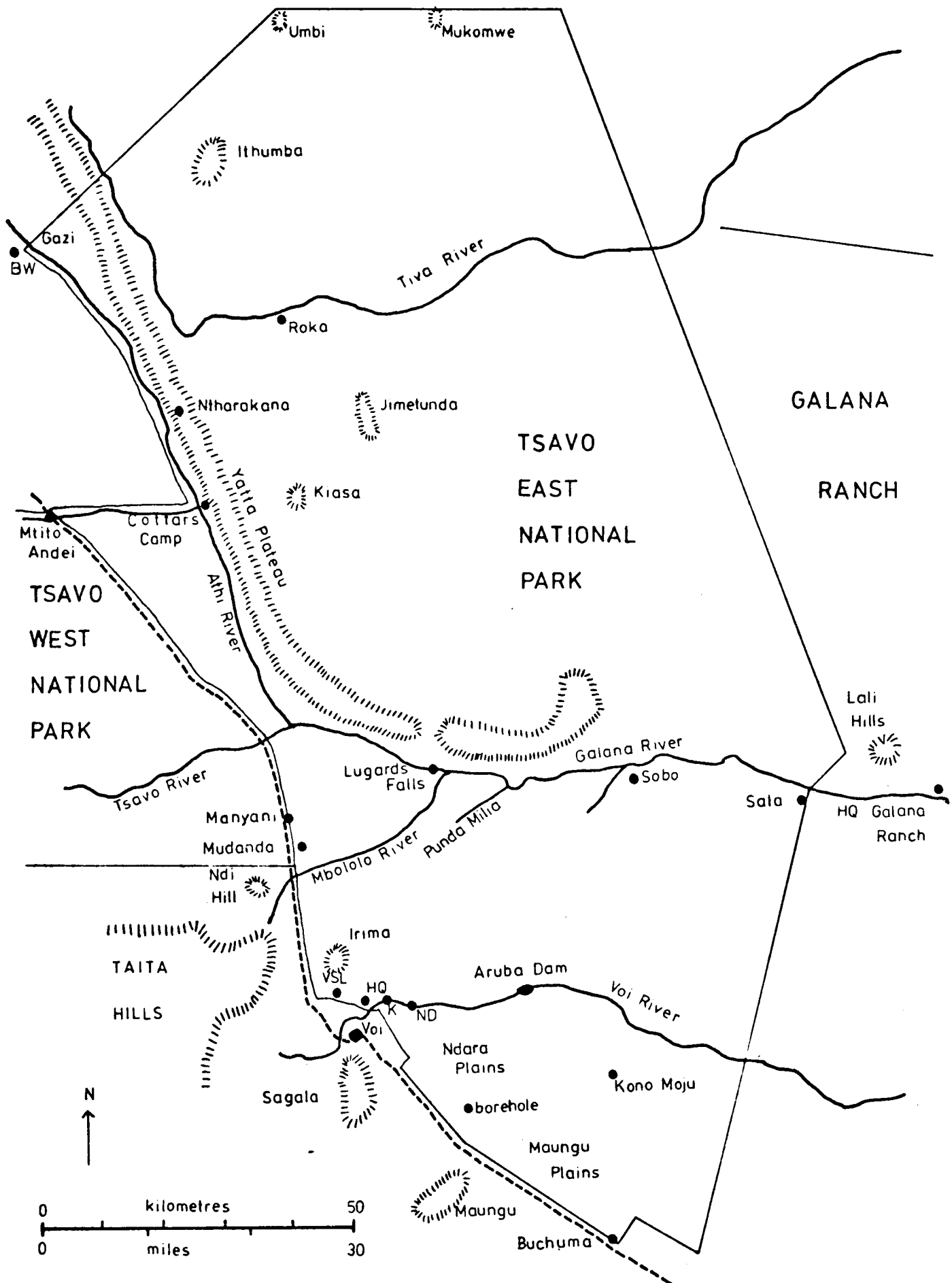


Fig. 2.1 Map of Tsavo East National Park, showing main localities. VSL - Voi Safari Lodge; BW - Bushwhackers Safari Camp; K - Kanderi; ND - Ndololo Campsite; HQ - Park headquarters. — - Park boundary; ---- - Nairobi to Mombasa road and railway.

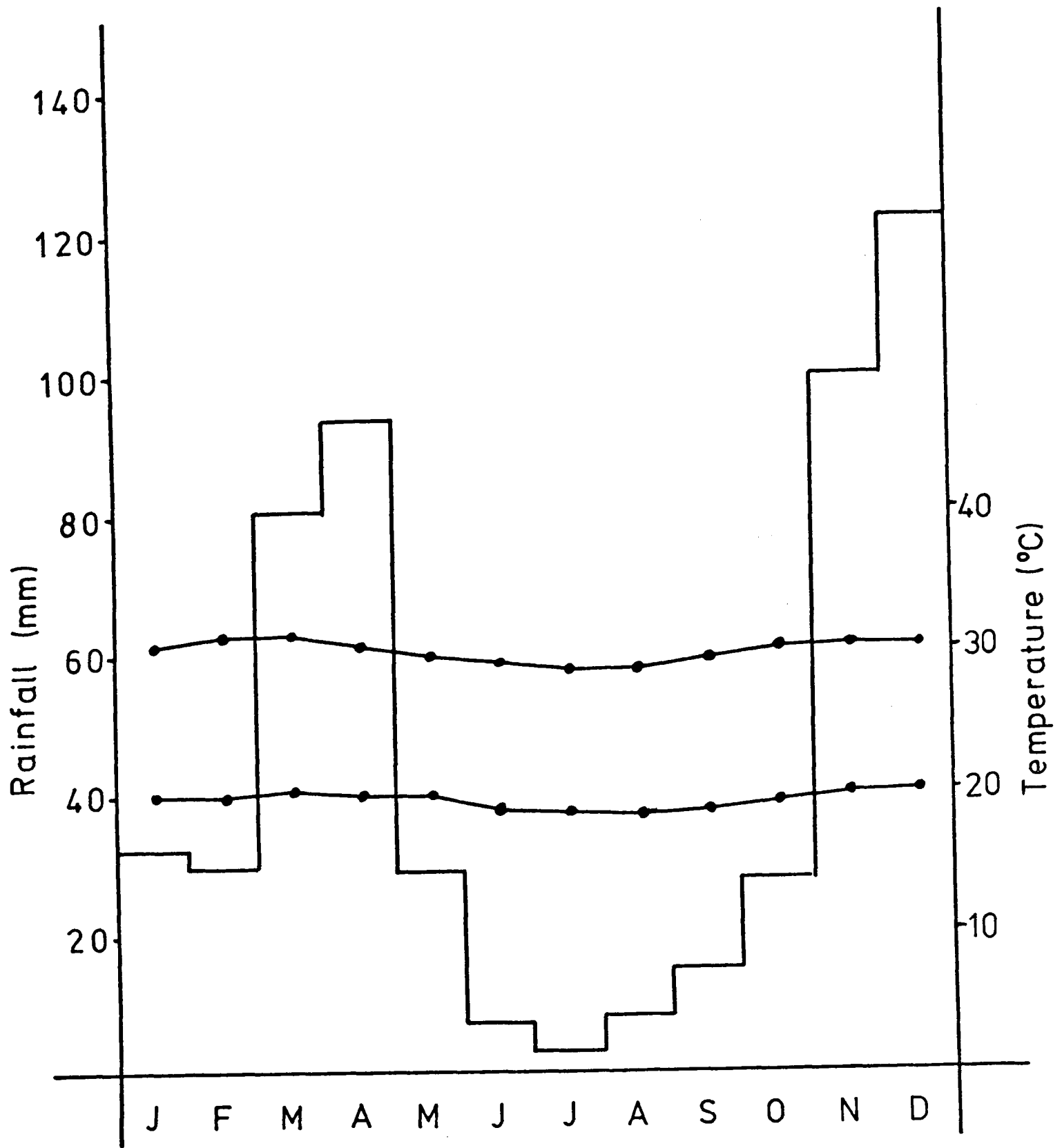


Fig. 2.2 Mean monthly rainfall at Voi Station over 67 years (bars), and mean monthly maximum and minimum temperature at Voi Station over 31 years (lines).
Records from reports of the East Africa Meteorological Department.

February is caused mainly by years in which rain fell in these months instead of, and not as well as, December and/or March. It should also be noted that, contrary to most of the rest of Kenya, the so-called 'short rains' of November-December are more predictable in Tsavo than the 'long rains' of March - early May (Tyrell & Coe 1974) and, as will be seen below, the latter were very poor in many areas of Tsavo in both 1975 and 1976 during this study.

The seasonal pattern of rainfall remains the same across the Park but the total rainfall at Voi Station (mean 549 mm per annum) is substantially higher than most of the Park, owing to the proximity of the Sagalla and Taita Hills. Fig. 2.3 shows the mean annual rainfall (1970-74) over the area of Tsavo East N.P. taken from the trend surface analysis of Cobb (1976). As can be seen, the total rainfall decreases as one moves east across the Park, although it increases again between the eastern boundary of the Park and the Indian Ocean coast. It should be noted that these data of Cobb (1976) are based on a climatic year starting on July 1st, and not a calendar year. It does not however, affect the general trends shown.

Kingston (1977) concluded that the five year 1970-74 rainfall mean was about 17% below the long-term average, and Buxton (1979) added that the five year 1972-76 mean was not significantly different from this. The monthly rainfall at seven stations in the Park (locations in Fig. 2.1) are given for my study period in Table 2.1. This shows that there were about average amounts in November and December of each year but that there was only just over half the average in April-May. Table 2.1 also shows two other features. In both years there was some unseasonal and fairly widespread rain in September. How much this affected bird populations is unknown, but it had a considerable effect on the elephant population, at least in 1975. In this year, elephants had just started to die of starvation in significant numbers, when the rain fell and delayed further deaths for about a month, and in so doing may well have prevented mortality such as occurred in 1970-71.

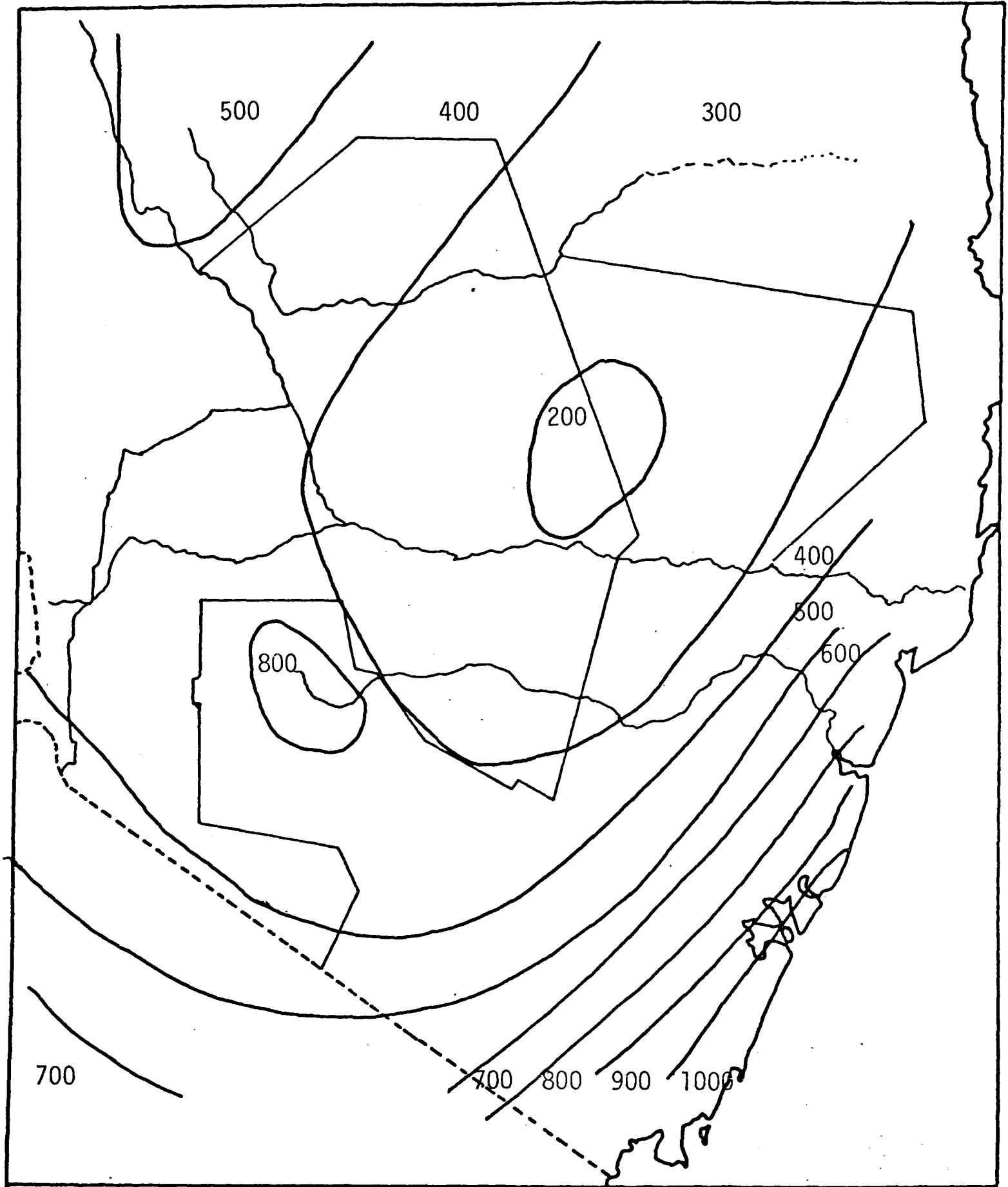


Fig. 2.3 Distribution of Mean Annual Rainfall (1970 - 1974) analysed by Trend Surface Analysis (after Cobb 1976 Fig. 2.3.5).

Table 2.1. Rainfall at seven stations in Tsavo East National Park, November 1974 - December 1976

	N	D	J	F	M	A	M	J	A	S	O	N	D	Total
Park HQ	98	58	8	0	33	19	9	0	1	0	x	91	154	335
Aruba	53	67	5	0	1	9	22	0	2	13	1	43	27	124
Buchuma	33	56	39	0	20	40	69	2	15	29	8	25	47	295
Sala	111	65	8	0	33	43	12	0	0	24	3	14	42	182
Lugard's Falls	73	73	20	0	2	68	10	0	5	11	0	51	70	237
Manyani	66	44	10	1	0	34	20	0	0	5	0	97	87	254
Ithumba	129	6	x	0	3	0	54	0	1	21	3	95	17	194
Average	80	53	13	x	13	30	28	x	3	18	2	59	63	232
Park HQ			0	0	4	46	13	1	0	45	6	103	79	299
Aruba			0	47	6	57	26	3	0	42	22	82	74	367
Buchuma			2	4	19	49	78	29	2	63	0	8	15	280
Sala			1	0	0	80	9	0	0	78	6	3	5	192
Lugard's Falls			0	2	0	66	9	0	0	39	1	95	0	213
Manyani			0	0	0	13	1	0	0	46	0	100	8	169
Ithumba			1	2	x	18	29	0	0	9	0	12	46	117
Average			1	8	4	47	24	5	x	46	5	58	32	234

Notes:
1) All figures are mm. x = trace
2) For location of sites see Fig. 2.1

The second feature is illustrated most clearly in Table 2.1 by the Aruba figure for February 1976. This total, which is nearly 13% of the 1976 total at Aruba, was caused almost entirely by one thunderstorm on the afternoon of the 29th. Such local thunderstorms can have a considerable effect on the vegetation and animal populations within a very short distance. Many bird species, and mammals, will concentrate in such areas where rain has fallen recently.

There are two other climatic factors which might be important for my study. In addition to the rainfall, Fig. 2.2 shows the mean maximum and minimum temperatures recorded at Voi Station over 31 years. As in most tropical areas, temperature varies rather little through the year, but it should be noted that the shorter dry season is also hotter than the long one, due in part to less cloud cover. It is also likely that the average temperature will be higher further east than at Voi, but there are almost no data to demonstrate this. The other factor is wind speed. Table 2.2 shows the average wind speed at Aruba in each month of my study; it is considerably more windy between May and September than at other times of year, and this probably speeds up the drying out of the vegetation after the April rains.

Table 2.2. Average wind speed at Aruba in each month of my study (km per hour)

	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
1974	-	-	-	-	-	-	-	-	-	-	7.4	7.9
1975	7.4	7.6	9.2	13.3	15.4	19.0	17.7	17.6	14.8	12.9	7.9	6.9
1976	7.8	6.4	6.4	10.3	15.5	16.9	16.6	16.2	14.0	10.8	7.0	4.9

2.3. Topography, geology and soils

Tsavo East N.P. is a very gently sloping plain from about 300 m above sea-level on the eastern boundary, to 500-600 m a.s.l. on the western. Along the western edge of the Park there are a few gneiss inselbergs up to

about 250 m above the plain, and the northern and eastern bank of the Athi/Galana River is formed by the Yatta Plateau, which is here a tongue of lava mostly about 1 km wide and 150-200 m above the plain. The geology of the area has been described in outline by Sanders (1963), and W. van Wijngaarden has recently been carrying out a detailed soil survey of the Park.

The inselbergs provide nest sites for several birds, especially some birds of prey, swifts and swallows but, apart from this, neither the geology nor the soils are very important to birds except by way of their effect on the vegetation, but the relationships are only now being worked out by van Wijngaarden (in prep.).

2.4. Availability of free surface water

Most mammals are dependent on free surface water and, because this is scarce in the dry season, many species become restricted in distribution at this time (Cobb 1976). Birds are more mobile, but, in addition, many are able to obtain all their water needs from their food even at the end of the long dry season. A few, notably seed-eaters, are, however, water-dependent and may become restricted during the dry season. The most important sources of permanent water in the Park are the Tsavo, and the Athi/Galana Rivers, Aruba Dam, some pools in the main tributaries of the rivers and in the upper parts of the Tiva River as far east as Roka. Some artificial water supplies are present along the western boundary of the Park e.g. at Voi Safari Lodge and a few points along the Nairobi-Mombasa railway, and a few artificially-enlarged waterholes to the south of the Voi River usually retain water through much of the dry season. In the wet seasons the situation changes considerably. Seasonal watercourses, of which the most important are the Voi and Tiva Rivers, start to flow with the onset of the rains and, more important for animal dispersion, numerous shallow pans fill and retain water for varying periods into the dry season.

2.5. Vegetation

There have been two major schemes for classifying vegetation in East Africa: those of Pratt, Greenway & Gwynne (1966) and of Greenway (1973). The latter was the system used by Greenway (1969) for his check list of the plants of Tsavo East N.P., but it is rather unspecific in its definition of different types, and much of the vegetation in the Park today has been greatly modified from its original form by large mammals, and in some places by fire. I have therefore used Pratt et al.'s (1966) system as a basis.

Tsavo East N.P. falls into Pratt et al.'s ecological zone V, which is characterised by a semi-arid climate with the "woody vegetation dominated by Commiphora, Acacia and allied genera often of shrubby habit" (Pratt et al. 1966 p. 371). Within this zone they designate physiognomic types based on the canopy cover of the vegetation. Their main concern was rangeland and hence the amount of grass available, and chose as their critical canopy cover values of woody vegetation at 2% and 20%. I was more interested in the woody vegetation. Hardly anywhere in Tsavo East N.P. does the canopy cover of woody vegetation reach 20%, and a very few bushes or trees can make a substantial difference to the bird populations present. I have therefore defined my critical points for canopy cover at 1% and 10%.

On this basis I defined six major habitat types:

- G Grassland - <1% of bushes or trees
- BG Bushed Grassland - bushes 1-10%, trees <1%
- WBG Wooded and Bushed Grassland - bushes 1-10%, trees 1-10%
- B Bushland - bushes >10%, trees <1%
- WB Wooded Bushland - bushes >10%, trees 1-10%
- W Woodland/Woodland Thicket - bushes variable but usually >10%, trees >10%

I also worked along the Voi River and defined this as a seventh major habitat type

- R Riverine

When referring to specific habitat types on these definitions, the abbreviations are often used alone. The first five of these habitats (G, BG, WBG, B and WB)

show many similarities and as group they are referred to subsequently in this thesis as the Park savanna habitats (PSH).

When the Park was gazetted in 1948, the predominant vegetation type over much of the area was Woodland (mixed Commiphora-Acacia) grading to Woodland Thicket in places (Napier-Bax & Sheldrick 1963, D.L.W. Sheldrick pers. comm.). There has been considerable argument as to whether this, i.e. a mature climax vegetation, has been a permanent feature of the area of the Park for centuries, or whether there has been a continuous cycling process between this and more open country, a cycle mediated by the climate related to the phenology and generation time of the trees, and probably in conjunction with large mammals and/or fires. What is certain, however, is that since 1948 the vegetation inside the Park has changed very substantially.

Commiphora-Acacia mixed woodland does not now exist inside the Tsavo East N.P. boundary south of the Galana River. To the south and west of the main Nairobi-Mombasa road and in parts of the area of the Park north of the Galana River some large tracts do, however, still remain. These are very similar to the vegetation which used to cover the whole area (Sheldrick pers. comm.), although the areas outside the Park are now extensively used by domestic cattle, sheep and goats. Inside the southern area of the Park and to a lesser extent elsewhere large mammals, notably elephants Loxodonta africana and, in places, fires, have opened up the vegetation and modified it very considerably. Commiphora spp. and Acacia spp. are particularly susceptible to damage by elephants and, as a result, these genera which were dominant in the original woodland are now nearly absent. Thickets too have largely disappeared.

The results of these changes are that, although there were some more open areas in the original woodland, most of the habitat types now extant in the Park are derived from the woodland by destruction of woody vegetation. Unfortunately there has been hardly any detailed quantitative work on these changes, but the general impressions are confirmed by the few data in Agnew (1968) and Leuthold (1977a).

What follows is a general description of the main habitat types present in the area today. The vegetation on the plots used to estimate bird density (see ch 3) are described in more detail in Appendix 2. All plant nomenclature follows that in Greenway (1969).

a) Woodland/Woodland Thicket

The trees are predominantly Commiphora spp., and Acacia spp. (especially A. tortilis and A. thomasii) which have an open canopy at 7 - 8 m, although in places up to 10 m, and with occasional emergents. Interspersed with these are several other species of tree, notable among which are Delonix elata, Melia volkensii, Boswellia hildebrandtii, Lannea alata, Platycelyphium voense, Sterculia (3 spp.) and in places the baobab Adansonia digitata. The bush layer, up to 2 - 3 m high, is variable from very scattered to nearly impenetrable thickets, with Grewia spp. and, in thickets, Sansevieria spp. prominent. Grasses are usually sparse, especially outside the Park in parts inhabited by cattle and other domestic animals.

b) Park savanna habitats

The dominant tree species in the Park savanna habitats are those which are relatively unused by elephants for food: Delonix elata, Melia volkensii, and Platycelyphium voense (Leuthold 1977a). They tend to be widely scattered and hardly anywhere reach more than 5% canopy cover. There have also been changes in the bush and shrub composition, but whether this is directly due to elephant destruction, or indirectly due to the reduction in shade by trees is unknown. Grewia spp. and Sansevieria spp. have largely disappeared, and dominants now include Premna (2 spp.), Erythrochlamys spectabilis, Bauhinia taitensis, and especially Sericocomopsis (2 spp.). The last may occur in nearly pure stands. Other locally important species are Boscia coriacea and Thylachium thomasii, both of which are evergreen, and the former of which may grow up to 5 - 6 m as a small tree,

and Dirichletia glaucescens. Grass cover varies from very little to over 75% but most areas range from about 25% to 50%. Dominant genera include Aristida, Brachiaria, Cenchrus, Chloris, Digitaria, Eragrostis, Panicum, and Sporobolus.

The most common habitat types in the Park are Bushed Grassland, and Wooded and Bushed Grassland, and together these cover nearly three-quarters of the southern area of the Park. In general, the western parts which have a higher rainfall, support a denser vegetation, with a few fairly extensive areas of Bushland and Wooded Bushland although small patches of these habitat types may be interspersed anywhere. The habitat is usually very open near permanent water due to heavy grazing and trampling by mammals. Grassland is, however, rare, being almost restricted to alluvial deposits such as those near Irima Hill. There are some areas near Aruba where there is very little living vegetation at all (including grass), but with a number of dead trunks, and this is also classed as Grassland.

In general, the northern area has a denser vegetation, especially away from the Galana and Tiva Rivers and some areas differ in their species composition, including for example Terminalia orbicularis and Cassia abbreviata. Also, along the western side of the Park, and especially on the Yatta Plateau, Adansonia digitata is important locally, although this too has been subjected to heavy elephant damage.

c) Riverine vegetation

The upper reaches of the Voi River in the Park support a small area of riverine forest. It extends about 10 km into the Park but is rarely more than 150 m wide. There is a nearly closed canopy at about 20 m comprising Newtonia hildebrandtii, Dobera glabra, Kigelia africana and Acacia spp. as dominants, and in places there are several Ficus spp. The bushes may be very thick with, for example, Capparis sepiaria, Salvadora persica, Azima tetracantha and Pluchea (2 spp.) as important components. Grasses are

usually thick and matted around the edges and in clearings but sparser inside the forest, East of Ndololo the forest starts to thin out eventually becoming a fringe of trees.

The surroundings of the Galana and Tiva Rivers are somewhat different from the Voi River. There is hardly more than a fringe of trees along either although there was evidently much more before the 1960-61 floods. There are two main types: Acacia elatior fringes, and stands, often pure, of the doum palm Hyphaene coriacea. At intervals along both rivers there are some thickets of the succulent bush Suaeda monoica, and indicator of salination.

d) Other habitats

Around waterholes there may be a more luxuriant vegetation than in the surrounding area, both of bushes especially Lawsonia inermis and grasses.

In the west there are a few rocky hills e.g. Irima, several near Voi, and several in the northern area such as Ithumba and Kiasa. They are usually rather thinly covered with trees and bushes, often of species not occurring elsewhere (Greenway 1969).

The Yatta Plateau provides a slightly different habitat type, having a very thick bush cover indeed on the top, especially in the northern parts, and as said above baobabs are particularly numerous here.

Finally a minor but important habitat for a few species such as swifts Apodidae and swallows Hirundinidae to nest on is artificial structures, mainly buildings and culverts.

Postscript

As a postscript it should be noted that since early 1977 and the end of my fieldwork, there have been exceptional rains in Tsavo N.P. and these, together with a reduction in the numbers of elephants due both to drought over the previous few years and poaching, have led to a great increase in the growth of the vegetation.

CHAPTER 3 Bird Census Methods

3.1. Introduction

The most important data required for this study were the numbers of birds in each habitat at each season. The methods had, therefore, to be comparable over the seven major habitat types, between wet and dry seasons, and be applicable to all species. The Park, too, is very large and I wanted to sample as large a part of it as possible.

I tried to cover fairly thoroughly the southern area of the Park east to a line joining Maungu, Mukwaju, and Lugard's Falls, and the woodland just to the south and west of the main Nairobi/Mombasa road - an area of about 2500 km². In practice, much of this was covered once each month during the first year (1975) and once every six to eight weeks during the second (1976). Periodic visits were made to the remainder of the southern area, some parts of the northern area such as Ntharakana, Gazi, Umbi, Mukomwe, and the Tiva River around Roka, and some parts of the Galana Ranch within about 15 km of Tsavo East N.P. boundary. There is, however, a large section of the Park on the eastern side of the northern area which was not visited at all, due largely to the distances involved and difficulty of access. The main localities are marked on Fig. 2.1.

Methods of carrying out censuses were extensively reviewed by Kendeigh (1944). There are two main types of census; those which give an index of relative abundance (Type I), and those which give an estimate of the density of birds on the ground (Type II). Ideally one would carry out Type II censuses in all cases, but they are much more time-consuming than Type I, which is important since I wanted to cover a wide area and secondly in many conditions Type II censuses imply a degree of precision which may be unjustified. For some purposes Type II censuses are essential and I have used them when considering the bird community as a whole in each habitat

type, but for many comparisons involving the ecology of individual species and their close relatives, I considered indices of abundance to be adequate and I have relied on them here for this purpose.

There are three practical problems to consider with censuses; weather, time of day, and most important, size of census unit. Birds, just as humans, tend to take shelter in bad weather and they are therefore less visible. This was, however, very little problem in Tsavo as one can almost guarantee fine weather - censuses had to be abandoned due to rain or drizzle on only three mornings in two years. Wind is, however, stronger from May to September than at other times (Table 2.2) and may reduce numbers seen slightly.

It is "well-known" that in both tropical and temperate habitats, one sees more birds early and late in the day than around midday, although it has very rarely been quantified. Because of this I carried out all my censuses in the mornings and most before 10 a.m. I did, however, quantify the effects by walking the same path at intervals through the day on nine occasions spanning all seasons. The average number of individuals seen at each hour is shown in Fig. 3.1 (those flying over are excluded). In a few cases where I did not census at a particular hour on a day I have taken the average of the two adjacent ones. Fig. 3.1 shows the expected peak in numbers early in the morning and decrease later in the day. There is a slight but not significant increase before dusk. In Tsavo, many species seem to go to roost early, as shown by a pair of the weaver Malimbus rubriceps which came to roost in my house from September to December 1976, at between 5 and 5.30 p.m. which is over an hour before dark. The only other published figures that I know of from Africa for the diurnal rhythm of numbers seen are those of Winterbottom (1972b), in a garden in the Orange Free State. My figures agree with these except that he found as large a peak just before dusk as there was in the morning.

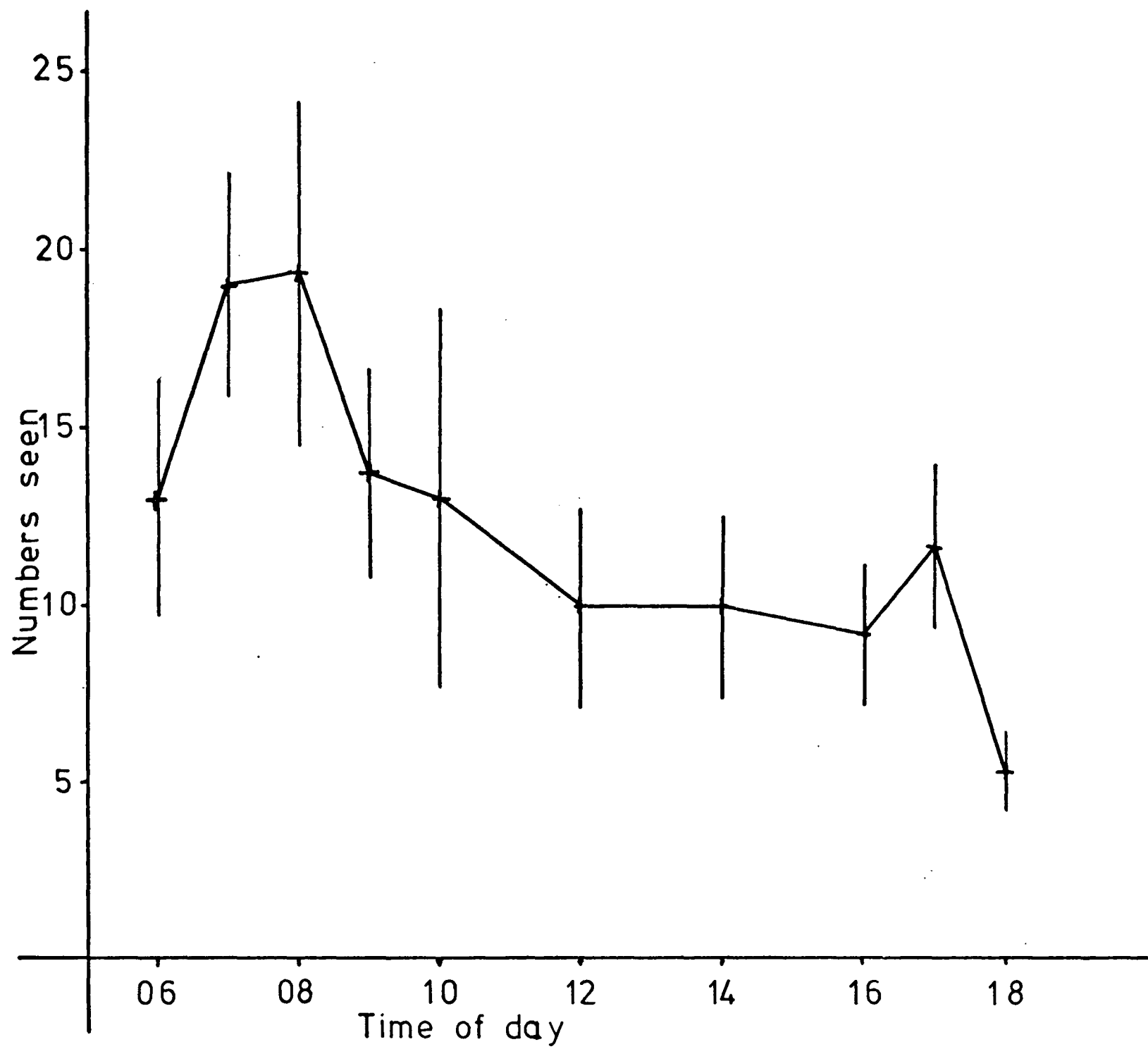


Fig. 3.1 The number of birds seen on a transect near Park headquarters at different times of day. The vertical lines are one standard error either side of the mean,

There were several factors which influenced the decision on size of census unit, among which were:

- a) I wanted to sample over a wide area but had only three or four hours per day were suitable, due to the decrease in numbers visible after 10 a.m. (Fig. 3.1).
- b) Habitats may intermingle fairly closely and I wanted to ensure that each unit only sampled one habitat.
- c) The presence of large mammals, notably rhinoceros (Diceros bicornis), made walking in thick bush potentially hazardous, so I did not want to work too far from a road and the car.
- d) Bird density is often very low indeed; and so very small plots were inefficient and could make for great inaccuracies and high variance.
- e) Sample units should be the same in each habitat and at each season.

Some of these factors conflict with each other and so the final decision had to be a compromise.

Two final, general, points should be made regarding censusing. The number of observers has been shown to make a difference to the numbers of birds seen in forest (Lack 1976 p. 34), but the effect is unimportant to this work as almost all censuses were carried out on my own; and I was using a portable tape-recorder for taking field notes to avoid looking down at a notebook continually.

One factor, however, that cannot be quantified is my increasing familiarity both with the area and the birds. This obviously made identification quicker and easier as time went on, particularly with calls. To identify birds I used all the cues available though I never counted a bird I did not see.

3.2. Census Methods Used

By far the most commonly used base for relative indices is time. I have used this here, and I standardised all censuses to units of 15 minutes.

A variety of methods have been used for estimating bird density, and they have been recently reviewed by Emlen (1971), who defined six previous methods and added one of his own. He (Emlen 1977) has now added a modification of this last to produce an eighth method. The methods are: 1) mark, release, recapture, 2) map nests, 3) map singing males, 4) count in narrow strip, 5) count to flushing distance, 6) count $\times$ effectivity (the percentage missed calculated from separate intensive studies), 7) count $\times$ detectability (the percentage missed calculated directly on the transect from lateral detection distances) and 8) which was described after I had finished my fieldwork, is a modification of no. 7 allowing for the frequency of production of detection cues by the bird. I wanted a method which was applicable and efficient over a wide area, different habitats, different seasons and for all species. These requirements immediately excluded nos. 1, 2, and 3. No. 5 is only really applicable to game birds, and no. 6 needs other separate studies. This left nos. 4 and 7 (and 8) of which no. 7 is a refinement of no. 4 (no. 8 is a refinement of no. 7 and is applicable in the breeding season only (Emlen 1977)). To calculate detectability one has to a) make accurate lateral distance estimations for every individual located, and b) assume you are seeing every bird (or know the frequency of production of detection cues) in a defined narrow strip. Inevitably there will be inaccuracies in the distance estimations and the assumption is the same as that using method no. 4. Further, for each species, there will be different detectability values for each habitat and each season. Many of these will be fairly arbitrary, apart from taking up a great deal of extra labour in their calculation; and so, as long as a strip of reasonable size was used (not too large) I considered method no. 4 would give an adequate estimate of density, with the two provisos that all figures calculated would be minima, and that the figures for the thicker habitat types, and in the wet seasons, would be likely to be underestimated more than figures for the thinner habitat

types and in the dry seasons. In practice I modified the method slightly and used plots rather than single transects in most habitats (see below).

Detailed organisation of the censuses on the ground was as follows:

a) Park savanna habitats

Type I - Fifteen minute censuses were carried out at one or two kilometre intervals along the Park roads. The first point of a series was determined by the first (or second) km change, recorded on my car's odometer, after a fixed point, usually a road junction. During the census the path walked varied a little but was usually a complete semi-circle (i.e. including the diameter which was the road) of radius about 150 m. The area sampled was not measured but was usually about eight hectares. During the census time, all individual birds seen and identified were counted, it was noted whether they were perched or flying over, and a list was made of any other species heard. No individual bird was knowingly counted twice.

Type II - In the first week of each month six days were spent covering six groups of plots. All these, and those for Woodland and Riverine, are located in Fig. 3.2 and their vegetation is described in Appendix 2. They were chosen to represent the range of 'typical' types within each of the five habitats and were each 400 x 175 yards (= 5.7 ha). During the census, I walked slowly over the plot to a set plan (Fig. 3.2 inset) and stopped briefly at least every 25 m. I recorded every bird seen on the plot or (separately) in the airspace over it during the time I was on it. Total time on a plot varied from 12 to 35 minutes (average about 17 minutes). I never knowingly counted the same bird twice but, as I was likely to be underestimating rather than overestimating the total with this method, if there was a doubt, the bird was recorded a second time. A list of additional species heard was noted.

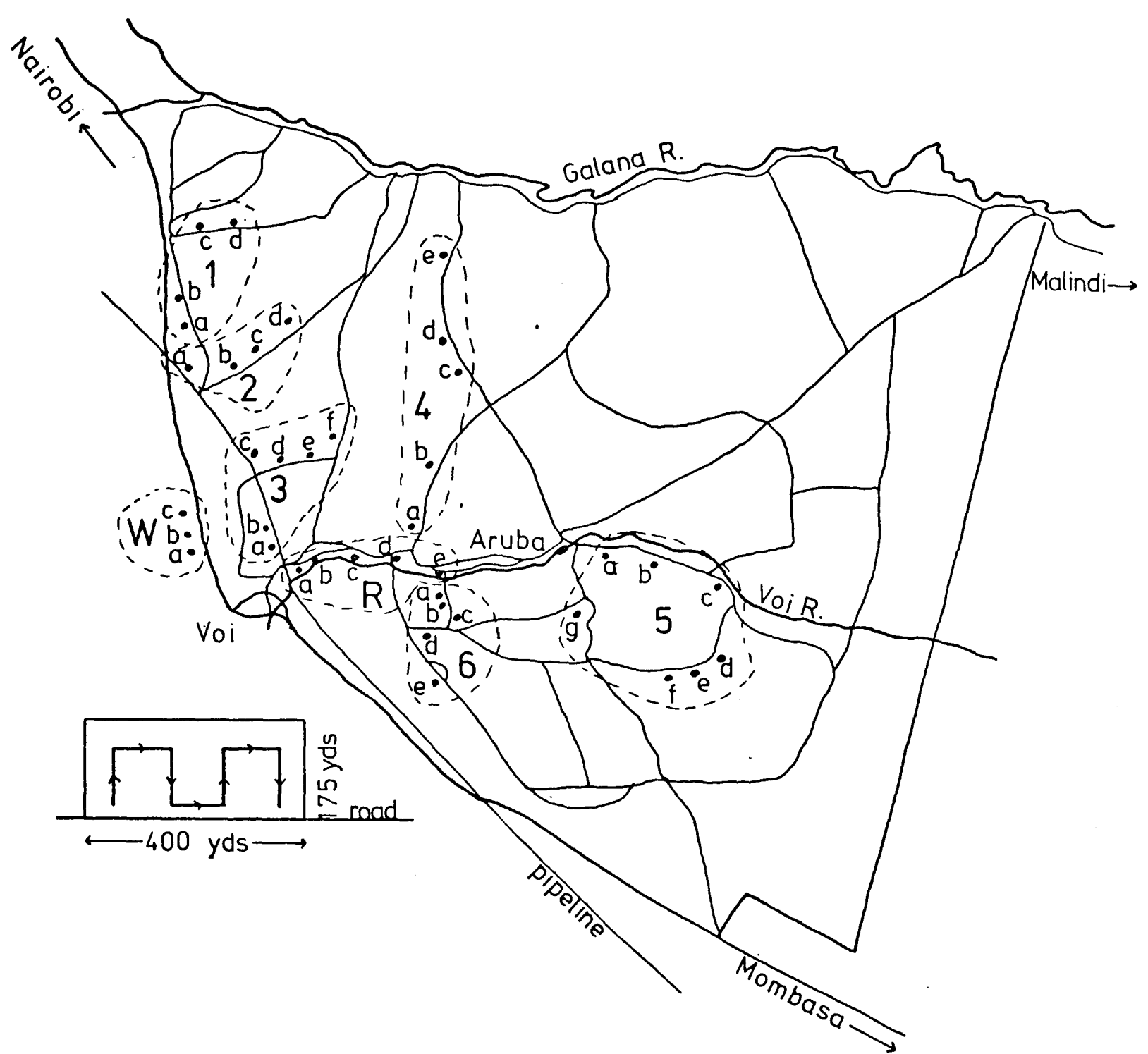


Fig. 3.2 The southern area of Tsavo East National Park showing the location of census plots. The dotted lines surround the plots in each group. The groups of plots in the Park savanna habitats are labelled 1 to 6 and the Woodland and Riverine groups are labelled W and R respectively. Within each group the plots are marked a, b, c etc. in the order they were censused. More details about each plot are in Appendix 2.
Inset - the route walked in each plot in the Park savanna habitats.

I always tried to census the plots of one group in the same order, but the presence, on the plot, of large mammals occasionally made this impossible. The order of groups was, however, not systematic over the six days, and indeed I usually avoided doing groups 1 and 2 (all were B or WB), and 5 and 6 (all were G, BG or WBG) on consecutive days. The number of plots in each group was between four and seven and no one habitat was always censused earlier or later in the day than the others except Grassland. Grassland plots averaged the fourth covered each day, the rest the third - ideally each would be the 3.1th each day. In this way the effects of time of day were eliminated.

b) Woodland

For this habitat I relied almost entirely on existing paths. For Type II censuses I walked a fixed distance along each of three paths just to the north of Voi recording every bird perched within 50 m (comparable to other habitats) on each side of the path. For Type I censuses I divided these into 15 minute units extending where necessary to complete 15 minute periods and noting any extra birds seen outside the 50 m; and some similar paths, elsewhere, were also walked, again divided into 15 minute units.

c) Riverine

Being mainly just a strip of vegetation along the rivers, which is often very thick and full of large mammals, regular plot or transect censuses were impracticable and/or very hazardous. As a result, the census format was inconsistent from point to point, and as for Woodland censuses, Type II censuses were a subset of the Type I censuses. For Type II, five areas were censused along the upper reaches of the Voi River. Two censuses were carried out while staying more or less stationary at points between Park HQ and Kanderi where the road is close to the river. Censuses were carried out for 15 minutes and all birds seen were recorded as before.

The third site, Ndololo Campsite, was treated as a plot and walked to a set plan (divided into 15 minute units for Type I figures). The fourth and fifth sites were by each of the two crossings of the Voi River about 10 km east of Voi. They both involved a short transect, along the access road in the first instance, and along the edge of the strip of vegetation in the second. Further censuses for Type I were carried out further down the Voi River, nearer Aruba, where the habitat was similar to the last of those above.

3.3. Other data collected

3.3.1. Road counts

Some species cannot be censused accurately using the above methods. This is especially for two groups of bird a) large wide-ranging species such as birds of prey and b) aerial feeders - swifts and swallows (Apodidae and Hirundinidae). Smeenk (1974) gives some seasonal relative abundance indices for the birds of prey, and although I noted these species when they were seen I have not included them in any analyses.

As will become clear, swifts and swallows were unimportant in the ecology of the area, except for the European Swallow Hirundo rustica at certain times of year. The relative numbers of this and other species were estimated by a series of road counts. Along fixed routes once each month, I counted all identified birds seen, especially swifts and swallows. A total of 189 km was counted, about 25 km of which was counted twice but in opposite directions. I did the count using a tape-recorder while driving at a speed of around 40 km per hour. Smeenk (1974) used this method for birds of prey, though with separate driver and observer and it has been used for recording geographic movements by Pettet (1975) in Nigeria, and by Brown & Brown (1973) for relative numbers of three species of rollers (Coraciidae) in Kenya. Efficiency varies with the bird species and speed of travel.

For "conspicuous" perching species I was probably only seeing half those that a separate observer would have done. On one occasion (February 1976) A.D. Forbes-Watson was with me. Independently (and unknown to me) he counted all the rollers he saw on the 42 km of road I counted on that day. I saw 11 Coracias garrulus, 6 C. caudata and no C. naevia as against 30, 6 and 1 respectively (this also reflects the choices of perch used by the three species). Unfortunately there were very few swallows that day but he thought (pers. comm.) that I was more efficient with these and flying birds are more obvious than perched ones. However, as my method was constant, seasonal comparisons are valid.

3.3.2. Mist-netting

A small amount of mist-netting was carried out mainly in the woodland just outside the Park. It was not used for censusing but it did reveal one or two rare species I had not otherwise recorded (e.g. the warbler Locustella fluviatilis and the chat Lusciniamegarhynchos and confirmed the identity of one or two others (e.g. the bunting Emberiza poliopleura as distinct from E. flaviventris).

3.3.3. Feeding behaviour

During censuses and at other times observations of birds seen feeding were recorded. If observations were made during censuses (only rarely did this take up more than a minute), the census time was made up at the end. Feeding data included:

- 1) type of food - insect, fruit, seed etc.
- 2) from where and how the food was obtained
- 3) activity of the bird - perched, flying etc.
- 4) position in the vegetation, and/or position of perch before and after feeding movement
- 5) the height of the vegetation and the height of the bird in it
- 6) the distance travelled to food

- 7) if the bird was feeding in a bush or tree I also assigned it to the edge (up to about 0.2 m into the vegetation), just inside (about 0.2 to 1.0 m from the edge), or inside (more than 1.0 m from the edge). These three categories correspond approximately to the terminal twigs, larger twigs, and branches (including the trunk) respectively.

It became clear that several species were feeding in a similar way by sitting on a prominent perch and pouncing to the ground for food (or sometimes catching in the air). For these, in addition to casual observations, individuals were watched for periods up to 15 minutes, and all feeding activity and other movements were noted. In most cases I was able to continue watching for a predetermined multiple of five minutes, but sometimes the bird flew out of sight or too far for observation before this time was up.

As with censuses, most observations were made in the morning when peak numbers of birds were visible, and therefore, presumably, birds were most active. Hence all feeding rates calculated are high if one is considering the total daily intake. Data are, however, comparable between species. The few observations I have suggest that, for these species at least, the reduction in numbers seen after 10 a.m. was not due to reduced activity among those that were feeding, but to some individuals going into the shade and (presumably) resting. This obviously has important consequences for the energy budget of the species, but is beyond the scope of this study.

In addition to the above observations all road casualties, and other dead birds, found in the area were collected and their stomach contents preserved for later identification. These are the subject of a separate publication (Lack & Quicke 1978). Specific collecting was not permitted within the boundaries of the National Park.

3.3.4. Breeding season and Annual cycle

During censuses and at other times any signs of breeding activity were noted, for example courtship, carrying nest material, feeding fledglings

etc., and records were kept of all nests found. In addition, all mist-netted birds (and casualties) were examined for moult and a brood patch but these latter data are not used in summaries of breeding season, as netting was not carried out at all times of year.

CHAPTER 4 Food Availability

4.1. Introduction

There are five major types of food used by land-birds in Tsavo: fruit, nectar, grass seeds, arthropods (mainly insects) and small vertebrates (small mammals and lizards). Only a few of the species I was studying take small vertebrates, and in no case were they a major part of the diet; and I have no figures for relative abundance. In a fairly similar semi-arid area, in south Turkana, Coe (1972) found an overall, corrected, biomass figure of about 5 kg per ha for small mammals, and Western (1974) a figure of about 1 kg per ha for lizards, with perhaps a similar biomass of snakes. Neither author, however, gives any indication of any seasonal changes in abundance.

I present here figures for the relative abundance through the year of fruit, nectar, grass seeds, and arthropods.

4.2. Methods

Figures for relative abundance of the four food types were obtained once per month during 1976.

4.2.1. Fruit

The abundance of fruit was measured on the plots used for estimating bird densities. 70-100 bushes and about 15 trees (if present) were scored on a scale 0 to 3 for the numbers of fruits, and the main species were identified. For the results presented here these scores have, however, been reduced to presence or absence of fruit on each plant.

4.2.2. Nectar

The amount of nectar available has been assumed to be proportional to the abundance of flowers. The abundance of flowers on woody vegetation was measured in an exactly similar way and at the same time as fruits.

Very few herbs produce conspicuous flowers and I did not record any birds visiting them. They were therefore ignored.

4.2.3. Grass seeds

These too were measured on the bird density plots and I only scored seeds that were still on the stem. I recorded the seeds by noting what, in terms of vegetation, was directly in front of my foot on every other step, for about 100 points on each plot. There were five categories: bare ground, grass with seed, grass without seed, herb (if flowers or seeds were present they were noted separately) and litter. From this a percentage cover of the ground of seed stems (and total vegetation cover) were calculated.

4.2.4. Arthropods

a) on the ground

Each month in each of six sites (in woodland, at Ndololo, by my house (Voi Gate), about 3 km east of Park HQ (Aruba Road), and two sites along the Pipeline (Irima and Mzinga)) I put out 10 pitfall traps, consisting of 1 kg jam tins, each partially filled with water, and a drop or two of detergent to make the arthropods sink. The traps were placed in two rows of five, 50 m apart, each being 10 paces (6 - 8 m) from the next. As far as possible the same holes in the ground were used each month. After 48 hours the contents of each trap were collected and taken to the lab where they were sorted in a kitchen sieve. Arthropods were identified to order where possible, counted and then dried for 24 hours at 105°C after which they were weighed. Any individual more than 0.10 g dry weight was weighed separately.

b) in the grass layer vegetation

In five of the sites above (all except the woodland where there was no grass layer vegetation) three sweep-net samples were taken. Each sample consisted of 50 sweeps through the grass layer, though in places, especially

at the Aruba Road site, this layer was often very sparse. The net was not passed over bare ground. The contents of the net were put in a killing bottle containing ethyl acetate. In the lab they were sorted, where possible identified to order, counted, and then weighed fresh, and after drying as above. In all samples except February, grasshoppers, lepidopteran caterpillars and single, large individuals were weighed separately.

c) in the woody vegetation

Herbivorous insects in the woody vegetation feed to a great extent on leaves and especially new leaves (e.g. Feeny 1970). On this basis the seasonal leaf abundance should give an indication of the insect abundance, and this was measured at the same time and in the same way as for fruits and flowers.

d) termites (Isoptera)

Termites are one of the most abundant groups of insects in Tsavo and are a very important food source for many birds, but neither pitfalls nor sweep netting catch significant numbers. R.D. Buxton was studying termites in Tsavo for about the same period that I was there, and he has kindly allowed me to quote some figures for termite activity on the ground. This was measured by the dry weight of wood eaten by termites in the 30 days to the middle of each month, on eight transects in the southern area of the Park.

4.3. Results

4.3.1. Fruit

There are very few fruits in Tsavo that are eaten in any quantity by birds, and all except Premna spp. (mainly P. resinosa) only occur in woodland or along rivers. The five major fruits that are eaten, however, show three different seasonal regimes;

a) Fruit in wet seasons - Premna spp. and Grewia bicolor

Premna is one of the commonest bush genera in the whole Park at present, but it was probably considerably rarer in the past as I found only small numbers in woodland. Grewia bicolor is now, however, almost restricted to this habitat and all my data for this species are from it. The seasonal pattern of abundance of fruits of the two is shown in Fig. 4.1. They fruit at the end of each wet season and, particularly for Premna, the fruit is only available for a month or so. I have included two lines for G. bicolor, the solid line is that for fruits recorded on the bird density plots, and the dotted line is from a second area just to the south of Voi (this area was sampled in the last ten days of a month and I have plotted the figures one month ahead (the March figure was measured in late February etc.) to make the comparisons more valid). It is included to show, firstly, that given sufficient rain, G. bicolor may fruit in either wet season and may do so in both - on 4th January 1977 the figure in the second area was 11% in fruit (flowers measured at the same time on a similar scale were on 63% of the bushes) - and, secondly, that even over the space of about 10 km there may be substantial differences in the abundance of fruit at any one time.

b) Fruit in the dry season - Commiphora spp. and Salvadora persica

Throughout this thesis Commiphora spp. refers only to the common species with small (up to 5 mm diameter) fruits, which include C. africana, and not to those with much larger fruits for example C. boiviniana.

Commiphora spp. are the most important fruit producers in the Tsavo area, and, as mentioned in ch 2.5, are, at least in the southern area, almost restricted to areas of woodland outside the Park boundary. The seasonal pattern of abundance of the fruit is shown in Fig. 4.2. It is totally different from Premna spp. and Grewia bicolor, with the fruit being at its peak abundance in the long dry season from July to September, though a few fruits are available for much of the year, except perhaps the short rains.

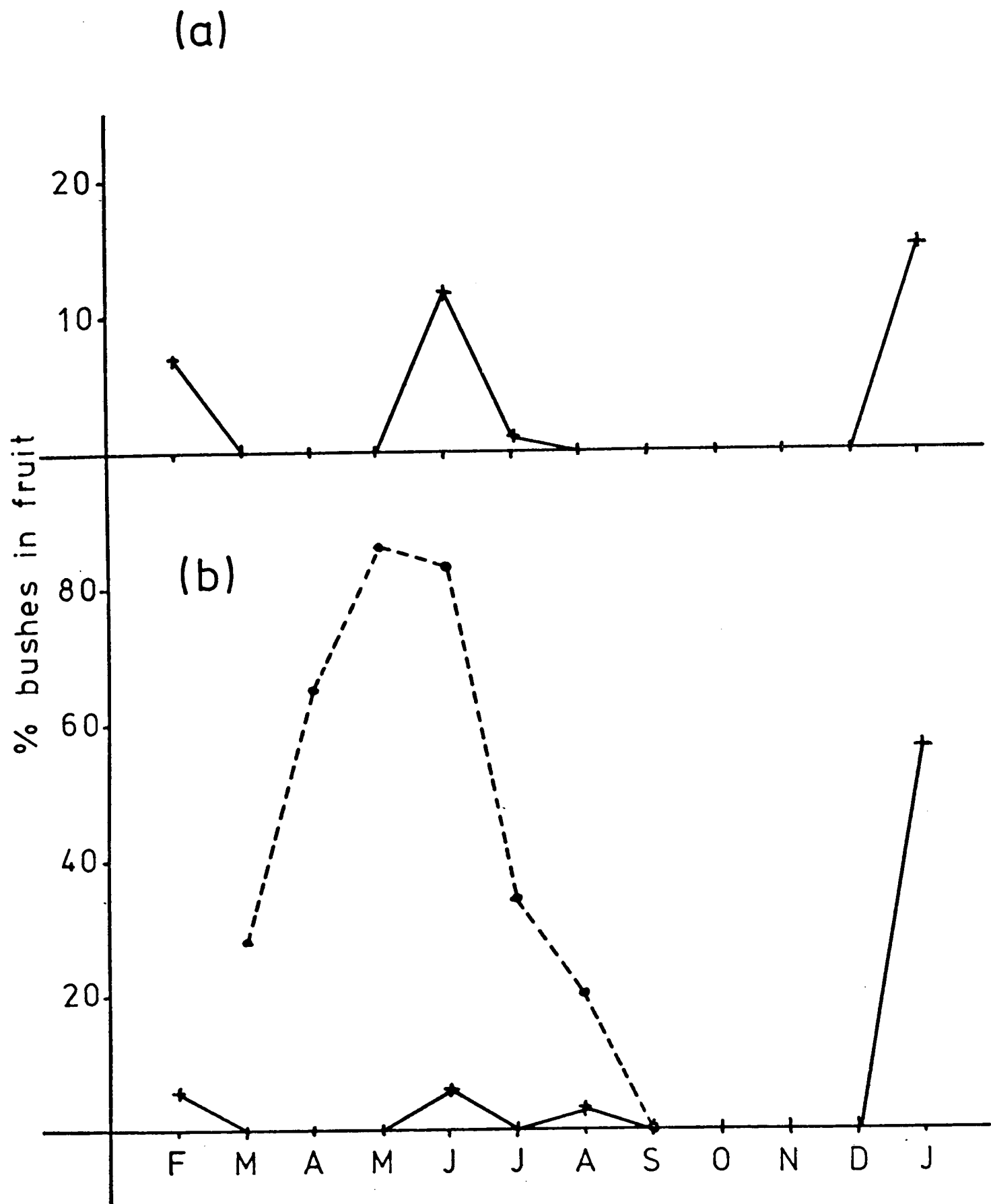


Fig. 4.1 The seasonal pattern of abundance of the fruits of
 a) Premna spp. and b) Grewia bicolor.
 For the explanation of the two lines in (b) see text.

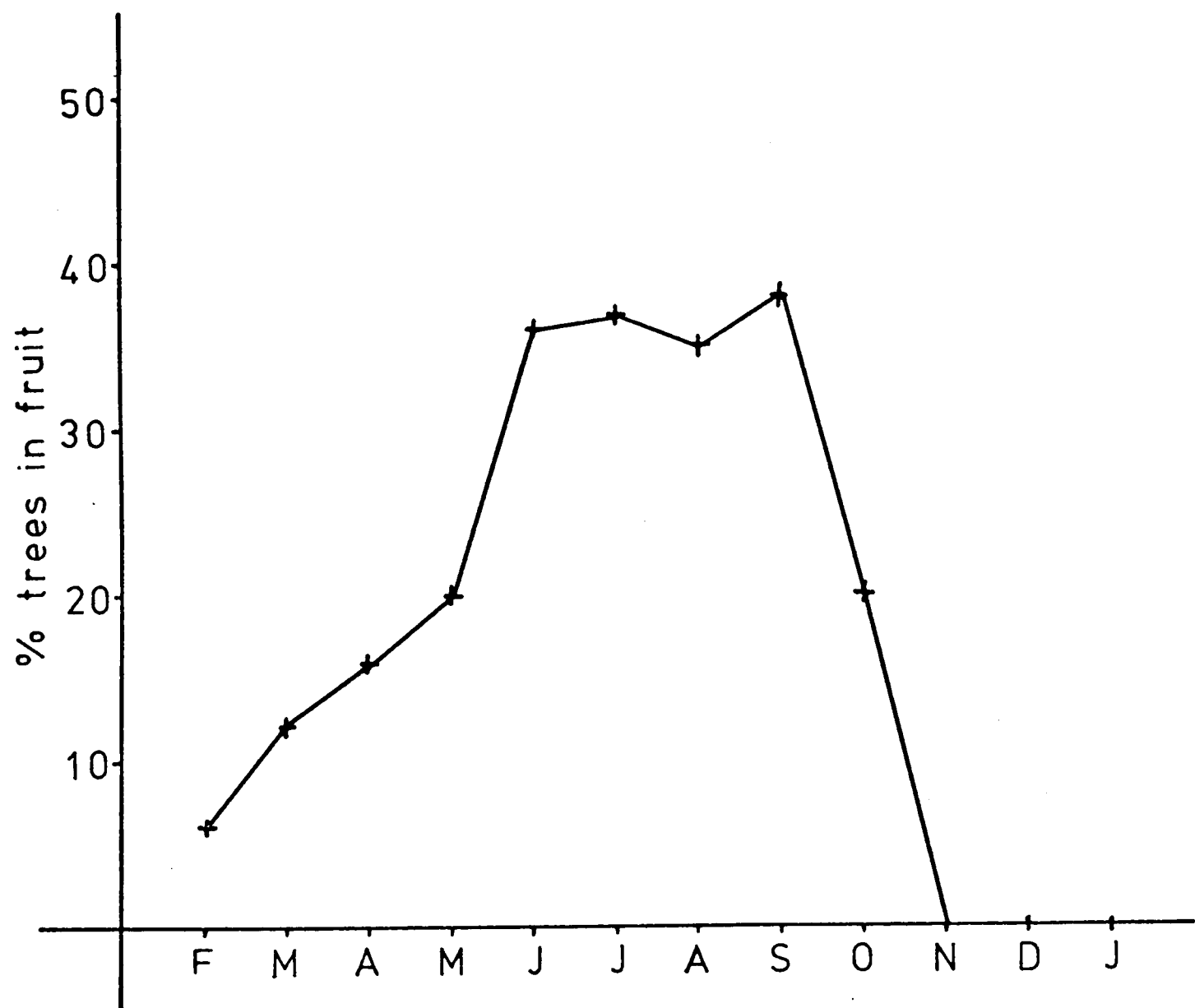


Fig. 4.2 The seasonal pattern of abundance of the fruits of Commiphora spp..

There may be variation in the total amount of fruit available between years; subjectively there was more fruit present in 1975 than in 1976.

Salvadora persica primarily occurs in the damper areas particularly along rivers. It occurred very rarely on my sample plots (Table 4.1) but the seasonal pattern shown is confirmed by qualitative observations along the Voi River. There was a great deal of fruit available in July and August, much less by September, and none at all was noticed at other times.

c) Fruit at any season - Ficus spp.

Ficus spp. occur along the Voi River and probably fruit in a mosaic manner, i.e. trees do not fruit all at the same time, but whether or not there are always one or more trees in fruit along the river is unknown. At Ndololo Campsite, two trees were fruiting in April and May, one in each of July and December (a total of four different trees) and none at other times.

d) Other fruits

The fruits of some other species were recorded as being eaten by birds especially in the woodland. In addition to Salvadora persica Table 4.1 shows data for Boscia coriacea, Strychnos decussata and for all species combined (including unidentified ones) recorded on the woodland transects, except for Commiphora spp., Grewia bicolor and Boscia coriacea (see separate figures), and Acacia spp. (not eaten by birds). B. coriacea and S. decussata are both shown to fruit in the dry season although very few of the former produced fruit in 1976. The woodland is shown to have some fruits available all the year, perhaps with more available in the wet seasons, coinciding with G. bicolor, but complementary to Commiphora spp. These species include Maerua spp. and some creepers.

4.3.2. Nectar

In the Park savanna habitats there were only two species of woody plant which produced conspicuous flowers, and which were visited regularly

Table 4.1. The percentage of bushes in fruit through the year for four 'species'

	F	M	A	M	J	J	A	S	O	N	D	J
<u>Salvadora persica</u>	-	-	-	0 (1)	-	0 (1)	43 (7)	0 (11)	0 (6)	0 (3)	-	0 (3)
<u>Boscia coriacea</u>	0 (100)	1 (141)	0 (154)	0 (116)	1 (199)	0 (233)	0 (220)	3 (244)	1 (185)	2 (175)	2 (180)	0 (147)
<u>Strychnos decussata</u>	0 (16)	0 (23)	0 (14)	12 (24)	34 (35)	20 (52)	15 (78)	14 (51)	9 (35)	6 (79)	2 (60)	1 (67)
Other woodland species	0 (16)	12 (17)	28 (39)	7 (42)	24 (21)	14 (43)	18 (33)	5 (39)	5 (44)	4 (57)	10 (40)	34 (35)

Notes:

- 1) The figure given is the percentage of bushes and/or trees that were in fruit
- 2) The figure in brackets is the number of bushes and/or trees used in the calculation
- 3) 'Other woodland species' are all the species recorded on the woodland transects, including unidentified ones, but excluding Commiphora spp., Grewia bicolor, Boscia coriacea and Acacia spp. (see text).

by birds: Platycelyphium voense and Delonix elata. The seasonal pattern of abundance of flowers of each is shown in Fig. 4.3. P. voense (Fig. 4.3a) has a flowering peak in April just before the rains and D. elata (Fig. 4.3b) at the end of each wet season.

In woodland and riverine the flowers of several other species of both bush and tree were visited but there was no obvious general seasonal pattern of abundance. Most flowers were fairly small and only rarely was a plant covered in them.

4.3.3. Grass seeds

The seasonal abundance of grass seeds is shown in Fig. 4.4. The major peak in January and February followed the short rains, and the two other increases in June and November followed the poor long rains and the unseasonal rain in September respectively.

4.3.4. Arthropods

a) on the ground

The mean dry weight of arthropods caught in the pitfall traps is shown for each of the six sites in Fig. 4.5, and the combined mean in Fig. 4.6. As expected, the peaks of abundance are in the latter part of each wet season. The lower line in Fig. 4.6 excludes all individuals which weighed more than 0.10 g and it shows the relative importance of these large individuals in the wet season, and that they are responsible for the major part of the variance. I also caught a few mice, frogs and lizards but these are left out of the analyses, and I caught too few for separate analysis.

b) in the grass layer

The mean dry weight of the three samples at each of the five sites is shown in Fig. 4.7, and Fig. 4.8 shows the combined mean. The variance in all these figures is very high but the main peak of abundance is shown, as before, to be in December and January. The lower line in Fig. 4.8 shows

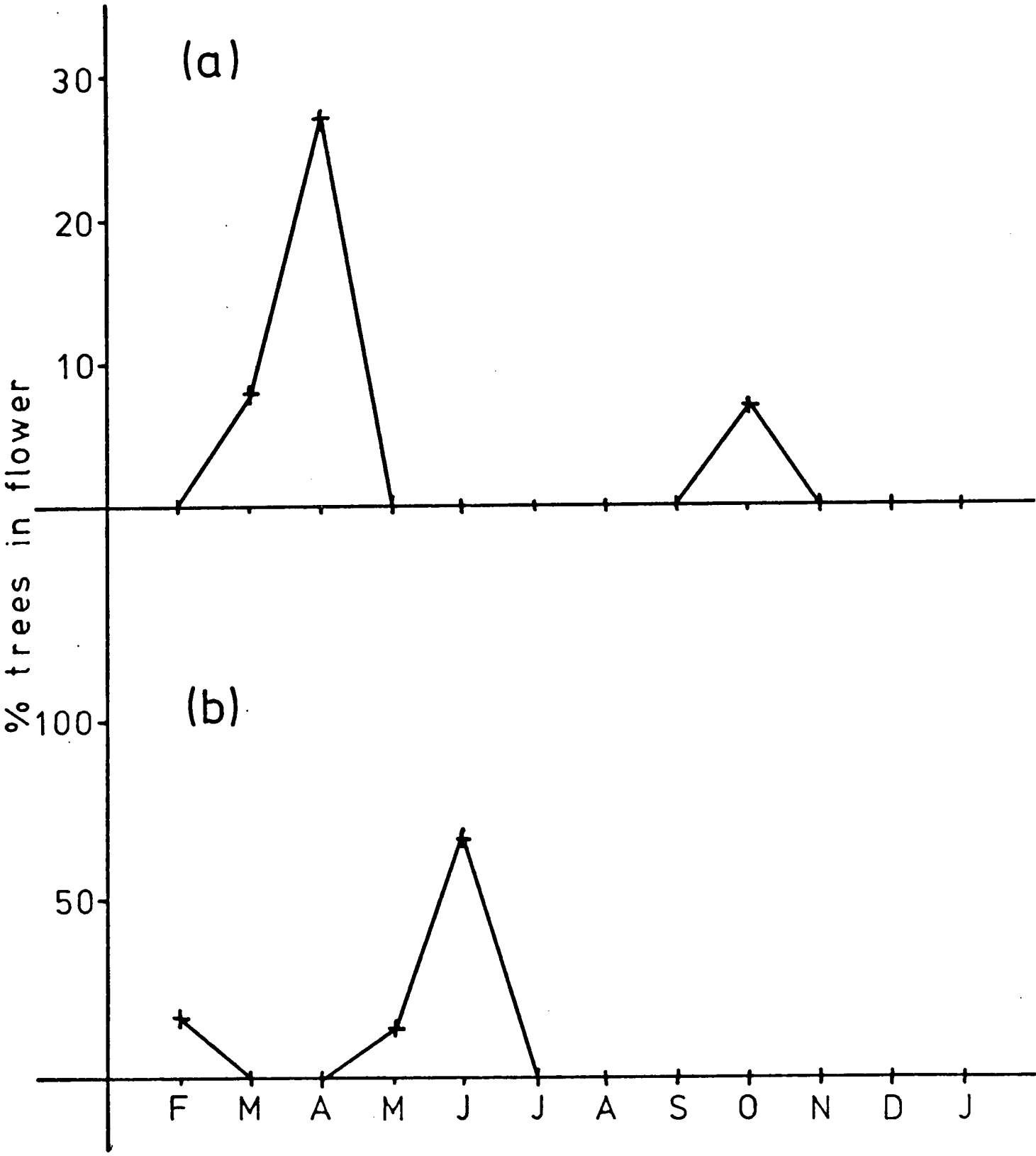


Fig. 4.3 The seasonal pattern of abundance of the flowers of
a) Platycelyphium voense and b) Delonix elata.

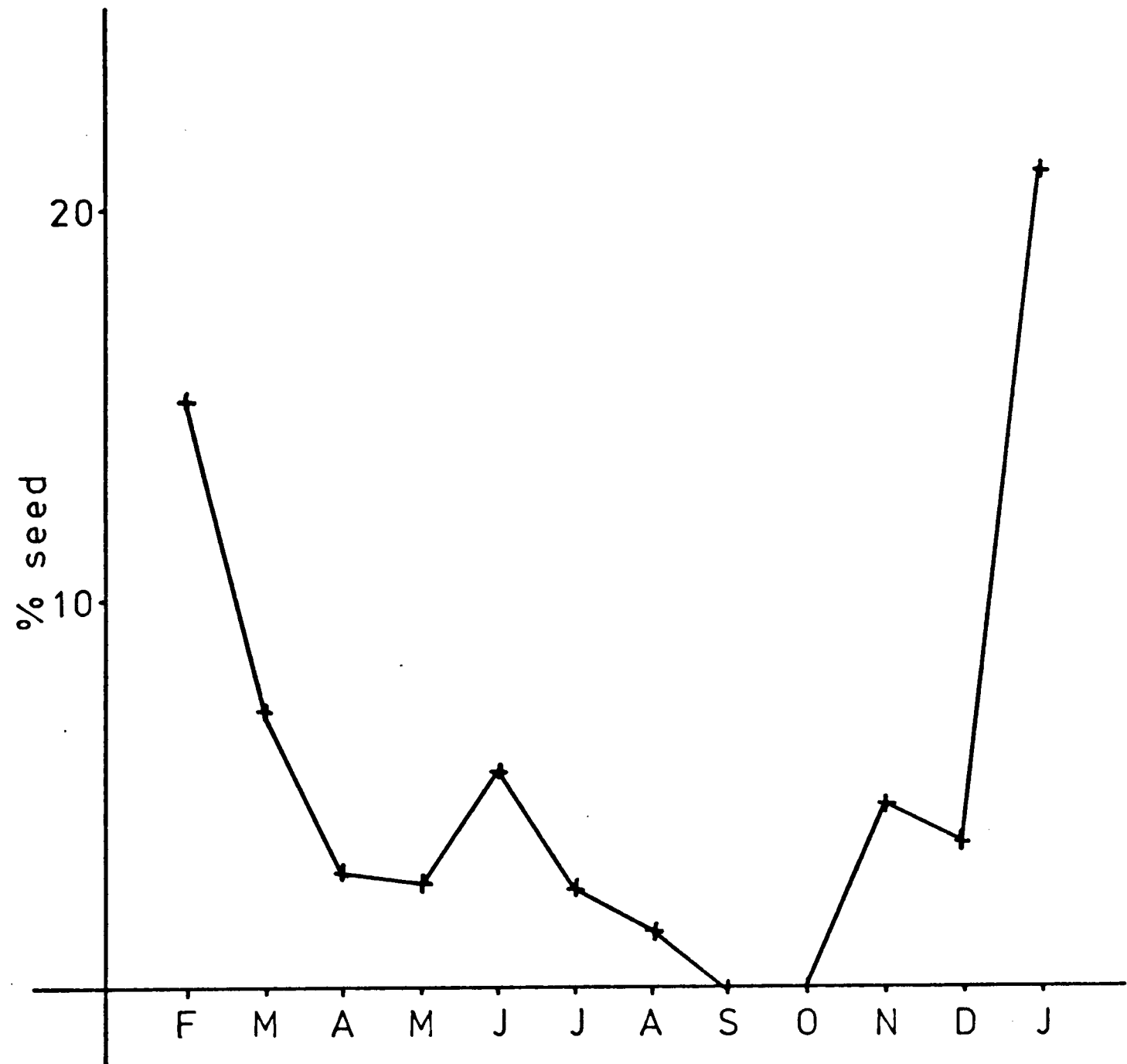


Fig. 4.4 The seasonal pattern of abundance of grass seeds.

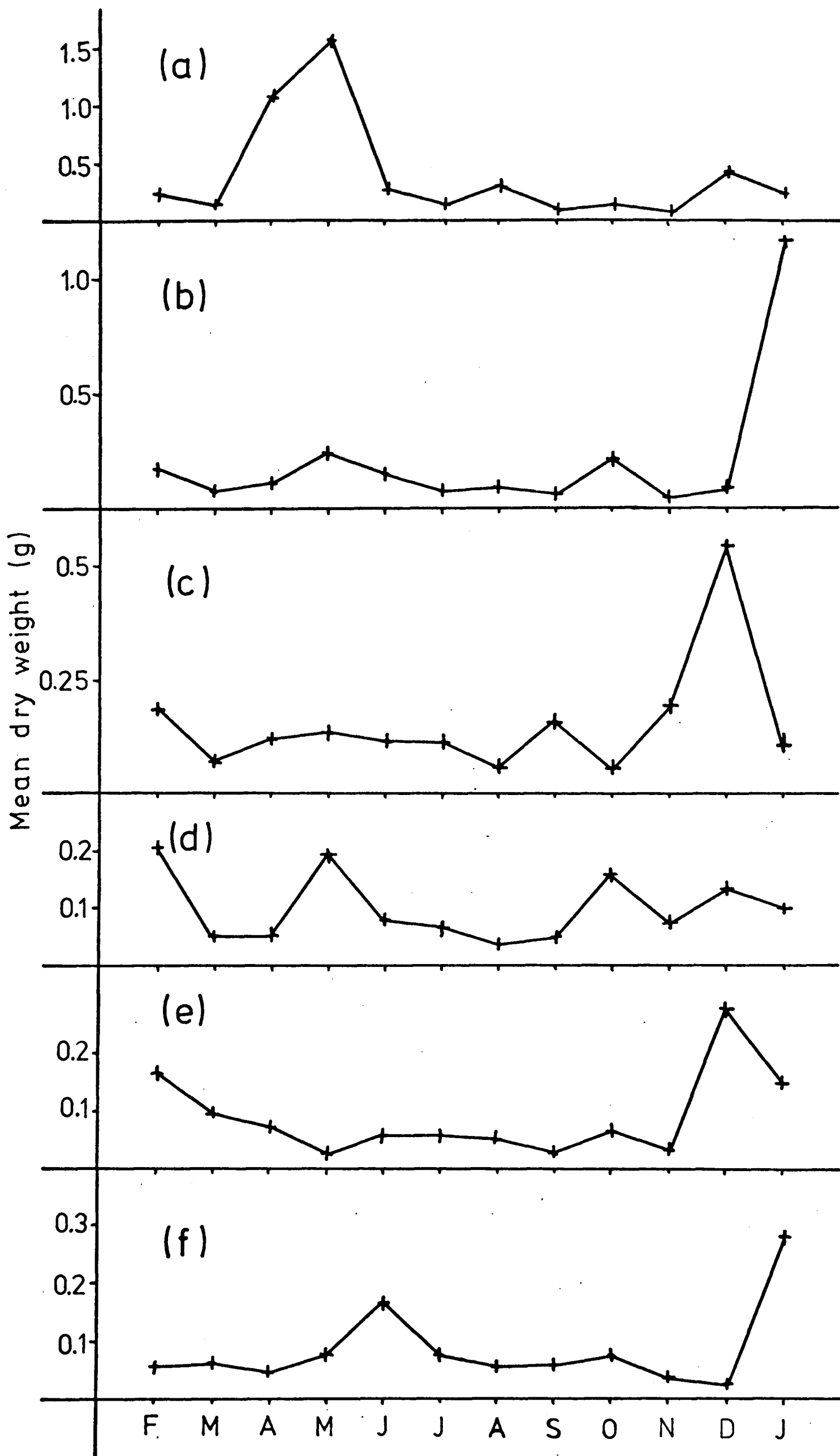


Fig. 4.5 The seasonal pattern of abundance of arthropods in pitfall traps at a) Ndololo, b) Voi Gate, c) Mzinga, d) Woodland, e) Irima, and f) Aruba Road.

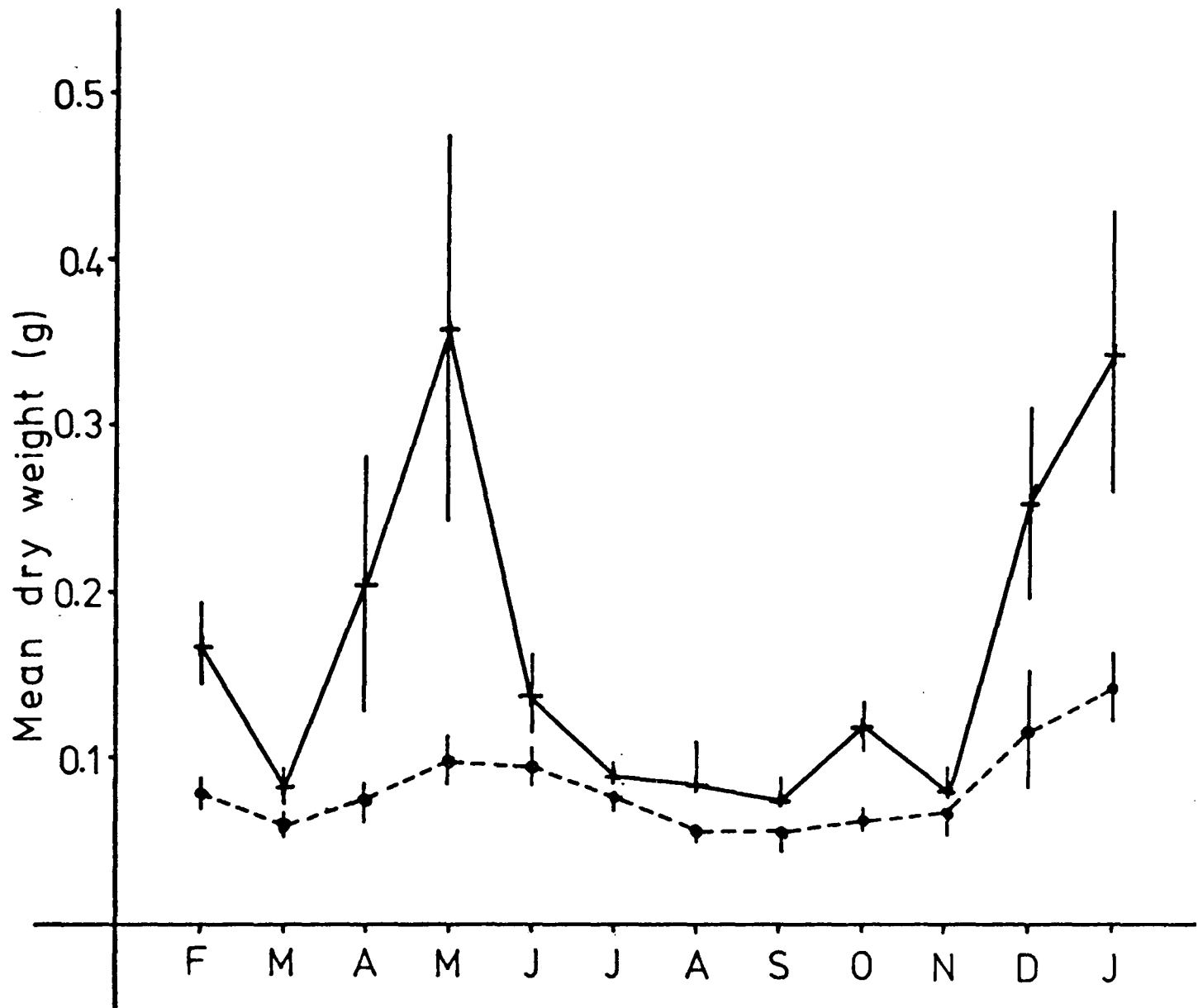


Fig. 4.6 The seasonal pattern of abundance of arthropods in pitfall traps: mean with one standard error either side. The lower (dotted) line excludes all items more than 0.10 g dry weight.

the mean dry weight of grasshoppers. The proportion of the total dry weight that were grasshoppers and lepidopteran caterpillars is shown in Table 4.2. The proportion of grasshoppers is fairly constant and high at around 75-80%. Lepidopteran caterpillars were restricted to periods after rain, and were only a small proportion of the total.

Table 4.2. The percentage of grasshoppers and lepidopteran caterpillars in the sweep-net samples

	Month											
	F	M	A	M	J	J	A	S	O	N	D	J
Grasshoppers n.m.	55	70	66	75	81	86	88	72	74	80	81	
Caterpillars n.m.	2	3	0	5	0	0	0	0	4	0	7	

Notes:

- 1) Figures are the percentage of total dry weight of insects caught in the fifteen sweep-net samples (three at each of five sites)
- 2) n.m. = not measured

c) in the woody vegetation

The proportion of bushes and trees in leaf over the 34 plots (Park savanna habitats and woodland) is shown in Fig. 4.9. It shows ^{about} equal peaks in the two wet seasons.

d) termites

The average weight of wood eaten by termites on the eight transects is shown in Fig. 4.10. The data run from June 1976 to April 1977 but I have drawn the figure to correspond to my other data. It shows the expected peak in the wet seasons and, more important, this peak continues into the dry seasons, especially the long dry season.

4.4. Discussion

4.4.1. Fruit

The results show that there is a temporary fruit supply in the Park savanna habitats in the latter part of each wet season, probably a continuous

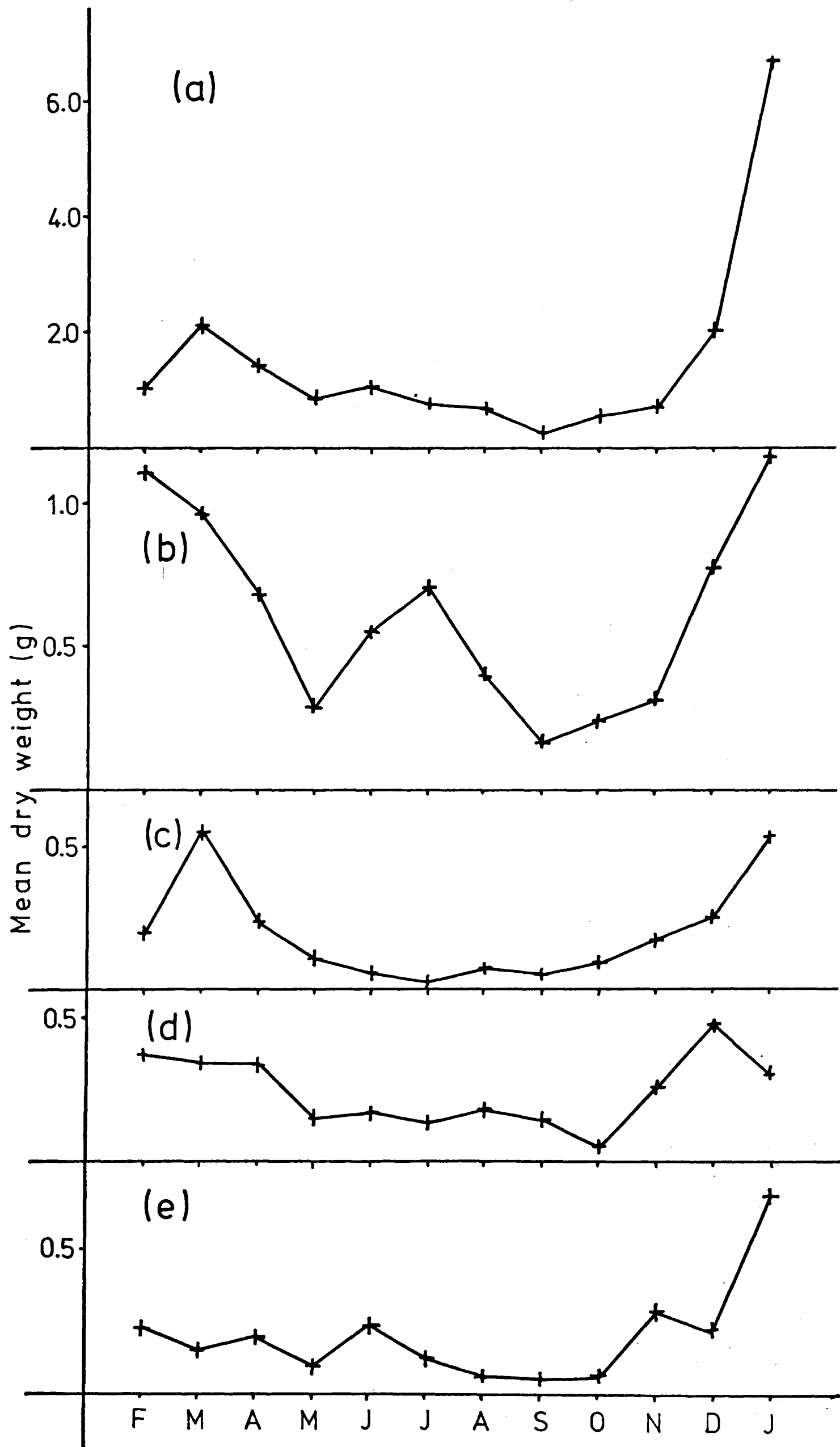


Fig. 4.7 The seasonal pattern of abundance of arthropods in sweep-net samples at a) Ndololo, b) Voi Gate, c) Mzinga, d) Irima, and e) Aruba Road.

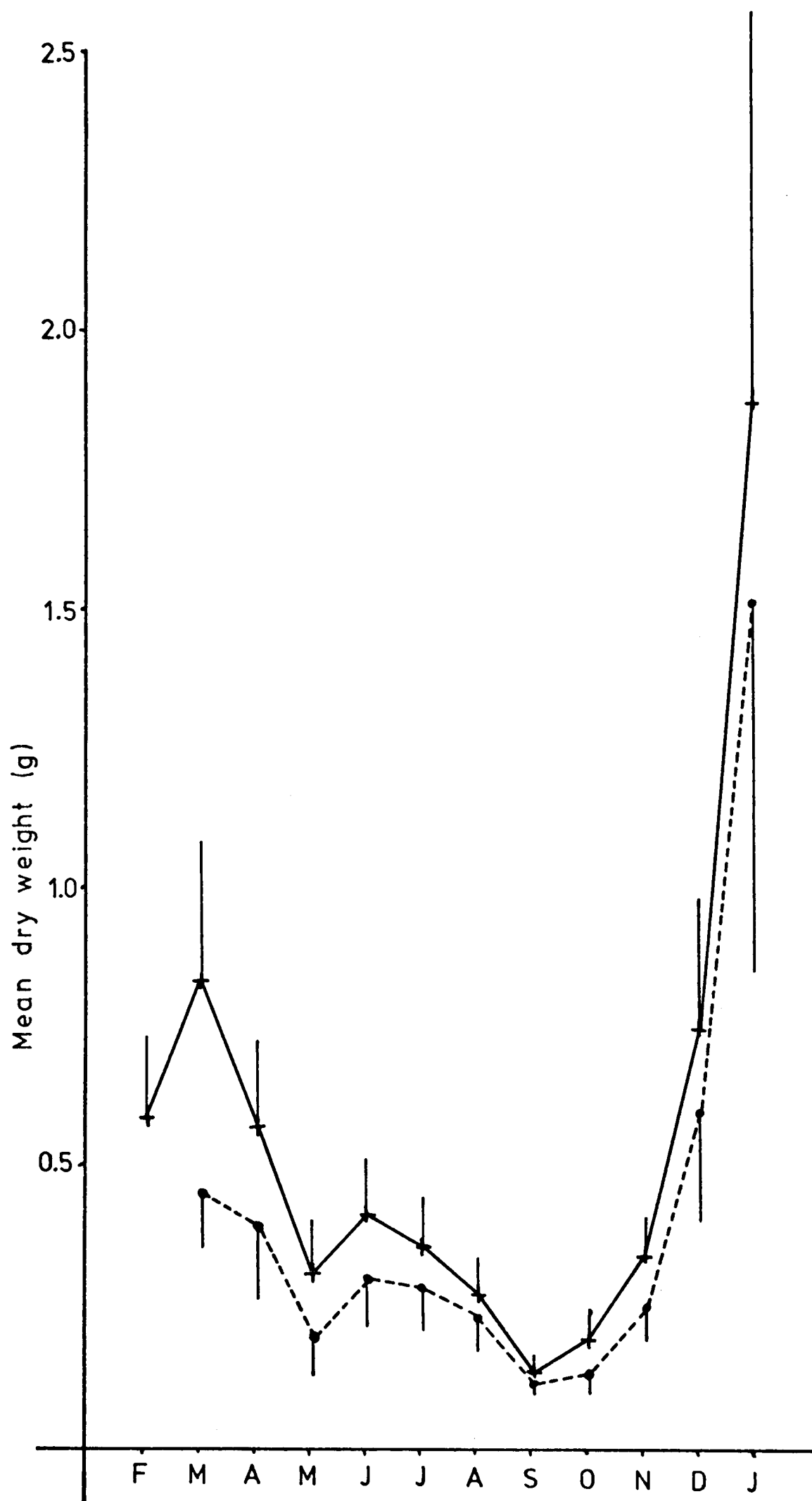


Fig. 4.8 The seasonal pattern of abundance of arthropods in sweep-net samples: mean with one standard error shown. The lower (dotted) line is the abundance of grasshoppers.

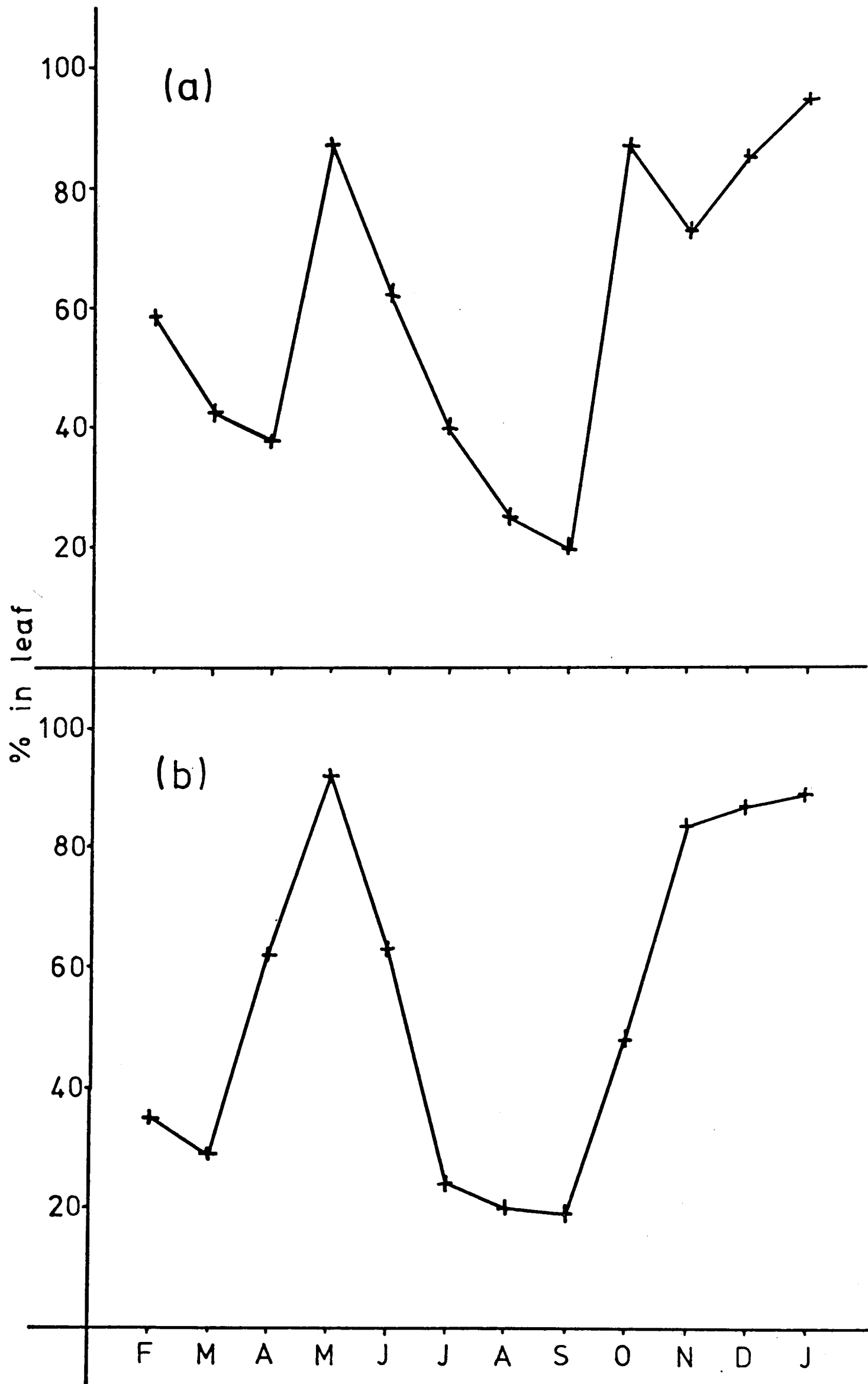


Fig. 4.9 The seasonal pattern of abundance of leaves on
a) bushes, and b) trees.

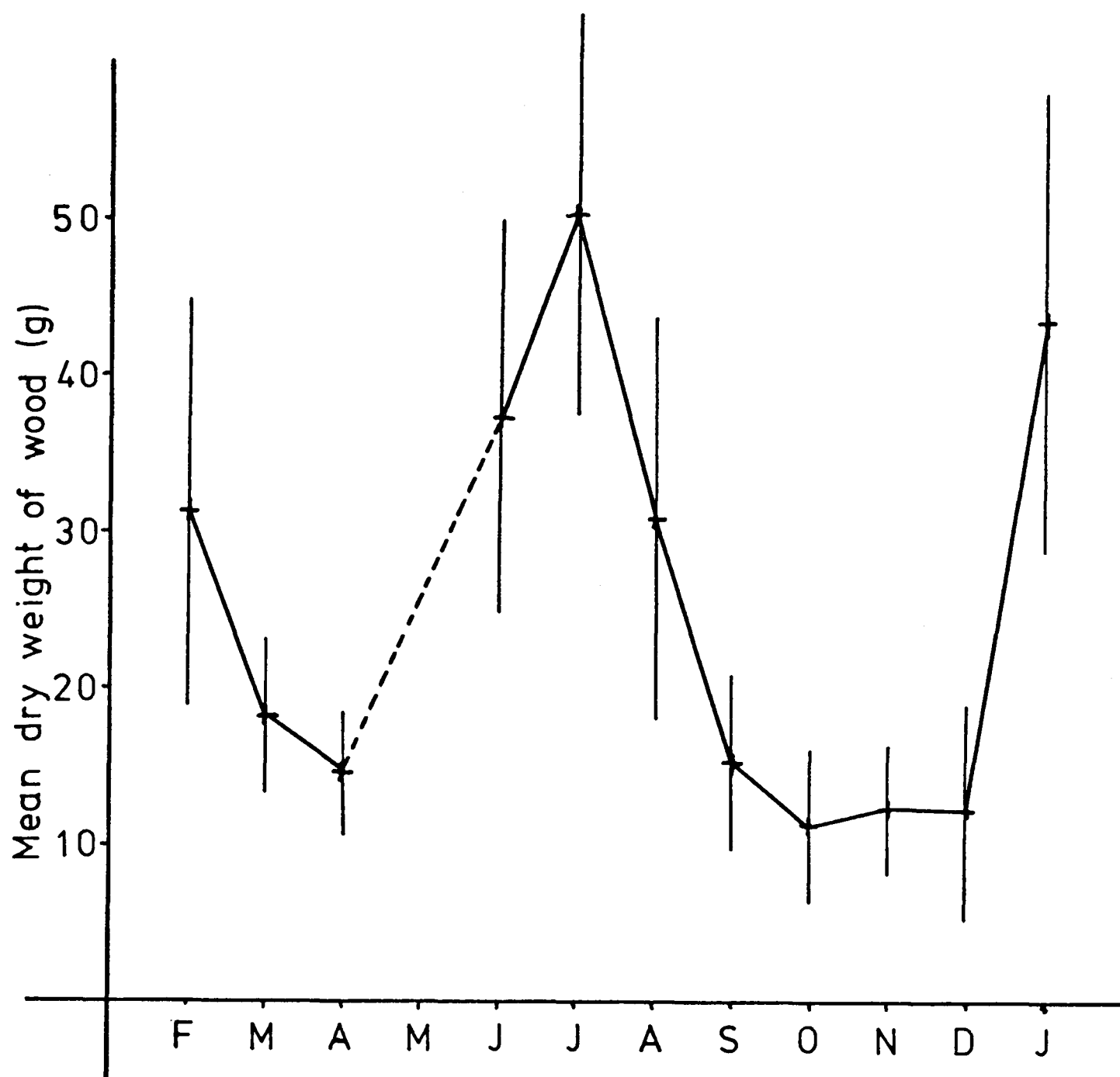


Fig. 4.10 The seasonal pattern of abundance of termites: the mean amount of wood eaten by termites on eight transects, with one standard error on either side. Data from R.D. Buxton (pers. comm.).

supply in woodland and possibly the same in Riverine. Plants in both these latter habitats, however, have substantial fruiting peaks in the early part of the long dry season. Fruit is therefore likely to be at its most scarce during the latter part of the dry seasons in October and March. There is unfortunately almost no other data to compare with this. For his plot in Senegal, Morel (1968) gives the highest fruit production of species eaten by birds (in this case especially Balanites, Boscia and Ziziphus) as December to March with very little between June and October. This peak is about two months into the single dry season with the trough falling in the wet season, a regime which closely parallels the woodland in my study. A specific difference is, however, noted by Coe (1972). In south Turkana Salvadora persica fruits in a mosaic manner, almost throughout the year, and sustains a wide variety of birds and small mammals. So, whether or not the Tsavo situation is typical of semi-arid savanna is as yet uncertain. It is likely too that there are differences between years, perhaps large. These are in turn likely to be related in some way to the rainfall, but the dynamics are unknown.

4.4.2. Nectar

Platycelyphium voense is one of the few plants (or animals) which is geared almost entirely to the April rains for reproduction and it, in common with some other tree species, produces flowers before the rains begin and before leaf production. This behaviour is fairly common in the tropics and is thought to aid conspicuousness for pollinators (Janzen 1967).

The data presented here for Delonix elata are based on only four to nine trees each month and the total spread of flowering is greater than that shown in Fig. 4.3b (see ch 5.4.3). Further, it is significant for the birds visiting them that this species of tree is widely scattered and, more important, there are few individual flowers at a time on any one tree.

Some other species of bush in the Park savanna habitats produce conspicuous flowers, especially in the wet seasons, for example Dirichletia glaucescens, Bauhinia taitensis and Erythrochlamys spectabilis but I did not record birds visiting them.

4.4.3. Grass seeds

Grass seed production seems to be directly proportional to the amount of rain that has fallen a month to six weeks previously (the correlation coefficient between the percentage seed (Fig. 4.4) with the average rain in the previous month (Table 2.1) = 0.59, df 10, $P < 0.05$). In very poor years it will probably also be related to the amount of seed set in the previous rains.

My data take no account of seeds that have fallen to the ground. For these, the peaks will be slightly later than those shown in Fig. 4.4, and slightly lower due to some being eaten on the stem. The troughs will not be so low except at the start of the rains, due to germination. In Thiollay' (1971) area, seeds that fell to the ground were unavailable to birds until the grass cover had been thinned, in his case by fires, a month or so after the seed was set. This effect is unimportant in Tsavo as the grass cover was rarely very dense or high, and was subject to heavy grazing pressure by large mammals which served to keep it more open.

4.4.4. Arthropods

The Ndololo site recorded a considerably larger biomass of arthropods than the other sites, both in the pitfall and the sweep-net samples. The reason is probably that there was a greater volume of grass and litter at this site. The other sites, which were in different habitats ranging from thin Bushed Grassland to Woodland, were all similar to each other. Hence except for the riverine, the ground and grass layer arthropod biomass (almost all insect) does not seem to be affected by the

habitat changes. There was a slight difference in seasonal patterns of abundance, especially in the pitfall data, at the Irima and Mzinga sites as compared to the others. The Irima and Mzinga sites showed almost no increase in April and May whereas the others showed a small peak although delayed until June at the Aruba Road site and not significant at Voi Gate. In the others, the peak is significantly different from the months on either side (d-test on figures from the individual traps). It was probably the result of differences in rainfall. The Irima and Mzinga sites recorded almost no rain in April and May whereas the others received up to about 50 mm, despite being only 5 - 10 km distant.

The seasonal occurrence of insects, with an increase in the wet season, has been "known" for many years but very few studies have quantified it. All investigators agree that there is a major increase in the wet season, whether the samples have been taken by hand (Morel 1968), with sweep-nets (Dingle & Khamala 1972), a light trap (Owen 1969a, Sinclair 1978) or a Malaise trap (Owen 1969a,b) but two other important points emerge from these studies. My data agree with both and both have important consequences for the birds. Firstly, where there is more than one wet season, the season with the more predictable rainfall produces a greater flush of insects, and this peak is less dependent on the actual amount of rain in a given year. Secondly, among most groups of insects the difference between the average peak abundance and the average lowest abundance is a factor of only about five or six. Most casual observers have assumed this difference to be much greater. The fallacy is due I think to the mass of insects that come to lighted windows for a few days (only) after the first storms of a wet season. These are all adult insects and I agree with Sinclair (1978), and others, that many of them are likely to be insects coming into the area with the intertropical front, as do the rains themselves, and are not of local origin. I would suggest further that their behaviour closely resembles that of many birds at the same time. Some will no doubt stay and breed

in the area in response to the flush of green vegetation associated with the rain, but others will only be passage migrants and therefore unavailable as food for local birds except on a very temporary basis. Thus the very large increase in the total abundance at light traps and lighted windows for the few days at the start of a wet season gives a false impression of the availability of insects for birds, and this is further enhanced because adult insects are, in general, less palatable than larvae.

One group of insects that probably does show a larger increase in the wet seasons is those living in the woody vegetation, but I do not have the data. Morel (1968), however, provides some for his plot in Senegal although his analyses excluded some important groups notably those living on the bark and trunks. He found that the biomass of insects in the foliage of the woody vegetation increased by a factor of 17 in one year, and 60 in another, in the wet season over the preceding dry season. This obviously has very important consequences for the birds taking food from vegetation, but it should be noted that these insects never contributed more than 5% to the total insect biomass and that the bark and trunk living ones are likely to provide a fairly substantial and more constant biomass thus reducing these factors. In the same place the 95% or more living on the ground only showed increases of a factor of three and eight in the two years respectively.

4.5. Conclusions

The methods I have used to show the seasonal occurrence of the foods were designed to reflect the availability rather than the total abundance per se. These two may be rather different quantities as I have suggested in the penultimate paragraph above, and as Thiollay (1971) showed for seeds.

Almost all foods are very seasonal in their occurrence, but it is unlikely that any are entirely absent at any period.

CHAPTER 5 The Land-birds of Tsavo East National Park

5.1 Introduction

Gause's competitive exclusion hypothesis states that "complete competitors cannot coexist" (Hardin 1960), and it is one of the central tenets of competition theory. Intensive studies, even of closely related species which are coexisting in an area, and appear to be occupying the same niche, have usually revealed significant differences in ecology between species (see Lack 1971). Species may compete and exclude each other from any essential resource but the most common of these are thought to be somewhere to live (in particular to nest), and food. Four major isolating mechanisms have been found to operate between species occupying an area. Firstly they may occupy different habitats, e.g. one species may be in woodland and another in grassland. Secondly, they may feed at different times, either diel e.g. one by day and another by night, or more often, seasonal e.g. one in the wet season and another in the dry. Thirdly, they may feed or nest in different parts of the same habitat, e.g. one on the ground and another in the woody vegetation. And fourthly, even if feeding in the same part of the habitat they may take different types of food, e.g. one taking fruit and another insects, or different sizes of food. The first three of these isolating mechanisms are quantifiable from observations on the living birds as can, in broad terms, the types of food eaten. This last, however, and particularly the size of items taken can only be examined critically by collection and analysis of gut contents, a method which was not available to me in this study because I was working in a National Park. As noted earlier, though, any dead birds found were examined (see Lack & Quicke 1978).

Some indication of the size of food items taken can be obtained by assuming a relationship between the size of items and the size of bird. Only few studies have tried to correlate the two but they have found it to be largely correct within a small taxonomic group and/or feeding method. For example, Hespenheide (1971) has shown for some New World flycatchers (Tyrannidae) that, within a feeding type, prey size is highly correlated with bird body weight and less so with some bill characteristics, and Abbott, Abbott & Grant (1977) have shown for Darwin's Finches (Geospizinae) that the size and hardness of seeds eaten is related directly to bill characteristics especially depth.

On question arising from comparisons between species is "how different do two species have to be in order to be able to co-exist?" or, in other words, "how much overlap can be tolerated?" Workers are usually content, however, to show that there is a statistically significant difference between two co-existing species on at least one resource dimension. The degree of overlap is sometimes measured at the same time (see Cody 1974) but widely applicable general "rules" for the degree that can be tolerated can only really be formulated for the size dimension. This has been done by arguing from species which do co-exist and appear to be segregated by the size of food items taken, but even here the authors emphasise that their results are only indications of the necessary differences. Grant (1968) suggested that for bill measurements a minimum difference of 15 per cent of the smaller species is necessary in at least one dimension, usually length. Similarly for body weight, Diamond (1972) suggested that the larger species needs to be double that of the smaller.

When a resource is not in short supply, ecological differences between species will not be necessary for coexistence. Nevertheless, they can easily, and often do evolve in such cases as Hespenheide (1973) shows. He was only considering size of prey taken and character

displacement, but the argument can be generalised to include habitat preferences and feeding stations. Therefore one would expect that even if a resource, such as food, is superabundant, the various species using it will be different from each other, taking it in different habitats, in different ways, or from different sites etc. A resource will of course only be superabundant for the user if either some other essential resource is limiting, or predation is so high that numbers are kept below the carrying capacity of the habitat. The most likely limiting resource for birds in Tsavo, other than food, is nest-sites, but, except perhaps for holes in trees, these appear to be widely available, although the precise requirements of most species are unknown. There are very few estimates of the effect of predators, or the amount of predation on bird populations in the tropics, but it is generally agreed that predation is much increased over temperate areas, and predation has been suggested as the cause of the increased species diversity of many groups of animals found in the tropics (see Pianka 1966).

One would expect therefore to find differences in feeding ecology between species whether or not food is limiting. This is, however, assuming that the environment and resource supplies are relatively constant and predictable from year to year. This is far from the case in Tsavo. As shown in ch. 2.2 the climate is very unpredictable, and as food abundance is largely dependent on the climate (see ch 4) one must assume that food availability is also unpredictable. Furthermore, there have been major changes in the habitat over the past 20 years and it seems likely that the bird populations are still changing as a result.

Three hundred and twenty four species of land-bird and a further 52 species of bird of prey have been recorded in Tsavo East N.P. (Lack, Leuthold & Smeenk 1980). In this chapter each family of birds, or in a few cases grouped into subfamily or two closely related families, is

considered in turn. The species are discussed in terms of status, habitat preferences and seasonal occurrence in Tsavo, based on censuses giving indices of relative abundance (Type I), and feeding ecology. The discussion is directed primarily at the differences between species, especially between those closely related taxonomically. The final part of the chapter discusses the commoner species grouped into their main food types.

5.2 Explanations of terms and figures used in this chapter

5.2.1 Nomenclature

All birds names follow Forbes-Watson (1971). This, with a few minor modifications, follow White (1965) for non-passerines and Hall & Moreau (1970) for passerines. A complete list of all land-bird species recorded in Tsavo East N.P. is given in Appendix 1.1, together with some of their major characteristics. The species number in Mackworth-Praed & Grant (1957-60) is also given.

Plant names follow Greenway (1969).

5.2.2 Sources of data

The text in each section contains a subsection 'Data from Tsavo'. These are data collected during the fieldwork for this study. Two short specific papers 1) on the lark Mirafrapa pulpa (Lack 1977) and 2) on the stomach contents of some birds found dead in Tsavo (Lack & Quicke 1978) have been published and details of specific records of rare species and a brief summary of the status of the rest are given in Lack, Leuthold & Smeenk (1980).

A subsection 'Data from the literature' is included where data which did not originate in Tsavo, are used in subsequent classification and analysis, or where information in the literature warrants further

discussion e.g. of movements. However, the only information available about the ecology of most of the species discussed in this study is that contained in the standard handbooks where it is usually only noted in very general terms. To save repetition these are not usually quoted individually but those consulted are Jackson (1938), Mackworth-Praed & Grant (1957-60) (abbreviated where necessary as MPG) and Williams (1967, 1969) for East Africa; Benson et al. (1973) for Zambia; and McLachlan & Liversidge (1977) for South Africa.

5.2.3 Previous information on Tsavo

Unless otherwise stated, all references to the status or occurrence of species "formerly" refer to the period 1959-60, and all are personal communications from A.D. Forbes-Watson.

5.2.4 Bird counts

All figures quoted for habitat preferences and seasonal occurrence are of the number of individual birds seen per 10 hours, derived from the Type I censuses. Individuals only seen flying over are excluded.

Table 5.1 gives the number of 15 minute censuses carried out in each major habitat type for each of the 25 months of the study. These are the figures used to calculate all relative abundances given in this chapter, unless otherwise stated. Each month the habitats were covered to about the same extent relative to each other. In addition to those figures in the table that are marked (the largest single deviations) it should be noted that December 1976 was very atypical, both in the distribution of time spent in each habitat, and in the total time spent (very low), and also that after August 1976 there was a relatively low coverage of Bushland and Wooded Bushland, and relatively high of Bushed Grassland and Wooded and Bushed Grassland; but I do not think these deviations have a very significant effect on the bird abundance figures.

Table 5.1 The number of 15 minute censuses carried out in each habitat in
each month

Months	Habitat							TOTAL
	G	BG	WBG	B	WB	W	R	
1974								
December	9	15	34	5 ^a	19	21	13	116
1975								
January	13	32	28	19	21	29	17	159
February	12	59 ^a	32	18	13	27	13	174
March	9	21	27	13	13	23	7	113
April	11	40	38	16	13	26	11	155
May	8	27	38	9	25 ^a	13	11	131
June	12	33	33	21	18	26	7	150
July	7	22	28	15	10	19	8	109
August	5	15	31	7	24 ^a	13	8	103
September	10	31	36	22	14	22	7	142
October	8	35	34	16	13	14	6	126
November	12	27	36	21	14	26	8	144
December	5	5 ^a	18	8	10	19	8	73
1976								
January	7	20	17	12	8	26	8	98
February	4	12	12	6	8	13	7	62
March	2	22	38	10	23	27	7	129
April	6	29	12 ^a	13	29	30	7	126
May	9	19	24	10	8	17	12	99
June	2	17	26	10	6	12	6	79
July	4	20	21	13	28 ^a	34	10	130
August	4	18	24	3	7	10	6	72
September	2	22 ^a	12	4	4	15	6	65
October	3	14	34 ^a	7	7	18	6	89
November	4	23	30	6	10	17	7	97
December ^a	0	4	18	1	1	18	7	49
TOTAL	168	582	681	285	346	515	213	2790

Notes:
a) rather low or rather high in proportion for that month. December 1976 is
very atypical (see text).

The greatest problem with all comparisons of censuses is that of bird conspicuousness. In this study the effects of conspicuousness come under three headings.

a) Comparison between species

A species is likely to be more conspicuous, and easier to identify if, compared with others, it is large, has bright colours, is vocal and feeds in the open rather than inside the vegetation. The most important comparisons, however, involve closely related species and these, almost by definition, have many similar characteristics, and hence are conspicuous to the same degree.

b) Comparison between seasons

There are two seasons in Tsavo for this purpose, wet and dry. During the wet season the presence of more or less dense foliage makes all habitats more difficult to see through. One would therefore expect birds to be less conspicuous in the wet season despite some birds 'showing off' more to attract mates and exclude rivals; hence any increases in numbers recorded then are probably underestimates, and only decreases should be treated with caution. A few species were found to increase in the long dry season but for many it was only for part of the dry season, and for some the increase could be attributed to an increase in the available food supply. I found no sharp decreases over the period at the start of either wet season, and indeed for a large number of species there was a considerable increase.

c) Comparison between habitats

A habitat with a greater volume of vegetation is more difficult to see through, and hence one would expect birds to be less conspicuous. The main factor affecting visibility in any habitat is green foliage, but except in Riverine, which remains to a large extent evergreen, leaves are only on the trees for a quarter of the year, and, although twigs

make a difference between the thickest habitats and the thinnest, they are not a significant factor for the finer divisions. Further, the screening effect of one habitat over another is consistent whether or not the trees and bushes are in leaf. The comparison that is most affected is Riverine versus the remainder. As with the seasonal comparisons, however, it is only differences in one direction that should be treated with caution. The comparison between Woodland and the remainder is potentially the next most affected and is one of the most crucial to the whole study, but even here differing conspicuousness is relatively unimportant. The predominant direction of the changes in numbers over the next thinner habitats (Wooded Bushland and Bushland) is that of an increase in Woodland, which is likely to be real, and for those species that show a decrease, it is usually a continuation of a trend shown through other habitats, and/or there is evidence from the literature that the species concerned is likely to be commoner in the more open habitats.

Differences in conspicuousness, therefore, exist and may affect the accuracy of the figures which follow, but they will not affect the arguments presented since they have tended to minimise rather than exaggerate the differences in observed numbers of birds.

5.2.5 Feeding records

It was often difficult and sometimes would be misleading to count the total number of individual food items eaten. Where a bird was "seen feeding" at a site, five items have been scored, and the sum of all these is the score used in determining food preferences and feeding methods. The effects of this limit of five items are to reduce slightly the score of common feeding methods, and increase the rarer ones. The limit also reduces the importance in the total score of a method used with a very temporary abundance of food, which may be atypical.

When calculating position in the vegetation, however, both horizontally and vertically, I have used only one figure per bird seen. If a bird used more than one horizontal position, the predominant one has been scored. For vertical positions the mean has been calculated. All figures for height (and distance flown) are quoted as mean $\pm$ standard error (number of individuals). All such figures are in metres.

Feeding rate has been calculated from the timed feeding observations by dividing the number of food items taken by the total time observed.

5.2.6 Statistical Treatment

a) Habitat Preferences

Preferences of one species -- where required these have been analysed using χ^2 . The seven major habitat types have often been divided into broad groupings for this purpose. Firstly, thick habitats (B, WB, W and R) and thin habitats (G, BG, WBG), and from Table 5.1 these are shown to have been censused in the proportion 49 per cent thick and 51 per cent thin. It is these percentages which are used to calculate expected numbers. A second division is those with trees (WBG, WB, W, R) totalling 63 per cent of census time, and those without (G, BG, B) totalling 37 per cent. Differences between species -- these also have been analysed using χ^2 . In some cases to avoid low expected numbers, two, or occasionally three, habitats have been merged for these calculations. In each, the χ^2 value, the degrees of freedom (df) and the probability value attached are given. Throughout, N.S. means "not significant" at $P < 0.05$. In addition, an indication of which habitat or habitats are most responsible for the magnitude of the χ^2 value is given. The figure calculated is the percentage of the total χ^2 value contributed by each habitat, and the largest one (or two if they contribute about the same percentage) is mentioned.

b) Seasonal occurrence

Both in this chapter when considering an individual species's abundance in different months, and in the next chapter when considering the density of birds similarly, the year is considered as a circle, with the months represented by sectors around its circumference. Data from the two years are summed and the months weighted for different effort expended if necessary. The abundances in each month are then tested for uniformity. The abundance in each month is taken as a vector from the central point. The test involves calculating the magnitude of the resultant vector $R = \text{square root of } ((\sum n \sin A)^2 + (\sum n \cos A)^2)$ where n is the abundance in each month, A is the angle of the sector representing that month (January was arbitrarily selected as having angle zero), and the summation in each case done over the year. Five percent and one per cent critical values of R/N (N = total numbers seen over the year) are given in Table 56 of Pearson & Hartley (1972) for $N \leq 200$ and are reproduced in Appendix 1.4. For $N \geq 20$, with increasing accuracy as N increases, $2R^2/N$ is found to be approximately distributed as χ^2 with 2 degrees of freedom (see Pearson & Hartley 1972 p.124). In each case large values indicate that a seasonal pattern is present in the data. The modal date of the peak can also be calculated ($= \tan^{-1} ((\sum n \sin A)/(\sum n \cos A))$ and A as before) and then equating degrees with days from the arbitrary date assigned to $A = 0$ (15 January in this case). Dates are given here as quarter months e.g. January 2 is the second week of January, February 4 the last week of February etc.

This test will show up a seasonal effect for single peak distributions. A few species appear to show a more complex pattern of occurrence in Tsavo, with two or occasionally more peaks of abundance in the course of the year, for example a peak in both wet seasons. By making the higher abundance more spread out and the average over the period of both peaks lower, the value of R/N (and $2R^2/N$) will be reduced.

There is no single statistic similar to R/N to describe such distributions, and each case is treated individually in the discussions which follow.

c) Other data

Statistical tests have been used where appropriate, in particular the d-test for the difference between means. In all cases the d-test has been used, and not the t-test, because the latter assumes that the variances of the two distributions to be distinguished are the same (see Bailey 1958).

I do not have sufficient critical data for all situations, in particular for the rarer bird species. In some cases I have given a subjective impression from my own casual observations in Tsavo as an indication of what occurs. These are all clearly marked as such and no critical analyses stem from them.

5.2.7 The summary tables at the end of each section

The main methods of ecological separation are tabulated using the following code:

H	Habitat
F	Feeding station
T	Type of food
O	Seasonal occurrence
S	Body size

Very often two or more methods seem to operate. In such cases all are mentioned, but if one is of lesser importance it is placed in brackets. Further, some species are mainly separated by one method, but may have a considerable zone of overlap. Differences which operate in the overlap zone are placed after a dash.

For example the summary table

	A	B
species A	-	-
species B	T-F	-
species C	H(0)	H

shows that species C occurs in a different habitat to A and B, and also at a different time of year to species A. Species A and B eat mainly different food types, but where they are eating the same food, they take it from different sites.

5.3 The land-birds

The relative abundance of each species in each habitat is given in Appendix 1.2. Appendix 1.3 gives the relative abundance of each species in each month.

5.3.1 Struthionidae - Ostriches

Data from Tsavo - Two races of Struthio camelus meet at the course of the Nairobi-Mombasa railway, with S. c. molybdophanes to the east and north (including Tsavo East N.P.), and S. c. massaicus to the south and west (including Tsavo West N.P.). The latter has, however, been seen four times in Tsavo East N.P. all within about 5 km of the railway.

From an ecological point of view S. camelus can be classed as a large herbivorous mammal, and Cobb (1976) included it in his survey of these. He found, from aerial surveys, that it is primarily an open country species, and my few data confirm this, although S. c. molybdophanes is tolerant of thicker scrub than S. c. massaicus (Cobb 1976).

Data from the literature - It is mainly herbivorous and S. c. molybdophanes is thought to be more of a browser than other races (MPG).

S. c. molybdophanes is one of several forms which has been expanding its range south in recent years; it was not recorded south of the Tana River, about 75 km north-east of Tsavo East N.P. at its nearest point, by MPG.

5.3.2 Phasianidae - Gamebirds; and Numididae - Guinea-fowl

Date from Tsavo - Four gamebirds and three guinea-fowl have been recorded. Francolinus hildebrandti is entirely restricted to rocky hills and hence was not seen in censuses. It is larger than the other three species but only just under half the size of the three guinea-fowl.

F. leucoscepus is the next in size. It is resident but there is a slight seasonal variation in numbers ($R/N = 0.31$, $N = 56$, $0.01 < P < 0.05$, peak February 1).

It occurs primarily in Riverine. F. sephaena, also a resident ($R/N = 0.17$, $N = 97$, N.S.), is commonest in Woodland, but it occurs regularly in Riverine, and more rarely in other habitats. Coturnix delegorguei is much smaller.

It may occur in large numbers in any area where there is a high grass cover, especially the more open habitats ($\chi^2 = 98$, $df\ 1$, $P < 0.001$). It is common in December and January although much smaller numbers occur between October and May ($2R^2/N = 760$, $N = 459$, $P < 0.001$, peak Dec 4).

Of the three guinea-fowl species, Guttera pucherani has not been seen in the Park since November 1973. Previous to that it was seen sporadically in the Voi River forest (W. Leuthold pers.comm.). Numida meleagris is uncommon in Woodland but is rare outside this in the other thicker habitats. It was seen feeding at times in more open areas when these were nearby e.g. near Irima Hill. There is a large resident flock of Acryllium vulturinum around Park HQ, otherwise I only saw it very rarely in thicker habitats (none in censuses). I did not see it in riverine forest.

The two commoner Francolinus spp. and the three guinea-fowl have all decreased very much in numbers in the last few years. This is partly due to the habitat changes but the decrease is especially marked among

these species. Perhaps the recent series of dry years has had a greater effect on these species than on most others.

All seen feeding were on the ground.

Data from the literature - All these species are mainly vegetarian, eating seeds and shoots, and digging up small tubers etc. And, with the exception perhaps of C. delegorguei, they all eat some insects. All food is taken from the ground. By analysing stomach contents Swank (1977) found that the major food of F. leucoscepus, F. sephaena and N. meleagris in Kajiado was Cyperus bulblets (as also found by Stonach (1966) for F. leucoscepus in Mkomasi) with insects, especially termites, forming 25-30 percent of the diet of the two Francolinus spp., and 10 percent of that of N. meleagris. Swank (1977) also found a direct relationship between size of bird and size of prey although there was considerable overlap.

Summary of differences

	<u>F.s.</u>	<u>F.h.</u>	<u>F.l.</u>	<u>C.d.</u>	<u>N.m.</u>
<u>F. sephaena</u>	-	-	-	-	-
<u>F. hildebrandti</u>	H	-	-	-	-
<u>F. leucoscepus</u>	H	H	-	-	-
<u>C. delegorguei</u>	H	H	H	-	-
<u>N. meleagris</u>	S	H	H-S	H	-
<u>A. vulturinum</u>	S	H	H-S	H	?

5.3.3 Turnicidae - Button Quails

Data from Tsavo - Two species occur and both are regular but uncommon. Turnix sylvatica is very similar to the quail Coturnix delegorguei (ch 5.3.2), both in its habitat preferences and seasonal occurrence, but it is only half the size. However, it is much less common (only four seen in Type I censuses). Ortyxelos meiffrenii is a resident ($R/N = 0.06$, $N = 24$, N.S.) which is widespread in low numbers.

Subjectively it seemed less dependent on high grass cover than T. sylvatica although it did not occur in areas with a cover of less than about 25 percent. It is probably commoner than it appears to be from my data as I only saw it when I flushed it at my feet. I did not record it in Woodland and it too seems to have been expanding its geographical range recently, due to the habitat changes (see Lack 1975).

All seen were on the ground.

Data from the literature - Both species feed mainly on grass seeds taken from the ground.

Summary of differences

	<u>T.s.</u>
<u>T. sylvatica</u>	-
<u>O. meiffrenii</u>	H-OS

5.3.4 Otididae - Bustards

Data from Tsavo - Five species are recorded. The two largest are very rare: Otis kori is a sporadic visitor to open grass areas, and there are only two records of Neotis heuglinii. Eupodotis hartlaubii occurs in small numbers in Grassland where there is a high grass cover, and I only saw very few away from this. E. senegalensis is similar but a little more widespread. E. ruficrista is by far the commonest species. It is resident (R/N= 0.12, N= 136, N.S.) in all habitats except Grassland and Riverine. It is very secretive but it calls frequently. The call is very loud and the bird was heard in just over 50 percent of all 15 minute census units, although seen only 1.9 times per ten hours censusing.

All seen feeding were taking vegetable matter from the ground.

Data from the literature - All species feed entirely on the ground and take both vegetable matter and insects.

Summary of differences

	<u>E.r.</u>	<u>E.s.</u>
<u>E. ruficrista</u>	-	-
<u>E. senegalensis</u>	H	-
<u>E. hartlaubii</u>	H	?

5.3.5 Charadriidae - Plovers

Data from Tsavo - There are ten species recorded which live mainly by water. One of these, Charadrius pecuarius, was recorded twice in censuses, but here I am only concerned with the four dry land species.

Vanellus lugubris is an uncommon visitor to any habitat from June to August and may not occur every year (I only recorded it in 1976).

V. tectus is resident and fairly common ($2R^2/N = 3$, $N = 232$, N.S.).

V. coronatus is present all the year but shows some seasonal variation in numbers ($R/N = 0.26$, $N = 112$, $P < 0.01$, peak Feb 2). The habitat preferences of the two (and Charadrius asiaticus) are shown in Fig 5.1. V. coronatus occurs in more open habitats than V. tectus ($X^2 = 77$, $df\ 5$, $P < 0.001$, 30 per cent due to G, 30 percent to BG). Subjectively V. coronatus also seems to prefer areas with more grass, and this seems to be the main difference between it and C. asiaticus ($X^2 = 18$, $df\ 3$, $P < 0.001$, 70 percent due to the concentration of C. asiaticus in G). The latter occurs mainly to the south and east of Aruba where there is almost no grass at all. It is a Palaearctic migrant being fairly common from September to March, and especially on autumn passage in September and October ($R/N = 0.61$, $N = 27$, $P < 0.001$, peak Dec 2).

Plovers can regularly be heard calling at night while flying and moving around. V. coronatus is known to do this (e.g. MPG), but whether other species are involved as well is unknown.

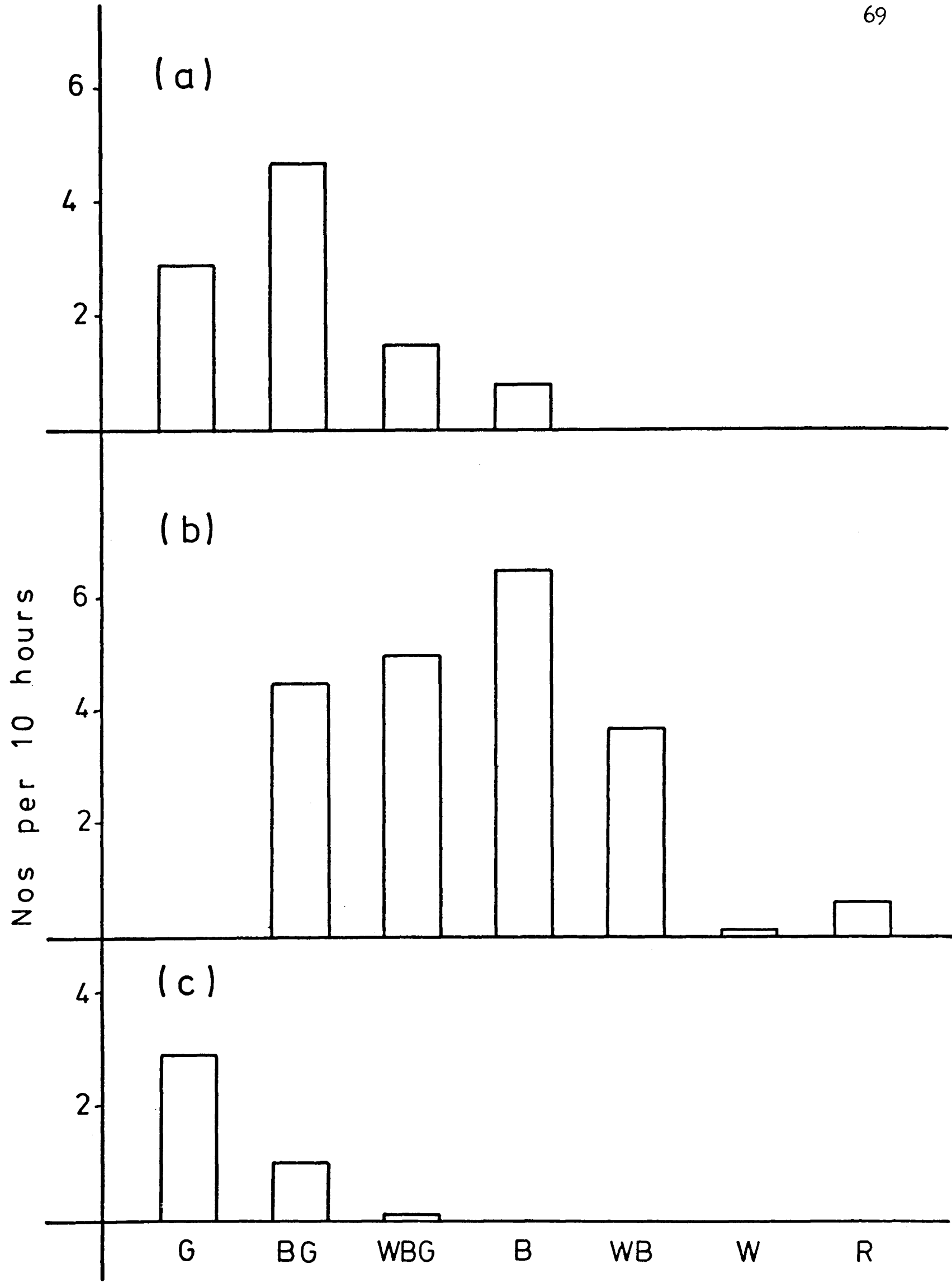


Fig. 5.1 The habitat preferences in Tsavo of three plovers; a) *Vanellus coronatus*, b) *V. tectus*, c) *Charadrius asiaticus*. In this and subsequent Figures of habitat preferences in this chapter the habitat abbreviations are as in ch 2.5. The amount of time spent censusing in each habitat is given in Table 5.1.

Data from the literature - All species feed mainly, if not entirely, on animal food, taking it from the ground. All species may feed partly at night.

Summary of differences

	<u>V.t.</u>	<u>V.c.</u>
<u>V. tectus</u>	-	-
<u>V. coronatus</u>	H	-
<u>C. asiaticus</u>	H	H

Note: The habitat preferences of V. tectus and C. asiaticus are different ($\chi^2 = 49$, df 3, $P < 0.001$, 80 percent due to G with BG).

5.3.6 Burhinidae - Thickknees

Data from Tsavo - Two species are recorded, but one, Burhinus vermiculatus is a waterside species. B. capensis is regular, but rare, usually among thick bushes. I only saw it rarely by day.

Data from the literature - It is mainly nocturnal (so it may be commoner than it appears). It feeds predominantly on insects taken on the ground, and is considerably larger than any other plover or courser which might be a potential competitor.

5.3.7 Glareolidae - Coursers (Pratincoles)

Data from Tsavo - There are five courser species and one pratincole Glareola pratincola recorded. The last is a water species, there is only one record of Cursorius africanus, C. cursor is a sporadic visitor to areas east of Aruba, and C. chalcopterus is only very rarely seen on the roads at night especially between December and May. The other two are relatively common. C. temminckii occurs in open habitats, mainly to the south and east of Aruba. It is more often seen between May and October (7 of 10 seen in Type I censuses) but is probably resident. C. cinctus, like C. chalcopterus, is said to be mainly nocturnal and I only saw it rarely.

It occurs in all habitats except Grassland and Riverine, and is present all the year although it seems commoner in the dry season ($R/N = 0.52$, $N = 49$, $P < 0.01$, peak Aug 2). It was usually flushed from under a bush and not seen out in the open as was C. temminckii.

C. temminckii was seen feeding on open ground like a plover. I have no data for C. cinctus.

Data from the literature - Both species take insects from the ground.

Summary of differences

	<u>C.c.</u>
<u>C. cinctus</u>	-
<u>C. temminckii</u>	H

Notes: X^2 for the difference in habitat preferences = 4.3, df 3, N.S.. However this is probably due mainly to the low numbers of C. temminckii (only 10). Subjectively the difference is real and the bare figures do not include some of the other points noted above.

5.3.8 Pteroclididae - Sandgrouse: and Columbidae - Pigeons, Doves

There is some argument about the taxonomic relationships of these two families, but as their ecological requirements are similar, they are considered together.

Data from Tsavo - There are two sandgrouse species and nine dove species recorded. I did not see the doves Columba guinea, Treron australis or Turtur tympanistria. They have appeared occasionally in the Voi River forest, the first two at least coming in for fruit. I only saw the sandgrouse Pterocles exustus between May and September 1976 when a few flocks were seen, mainly in the very open areas to the south and east of Aruba.

The remaining species are all fairly common at least at some seasons. The dove Streptopelia decipiens is the least numerous, being strictly limited to fringes of trees, especially those of Acacia elatior, along rivers, although in these it is common. It was not seen in the Voi River forest. The other six species fall into three pairs based on body size. The large sandgrouse P. decoratus is very common all the year, although slightly seasonal ($2R^2/N = 26$, $N = 859$, $P < 0.001$, peak Jun 2), in all the Park savanna habitats except Grassland, but is very rare in Woodland and Riverine (Fig. 5.2). Like other sandgrouse, this species is very stereotyped in its drinking habits - between 0700 and 0830 local time - and concentrations at water in the dry season were sometimes very spectacular e.g. at Roka on the Tiva River. The other large species, the dove Streptopelia semitorquata, is a resident ($R/N = 0.12$, $N = 122$, N.S.), has completely different habitat preferences (Fig. 5.2) ($X^2 = 820$, $df\ 5$, $P < 0.001$, 50 per cent due to W, 40 per cent to R), and subjectively I found it considerably more arboreal than any other species in these families. This probably means it eats some fruit but I have only one record of it doing so (on the bush Salvadora persica).

The small pair, the doves Oena capensis and Turtur chalcospilos, have similar habitat preferences to the above pair with O. capensis in the open habitats; but T. chalcospilos is more widespread in the thicker Park savanna habitats than S. semitorquata (see legend to Fig 5.2). T. chalcospilos is a resident ($R/N = 0.20$, $N = 117$, N.S.), but O. capensis is seasonal in occurrence ($R/N = 0.50$, $N = 177$, $P < 0.01$, peak Feb 3). It is absent in the long dry season, increases in the short rains and remains in slightly reduced numbers until about mid-June. My few specific records suggest that both species are entirely granivorous.

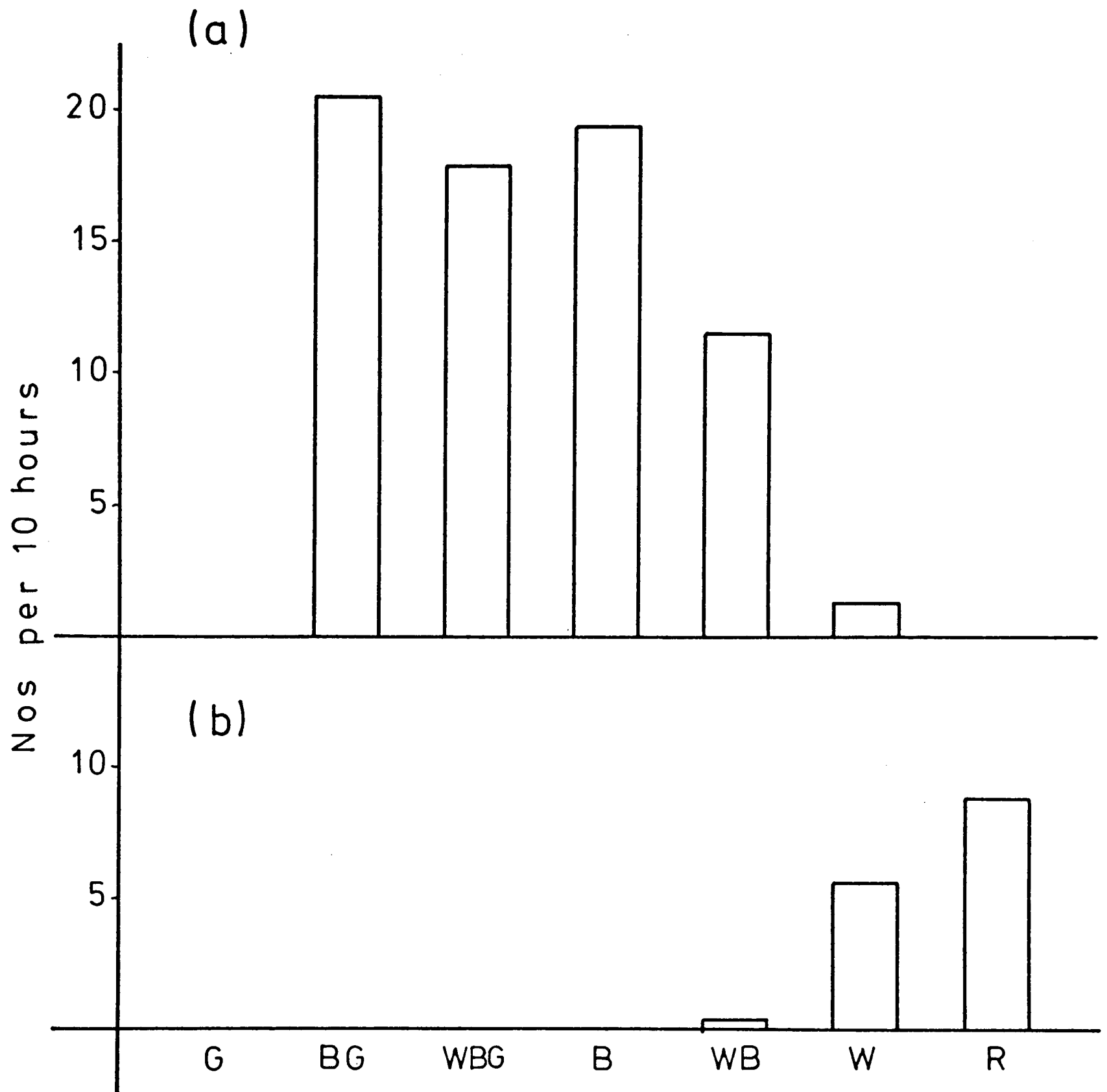
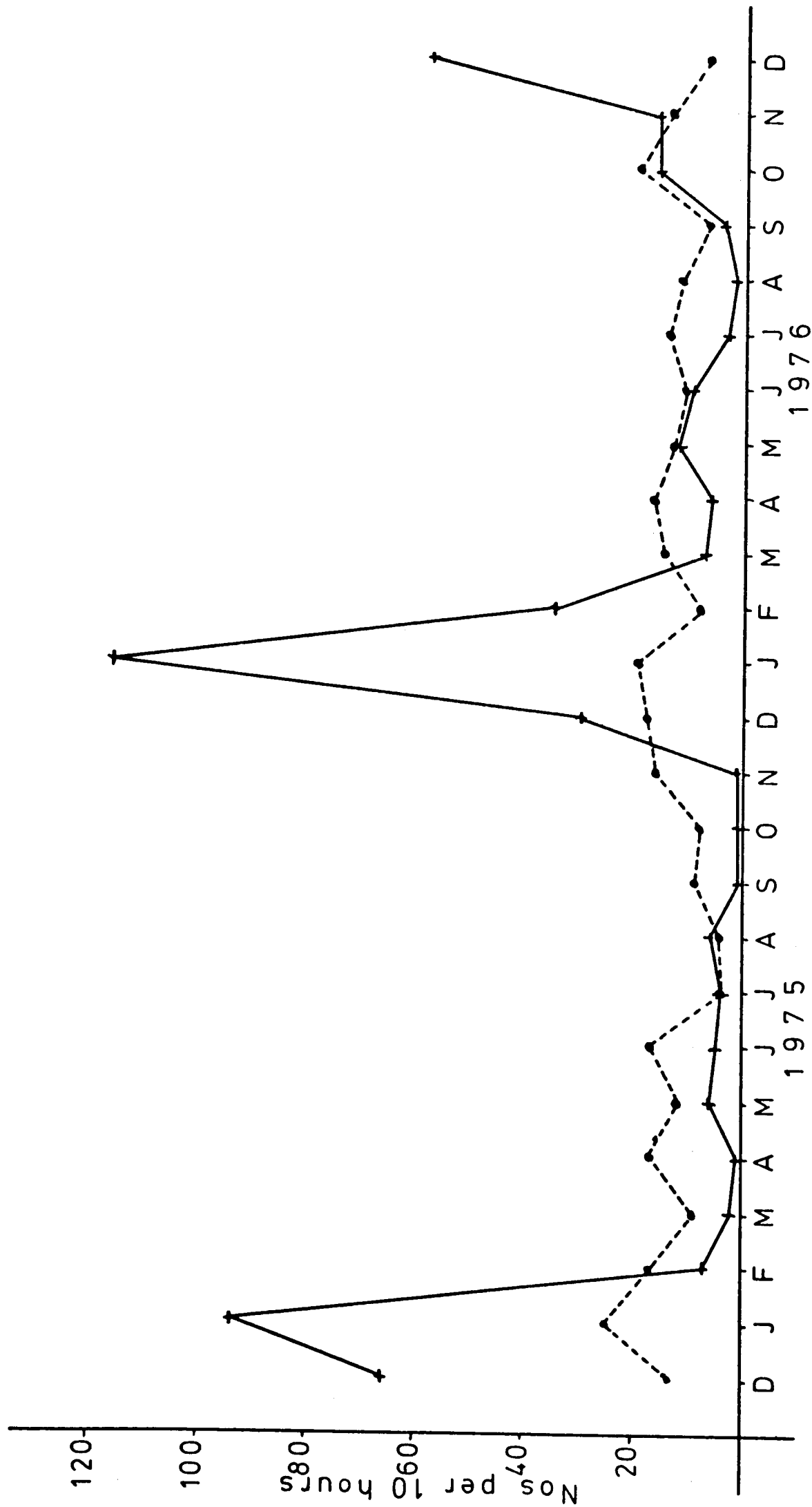


Fig. 5.2 The habitat preferences in Tsavo of two large Columbiformes; a) *Pterocles decoratus*, b) *Streptopelia semitorquata*.

The habitat preferences of the dove *Oena capensis* are fairly similar to *P. decoratus* ($\chi^2 = 42$, df 4, $P < 0.001$, 55% due to WBG) and those of the dove *Turtur chalcospilos* to *S. semitorquata* ($\chi^2 = 14$, df 3, $P < 0.01$, 65% due to WBG with B). *O. capensis* and *T. chalcospilos* differ very significantly ($\chi^2 = 234$, df 5, $P < 0.001$; 40% due to W, 30% to WBG) as do those in the figure above.

The middle sized pair, the doves Streptopelia capicola and S. senegalensis, are both fairly common in all habitats, although statistically their preferences are different ($\chi^2 = 63$, df 6, $P < 0.001$, 45 per cent due to W, 35 per cent to G). Their patterns of seasonal occurrence are very different (Fig. 5.3). S. capicola is common all the year with a slight increase in the wet seasons ($2R^2/N = 41$, $N = 955$, $P < 0.001$, peak Feb 2). S. senegalensis is present all the year in very small numbers; and these are in Woodland and/or near permanent water. There is a large influx, though, in December and January ($2R^2/N = 1200$, $N = 1318$, $P < 0.001$, peak Jan 1) to all habitats - there is a highly significant difference in its distribution over the habitats between January and the rest of the year ($\chi^2 = 162$, df 6, $P < 0.001$, 40 per cent due to BG, 35 per cent to W). S. capicola also becomes slightly more widespread then (habitat preferences in January: the rest of the year $\chi^2 = 13$, df 6, $P < 0.05$, 50 per cent due to WB). This suggests that in the dry season there are not enough seeds (both species seem to be entirely granivorous in Tsavo) to accommodate both species and hence competition is occurring. This suggestion is supported by the increased difference between the two species in their habitat preferences when both are commoner, in January, than during the rest of the year ($\chi^2 = 89$ (60 per cent due to W) for January, cf $\chi^2 = 21$ (35 per cent due to BG) for the rest of the year, both with df 6), and this occurs despite January being the time of greatest seed abundance.

Data from the literature and discussion - where the January influx of S. senegalensis, O. capensis (and many other species (see later sections)) comes from is not known. S. senegalensis is reported as migratory or nomadic in several other parts of southern and eastern Africa although in many parts, as in Tsavo, it is partially resident. It occurs only after good rains in the Kalahari (Maclean 1970). But in Zambia Benson et al. (1973) say that the "largest numbers by far" occur from April to November, which is the dry season, and there are evidently more birds after poor rains.



g. 5.3 The seasonal pattern of occurrence in Tsavo of two doves; +—+ Streptopelia senegalensis,
 •—• S. capicola.
 In this and subsequent Figures of seasonal pattern of occurrence in this chapter, the amount of
 time spent censusing in each month is given in Table 5.1.

This is of course the period when they are absent from Tsavo, but Benson et al. (1973) think that the influx to Zambia is from the south, though they provided rather little evidence. Possibly Zambia is used as a fallback area in times of low food abundance, but there is really too little documentation of movements in other parts of the species's range to be sure.

The handbooks say that all seven commoner Tsavo species are entirely granivorous picking up seeds from the ground. Support for my suggestion that S. semitorquatus may be partially a fruit-eater does, however, come from Goodwin (1967) who, after saying it is mainly granivorous, adds that "it does also eat berries in trees", and Thiollay (1971) who says it is entirely a fruit-eater at Lamto, Côte d'Ivoire.

All species are said, too, to be water-dependent, in common with most seed-eaters, and^{to} need to drink at least once per day. But this does not seem to restrict their distribution in the southern area of Tsavo East unlike some mammal species. Sandgrouse are known to travel quite long distances to water (up to 80 km each way in the case of P. burchelli in the Kalahari (Maclean 1968)).

Irving and Beesley (1976) found a further difference between S. capicola and S. senegalensis in their feeding habits. On grain crops S. capicola fed mainly from the heads of standing crops with S. senegalensis feeding on fallen seeds on the ground, but in Tsavo both species fed mainly from the ground.

Summary of differences

	<u>P.d.</u>	<u>S.sem.</u>	<u>S.d.</u>	<u>S.c.</u>	<u>S.sen.</u>	<u>O.c.</u>
<u>P. decoratus</u>	-	-	-	-	-	-
<u>S. semitorquatus</u>	H	-	-	-	-	-
<u>S. decipiens</u>	H	H	-	-	-	-
<u>S. capicola</u>	S?	H-S?	H	-	-	-
<u>S. senegalensis</u>	O(S)	H-S	H	O(H)	-	-
<u>O. capensis</u>	SO	H	H	SO	S	-
<u>T. chalcospilos</u>	H	S	H	H-S	H-SO	H

5.3.9 Cuculidae - Cuckoos

Date from Tsavo - There are only very few records of Ceuthmochares aereus, and only two of Chrysococcyx cupreus.

Of the remaining eight species, none is very common and all are probably migratory to some degree. There are two small species Chrysococcyx klaas and C. caprius. C. klaas is rare in Wooded Bushland and Woodland. It was very rarely seen and only became obvious when it started calling in the wet seasons. I saw only three in censuses and one was in each of June and July when I saw no other cuckoos except a few Centropus superciliosus. This suggests that C. klaas is at least partially resident (as said or implied by the handbooks). C. caprius is a visitor, spending November (from the start of the rains) to January, and April to May in Tsavo, although a few may stay through the short dry season ($R/N = 0.72$, $N=54$, $P < 0.01$, peak Dec 4). It occurs in all habitats except Grassland but is commoner in those with ^{trees} ($X^2 = 18$, $df\ 1$, $P < 0.001$). Despite this habitat preference, the few data I have for C. caprius suggest that it feeds mainly in the bushes (6 of 7 birds seen feeding). I have no data on the feeding of C. klaas.

Of the larger species C. superciliosus is the largest. A few individuals are present all the year (despite the data in Appendix 1.3), but it mainly is a wet season visitor ($R/N = 0.61$, $N = 55$, $P < 0.01$, peak Jan 3). It occurs fairly commonly in thick bushes, especially along rivers and small watercourses, but the few in the dry season are all along the main rivers. It was rarely seen far from bushes and all four food items seen taken were from the ground.

Cuculus solitarius and C. clamosus are both rare (almost all my records are of birds calling), were recorded only in Woodland, and only in the wet seasons. Clamator glandarius, another wet season visitor ($R/N = 0.96$, $N = 14$, $P < 0.01$, peak Dec 3), occurs wherever there are trees especially Wooded and Bushed Grassland (8 of 14 seen in censuses) but is again rare. It has bred in the Park (Trevor & Lack 1976), but whether the birds coming in are all African residents or whether Palaearctic birds are involved as well is unknown. Clamator jacobinus is slightly smaller and is more common. It was usually seen low down in thick bushes (none of 13 food items seen taken were from higher than 1m in the woody vegetation though it is still commoner in habitats with trees present ($\chi^2 = 14$, $df\ 1$, $P < 0.01$)). C. jacobinus occurs from November to January and returns in smaller numbers in April ($R/N = 0.77$, $N = 51$, $P < 0.01$, peak Dec 3). There is a breeding record for January (Turner 1977) suggesting, as for C. glandarius, that some are of African origin; but many East African birds are thought to be migrants from the Indian subcontinent (Friedmann 1964).

The final and commonest large species is Cuculus canorus. Both the Palaearctic race C.c. canorus and the African C.c. gularis occur, but I have too few positive identifications to know the proportion of each. The species is commonest in habitats with trees ($\chi^2 = 15$, $df\ 1$, $P < 0.01$), and was usually seen in the trees. It occurs from late October to January and there is quite a large passage in April ($R/N = 0.39$, $N = 64$, $P < 0.01$, peak Dec 3; April mean = 3.1 per 10 hours ($\pm S.E. 0.2$) ($n = 2$); from March and May (both 0 seen per 10 hours) $t = 12.7$, $df\ 1$, $P < 0.05$).

Data from the literature and discussion - Most of the species eat hairy caterpillars, and this separates them from other bird species in Tsavo except the cuckoo-shrike Campephaga flava, but this species is

rare (see ch 5.3.29). C. superciliosus eats large insects mainly from the ground and is also known to take young birds and other small vertebrates.

Summary of differences

	<u>C.can.</u>	<u>C.cl.</u>	<u>C.so.</u>	<u>C.g.</u>	<u>C.j.</u>	<u>C.k.</u>	<u>C.cap.</u>
<u>C. canorus</u>	-	-	-	-	-	-	-
<u>C. clamosus</u>	H	-	-	-	-	-	-
<u>C. solitarius</u>	H	?	-	-	-	-	-
<u>C. glandarius</u>	?	H	H	-	-	-	-
<u>C. jacobinus</u>	F	H-?	H-?	F	-	-	-
<u>C. klaas</u>	S	H-S?	H-S?	S	FS	-	-
<u>C. caprius</u>	FS	H	H	S	S	H?	-
<u>C. superciliosus</u>	F(H)	H	H	F	HS	S	HS

5.3.10 Psittacidae - Parrots

Data from Tsavo - The one species, Poicephalus rufiventris, is a common resident ($R^2/N = 8.5$, $N = 245$, $0.01 < P < 0.05$) in Woodland and Riverine. It is also fairly common in Wooded Bushland.

All those I saw feeding (43 birds) were eating fruit except for one eating leaves and one probably flowers. It seems fairly catholic in its choice, including some of the plant species with larger fruits e.g. Commiphora boiviniana in addition to the small Commiphora spp. and others. It feeds in both bushes (10 birds) and trees (33 birds).

5.3.11 Musophagidae - Turacos

Data from Tsavo - Two species are recorded but there are no recent records of Tauraco porphyreolophus. The other, Corythaixoides leucogaster, is a common resident ($2R^2/N = 9$, $N = 206$, $0.01 < P < 0.05$) in Woodland, with a few occurring in Wooded Bushland and in riverine fringes. I did not see it in the Voi River forest.

I have only few data as it is rather shy, but, like the parrot Poicephalus rufiventris, it seems to be largely a fruit-eater (8 of 12 birds but see below), and mainly in the trees (10 of 12 birds). I also recorded it eating the flowers of Acacia mellifera (4 birds but 3 were on one day).

Data from the literature - The suggestion in the handbooks that C. leucogaster is dependent on acacias seems to be based on Jackson's (1938) statement that "its food consists to a large extent of buds, seeds and young pods of acacias" (my emphasis). Moreau (1958) is uncertain, although acacias often dominate the vegetation in areas where this species occurs. I found no evidence for such a dependence.

5.3.12 Tytonidae and Strigidae - Owls

Owls were not studied in detail but are included here for completeness. All are nocturnal, I saw nonevery often and much of this section is based on casual observation.

Data from Tsavo - Six species are recorded, two of which I never saw - Tyto alba has occurred in Voi and on Ndara Plains, and Otus leucotis has been seen along the Galana River.

Otus scops occurs rarely along rivers, and very rarely elsewhere. It was formerly fairly common. Next larger is Glaucidium perlatus, probably the commonest species. It is common along rivers, and also occurs more rarely wherever there are trees, and it was fairly often heard calling by day. The two eagle owls are much larger. Bubo africanus occurs throughout the Park and was usually seen roosting on or near the ground. One used the same shelter on Ndara Plains in 1975 and 1976 as a Tyto alba had done in 1972 (C. Smeenk pers. comm.). B. lacteus on the other hand was seen only in large trees especially along rivers and watercourses.

The only data I have on the food of these species is of a G. perlatus catching a flying termite, and the analysis of some pellets of B. africanus collected in the shelter noted above. These pellets yielded mainly beetles but there were some bird and rodent remains (G.R. Cunningham van Someren pers. comm.).

Summary of differences

	<u>O.s.</u>	<u>G.p.</u>	<u>B.a.</u>
<u>O. scops</u>	-	-	-
<u>G. perlatus</u>	S	-	-
<u>B. africanus</u>	HS	S	-
<u>B. lacteus</u>	S	S	H

5.3.13 Caprimulgidae - Nightjars

As with the owls, I know very little about the nightjars due to their nocturnal habits.

Data from Tsavo - It is probable that most, if not all species in Tsavo are migratory, and only come into the Park during, and for the period soon after, the rains (but see below). Almost all positive specific identification refer to specimens, most of which were road casualties. The eight species which have been recorded are: Caprimulgus europaeus, C. nubicus, C. fraenatus, C. donaldsoni (probably the commonest), C. inornatus, C. tristigma, C. fossii (also fairly common), and C. clarus. Of these, there are breeding records for C. donaldsoni - including a recent fledgling found dead in early August which suggests that some of this species might be resident; and C. fossii - a pair of birds collected with an egg near the Tsavo River in April 1934 (Peters & Loveridge 1937). This pair was collected and published as C. nubicus, but the specimens were kindly checked for me by R.M. Paynter Jr. and found to be C. fossii.

Stomach contents of 11 individuals of five species were analysed by Lack & Quicke (1978) and the diets were shown to be very generalised. One interesting find was that a C. fraenatus had taken 13 grasshoppers (Acrididae) with red hind-wings, which might be thought of as a flashwarning colouration. Obviously this would be much less visible to a nocturnal predator. Further, grasshoppers do not usually fly unless flushed, especially at night, and so it is likely that this bird had been following large mammals. .

5.3.14 Apodidae - Swifts

As explained earlier, swifts, and swallows Hirundinidae (ch 5.3.27), were not studied in detail in this study and most of both these sections is based on casual observations only.

Data from Tsavo - There are three resident species. Apus affinis occurs commonly around its nest-sites which are mostly on buildings, but is rare away from these; A. caffer is less common where it occurs, but it is more widespread than A. affinis because it more often nests in culverts; and Cypsiurus parvus occurs commonly wherever there are doum palms Hyphaene coriacea, but was seen in other areas at times. The remaining species are all uncommon or rare visitors, and were seen most commonly along the Voi River. I recorded Apus apus, A. barbatus (probably), A. melba, A. aequatorialis, A. niansae, and Telacanthura ussheri, and others have reported A. horus and Neafrapus boehmi in addition.

5.3.15 Coliidae - Mousebirds

Data from Tsavo - Three species have been recorded, but I only saw Colius leucocephalus twice ⁱⁿ -/the same place in Woodland in May and July 1976. C. striatus is an uncommon resident ($R/N = 0.15$, $N = 63$, N.S.) in Riverine, but also occurs rarely in other habitats. C. macrourus is common all the year although shows a small peak of numbers coinciding with the fruiting of Commiphora and Salvadora persica ($2R^2/N = 15$, $N = 452$, $P < 0.001$, peak Aug 2). It is commonest in Riverine but is more widespread than C. striatus occurring fairly commonly wherever there is woody vegetation (χ^2 for the difference = 45, df 5, $P < 0.001$, 50 per cent due to R and the concentration of C. striatus there).

I did not record either species eating anything except fruit, and I found no difference between the fruits eaten by the two species. Both

seemed to take whatever was available, and for both species the majority of fruits taken were in bushes not trees (C. macrourus 67 of 78 birds in bushes, C. striatus 11 of 15 birds), and despite their habitat preferences I did not record either in Ficus trees.

Data from the literature - Both species are almost omnivorous though eating predominantly green vegetation. A.D. Forbes-Watson adds (pers. comm.) that C. macrourus certainly regularly eats leaves whereas C. striatus is more limited to fruit.

Summary of difference

	<u>C.m.</u>
<u>C. macrourus</u>	-
<u>C. striatus</u>	H-T?

5.3.16 Trogonidae - Trogons

Data from Tsavo - One species Apaloderma narina, used to be fairly common along the Tiva River (D.L.W. Sheldrick pers. comm.) but there is only one recent record.

5.3.17 Alcedinidae - Kingfishers

Data from Tsavo - Six species are recorded. Two are fish-eating waterside species: Alcedo cristata is seen rarely near water, and Ceryle rudis is uncommon along rivers especially the Galana. Three of the four land species are nearly restricted to vegetation by watercourses, and the fourth is commonest there. Two are rare: Ceyx picta, which I o saw three times, and Halcyon albiventris, which occurs only in riverine forest and all my records (eight in censuses) were between December and June. H. leucocephala is primarily a riverine species but it was occasionally found elsewhere, usually near waterholes, during the wet seasons. It shows a pronounced seasonal pattern of occurrence (Fig. 5.4) (R/N = 0.58, N = 160, P < 0.01, peak Jan 4), being present from November to

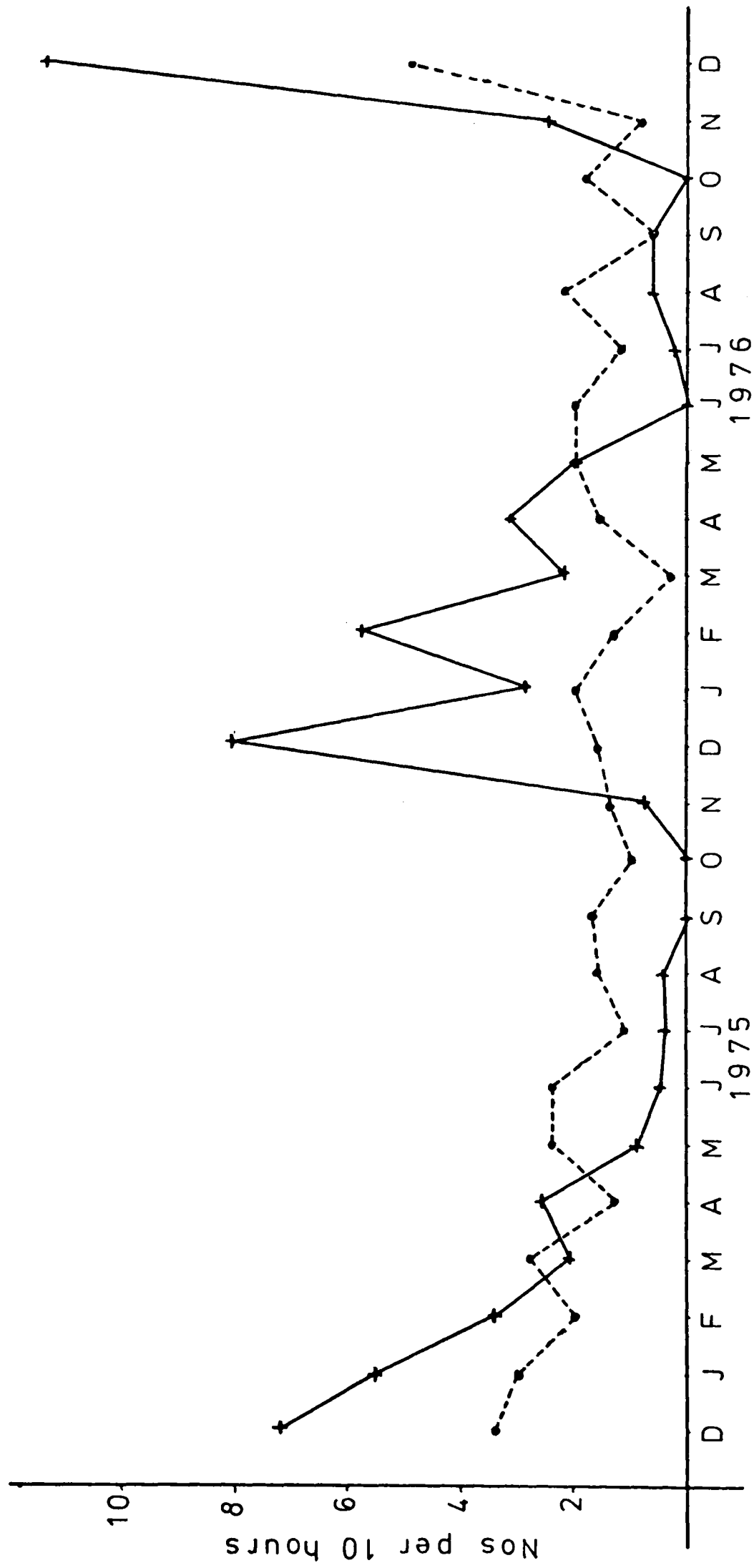


Fig. 5.4 The seasonal pattern of occurrence in Tsavo of two kingfishers; +---+ *Halcyon leucocephala*,
 •---• *H. chelicuti*.

Table 5.2. Feeding behaviour of two kingfishers Halcyon in Tsavo

	<u>H. leucocephala</u>	<u>H. chelicuti</u>
Number of items	59	46
Pounce to ground (%)	80	85
Items taken from the air (%)	8	11
Items taken with bird in flight (%)	31	41
Height of perch used to reach for prey (m) ^a	4.4 ± 0.4 (41)	4.9 ± 0.5 (31)
Distance flown (m) ^a	10.2 ± 1.8 (38)	13.4 ± 3.7 (30)
Perches on trees (%)	76)	53)
	)(n = 54)	)(n=45) ^b
bushes (%)	24)	40)
Feeding rate (items/minute)	0.13 (13 items)	0.12 (24 items)

Notes:

a) Heights and distances are quoted as mean ± standard error with sample size in brackets.

b) 7% on electricity wires.

June though a very few could usually be found in all months. H. chelicuti is smaller and is resident (Fig. 5.4) ($R/N = 0.09$, $N = 128$, N.S.). It occurs fairly commonly in all areas with large trees which have open ground underneath, but is especially common in Riverine (6 per 10 hours cf a maximum of 4 in any other habitat).

Data on the feeding behaviour of the latter two species are given in Table 5.2. The two are very similar. Both species were usually seen on horizontal branches near the base of tree canopies from where they pounced to the ground. H. albiventris seems similar, but I have very few data.

Data from the literature - Some H. leucocephala may spend the rest of the year around Kitui where it was found between July and October and from mid-February to April (Tennent 1962). There are also two ringing recoveries in Kenya, in November and March, of birds ringed in Ethiopia in October (Ash 1976), so some birds may go further.

Summary of differences

	<u>H.c.</u>	<u>H.l.</u>
<u>H. chelicuti</u>	-	-
<u>H. leucocephala</u>	O(H)-?	-
<u>H. albiventris</u>	O(H)-?	?

5.3.18 Meropidae - Bee-eaters

Data from Tsavo - Six species (one with two races) of three size classes have been recorded, but one of the large species, Merops nubicus, is only a rare visitor, in February and March. Of the remaining large forms, considerable numbers pass over Tsavo south between late August and October, and north in April and early May. These include M. apiaster, M. superciliosus persicus and probably M. s. superciliosus, but most fly too high for positive identification. M. apiaster and M.s. persicus stopped only rarely. M. s. superciliosus is rather mysterious. It occurs fairly commonly in Woodland and Riverine and rarely in other

habitats, from November to late March ($R/N = 0.81$, $N = 65$, $P < 0.01$, peak Jan 4). Outside this period I had only one record - of six by the Voi River in September 1976. But W. Leuthold (pers. comm.) saw some which were probably breeding on the Athi River in August 1974, and J. Mulder (pers. comm. to C. Smeenk) saw one feeding a fledgling Indicator indicator by the Galana River in July 1976.

M. albicollis is the only medium-sized species in Tsavo. It is present there from November to April ($R/N = 0.68$, $N = 91$, $P < 0.01$, peak Jan 2), in open habitats and Riverine.

The final pair are both small and resident, but have quite different habitat preferences. M. pusillus ($R/N = 0.17$, $N = 96$, N.S.) occurs by rivers or, when away from these, in watercourses or other damper areas; by contrast M. revoilii ($R/N = 0.11$, $N = 74$, N.S.) occurs only in the Park savanna habitats, except Grassland (χ^2 for the difference = 78, df 5, $P < 0.001$, 50 per cent due to R, 25 per cent to BG), and often in very dry areas.

The feeding ecology of the four commoner species is summarised in Table 5.3. All are entirely insectivorous and take the majority of their food in the air while in flight. It was often noted that the insects caught were relatively large, but I could not tell whether there was an abundance of bees and wasps in the diet as in many places (Fry 1972). The differences between the species mainly reflect their habitat and size differences, the larger species feeding higher in the air, using higher perches to wait for prey, and flying further out to feed. In particular M. s. superciliosus used the electricity wires running parallel to the main Nairobi-Mombasa road as perches, and these were considerably higher than any other perch nearby.

TABLE 5.3. Feeding behaviour of four common bee-eaters Merops in Tsavo.

	<u>M. s. superciliosus</u>	<u>M. albicollis</u>	<u>M. pusillus</u>	<u>M. revoilii</u>
Size (weight)	Large (43 g)	Medium (25 g)	Small (14 g)	Small (14 g)
No. of items	108	223 ^c	238	80
% taken in air	100	98	96	80
% taken from ground	0	2	4	20
Height of capture (m) ^a	8.7 ± 1.1 (40)	3.3 ± 0.8 (46)	1.7 ± 0.3 (45)	1.2 ± 0.2 (34)
Height of perch used to wait for prey (m) ^a	10.8 ± 0.8 ^b (46)	3.7 ± 0.7 (54)	1.5 ± 0.3 (62)	1.1 ± 0.1 (33)
Distance flown to food item (m) ^a	28.9 ± 4.0 (35)	14.3 ± 3.6 (15)	6.3 ± 1.1 (34)	5.0 ± 1.2 (30)
Feeding rate (items per minute)	0.30 (28 items)	0.71 (19 items)	0.68 (81 items)	0.56 (34 items)

Notes:

- a) Heights and distances are quoted as mean ± standard error with the sample size⁺ in brackets.
b) If 17 birds on electricity wires at 15 m are excluded this figure becomes 8.2 ± 1.0 (n = 29)
c) This includes records of 3, 5, 8, 10, and 12 birds all taking 'several' in the air. If these are excluded there remains n = 33 with 12% from the ground.

Data from the literature and discussion of movements - The movements of M. s. superciliosus are further confused by data in the literature. For East Africa MPG say it is present only from May to September, and replaces M. s. persicus at that time. Williams (1967) allows a resident population, but adds that it is augmented from May to September. Further south, it occurs in South Africa between September and January (McLachlan & Liversidge 1977), and passes through Zambia in September and April (Benson et al. 1973). In Madagascar, it is a resident but is reduced in numbers from May to September (Milon et al. 1973), and it is thought that the migrants go to the African mainland. Further north than Tsavo, it is thought to be a resident in Somalia (Archer & Godman 1961).

Obviously there are extensive migrations and there may be some partially distinct populations; but there is little or no plumage variation (Fry 1969), despite Clancey (1968) who has differentiated a breeding population in SW Africa. Where the birds coming into Tsavo in November are coming from is difficult to tell, but I think it likely they are from Somalia following the rain belt south, in common with many other species. November to March is a dry period in Somalia (Archer & Godman 1937), and over much of Africa several years to 1977 were drier than some in the past. Perhaps the movement is recent. More likely, the species is only partially resident in Somalia (pace Archer & Godman 1961). The few birds seen in Tsavo between April and October are no doubt Madagascan or South African birds.

Some authors have suggested that the two races of this species, which have often been considered separate species, are ecological equivalents. This seems not to be the case. In my limited experience, and confirmed by some of the literature, there is a habitat difference; M. s. persicus being almost always near water e.g. Lake Jipe in Tsavo West N.P. and M.s. superciliosus in any light woodland.

M. albicollis is a well-known intra-African migrant which breeds mainly in the Sahel zone (Snow 1978), and moves south after breeding. There are, however, a few breeding records further south, even as far as southern Kenya (Cunningham van Someren 1971).

Summary of differences

	<u>M.s.s.</u>	<u>M.a.</u>	<u>M.p.</u>
<u>M. s. superciliosus</u>	-	-	-
<u>M. albicollis</u>	HF	-	-
<u>M. pusillus</u>	SF	F	-
<u>M. revoilii</u>	HFS	F	H

5.3.19. Coraciidae - Rollers

Data from Tsavo - Four species are recorded. Coracias garrulus, a Palaearctic migrant, is fairly common in all the Park savanna habitats after the onset of the rains in November, and becomes steadily less common as the winter progresses (Fig. 5.5), although during rain and during the spring migration some large loose flocks can be seen passing through ($2R^2/N = 430$, $N = 385$, $P < 0.001$, peak Jan 2). It is rare in Riverine which is where C. caudata is commonest (X^2 for the difference = 150, df 6, $P < 0.001$, due 85 per cent/to the concentration in C. caudata in R). C. caudata is resident ($R/N = 0.12$, $N = 147$, N.S.). In addition to C. c. caudata a few of the northern race C. c. lorti visit Tsavo from December to March. C. naevia is larger and has similar habitat preferences to C. caudata ($X^2 = 5$, df 3, N.S.). It is rarer than the others and occurs mainly from April to June (Fig. 5.5) ($R/N = 0.60$, $N = 23$, $P < 0.01$, peak May 2). Brown and Brown (1973) also found an increase in March and April in this species, and in C. caudata, along the Nairobi - Mombasa road especially with good rains. Eurystomus glaucurus is present from November (after the onset of the rains) till April ($R/N = 0.77$, $N = 19$, $P < 0.01$, peak Dec 3) though it will also appear if there is unseasonal rain e.g. in late September 1976. It is

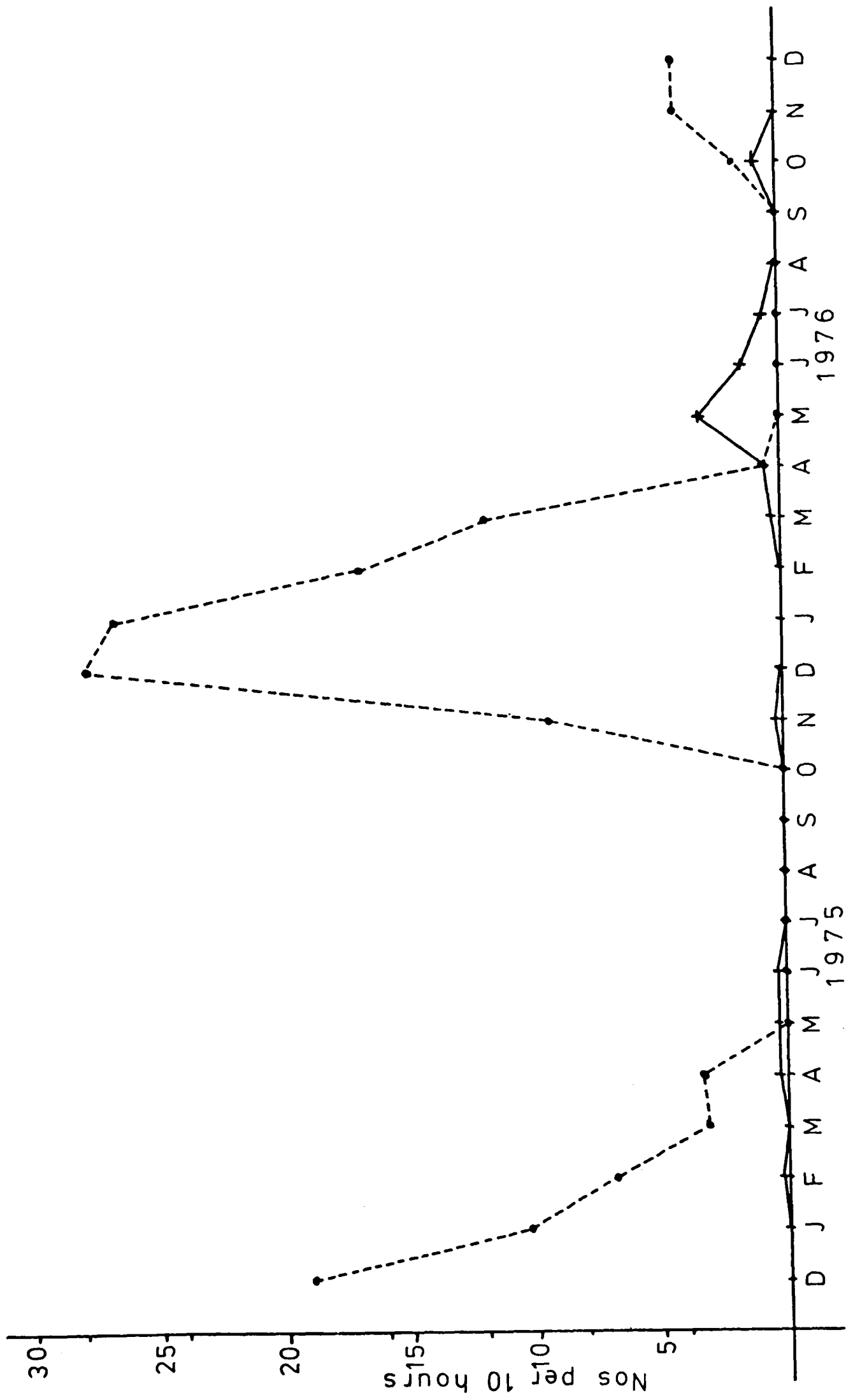


Fig. 5.5 The seasonal pattern of occurrence in Tsavo of two rollers; +---+ *Coracias naevia*,
 •---• *C. garrulus*.

Table 5.4 Feeding behaviour of three rollers Coracias in Tsavo

	<u>C. garrulus</u>	<u>C. caudata</u>	<u>C. naevia</u>
No. of feeding movements ^b	113 ^c	104	16
% from ground	91	79	69
% from air	8	19	25
Height of aerial capture (m) ^a	4.2 $\pm$ 1.9 (7)	6.8 $\pm$ 1.8 (13)	3.0 $\pm$ 2.2 (3)
Height of perch used to search for prey (m) ^a	2.9 $\pm$ 0.1 (79)	4.6 $\pm$ 0.3 (67)	6.5 $\pm$ 1.2 (9)
Distance flown to food (m) ^a	12.3 $\pm$ 1.2 (72)	16.0 $\pm$ 1.6 (65)	20.7 $\pm$ 4.7 (8)
Feeding rate (items per minute)	0.16 (42 items)	0.14 (51 items)	0.07 (8 items)

Notes:

- a) heights and distances are quoted as mean $\pm$ standard error with the sample size in brackets.
- b) in most cases one feeding movement is equivalent to one food item. But in a few cases, the bird flew down to a termite's or ant's nest, and ate several items before returning. These have been scored as one feeding movement in this table.
- c) I also had 4 records of 'several' birds catching flying termites in the air. These are not included in the table.

almost restricted to Riverine (all 19 in censuses) but it occurs occasionally elsewhere, especially where there are baobabs.

All species are primarily insectivorous (though they may take small vertebrates at times). I have very few feeding data for E. glaucurus but it nonetheless appears very different from the others. It was usually seen at the top of a large bare tree (mean height ($\pm$ S.E.) of 13 birds seen feeding and/or searching for food = 15.1 ± 1.2 m). From these it takes insects in the air, and only occasionally pounces to the ground, which is the predominant feeding method of the other species. Data on the feeding behaviour of the three Coracias species are given in Table 5.4. C. naevia is larger and feeds less often than the other two, and although it searches from higher perches and flies further out than either, the only significant difference is in perch height from C. garrulus ($d = 2.9$, $df\ 8$, $P < 0.05$). The largest difference between C. garrulus and C. caudata is the height of perch used to search for prey ($d = 4.7$, $df\ 89$, $P < 0.001$). This, however, is mainly a reflection of the difference in habitat preferences.

Data from the literature - E. glaucurus also feeds while circling around at a great height and may continue after dark, unlike the other species.

Summary of differences

	<u>C.g.</u>	<u>C.c.</u>	<u>C.n.</u>
<u>C. garrulus</u>	-	-	-
<u>C. caudata</u>	H(F)	-	-
<u>C. naevia</u>	?(SO)	S?	-
<u>E. glaucurus</u>	F(H)	F	F

5.3.20 Upupidae - Hoopoes

Data from Tsavo - Two races of Upupa epops occur. A race with a white bar on the primaries, either U. e. epops or U. e. senegalensis, is a rare visitor between November and February. The other, U. e. africana, is fairly common in thicker habitats between January and July, but is

very rare for the rest of the year ($R/N = 0.44$, $N = 108$, $P < 0.01$, peak Apr 3). It is commonest in Woodland.

All 97 food items recorded were insects taken from the ground and 80 per cent were from bare ground. It eats a large number of termites but what proportion of the total diet is termite is unknown.

5.3.21 Phoeniculidae - Wood-Hoopoes

Data from Tsavo - Four species have been recorded but two, Phoeniculus granti and P. cyanomelas are only very rare visitors. P. purpureus is a resident ($R/N = 0.16$, $N = 87$, N.S.) occurring only in habitats with trees particularly in Riverine. P. minor is only half the size, is also resident ($R/N = 0.06$, $N = 169$, N.S.), and occurs in all habitats except Riverine and Grassland but is commoner in the thicker habitats ($X^2 = 31$, $df\ 1$, $P < 0.001$) (X^2 for the difference between the two species = 129, $df\ 4$, $P < 0.001$, 75 per cent due to WBG).

The feeding behaviour of the two common species is very similar. They feed mainly by probing twigs, branches and sometimes fallen logs, and extracting insects from the bark, and they sometimes dig well into the bark pulling off pieces. There is however a major difference between the two: P. purpureus chooses larger branches (Table 5.5)

Summary of differences

	<u>P.p</u>
<u>P. purpureus</u>	-
<u>P. minor</u>	HF

5.3.22 Bucerotidae - Hornbills

Data from Tsavo - Three species are rare in Tsavo occurring almost entirely along rivers: Bycanistes brevis, Bucorvus cafer and Tockus alboterminatus.

Table 5.5. Feeding sites of two wood-hoopoes Phoeniculus

	Twig/stem diam.<0.5 in. (1.3cm)	Branch diam.>0.5 in. (1.3cm)	Main trunk	Fallen log	Live ^a wood ?size	Dead wood ?size	Other ^b
<u>P. purpureus</u> (n 45)	-	11	24	11	22	11	20
<u>P. minor</u> (n 45)	11	23	9	2	20	18	18

- Notes:
- 1) Figures are percentages
 - 2) Records of feeding and active searching have been included. Only one record per bird has been scored. If a bird was on more than one site while being watched, only the first site has been scored.
 - 3) P. purpureus feeds from larger branches. Taking the first three columns only the difference between the species is significant ($X^2 = 11$, df 2, $P < 0.01$).
 - a) For P. purpureus the 22% is made up 11% on "twigs" and 11% on "branches". For P. minor the 20% is made up 7% on "twigs" and 13% on "branches".
 - b) for P. purpureus the 20% is made up on 7% from the ground and 13% from unknown sites. For P. minor the 18% is made up of 5% from the air, 4% from leaves and 9% from unknown sites.

The other four species are all fairly common to very common, and some individuals of all are resident. Their habitat preferences are shown in Fig. 5.6. (χ^2 for the differences in habitat preference is significant at $P < 0.001$ between all pairs of species, with differences in Woodland and Riverine being the major contributors in most cases.) T. nasutus is resident in Tsavo ($R/N = 0.11$, $N = 120$, N.S.). T. flavirostris shows a slight seasonal pattern ($2R^2/N = 11$, $N = 188$, $P < 0.01$, peak Apr 3) but is present all the year. The other two show some rather erratic fluctuations in numbers, but if a running mean over three months is calculated, a seasonal pattern is apparent (Fig. 5.7). (Calculated on the original data: for T. erythrorhynchus $2R^2/N = 25$, $N = 540$ $P < 0.001$, peak Feb 3 ; for T. deckeni $2R^2/N = 21$, $N = 580$, $P < 0.001$, peak Jul 1). But this is an oversimplification. Fig. 5.8 shows the same data, but with the seasonal pattern in Woodland separate from that in other habitats. T. deckeni has a peak in Woodland coinciding with the peak of Commiphora fruit ($2R^2/N = 75$, $N = 450$, $P < 0.001$, peak Jul 4) but that for T. erythrorhynchus is not significant ($2R^2/N = 3.7$, $N = 201$, N.S.). The seasonal pattern of T. erythrorhynchus in the other habitats shows a peak of numbers from December to March coinciding with the peak insect abundance and a trough from July to September ($2R^2/N = 25$, $N = 347$, $P < 0.001$, peak Feb 3). T. deckeni is uncommon in other habitats than Woodland, but there is a similar pattern ($R/N = 0.58$, $N = 130$, $P < 0.01$, peak Feb 4). I have no evidence for or against some movement from the Park savanna habitats and Riverine into the Woodland in July, but a subjective impression of the numbers involved would suggest that there is some movement into and out of the Tsavo area, as a whole, in addition.

All four species eat both fruit and insects (Table 5.6). T. erythrorhynchus is shown to be much more insectivorous than the others and this explains its broader habitat preferences, and the dominance of the 'other habitats'

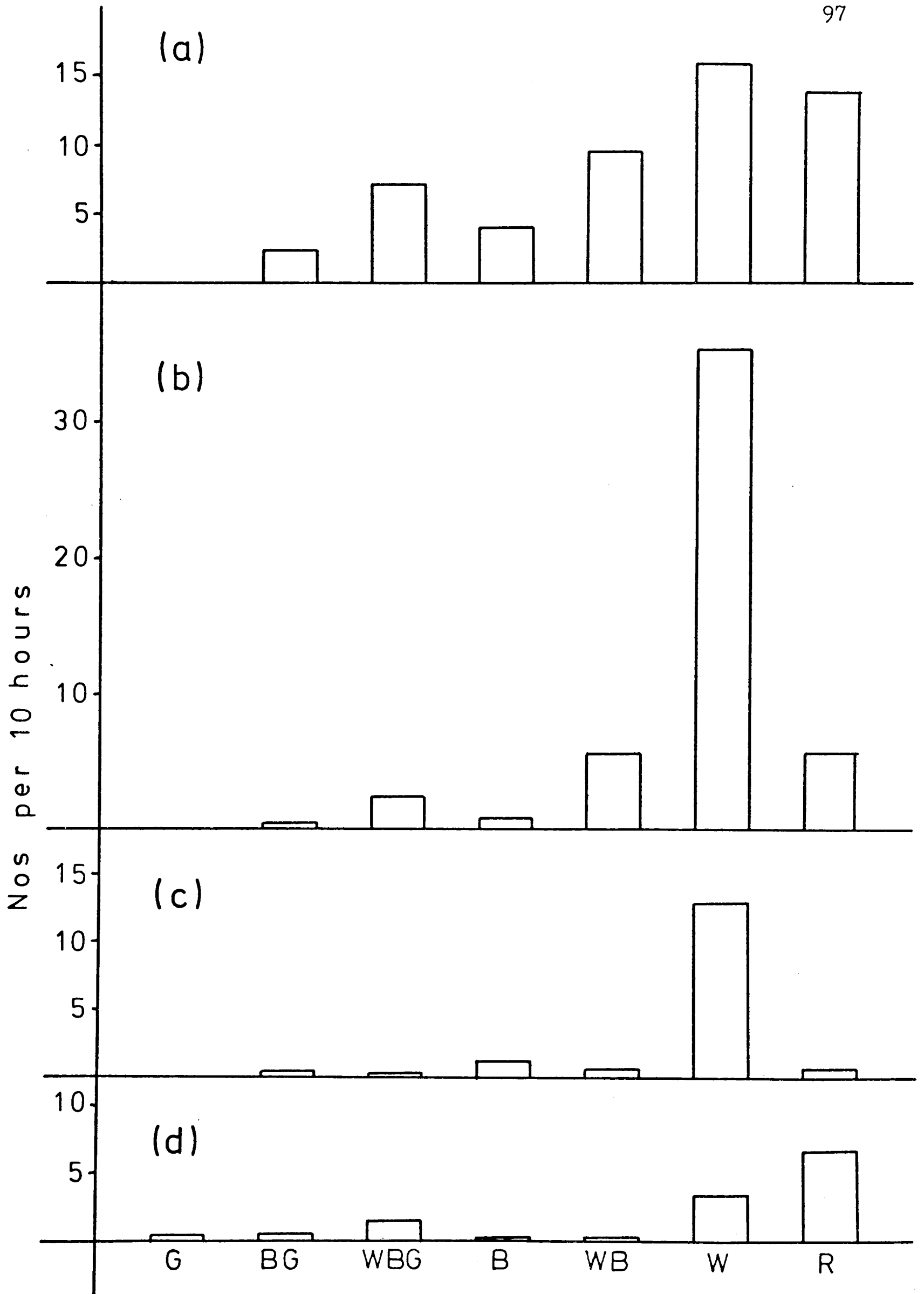


Fig. 5.6 The habitat preferences in Tsavo of four hornbills; a) *Tockus erythrorhynchus*, b) *T. deckeni*, c) *T. flavirostris*, d) *T. nasutus*.

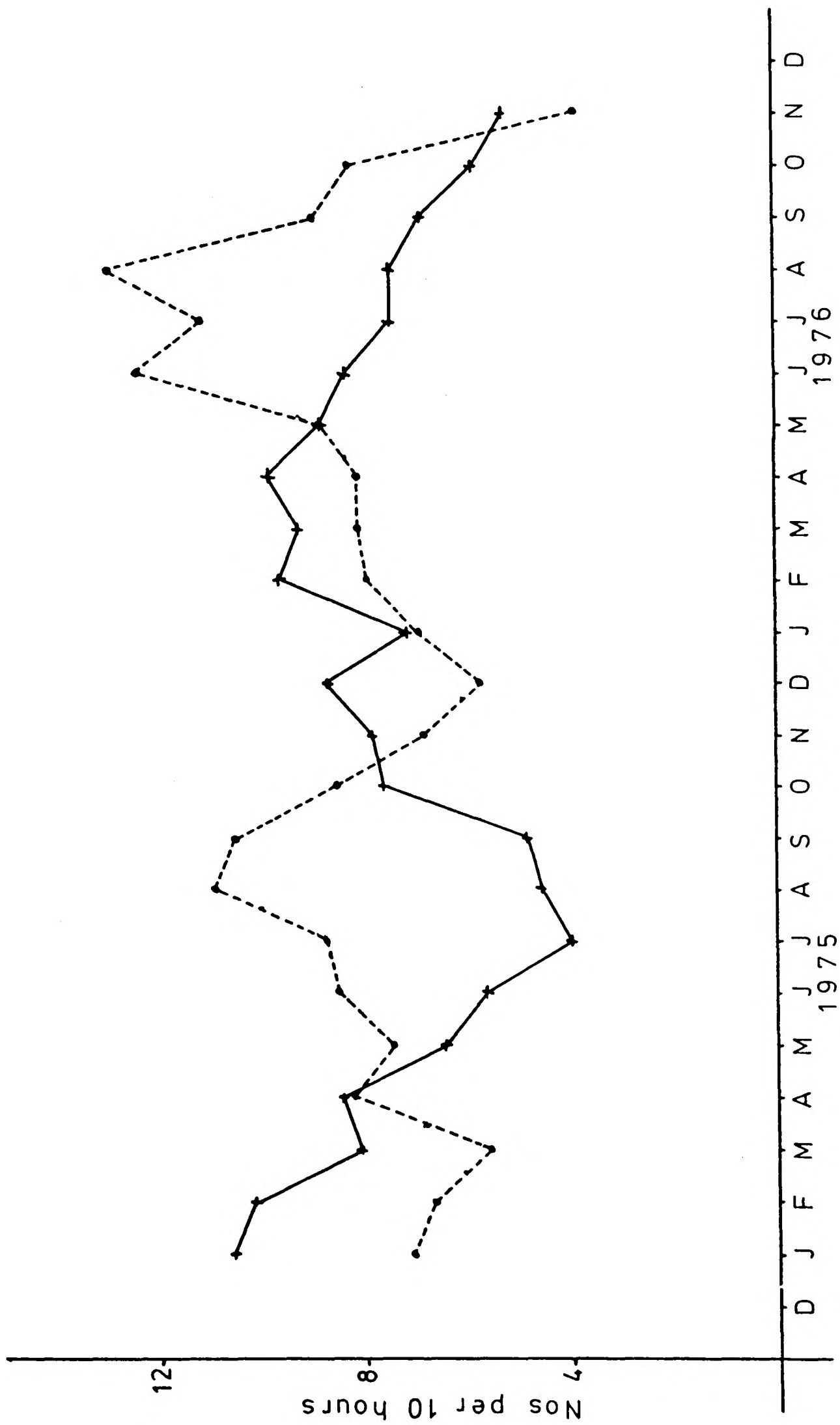


Fig. 5.7 The seasonal pattern of occurrence in Tsavo of two hornbills; +—+ *Tockus erythrorynchus*,
•---• *T. deckeni*.
Each point is the combined figure for that month and the two adjacent ones, creating a three-month running mean.

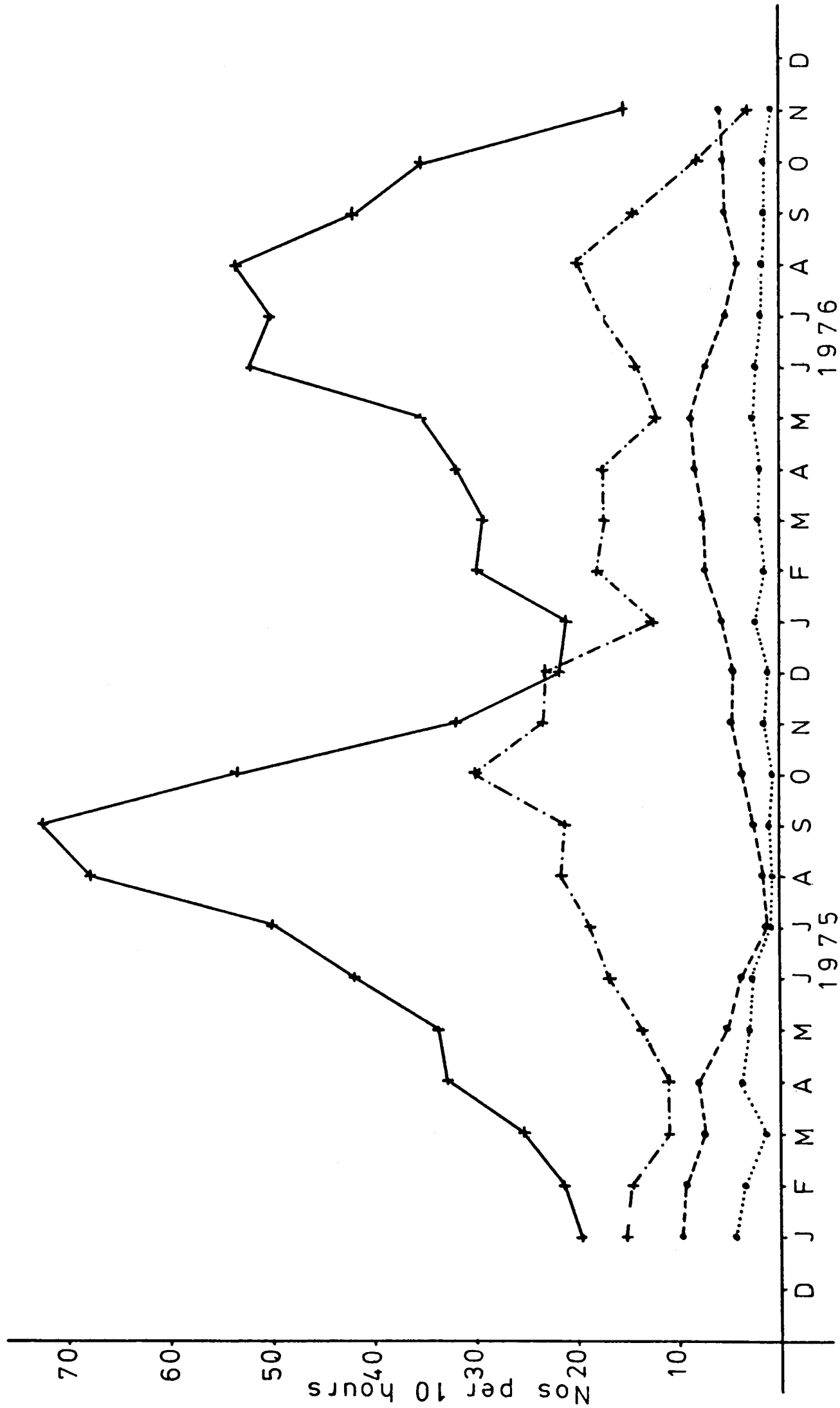


Fig. 5.8 The seasonal pattern of occurrence in Tsavo of two hornbills in Woodland and in other habitats; +---+T. deckeni in Woodland, and in other habitats; +---+T. erythrorynchus in Woodland, and in other habitats. Three-month running means have been calculated as in Fig. 5.7.

Table 5.6. Food items of four hornbills Tockus in Tsavo

	No. of items	Percentage on				
		Fruit	Insect	Other plant ^a	Other animal ^b	Unknown
<u>T. erythrorhynchus</u>	293	35	64	x	x	x
<u>T. deckeni</u>	226	69	29	2	-	-
<u>T. flavirostris</u>	83	63	37	-	-	-
<u>T. nasutus</u>	65	69	20	-	8	3

Notes:

1) x = less than 1%

a) Other plant: T. erythrorhynchus - 1 seed; T. deckeni - 1 seed, 5 flowers

b) Other animal: T. erythrorhynchus - 1 lizard; T. nasutus - 3 lizards,
1 frog, 1 egg.

in its seasonal cycle of abundance. The insects taken by this species (94 per cent of 175 items where site of capture is known), T. deckeni (93 per cent of 55 items) and T. flavirostris (97 per cent of 31 items) were almost all from the ground. All three take a large number of termites and T. erythrorhynchus was, several times, seen taking beetles and termites from dung piles especially those of éléphant and buffalo, Syncercus cafer. The fruits taken are correlated with habitat preference. Commiphora spp. accounted for 66 per cent of the fruit taken by T. deckeni, 83 per cent by T. flavirostris, but only 35 per cent by T. erythrorhynchus; and at least a further 19 per cent of the fruits taken by T. deckeni were of species largely confined to Woodland, e.g. Commiphora boiviniana, Grewia villosa and Maerua spp..

I have rather few data, but T. nasutus seems to be rather different. I only saw two birds eating Commiphora fruit, the insects were all single large items, and I did not record it eating termites, though all insects but two, of those for which the site of capture is known ($n = 10$), were taken from the ground.

Data from the literature - My data agree closely with those of Elliott (1972), who had all the same species except for a lack of T. flavirostris, in Kidepo N.P., Uganda. However, Kemp (1973) says that T. nasutus is entirely an insectivore, and that it forages in trees and not on the ground. Kemp had T. flavirostris and either T. erythrorhynchus (Kruger N.P., Transvaal) or T. monteiri (S.W.Africa) as potential competitors, and it is surprising that T. nasutus should be more similar to other species when there are three congeners, as in Tsavo, than in the Kruger N.P. and S.W. Africa where there are only two. The ecology of T. flavirostris and T. erythrorhynchus seems to be broadly similar in all these areas.

Summary of differences

	<u>T.e.</u>	<u>T.d.</u>	<u>T.f.</u>
<u>T. erythrorhynchus</u>	-	-	-
<u>T. deckeni</u>	TO(H)	-	-
<u>T. flavirostris</u>	T(H)	?	-
<u>T. nasutus</u>	T(H)	H	H

5.3.23 Capitonidae - Barbets

Data from Tsavo - Three species, Lybius leucocephalus, L. leucomelas and Pogoniulus bilineatus have not been seen in recent years, and there is only one record of L. torquatus.

All the remaining six species are resident (for statistics see below). Two are almost restricted to Riverine: L. melanopterus (R/N = 0.17, N = 42, N.S.) and L. lacrymosus (R/N = 0.05, N = 52, N.S.). The latter is half the size and occasionally occurs also in Woodland and along smaller watercourses. I did not see L. melanopterus outside riverine forest. L. melanocephalus (R/N = 0.02, N = 167, N.S.) is morphologically very similar to L. lacrymosus, but is almost confined to Woodland where it is common. P. pusillus (R/N = 0.30, N = 35, N.S.) is half the size of these latter, and is uncommon in both Woodland and Riverine. Finally, and rather different structurally, are the two Trachyphonus species. T. darnaudii ($2R^2/N = 1$, N = 288, N.S.) occurs almost entirely in the thicker habitats except Riverine (92 per cent of 288 seen were in B, WB and W), and T. erythrocephalus (R/N = 0.13, N = 137, N.S.) is in all habitats except Grassland.. (For the difference between the two species $\chi^2 = 124$, df 5, $P < 0.001$, 50 per cent due to WBG, 20 per cent to W).

Most species in Tsavo can be separated from each other by habitat and/or size differences. But there are some feeding differences too. L. melanopterus is almost entirely a frugivore (90 per cent of 77 items) and all items except two insects, taken on the ground, were in trees, especially in Ficus spp. L. lacrymosus eats both fruit and insects in

about equal amounts (56 per cent of 66 items were fruits). It eats all of its insects in the trees (although two were in the air near to trees) and 66 per cent of them were taken with the bird in flight. L. melanocephalus is also a frugivore - 97 per cent of 91 items, and 78 per cent of these were Commiphora spp.. P. pusillus is very like L. lacrymosus in eating both fruits (80 per cent of 37 items recorded) and insects (20 per cent), almost all taken in trees (90 per cent) and some while in flight (27 per cent).

The two Trachyphonus have further differences from each other in their feeding. T. darnaudii eats fruit (45 per cent of 77 items) and insects (55 per cent). All the insects were taken from the ground, and all were termites except for one bird (5 items scored) which was eating ants. Although fruit were taken in both bushes and trees (mean height of feeding ($\pm$ S.E.) = 3.8 ± 0.6 m (n=10)), the species was usually seen in bushes and not trees. By contrast, T. erythrocephalus is mainly an insectivore (83 per cent of 29 items (and the literature agrees)). All the insects seen taken were from the ground and 87 per cent were termites. The one bird eating fruit was on a Salvadora persica bush laden with fruit at the time.

Summary of differences

	<u>L.mp.</u>	<u>L.l.</u>	<u>L.mc.</u>	<u>P.p.</u>	<u>T.d.</u>
<u>L. melanopterus</u>	-	-	-	-	-
<u>L. lacrymosus</u>	TS	-	-	-	-
<u>L. melanocephalus</u>	H	H	-	-	-
<u>P. pusillus</u>	TS	S	TS	-	-
<u>T. darnaudii</u>	H	HF	TF	F	-
<u>T. erythrocephalus</u>	TF	F	HT	TF	H-F

5.3.24. Indicatoridae - Honeyguides

Data from Tsavo - Three species have been recorded but Indicator variegatus has only been seen once recently. I. indicator is rare south of the Galana River mainly in Woodland, but in parts of the northern area it is commoner. I. minor is uncommon in Woodland and Riverine. It is probably resident (R/N=0.39, N=18, N.S.) but is more often noted in

the wet seasons, probably because it calls more then.

I have no feeding data for I. indicator, and only three observations for I. minor, all of insects taken while in flight.

Data from the literature - They eat insects, especially larvae of Hymenoptera, and beeswax.

Summary of difference

	<u>I.i.</u>
<u>I. indicator</u>	-
<u>I. minor</u>	H-S

5.3.25 Picidae - Woodpeckers

Data from Tsavo - All three species recorded, are fairly common residents, at least in some habitats. Campethera nubica (R/N=0.05, N=133, N.S.) occurs wherever there are trees or large dead stumps. Dendropicos fuscescens (R/N = 0.09, N=114, N.S.) has similar habitat preferences, but is much less common in Riverine (1 seen per 10 hours cf. 4 for C. nubica) ($X^2=12$, df 5, $P<0.05$, 55 per cent due to R). Thripias namaquus (R/N=0.26, N=18, N.S.) only occurs where there are large trees, and as a result is almost restricted to Riverine (15 of 18 seen in censuses).

I have very few records of woodpeckers capturing prey, but only of birds actively searching. All three species seem to be typical woodpeckers. They search by tapping and hammering on twigs, branches and trunks. The size distribution of twigs and branches attacked by each species is shown in Fig. 5.9, and this clearly parallels the size difference of the birds. The distribution of sizes is significantly different between species: X^2 for D. fuscescens: C. nubica=16, df 3, $P<0.01$; and for C. nubica: T. namaquus=19, df 2, $P<0.001$ (the tables have been reduced from all the divisions shown in Fig. 5.9 to avoid too many low expected numbers). The medians follow a series D. fuscescens - 1.6 cm, C. nubica - 3 cm and T. namaquus - 11.4 cm.

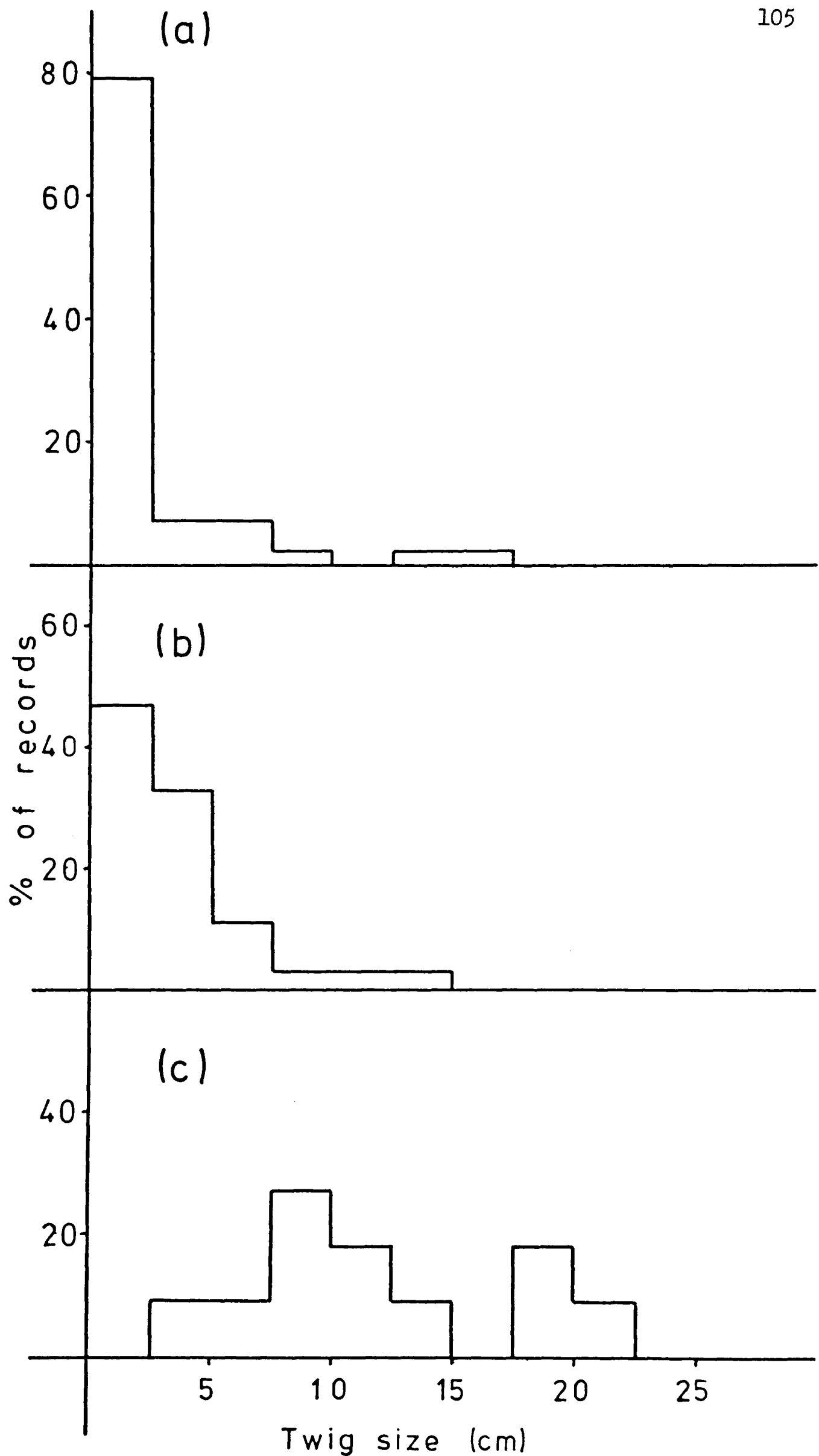


Fig. 5.9 The distribution of twig/branch size searched by three woodpeckers; a) *Dendropicos fuscescens* (n=44), b) *Campetheranubica* (n=36), c) *Thripias namaquus* (n=11).

Data from the literature - Short (1971), working in the Transvaal, found a similar difference between D. fuscescens and T. namaquus in size of branch searched, but added that D. fuscescens is a probing and tapping woodpecker, whereas T. namaquus taps, excavates, probes and picks at the surface in order of decreasing frequency. He did not study C. nubica.

Summary of differences

	<u>C.n.</u>	<u>D.f.</u>
<u>C. nubica</u>	-	-
<u>D. fuscescens</u>	F	-
<u>T. namaquus</u>	F	FS(H)

5.3.26 Alaudidae - Larks

Data from Tsavo - Five Mirafra species and three Eremopterix species have been recorded. There are only two recent records of M. rufocinnamomea. Of the other Mirafra spp., M. hypermetra is the largest and occurs primarily in Grassland. However it needs a few dead sticks or bushes for use as songposts. M. poecilosterna is probably the most widespread bird in the whole Park being very common in all the Park savanna habitats. It occurs in Woodland only where there are few bushes under the trees, i.e. it does not occur in areas of thicket. Both species are present in ^{large} numbers all the year but both show seasonal variations (M. hypermetra $2R^2/N = 29$, $N = 512$, $P < 0.001$ peak Feb 2; M. poecilosterna $2R^2/N = 12$, $N = 2527$, $P < 0.01$, peak Sep 3).

There is some doubt about the status of the other two Mirafra species. This is due largely to identification problems, especially early on in my study. M. cantillans has very similar habitat preferences to M. hypermetra ($X^2 = 3.6$, $df\ 2$, N.S.) but it is much less common. M. pulpa is found most commonly in Bushed Grassland and prefers the western half of the Park where it is wetter and there is a higher grass cover (M. pulpa: M. cantillans $X^2 = 9$, $df\ 2$, $P < 0.05$, 75 per cent due to WBG with

B with WB). Both species occur regularly from December to February and a few remain until May (M. cantillans $R/N = 0.63$, $N = 74$, $P < 0.01$, peak Feb 1; M. pulpa $N = 10$, Dec and Feb only). Their status in the remainder of the year is uncertain. I could only distinguish the two species when they were singing, which was only heard during the above periods. A few individuals of one or the other could be found at any time of year but most seemed to have moved away. And, as most of them were in Grassland and not Bushed Grassland, I think the majority were M. cantillans. For further notes on M. pulpa with comparative data on the other species see Lack (1977).

Of the three Eremopterix species, I never saw E. leucopareia. Formerly it was fairly common e.g. around Aruba (D.A. Turner pers. comm.). It has evidently been replaced by E. signata which was not seen until about 1965 (D.A. Turner pers. comm.). E. signata is now fairly common in all open habitats with a few in Bushland and Wooded Bushland. I did not record it in Woodland or Riverine. E. leucotis is less common and restricted to Grassland and Bushed Grassland (χ^2 for the difference with E. signata = 485, df 4, $P < 0.001$, 60 per cent due to WBG). The occurrence of E. signata over the seasons is rather erratic (Fig. 5.10), with peaks in April-May 1975, September-October 1975, February 1976 and May to September 1976 ($2R^2/N = 480$, $N = 1903$, $P < 0.001$, peak May 3). E. leucotis is, however, seasonal and more regular (Fig. 5.10) occurring, in flocks, only after rain ($2R^2/N = 910$, $N = 756$, $P < 0.001$, peak Mar 2, although none were seen in March itself - a statistical effect due to a peak in both wet seasons see ch 5.2.6)

All seen feeding were on the ground, the four commoner Mirafra species appeared to take both seeds and insects; M. hypermetra - 47 per cent of 32 items were insect, the rest unidentified; M. poecilosterna - 45 per cent of 60 items insect, the rest unidentified. M. cantillans - one record of

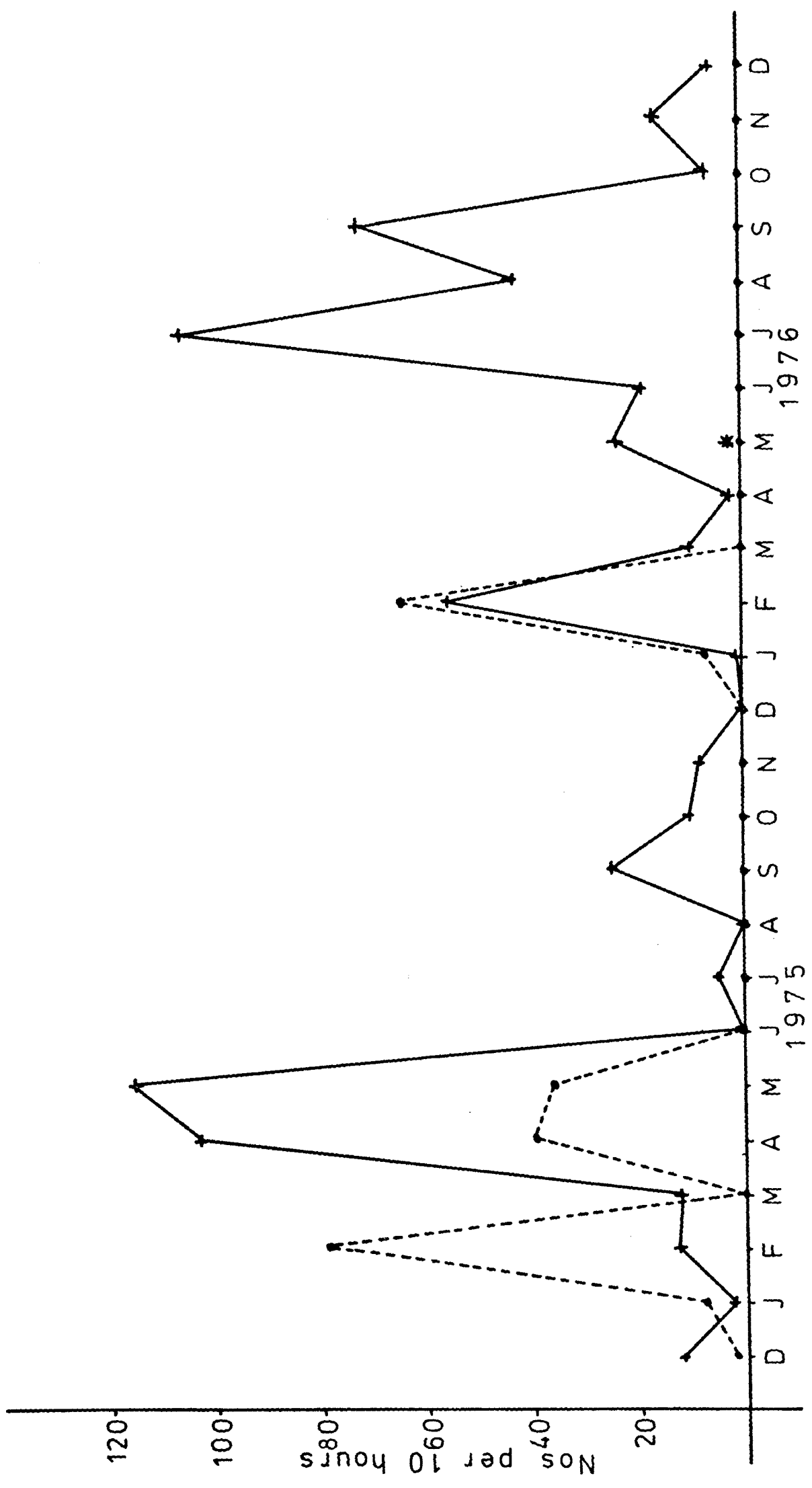


Fig. 5.10 The seasonal pattern of occurrence of two larks; + *Eremopterix signata*, • *E. leucotis*.

a bird catching flying insects; M. pulpa - the stomach of the bird collected in Tsavo East in January 1977 contained both seeds and insects (Lack 1977). The two Eremopterix species seemed to be largely or entirely granivorous: E. signata - 9 records of flocks; E. leucotis-5 records of flocks; although E. signata was seen carrying insects twice in April probably to its young.

Data from the literature - Mirafra cantillans is certainly migratory in some parts of its range e.g. in parts of Tanzania (MPG), and M. pulpa has three times come to the lights of Ngulia Safari Lodge in December suggesting this too is migrating. However in December 1976 a M. hypermetra also came to the lights there (G.C. Backhurst pers. comm.).

The Mirafra species eat both seed and insects and the Eremopterix species are largely granivorous.

Summary of differences

	<u>M.h.</u>	<u>M.po.</u>	<u>M.c.</u>	<u>M.pu.</u>	<u>E.s.</u>
<u>M. hypermetra</u>	-	-	-	-	-
<u>M. poecilosterna</u>	H	-	-	-	-
<u>M. cantillans</u>	O-S?	H	-	-	-
<u>M. pulpa</u>	O-S?	H-?	?(H)	-	-
<u>E. signata</u>	HT	HT	HT	HT	-
<u>E. leucotis</u>	HT	HT	HT	HT	O?

5.3.27 Hirundinidae - Swallows

See note at start of ch 5.3.14.

Data from Tsavo - Nine species are recorded but only one, Hirundo rustica, is at all numerous. This is a Palaearctic migrant which is common from the onset of the rains in November till mid-February, though it occurs from September to early May. Figures from the road counts are given in Fig. 5.11. It was seen flying over all habitats. It feeds low over the ground, and quite often follows large mammals catching the disturbed insects.

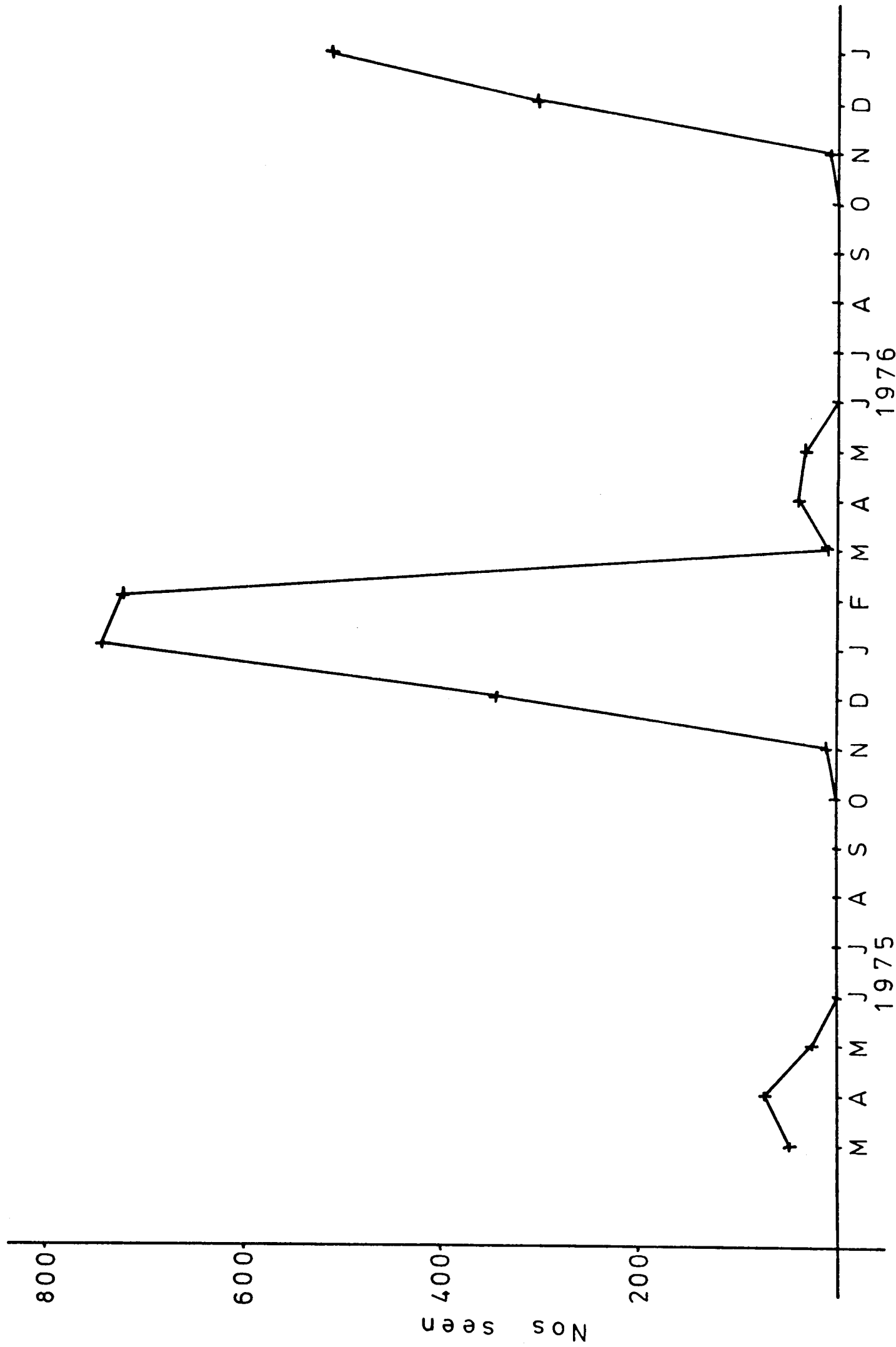


Fig. 5.11 The seasonal pattern of occurrence in Tsavo of a swallow Hirundo rustica. These figures are from the road counts - see ch 3.3.1.

Two other Palaearctic migrants occur rarely. A few Riparia riparia occur each autumn, mostly at Aruba; and a few Delichon urbica are usually seen each winter. Four other species are residents in very small numbers: H. smithii occurs only in the vicinity of water especially the Galana River; H. daurica occurs mainly around its nest-sites in culverts though it also nests more rarely on buildings; H. abyssinica is similar but the reverse; and H. fuligula occurs around rocky hills.

The final two species are both very rare: there is only one record of R. cincta; and only one recent record of H. senegalensis, although this was seen formerly.

Summary of differences

	<u>H.r.</u>	<u>H.s.</u>	<u>H.d.</u>	<u>H.a.</u>
<u>H. rustica</u>	-	-	-	-
<u>H. smithii</u>	H	-	-	-
<u>H. daurica</u>	H	H	-	-
<u>H. abyssinica</u>	H	H	H	-
<u>H. fuligula</u>	H	H	H	H

5.3.28 Motacillidae - Wagtails, Pipits

Data from Tsavo - Three wagtails Motacilla are recorded but there is only one record of M. cinerea. M. aguimp is fairly common by the Galana and Tiva Rivers and around buildings, but it is very rare away from these and hence very rare in censuses. The Palaearctic migrant M. flava, of one or more subspecies, occurs in small numbers in short grass ("lawn") areas, e.g. Aruba Lodge, between November and early May. Both species were seen feeding on insects captured on or near the ground.

Four species of pipit Anthus are known to occur but all are rare visitors mainly to short grass areas, especially south and east of Aruba. A. novaeseelandiae is the most often seen, but it is only a sporadic visitor occurring between November and April. A. cervinus is similar with records from December to March. There are two certain, and one

probable, records of A. trivialis, and two recent records of A. leucophrys but this latter formerly occurred more often in very open areas.

Two other species in this family are more common. Macronyx aurantiigula is fairly common all the year although more were seen in the wet seasons ($R/N = 0.27$, $N = 165$, $P < 0.01$, peak Mar 2; due to peaks in both wet seasons - see ch 5.2.6.). It occurs in areas with a high grass cover especially Grassland. Tmetothylacus tenellus is common in all the Park savanna habitats (a little less so in Grassland), though it may occur anywhere at times. It is very seasonal in its occurrence (Fig. 5.12), ($2R^2/N = 717$, $N = 895$, $P < 0.001$, peak Jan 2), but, as with many intra-African migrants, a few can usually be found at any season. Numbers increase enormously with the onset of the rains and, this species particularly may be very localised to areas which have had rain.

Both M. aurantiigula and T. tenellus are entirely insectivorous and feed almost entirely on the ground (99 per cent of 141 items for T. tenellus; both items seen taken by M. aurantiigula were taken in the air but it was usually seen on the ground in thick grass. There is however a difference between the two species: M. aurantiigula prefers the dense grass, like the lark, Mirafra hypermetra (ch 5.3.26), but T. tenellus is much more catholic, feeding at times even on almost bare ground (only 13 times recorded as certainly from the herbage/grass, and the rest on the ground.

Data from the literature - M. aurantiigula feeds on the ground.

Summary of differences

	<u>M.ag.</u>	<u>M.f.</u>	<u>M.au.</u>	<u>T.t.</u>
<u>M. aguimp</u>	-	-	-	-
<u>M. flava</u>	?	-	-	-
<u>M. aurantiigula</u>	H	H	-	-
<u>T. tenellus</u>	H	H-?	FO	-
<u>A. novaeseelandiae</u>	H	(H)	H	(H)-?

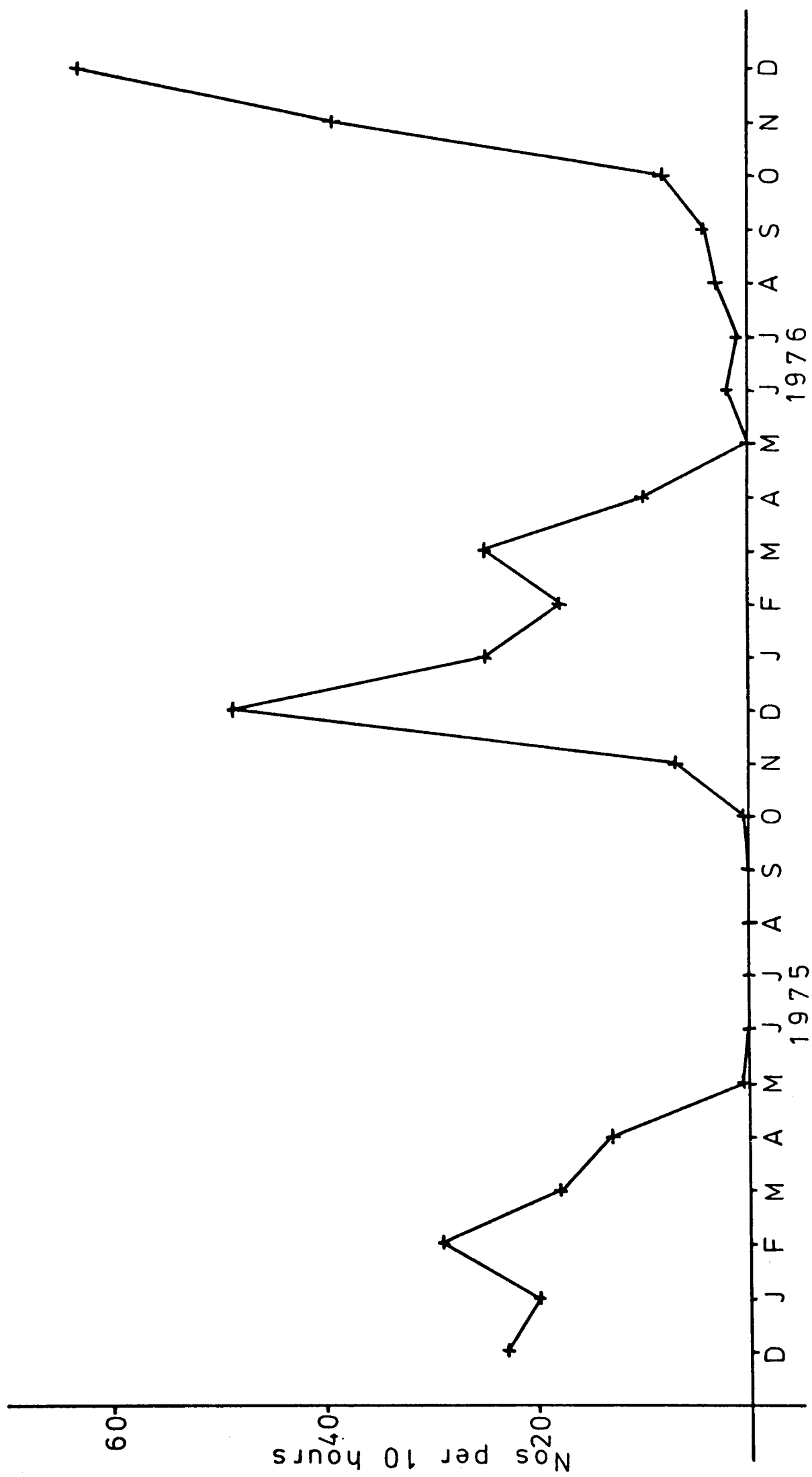


Fig. 5.12 The seasonal pattern of occurrence in Tsavo of a pipit *Tmetothylacus tenellus*.

5.3.29 Campephagidae - Cuckoo-Shrikes

Data from Tsavo - The one species, Campephaga flava, is rare and occurs in Woodland and Riverine. In the northern area, it also occurs rarely in other thick habitats. My records show it to be commoner from December to May ($R/N = 0.54$, $N = 70$, $P < 0.01$, peak Mar 1). It feeds on insects mostly off leaves (81 per cent of 21 items) and many are taken with the birds in flight (67 per cent).

Data from the literature - In common with the cuckoos (ch 5.3.9) it is said to take many hairy caterpillars.

5.3.30 Pycnonotidae - Bulbuls

Data from Tsavo - Five species are recorded, but there are only a few isolated records of Chlorocichla flaviventris from the Voi River. Nicator chloris is rare in the thickest parts of Woodland. I only saw it once, but heard it regularly during the wet seasons. Andropadus importunus another species much more often heard than seen is common in Woodland and Riverine. It was seen in all months except April but shows a seasonal pattern ($R/N = 0.42$, $N = 49$, $P < 0.01$, peak Nov 2). Phyllastrephus strepitans has very similar habitat preferences ($X^2 = 0.2$, $df\ 1$, N.S.) and is resident ($R/N = 0.21$, $N = 65$, N.S.). Pycnonotus barbatus, of which the well-marked subspecies P.b. dodsoni occurs, is a resident ($2R^2/N = 3$, $N = 275$, N.S.) is commoner (4 per 10 hours cf 1 for the other two species) and more widespread than any other member of this family. It is commonest in Woodland, then Riverine, but occurs regularly in Wooded and Bushed Grassland, Bushland and Wooded Bushland (to P. strepitans $X^2 = 20$, $df\ 2$, $P < 0.01$, 60 per cent due to PSH; to A. importunus $X^2 = 17$, $df\ 2$, $P < 0.001$, 60 per cent due to PSH).

All the three commoner species spend much of their time inside thickets, especially the former two. I only recorded A. importunus eating fruits (19 items). P. strepitans, however, seems to be entirely insectivorous (all 45 items). It creeps around, low down (mean height of feeding ($\pm$ S.E.) = 1.2 ± 0.2 m (n = 19)), rarely venturing away from bushes, taking insects off leaves (70 per cent), sometimes stems (9 per cent), the ground (16 per cent)/^{or} in the air (7 per cent). P. barbatus eats both insects (14 per cent of 139 items) and fruit (72 per cent) and was also recorded eating sisal flowers Agave sisalana. Considering its abundance in Woodland (5 seen per 10 hours) it is perhaps surprising that only four birds were seen eating Commiphora fruits and three of these were together in one tree. This probably serves to keep it separate from other fruit-eaters. Of the insects taken, half were termites, from the ground, but it also took some insects off leaves in bushes.

Data from the literature - A. importunus eats some insects as well as fruit. P. strepitans is entirely insectivorous. P. barbatus eats fruit and insects.

Summary of differences

	<u>A.i.</u>	<u>P.s.</u>
<u>A. importunus</u>	-	-
<u>P. strepitans</u>	T	-
<u>P. barbatus</u>	?	T

5.3.31 Laniidae - Shrikes

This family will be discussed in three groups, groups which are separate subfamilies in Forbes-Watson (1971) but which Benson et al. (1973) treat as separate families.

a) Prionopinae

Contrary to Forbes-Watson (1971) but agreeing with Benson et al. (1973) I have deferred discussion of Nilaus afer until the next section

as its ecology is much closer to those in the latter.

Data from Tsavo - The habitat preferences of the three species are shown in Fig. 5.13. As can be seen, Prionops retzii is entirely restricted to Riverine and P. plumata essentially to Woodland with a few extending further (X^2 for the difference = 450, df 3, $P < 0.001$, 80 per cent due to R). Eurocephalus rueppelli is more widespread, occurring particularly where there are trees ($X^2 = 79$, df 1, $P < 0.001$). All three species are usually seen in groups of three to six birds unlike other shrikes, except Lanius cabanisi at times, and all three have been shown to be co-operative breeders (review in Grimes 1976). All three have quite large resident populations although all three show a slight seasonal pattern in the data (P. plumata $2R^2/N = 11$, $N = 382$, $P < 0.01$, peak Sep 4; P. retzii $R/N = 0.29$, $N = 89$, $P < 0.01$, peak Oct 4; E. rueppelli $2R^2/N = 30$, $N = 819$, $P < 0.001$, peak May 3).

The feeding behaviour of the two Prionops species is similar but Eurocephalus is rather different. Data on the behaviour of the former pair are given in Table 5.7. Both species are usually seen moving slowly through the vegetation at the base of the tree canopy, and the difference in height of feeding can be attributed to this layer being at different heights in the species' major habitats.

E. rueppelli feeds mainly by pouncing to the ground from a perch (83 per cent of 213 items) and flycatching (15 per cent) (see Table 5.8). This is very different from the Prionops spp. and further discussion will be deferred to the section on Laniinae.

Summary of differences

	<u>P.p.</u>	<u>P.r.</u>
<u>P. plumata</u>	-	-
<u>P. retzii</u>	H	-
<u>E. rueppelli</u>	F	F

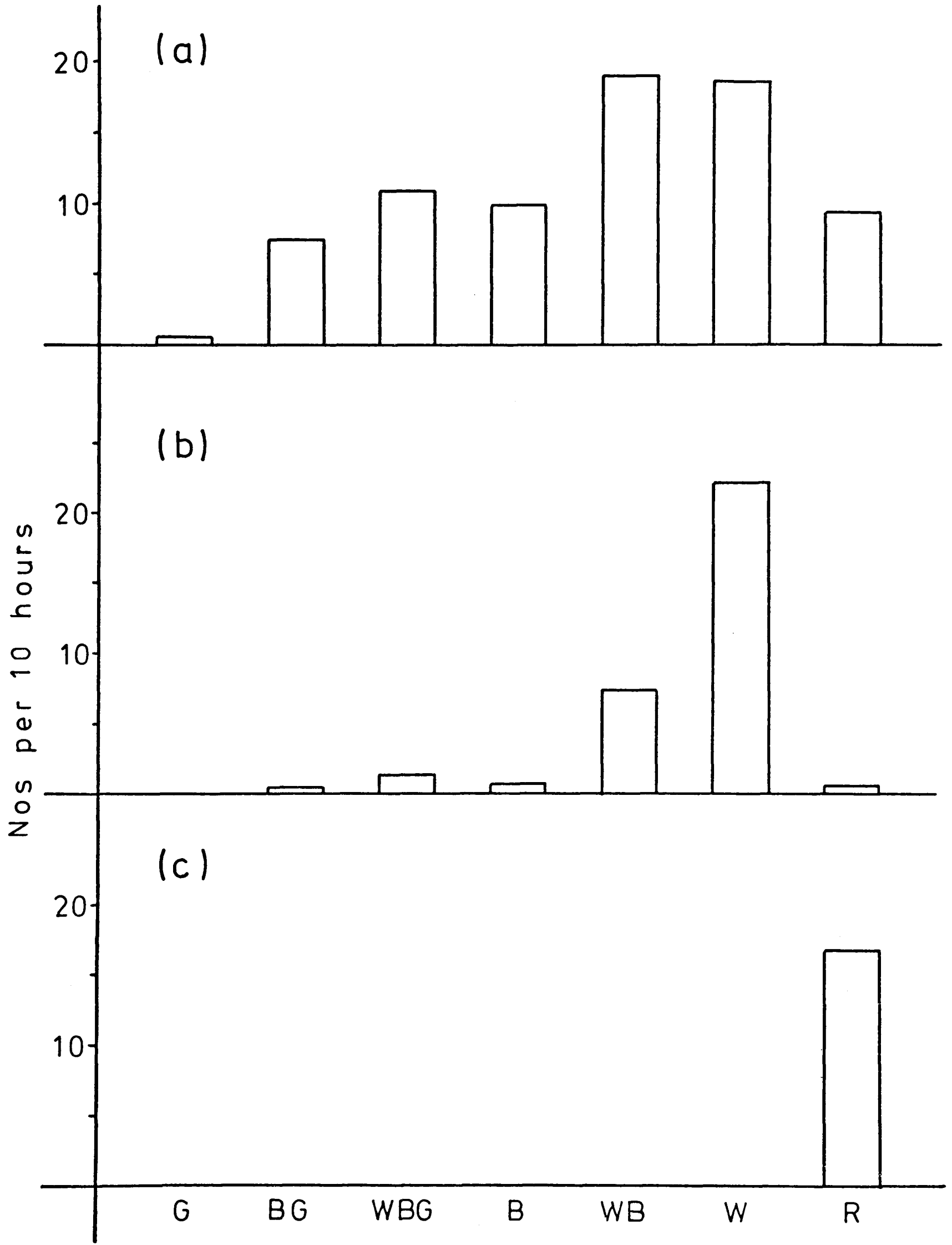


Fig. 5.13 The habitat preferences in Tsavo of three shrikes; a) *Eurocephalus rueppelli*, b) *Prionops plumata*, c) *P. retzii*.

Table 5.7 Feeding behaviour of two shrikes Prionops in Tsavo

	<u>P. plumata</u>	<u>P. retzii</u>
Number of items	76 ^a (1 = fruit, rest = insect)	46 (all insect)
Percentage taken from air	16	13
Percentage taken off twigs/stem	41	26
Percentage taken off branches/trunk	9	37
Percentage taken off leaves	9	15
Percentage taken off ground	19	9
Percentage taken from other	6	-
Percentage when perched	32	33
Percentage hovering	11	30
Percentage in flight ^b	49	35
Percentage pounce to ground	5	2
Percentage unknown	3	-
Height of feeding (m) ^c	3.0 $\pm$ 0.4 (56)	5.0 $\pm$ 0.8 (29)

- Notes:
- a) I have scored as one item (rather than five) each of three birds which pounced to the ground and then ate several termites as in each case only one movement was involved.
 - b) These are where the bird snatched an insect in passing without a significant pause.
 - c) Height is quoted as mean $\pm$ standard error with the sample size in brackets.

b) Malaconotinae

Data from Tsavo - Thirteen species are recorded but there is only one definite record and one possible record of Tchagra australis, only two of Laniarius ruficeps and no recent records of Malaconotus quadricolor. The other ten are in four genera containing two species each, all of which have superficially similar ecology, and two others which are rather separate. All for which I have data were entirely insectivorous, except where stated.

The two Dryoscopus species separate by habitat although neither is common. D. cubla occurs solely in Riverine especially the thicker parts. It is seen all the year but more in the wet seasons ($R/N = 0.45$, $N = 45$, $P < 0.001$, peak Jan 4). D. pringlii is rare in Woodland near Voi, but was seen more often in parts of the northern area, especially on the Yatta Plateau. The latter spends most of its time in the bushes (mean height ($\pm$ S.E.) of feeding birds = 2.2 ± 0.4 m ($n = 8$) cf. 7.4 ± 1.3 m ($n = 7$) for D. cubla; $d = 3.9$, $df = 7$, $P < 0.01$).

Of the two Tchagra species, T. senegala is uncommon in the thickest parts of Woodland (I only saw two outside this). T. jamesi is a resident ($R/N = 0.13$, $N = 111$, N.S.), occurs regularly in Bushland, Wooded Bushland and Woodland and rarely in other habitats where there are thick bushes. It feeds very low down in bushes (mean height ($\pm$ S.E.) = 0.3 ± 0.1 m ($n = 8$)). I have no feeding data for T. senegala.

I only recorded Laniarius aethiopicus (most were heard only) in the Voi River forest, during and soon after the wet seasons. L. funebris, however, is a common resident ($R/N = 0.6$, $N = 95$, N.S.) in Woodland. Outside this habitat it is restricted to bushes by watercourses but it was not seen along the Voi River. L. funebris feeds like T. jamesi, though also I saw it occasionally eating Commiphora fruits (34 per cent items recorded but fruit-eating is much more obvious in this and similar species).

I have no feeding data for L. aethiopicus.

The two Malaconotus species are both rare in Tsavo and, unlike the above pairs, are very different to each other in size. As before though, both species are more often heard than seen. M. sulfureopectus occurs rarely in Woodland and only very occasionally outside, and M. blanchoti is in both Woodland and Riverine. M. blanchoti is a resident ($R/N = 0.22$, $n = 18$, N.S.). Only five M. sulfureopectus were seen in censuses, all in December and January. I usually saw both species in trees, and my feeding data for M. blanchoti confirm this (mean height ($\pm$ S.E.) = 5.7 ± 1.4 m ($n = 8$)); I have ^{one} record of M. sulfureopectus feeding in a tree and one in a bush. Further, subjectively, M. blanchoti seems to catch items only rarely suggesting it is searching for larger prey.

Finally the two odd genera. Nilaus afer is an uncommon resident ($R/N = 0.02$, $N = 67$, N.S.) in habitats with trees except in Riverine (93 per cent of 67 birds in WBG, WB and W; $X^2 = 38$, $df = 1$, $P < 0.001$). It feeds by taking insects mostly from leaves (30 per cent of 33 items) or twigs (42 per cent) mostly while perched (79 per cent). It is usually found high in the vegetation (mean height ($\pm$ S.E.) = 6.5 ± 0.6 m ($n = 20$)) and near the outside rather than in the middle (21 per cent inside, 42 per cent just inside, 37 per cent at edge for 19 birds where recorded). The final species, Rhodophoneus cruentus, is a resident ($R/N = 0.07$, $N = 160$, N.S.) primarily in areas with bushes but without trees ($X^2 = 17$, $df = 1$, $P < 0.001$), though it does occur rarely with trees present even in parts of Woodland. Unlike any other shrike it feeds while running about on the ground in the open, picking up insects from the bare ground or grass (92 per cent of 50 items) or low bushes (8 per cent). It was rarely seen to venture more than 5 m or so from bushes and was usually seen where there was some grass, and not in large areas of bare ground.

Summary of differences

	<u>D.c.</u>	<u>D.p.</u>	<u>T.s.</u>	<u>T.j.</u>	<u>L.f.</u>	<u>M.b.</u>	<u>N.a.</u>
<u>D. cubla</u>	-	-	-	-	-	-	-
<u>D. pringlii</u>	H	-	-	-	-	-	-
<u>T. senegala</u>	H	S	-	-	-	-	-
<u>T. jamesi</u>	F	?	H-S?	-	-	-	-
<u>L. funebris</u>	H	?	?	H-?	-	-	-
<u>M. blanchoti</u>	S	FS	F	F	F(S)	-	-
<u>N. afer</u>	H	F	F(H)	F	F(H)	HS	-
<u>R. cruentus</u>	FH	F	F	F	F	FH	F(H)

c) Laniinae

Data from Tsavo - Four species, and a well-marked race of one, often considered a different species, have been recorded. Three forms are Palaearctic migrants. Lanius minor occurs in all habitats except Riverine. It only occurs on spring passage with records from late March to early May (in censuses only in April (R/N = 1.00)). There is a single autumn record, in 1971. L. collurio collurio follows a similar pattern of occurrence but it occurs on a regular, though rare, basis in autumn (Fig.5.14) (R/N = 0.83, N = 184, P < 0.01, peak Apr 1). As will be apparent from the figure, it appears to replace L. c. isabellinus in April. This latter becomes very common from the onset of the rains in November, then, after a peak in numbers from December to March, decreases very suddenly in April ($2R^2/N = 880$, N = 802, P < 0.001, peak Jan 3). But Fig. 5.15 shows it is not a simple question of replacement, as they are significantly different in their habitat preferences ($X^2 = 64$, df 6, P < 0.001, 35 per cent due to R, 35 per cent to WB). Because of this different ecology the two forms of this species are considered hereafter as different species.

The two African species are also differentiated from each other by their habitat preferences. L. dorsalis is a common resident ($2R^2/N = 1$, N = 708, N.S.) in all the Park savanna habitats, especially the open ones ($X^2 = 92$, df 1, P < 0.001). L. cabanisi (21 scattered records in censuses) is rare and occurs in similar habitats but, subjectively, is always in

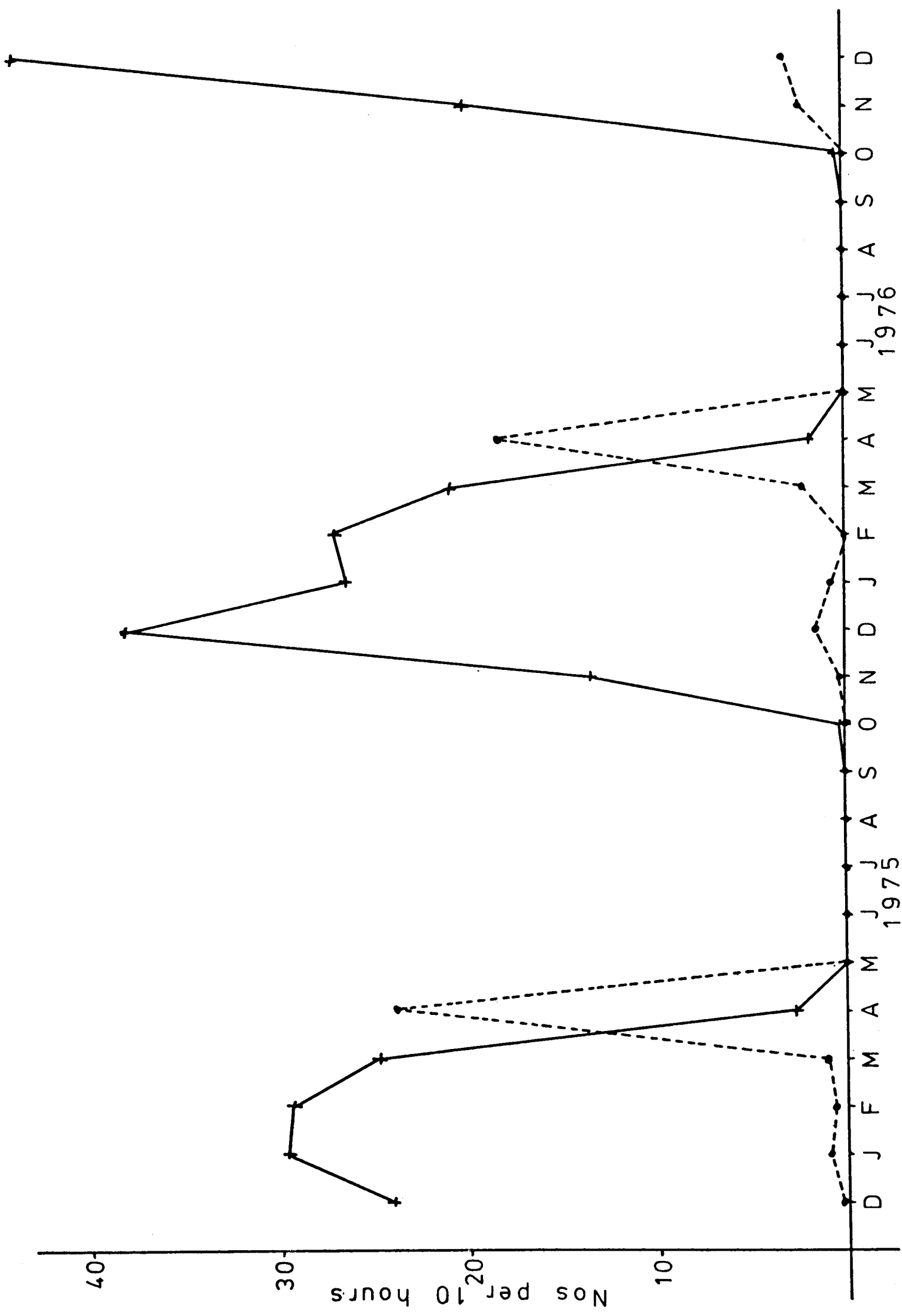


Fig. 5.14 The seasonal pattern of occurrence in Tsavo of two shrikes; +—+ *Lanius collurio* isabellinus, •—• *L. c. collurio*.

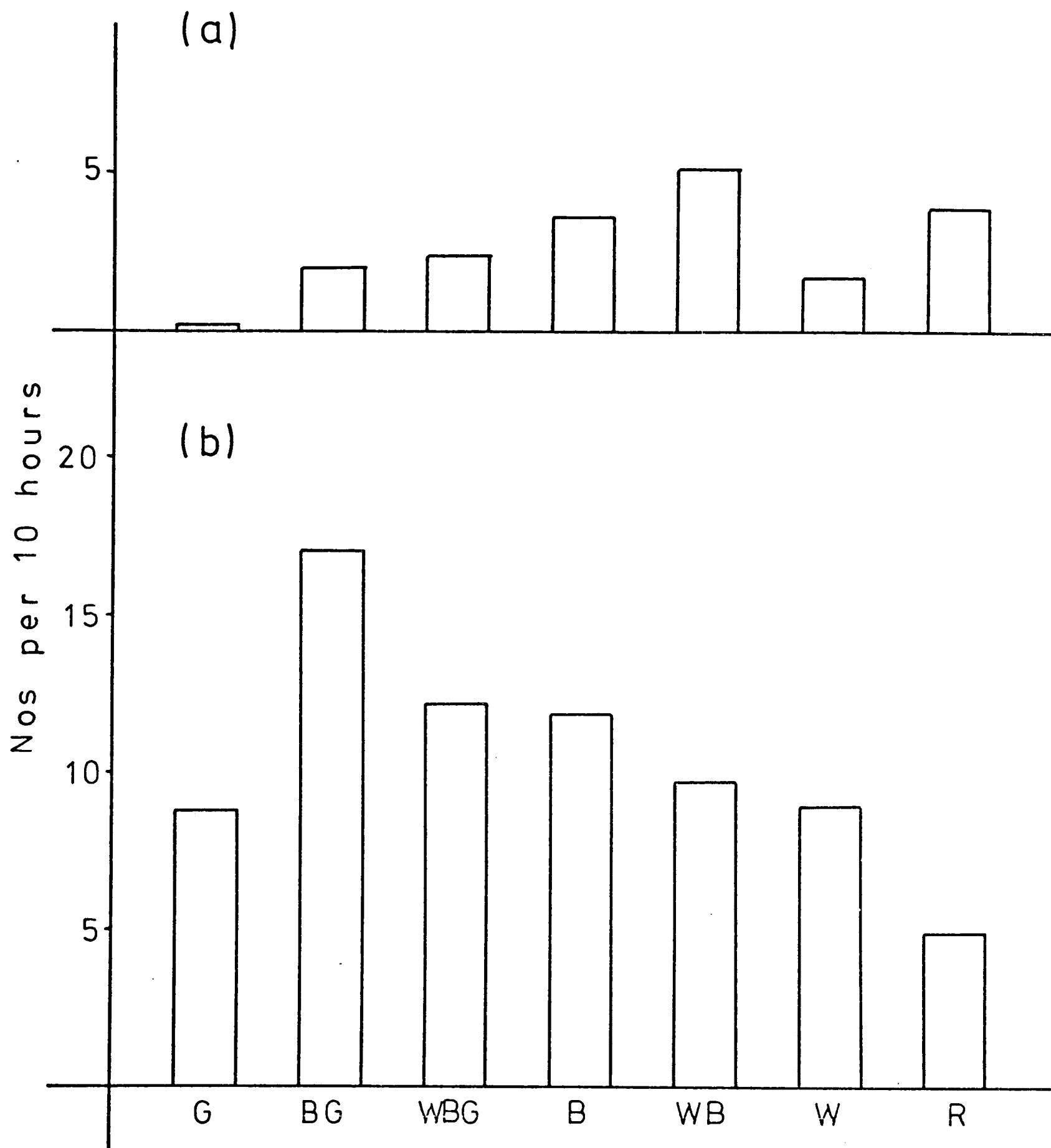


Fig. 5.15 The habitat preferences in Tsavo of two shrikes; a) Lanius collurio collurio, b) L. c. isabellinus.

the damper parts e.g. near rivers, and not on the open dry plains.

All these species and E. rueppelli feed mainly by pouncing to the ground from a prominent perch. Data on their feeding behaviour are given in Table 5.8. All six forms are very similar. The two smallest, L. collurio spp., in general, perch on lower bushes and fly out less far than the others, and the largest, L. cabanisi, does not flycatch probably due to its lack of manoeuvrability. E. rueppelli takes a higher percentage of its food in the air than any except L. minor and L. c. collurio, but these latter two are common only in April when there are more flying insects present due to the rain.

Data from the literature - L. minor is known to take a more westerly course on its autumn migration than in spring, and L. c. collurio similarly although the different course in this case is relatively slight (Moreau 1972).

Summary of differences (including E. rueppelli from the Prionopinae because of its similar feeding behaviour)

	<u>E.r.</u>	<u>L.d.</u>	<u>L.ca.</u>	<u>L.c.c.</u>	<u>L.c.i.</u>
<u>E. rueppelli</u>	-	-	-	-	-
<u>L. dorsalis</u>	H-?	-	-	-	-
<u>L. cabanisi</u>	(F)?	H	-	-	-
<u>L. c. collurio</u>	S	S(H)	S	-	-
<u>L. c. isabellinus</u>	(O)	(O)	(O)	S?	O

5.3.32 Muscicapidae (Turdinae) - Thrushes, Chats

Data from Tsavo - Eighteen species are recorded but five are very rare; there is only one record of each of Saxicola rubetra and Cercomela familiaris, and no recent records of Cercotrichas quadrivirgata, Cossypha heuglinii and Neocossyphus rufus. Two others are unimportant ecologically though there are several records - Myrmecocichla cinnamomeiventris which occurs sporadically on rocky hills (all records are from around Voi and there is often a resident pair at Voi Safari Lodge), and Luscinia megarhynchos

Table 5.8. Feeding behaviour of six shrikes, five Lanius spp. and Eurocephalus rueppelli in Tsavo

	<u>E. rueppelli</u>	<u>L. cabanisi</u>	<u>L. dorsalis</u>	<u>L. minor</u>	<u>L.c.collurio</u>	<u>L.c.isabellinus</u>
Number of items	213 ^a	81 ^a	135 ^b	41	74 ^a	175 ^a
% taken from ground (and herbage)	80	90	83	80	81	73
% taken from air	15	-	8	17	14	9
% taken from leaves in bushes	1	9	5	2	3	11
Height of aerial feed (m) ^c	7.6 ± 1.9 (17)	-	4.9 ± 1.4 (11)	4.7 ± 1.4 (7)	3.4 ± 1.2 (9)	9.8 ± 1.4 (16)
Height of perch used to search for prey (m) ^c	3.6 ± 0.3 (73)	2.3 ± 0.2 (44)	2.6 ± 0.1 (88)	2.7 ± 0.4 (20)	1.5 ± 0.1 (33)	2.1 ± 0.2 (112)
Distance flown to food (m) ^c	9.6 ± 1.0 (68)	10.8 ± 1.3 (44)	14.2 ± 1.3 (81)	12.7 ± 4.5 (19)	4.7 ± 0.7 (30)	8.0 ± 0.6 (105)
Feeding rate (items per minute)	0.31 (49 items)	0.23 (63 items)	0.17 (85 items)	0.27 (31 items)	0.41 (37 items)	0.25 (56 items)

Notes:

a) The following records have not been included in the above table:

E. rueppelli - 2 records of "several feeding on the ground"; 1 of "several feeding in the air", 1 of "several taking many in the air and several on the ground".

L. cabanisi - 4 records (of 1 bird each time) eating Salvadora persica fruits.

L. minor - 1 record of "many flycatching".

L.c. collurio - 1 record of "many flycatching".

L.c. isabellinus - 1 record of one bird eating fruits (unidentified species).

b) Of the records of L. dorsalis 2 are lizards and 1 is a small snake but these are included.

c) Heights and distances are quoted as mean ± standard error with sample size in brackets.

which has only been certainly recorded four times, from Riverine in March and April.

This leaves eleven species of which seven are Palaearctic migrants. Three of the four African species are resident and occur only in the thicker habitats. Turdus tephronotus ($R/N = 0.12$, $N = 48$, N.S.) is fairly common in Woodland. Outside this I only recorded it in Wooded Bushland, and almost all these were on the Yatta Plateau. Cichladusa guttata (only 3 in censuses) is rare in Woodland and was not seen outside this habitat. It is very secretive and keeps to the middle of the thickest bushes. Formerly it was fairly common, and also occurred along the Voi River. Cercotrichas leucophrys ($R/N = 0.08$, $N = 146$, N.S.) is the commonest of the resident species occurring fairly commonly in all thick habitats except Riverine and rarely in Wooded and Bushed Grassland and Bushed Grassland where there are thickets (Fig. 5.16). Finally, Oenanthe pileata is an uncommon visitor to open habitats mainly from March to June ($R/N = 0.88$, $N = 15$, $P < 0.01$, peak May 1).

O. pileata has three, and C. leucophrys one, congeneric potential competitors among the Palaearctic migrants. And both the other two resident species have similar sized potential competitors although not congeners: two for C. guttata and one for T. tephronotus. Monticola saxatilis is similar in size to T. tephronotus but has very different habitat preferences ($X^2 = 140$, $df\ 2$, $P < 0.001$, 75 per cent due to concentration of T. tephronotus in W), preferring the more open habitats ($X^2 = 24$, $df\ 1$, $P < 0.001$). It occurs throughout the winter arriving during November and staying until late March, but it is commonest, as are most Palaearctic migrants, in December and January ($2R^2/N = 220$, $N = 218$, $P < 0.001$, peak Jan 1).

The two potential competitors for C. guttata are Irania gutturalis and Luscinia luscinia. Both are commonest in Woodland though they do occur in other habitats.

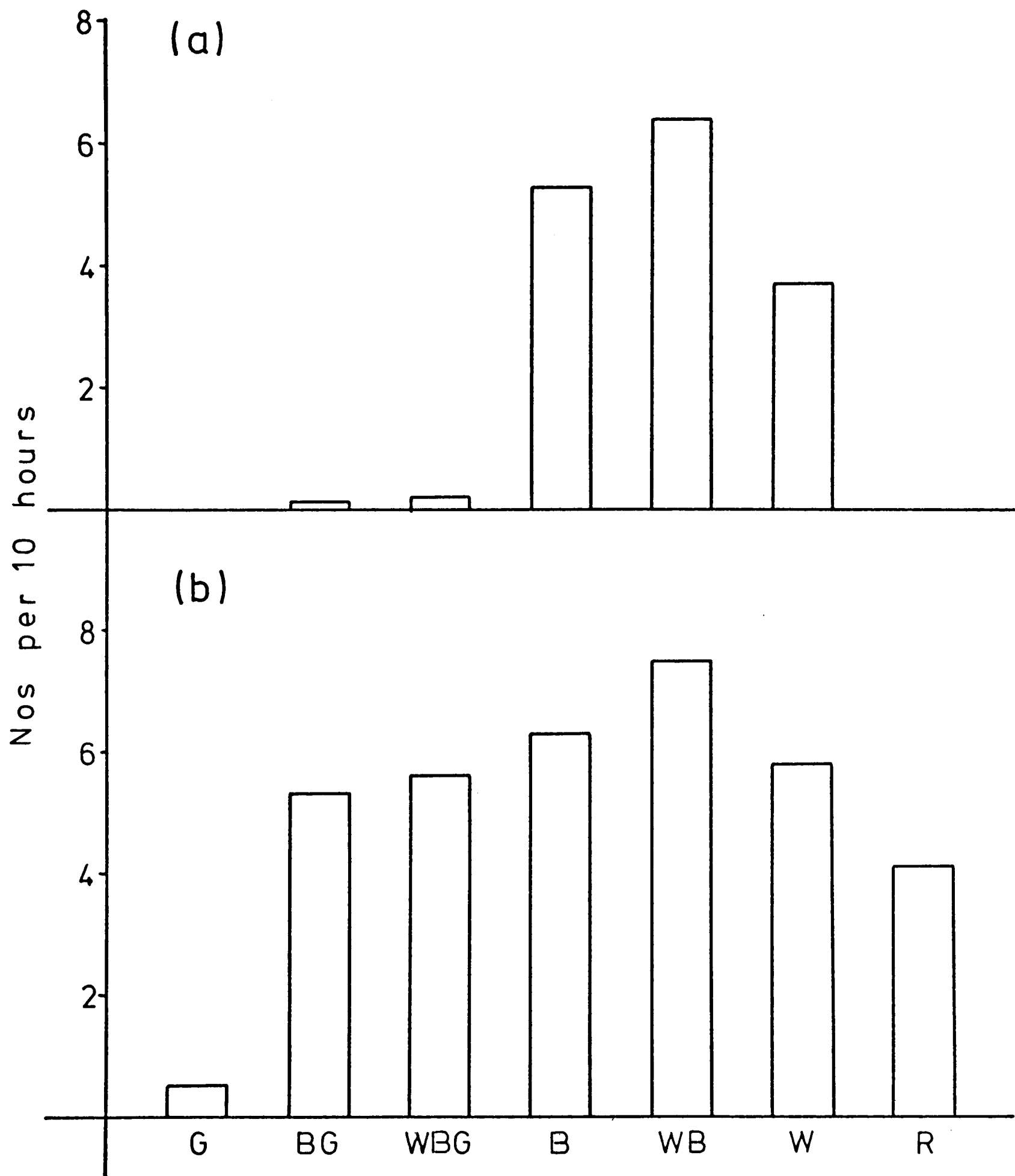


Fig. 5.16 The habitat preferences in Tsavo of two chats; a) Cercotrichas leucophrys, b) C. galactotes.

Both species occur from November to April with fewer seen (not statistically significant though) in January and February than the other months (I. gutturalis $R/N = 0.64$, $N = 39$, $P < 0.01$, peak Feb 1 (due to being equally common in December and March); L. luscinia $R/N = 0.67$, $N = 22$, $P < 0.01$, peak Dec 2).

Cercotrichas galactotes is the only Palaearctic species to meet a fairly common resident congener. Fig.5.16 shows that its habitat preferences overlap with those of C. leucophrys, but that it is more widespread (X^2 for the difference = 102, df 5, $P < 0.001$, 25 per cent due to G with BG, 25 per cent to WBG). It occurs all through the winter from November to March ($2R^2/N = 385$, $N = 381$, $P < 0.001$, peak Jan 2).

For the three Palaearctic Oenanthe spp., O. pileata can hardly be considered a competitor as it is so rare. It also occurs mainly after the Palaearctic ones have left for Europe (see above). Perhaps the latter prevent its arrival in Tsavo until later than it might otherwise, but unfortunately I can find no critical ecological data from areas where they coexist commonly.

The three Palaearctic species themselves are superficially very similar. All three, however, have different habitat preferences (Fig. 5.17). (For the differences O. pleschanka; O. isabellina $X^2 = 63$, df 4, $P < 0.001$, 30 per cent due to each of BG, WBG, and WB with W; O. pleschanka: O. oenanthe $X^2 = 10$, df 3, $P < 0.05$, 40 per cent due to each of G with BG and WB with W; O. isabellina: O. oenanthe $X^2 = 26$, df 4, $P < 0.001$, 50 per cent due to WBG). In the winter 1974-75 O. oenanthe and O. isabellina were not distinguished in the field, and the habitat preferences have been calculated only for birds seen after 1st July 1975. The number of hours used to calculate these are G - 23.5, BG - 86.75, WBG - 117.75, B - 46.0, WB - 57.0, W - 89.25, and R - 33.5 and not the totals shown in Table 5.1. The seasonal pattern of occurrence of the three species is shown in Fig. 5.18. All three show

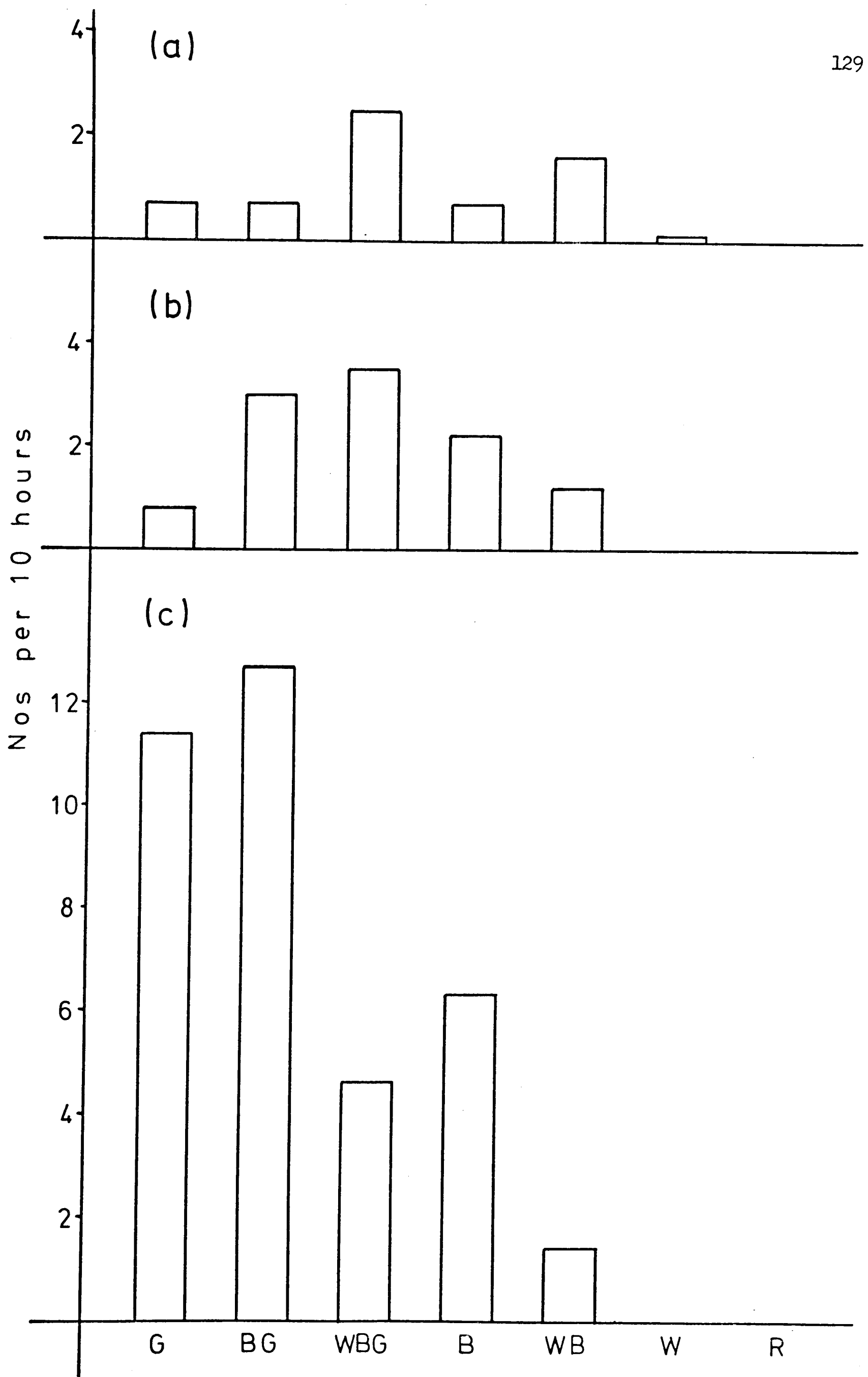


Fig. 5.17 The habitat preferences in Tsavo of three chats; a) *Oenanthe pleschanka*, b) *O. oenanthe*, c) *O. isabellina*. For *O. oenanthe* and *O. isabellina* only birds seen after 1st July 1975 are included - see text.

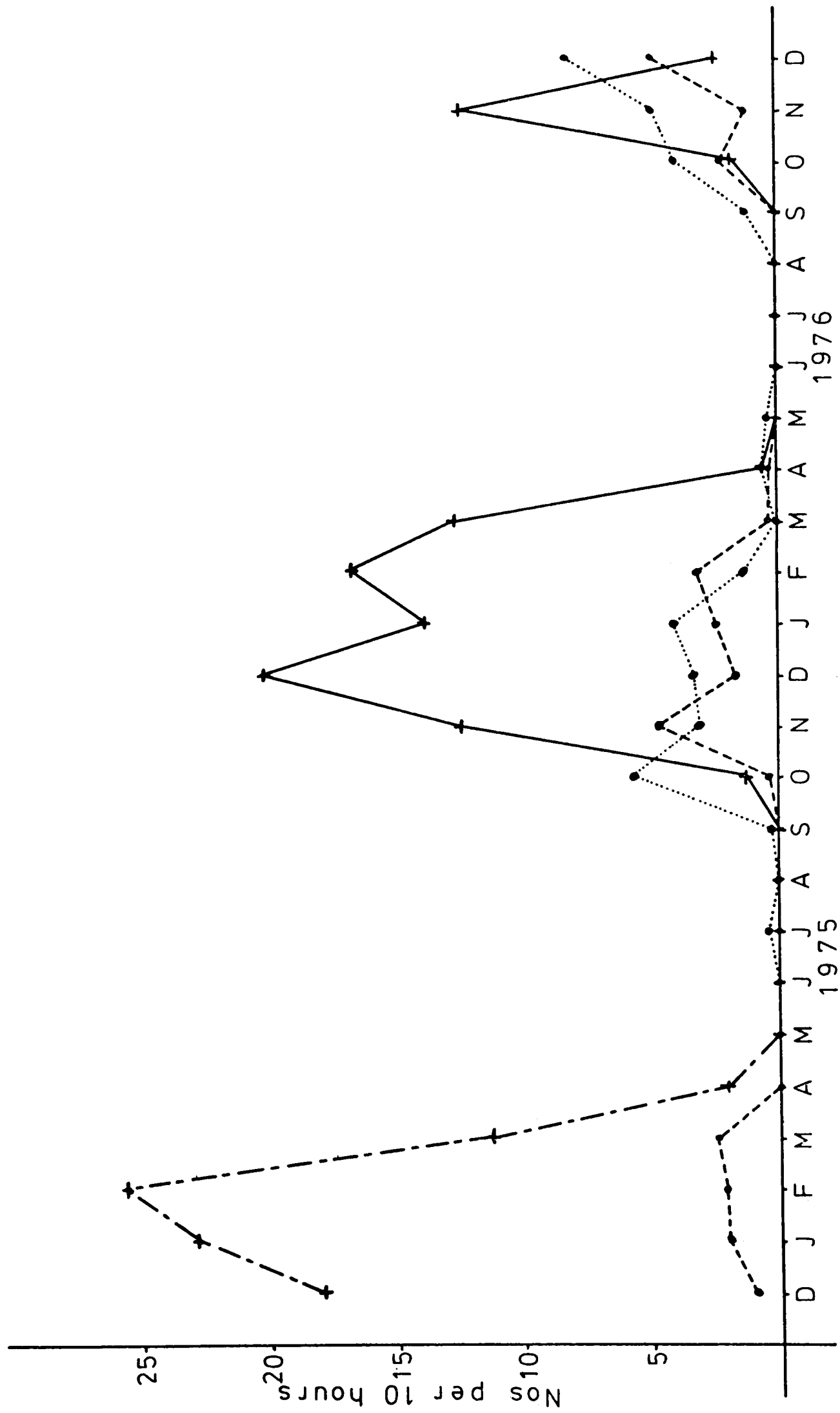


Fig. 5.18 The seasonal pattern of occurrence of three chats; +—+ Oenanthe isabellina, ••••• O. oenanthe, — — — — — O. pleschanka, +—+—+ O. isabellina and O. oenanthe combined (see text).

a typical Palaearctic migrant pattern having a peak of abundance in the early part of the winter with numbers remaining fairly constant from January to March and then dropping off sharply (O. pleschanka $R/N = 0.69$, $N = 75$, $P < 0.01$, peak Dec 4; O. isabellina $2R/2N = 230$, $N = 226$, $P < 0.001$, peak Jan 2; O. oenanthe $R/N = 0.68$, $N = 85$, $P < 0.01$, peak Nov 4). O. oenanthe indeed is one of the first Palaearctic migrants to arrive in Tsavo with a few seen in the last week of September.

All these species feed to a large extent, if not entirely, on the ground and most eat many termites. I have no data for T. tephronotus or C. guttata and very few for O. pileata (see below), I. gutturalis or L. luscinia. These last two both seem to stay inside and under the bushes. The two Cercotrichas species both feed almost entirely on the ground: C. leucophrys 98 per cent of 46 items, and C. galactotes 92 per cent of 165 items noted. Subjectively, the former stayed nearer the bushes than the latter, probably related to its habitat preferences.

M. saxatilis feeds mainly by pouncing to the ground from an elevated perch like the shrikes Lanius spp.. Unlike these, though, it usually eats several items while on the ground, perhaps running a few metres between each, before returning to its perch (96 per cent of 116 items were from the ground; 27 pounces to the ground were noted, on 13 of which the bird took several items before returning to a perch).

Data on the feeding behaviour of the three Palaearctic Oenanthe spp. are given in Table 5.9, and some differences stand out. O. pleschanka takes a third of its prey in the air unlike the others, which take the large majority from the ground. The major difference between the other two lies in the last line of the table and concerns the method of detecting prey. O. isabellina spends most of its feeding time actually on the ground running about, whereas O. oenanthe (and O. pleschanka) spend a considerable time sitting on elevated perches waiting for prey to become

Table 5.9 Feeding behaviour of three chats Oenanthe in Tsavo.

	<u>O. pleschanka</u>	<u>O. oenanthe</u>	<u>O. isabellina</u>
Number of items	100	201	268
% on herbage/ground	64	97	94
% in air	30	2	4
% in bushes	6	1	1
No. of items on ground/herbage	64	194	253
No. of movements to the ground from perch ^a	38 (59% of ground feeds)	72 (37%)	21 (8%)

1) No feeding records of O. oenanthe and O. isabellina before 1st July
1975 are included

a) see text

visible. How this affects any competition between the two species is unknown. The feeding method may be related to the size of prey item taken. Those waiting on perches should tend to move out only for larger items. The few data I have for O. pileata show it to be very similar (50 per cent of 10 items on the ground, 50 per cent in air, 2 movements to ground from a perch).

Data from the literature - T. tephronotus and C. guttata both fed mainly, if not entirely, on the ground, although the former takes a little fruit in addition.

My data on the feeding behaviour of Oenanthe spp. agree in many respects with those of Cornwallis (1975) working in south west Iran, especially the difference in behaviour between O. oenanthe and O. isabellina. The main difference between my data and those of Cornwallis is that, in Iran, all 37 items taken by O. pleschanka were from the ground and none from the air.

Summary of differences

	<u>C.gu.</u>	<u>T.t.</u>	<u>C.l.</u>	<u>C.ga.</u>	<u>O.o.</u>	<u>O.i.</u>	<u>O.pl.</u>	<u>O.pi.</u>	<u>M.s.</u>
<u>C. guttata</u>	-	-	-	-	-	-	-	-	-
<u>T. tephronotus</u>	S?	-	-	-	-	-	-	-	-
<u>C. leucophrys</u>	?	S	-	-	-	-	-	-	-
<u>C. galactotes</u>	H(F)	(H)-S	H-?	-	-	-	-	-	-
<u>O. oenanthe</u>	HF	H	H	?	-	-	-	-	-
<u>O. isabellina</u>	HG	H	H	(H)-?	F	-	-	-	-
<u>O. pleschanka</u>	HF	H	HF	F	HF	HF	-	-	-
<u>O. pileata</u>	HF	H	H	HO	O	O	HOF	-	-
<u>M. saxatilis</u>	HF	H-(F)	H(F)	S(F)	S	F(S)	FS	HFO	-
<u>I. gutturalis</u>	?	S	F	F	HF	F	F	HO	HF

5.3.33 Muscicapidae (Timaliinae) - Chatterers

Data from Tsavo - Neither of the two species recorded is common. Turdoides aylmeri is resident ($R/N \approx 0.06$, $N = 74$, N.S.) in Woodland especially the thicker parts, and also more rarely occurs in other thick habitats (5 per 10 hours in W cf 1 in B and WB). T. rubiginosus is a

little larger and occurs very rarely in thick bushes along rivers.

It was also occasionally seen in Woodland.

Both species occur in groups of about five individuals and were seen mostly in the middle of thick bushes.

Data from the literature - Both species are entirely insectivorous and feed on or close to the ground.

Summary of difference

	<u>T. a.</u>
<u>T. aylmeri</u>	-
<u>T. rubiginosus</u>	H

5.3.34 Muscicapidae (Sylviinae) - Warblers

Data from Tsavo - Of the 18 African and 13 Palaearctic forms recorded, eleven are very rare in Tsavo and/or have not occurred recently. These are:

- a) African species - Prinia subflava (2 records), P. somalica (1 record), Sylvietta isabellina (2 records, though 1 is of a nest with eggs), Parisoma boehmi (1 record); the latter two of these were more widespread formerly, and Acrocephalus gracilirostris, Sphenoeacus mentalis and Phyllolais pulchella also occurred formerly.
- b) Palaearctic species - Locustella fluviatilis (2 records), Acrocephalus scirpaceus (1 probable record), A. arundinaceus arundinaceus (3 birds caught and ringed) and Hippolais olivetorum (5 records).

Only four species of African warbler can be considered common in Tsavo. Camaroptera simplex is resident ($R/N = 0.12$, $N = 106$, N.S.), occurs mainly in Bushland, Wooded Bushland and Woodland, with only very few (10 per cent of 106 birds) seen in other habitats; Sylvietta brachyura, also resident ($R/N = 0.09$, $N = 122$, N.S.) occurs most commonly in Woodland (5 per 10 hours) and Wooded Bushland (3 per 10 hours) though it does occur in the other habitats (1 per 10 hours) except Grassland and Riverine.

Cisticola cinereola has a seasonal pattern of occurrence but is present all the year ($R/N = 0.27$, $N = 105$, $P < 0.01$, peak Mar 3). It occurs mainly in open habitats (99 of 105 seen in censuses). Cisticola nana has a similar seasonal pattern of occurrence ($R/N = 0.32$, $N = 83$, $P < 0.01$, peak Mar 3) and occurs in the more open parts of Woodland, and a few isolated areas of the Park savanna habitats where there are large trees with open areas underneath.

The feeding sites of the four are rather different to each other.

C. simplex is another species which feeds on or near the ground in thick bushes (for more^{see} details below), but it is considerably smaller than most others in this niche, particularly shrikes Laniidae (ch 5.3.31).

S. brachyura is like a nuthatch (Sittidae) both ecologically and morphologically. It walks and runs along branches and twigs taking insects from the bark (78 per cent of 80 items). C. nana feeds almost entirely on the ground where there is some grass with bare patches in between (62 per cent of 21 items from grass, 24 per cent from bare ground). C. cinereola was usually seen in thick grass but I have no specific feeding data to show it feeds there.

The other African warbler species are all uncommon or rare. The little I know of their ecology in Tsavo is summarised in Table 5.10.

Three of the nine Palaearctic forms are very uncommon though a few individuals are seen every year: Acrocephalus schoenobaenus occurs mainly in spring, to reedy margins or bushes near water; A. arundinaceus griseldis was seen in both spring (April) and autumn (December) especially in the Voi River vegetation and thickets; and Sylvia borin occurs in any thick bushes especially in December and January.

The habitat preferences and seasonal pattern of occurrence of the remaining six species are shown in Figs. 5.19, 5.20, 5.21, and 5.22. In the 1974-75 winter I had great difficulty distinguishing the two Hippolais species from each other, and some individuals in the 1975-76 winter were

Table 5.10. Ecology of some less common African warblers Muscicapidae (Sylviinae)

Species	Status	Preferred habitat	Feeding station	Other notes
<u>Cisticola chiniana</u>	?	WBG	?	Rare: records from near Voi, Irima and Mbololo River
<u>C. galactotes</u>	?	grass in damp areas	grass and reeds	
<u>C. aridula</u>	?	G	grass	much more obvious in the wet season when calling but may be resident
<u>Apalis flavida</u>	?	W (and WB in northern area)	trees and bushes	only seen May to October; formerly fairly common; see text
<u>Spiloptila rufifrons</u>	probably resident	B	bushes	formerly fairly common
<u>Camaroptera brevicaudata</u>	?	W and R	undergrowth	very rare
<u>Eremomela flavicrissalis</u>	probably resident	W (more open parts)	trees and bushes	

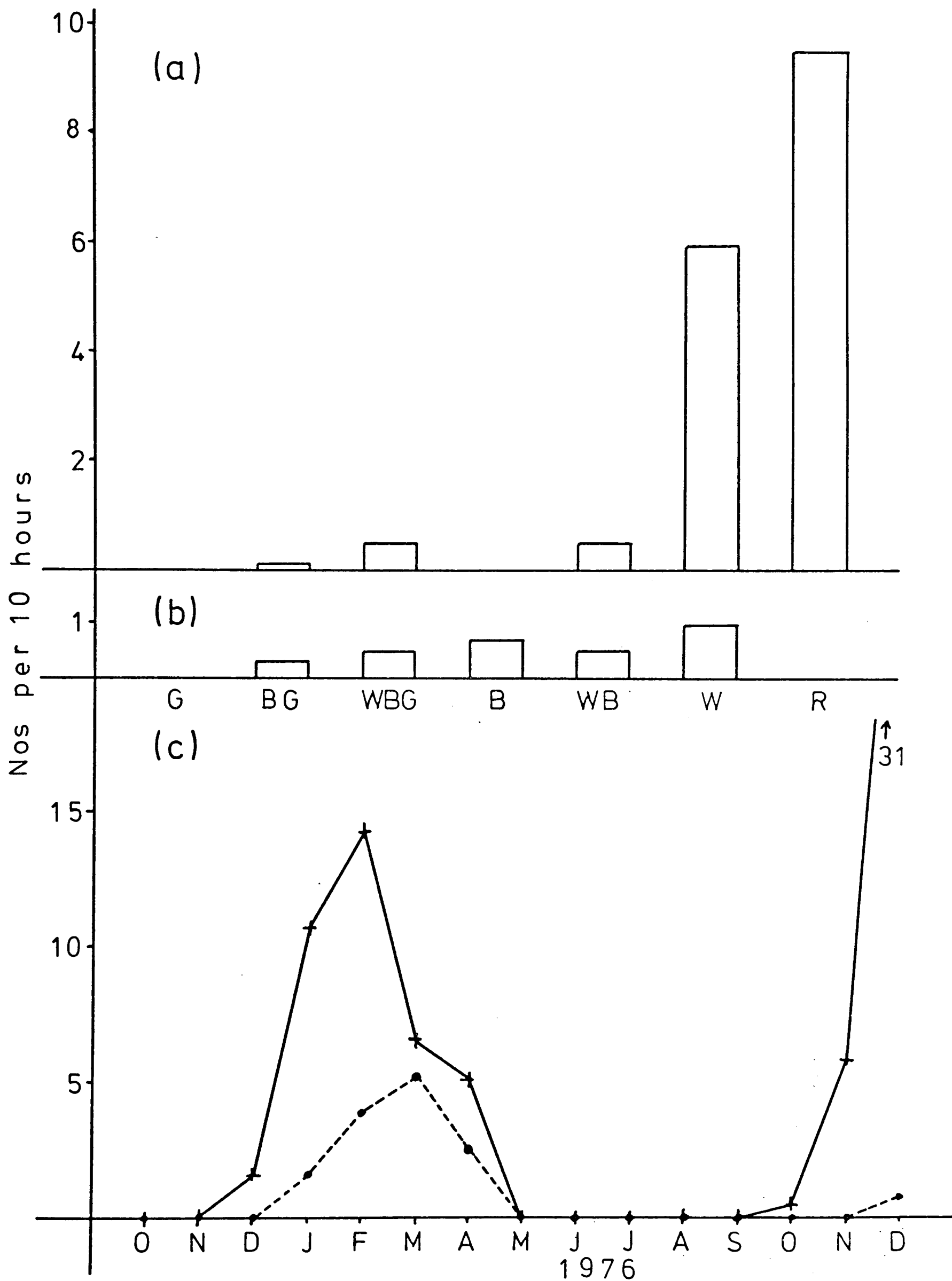


Fig. 5.19 The habitat preferences (a and b) and seasonal pattern of occurrence (c) of two warblers in Tsavo; a) habitat preferences of *Hippolais pallida*, b) habitat preferences of *H. languida*, c) seasonal pattern of occurrence of +—+ *H. pallida*, •--• *H. languida*.

also not distinguished. In all, only just under half the Hippolais spp. seen were positively identified and it is only these which are shown in Fig. 5.19. This figure shows that there is a difference in habitat preferences ($X^2 = 58$, df 3, $P < 0.001$, 40 per cent due to BG with WBG) - H. languida is more widespread though in smaller total numbers - and a slight seasonal difference - H. languida ($R/N = 0.86$, $N = 36$, $P < 0.01$ peak Mar 2) arrives and reaches peak numbers about a month after H. pallida ($R/N = 0.74$, $N = 146$, $P < 0.01$, peak Feb 1) although they both leave at the same time (median test on 1975-76 winter $X^2 = 6.0$ df 1, $P < 0.05$). Both these species are unusual among Palaearctic migrants (and other visitors) in being at peak abundance in the dry season (February and March).

The two Sylvia species also show different habitat preferences, with S. communis being commonest in habitats with trees ($X^2 = 42$, df 1, $P < 0.001$) although it is rare in Riverine, and S. nisoria being about equally common in all except Bushed Grassland and Grassland, including Riverine (Fig. 5.20.) (X^2 for the difference between the species = 24, df 5, $P < 0.001$, 90 per cent due to R). Seasonally they are different too (Fig. 5.22), with S. nisoria ($R/N = 0.66$, $N = 96$, $P < 0.01$, peak Jan 1) showing a peak a little after S. communis ($2R^2/N = 324$, $N = 309$, $P < 0.001$, peak Dec 4) (median test for the difference $X^2 = 13$, df 1, $P < 0.001$). S. communis also appears to show a peak in spring but this is not quite significant (mean of March : April figures $d = 3.2$, df 2, $P < 0.10$).

Acrocephalus palustris and Phylloscopus trochilus are both commonest in habitats with trees (A. palustris $X^2 = 46$, df 1, $P < 0.001$; P. trochilus $X^2 = 41$, df 1, $P < 0.001$) but P. trochilus is much rarer in Riverine (Fig 5.20) (for the difference $X^2 = 31$, df 5, $P < 0.001$, 65 per cent to R). A. palustris shows a seasonal pattern of occurrence typical of the Palaearctic migrants ($R/N = 0.84$, $N = 109$, $P < 0.01$, peak Dec 2), but P. trochilus has its main peak in spring (Fig. 5.21) ($R/N = 0.58$, $N = 134$, $P < 0.01$, peak Mar 2). There is a suggestion of two peaks but the figures in December are not significantly

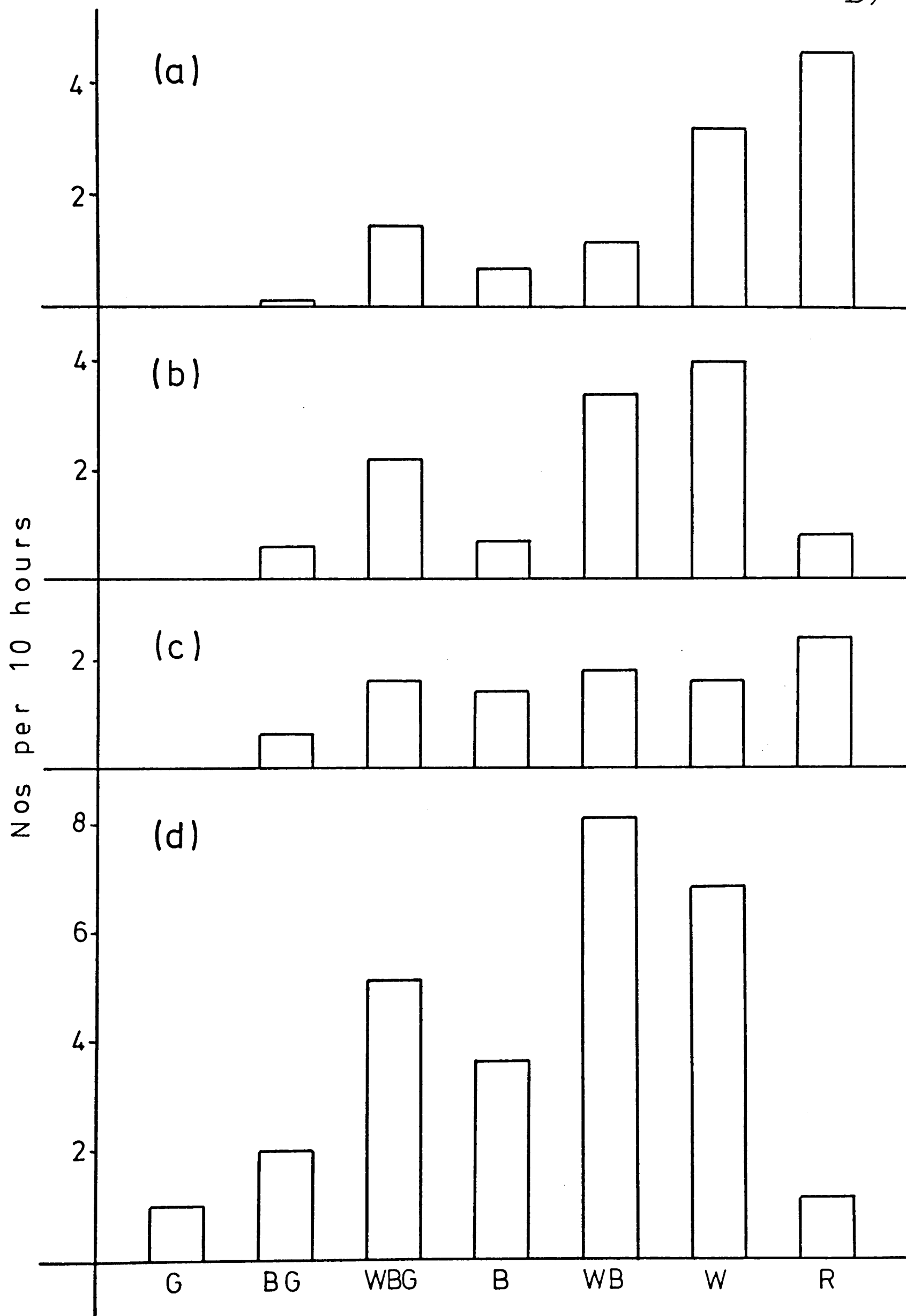


Fig. 5.20 The habitat preferences in Tsavo of four warblers; a) *Acrocephalus palustris*, b) *Phylloscopus trochilus*, c) *Sylvia nisoria*, d) *Sylvia communis*.

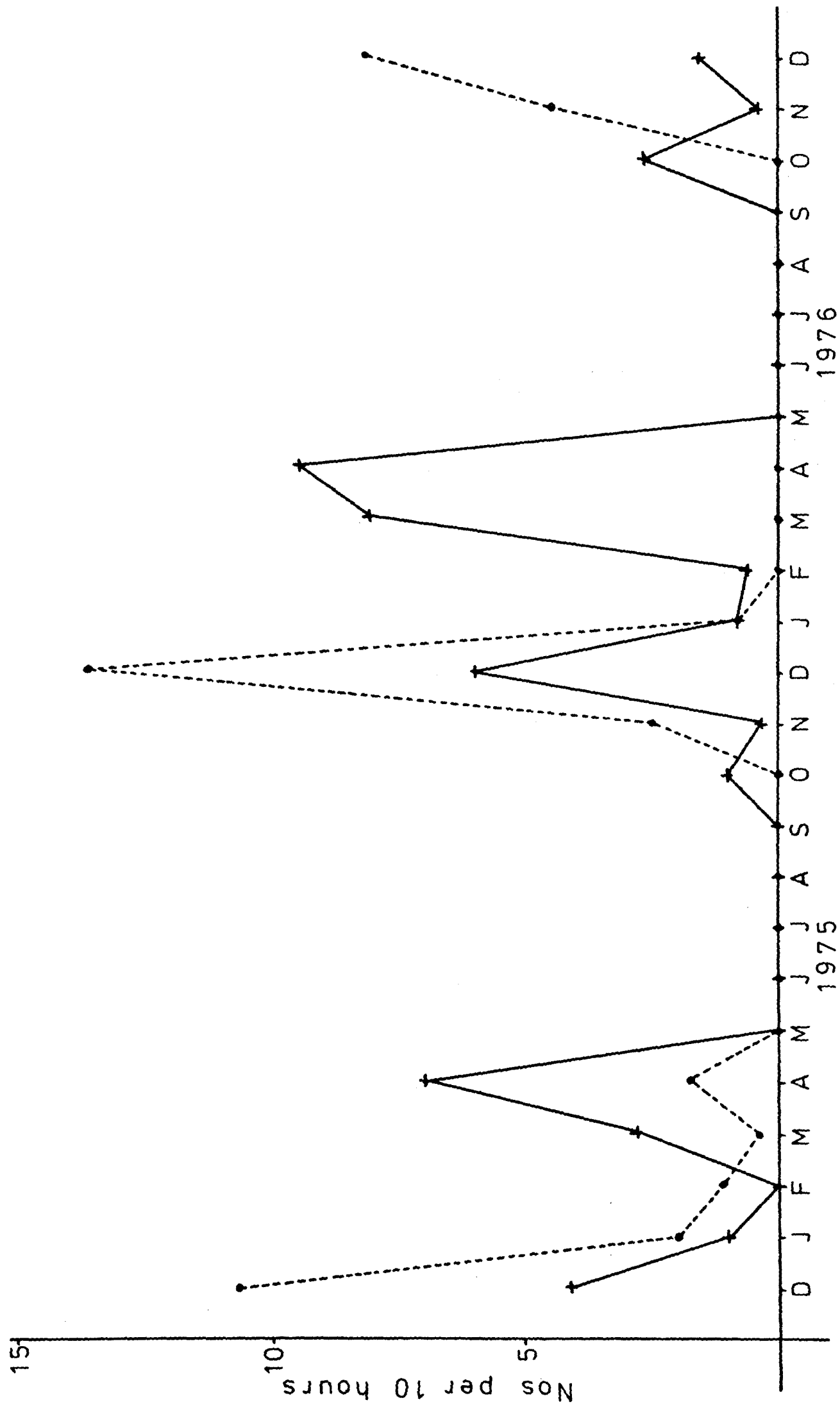


Fig. 5.21 The seasonal pattern of occurrence of two warblers; +---+ *Phylloscopus trochilus*,
 •---• *Acrocephalus palustris*.

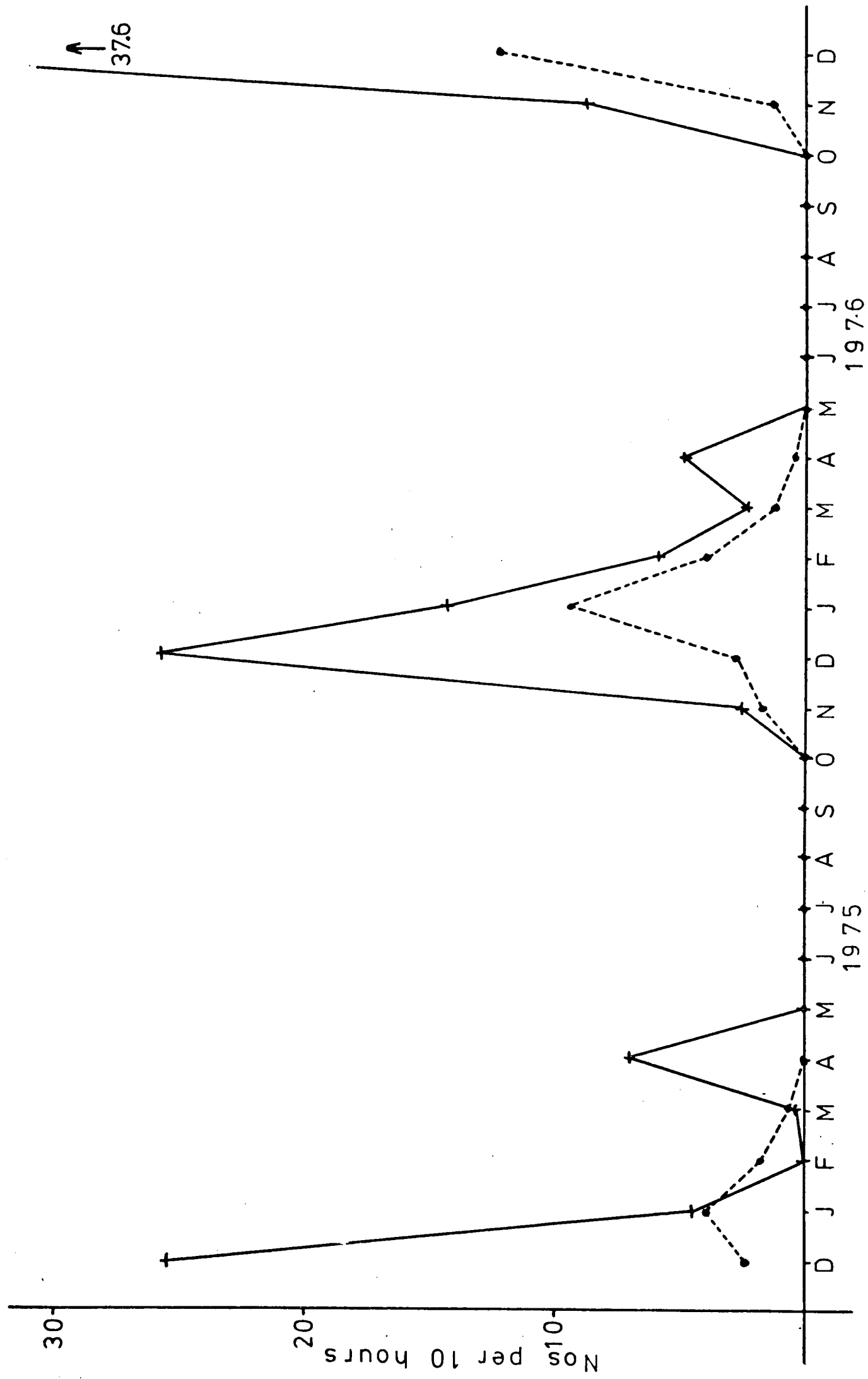


Fig. 5.22 The seasonal pattern of occurrence in Tsavo of two warblers; +— *Sylvia communis*,
 •—• *S. nisoria*.

higher than those for November ($d = 2.8$, $df\ 2$, N.S.) or January-February ($d = 2.6$, $df\ 2$, N.S.).

Data on the feeding behaviour of the six species are given in Table 5.11. It shows that all feed predominantly from leaves, though H. languida takes much of its food from twigs, and P. trochilus some from the air. The former is partly explained as when H. languida is commonest, in March, there are very few leaves on the bushes. Among the six species, three feed in the trees, and one in the bushes and two feed in both. Interestingly the bush feeder, S. communis, has a habitat preference for areas with trees (Fig. 5.20). Of the tree-feeders, P. trochilus stands out as occurring at the edge of the vegetation and not inside the tree canopy.

With six common Palaearctic species it is of particular interest to ask whether any of them potentially come into competition with resident African species. There are of course only four fairly common resident species which may itself be indicative of such. Furthermore three of the four are obviously different: S. brachyura and C. nana by their feeding site (bark and ground respectively), and C. cinereola by its habitat preferences (many more in Grassland and Bushed Grassland), and its presumed preference for feeding in grass. C. simplex is more closely similar but its only potential competitor in feeding station is S. communis. Forty-eight per cent of 56 items taken by C. simplex were from twigs, and a further 46 per cent were from the herbage layer and/or the ground, and only 3 per cent off leaves (cf. Table 5.11 for S. communis). C. simplex also feeds lower down ($\text{mean} \pm \text{S.E.} = 0.6 \pm 0.2\text{ m}$ ($n = 19$)) and this is significantly different ($d = 3.5$ $df\ 62$, $P < 0.001$). The next commonest African species is probably Apalis flava and here there is some evidence for competitive exclusion. Its feeding behaviour is very similar to an "average" Palaearctic warbler. Of 70 items recorded 81 per cent were from leaves, 14 per cent off twigs and 5 per cent from the ground (all following individual items down from a bush); 7 per cent were taken with the bird in flight;

Table 5.11 Feeding behaviour of six Palaearctic warblers Muscicapidae (Sylviinae) in Tsavo.

	<u>Hippolais</u> <u>pallida</u>	<u>Hippolais</u> <u>languida</u>	<u>Sylvia</u> <u>communis</u>	<u>Sylvia</u> <u>nisoris</u>	<u>Acrocephalus</u> <u>palustris</u>	<u>Phylloscopus</u> <u>trochilus</u>
No. of items	153	73	148 ^d	72 ^d	180	316
% from leaves	86	60	85	96	91	81
% from air	1	3	1	-	4	9
% from ground	-	-	-	-	3 (herbage)	-
% from twigs/stem	9	37	13	4	1	3
% with bird in flight	21	11	1	0	17	26
% inside tree/bush	57 (n=42)	54 (n=24)	80 (n=40)	85 (n=20)	50 (n=38)	38 (n=69)
% just inside edge	38	29	10	10	41	36
% at edge	5	17	10	5	9	26
Height of feeding (m) ^a	5.7 $\pm$ 0.5 ^b (44)	3.2 $\pm$ 0.5 ^b (27)	1.7 $\pm$ 0.3 ^c (44)	3.8 $\pm$ 0.8 ^c (21)	5.0 $\pm$ 0.7 (43)	5.2 $\pm$ 0.3 (81)

Notes:

- a) Heights are quoted as mean $\pm$ standard error with the sample size in brackets
b) The difference in feeding height between H. pallida and H. languida is highly significant; $d = 3.7$, df 66, $P < 0.001$
c) The difference in feeding height between S. communis and S. nisoris is highly significant; $d = 2.6$, df 56, $P < 0.02$
d) In addition 7 birds of each species seen eating fruit.

7 (of 10 birds for which it was recorded) were inside the vegetation, 2 just inside and 1 at the edge; and mean height of feeding ($\pm$ S.E.), excluding those insects chased to the ground, = 2.4 ± 0.4 m ($n = 13$). Hence from Table 5.11 it seems closest in behaviour to the two Sylvia species and between the two in mean height of feeding. However, the interesting point is that all my records of the species (ten separate occasions) fall between May and October - 2 in May, 1 in June, 2 in July, 2 in August, 1 in September and 1 in October ($R/N = 0.69$, $N = 9$ (others not in censuses), $P < 0.01$, peak July 4).

Data from the literature and discussion - That A. palustris should prefer habitats with trees, and feed in them, is interesting. In Europe it breeds in willow thickets etc near water (Voous 1960), and occurs in undergrowth of thickets and/or reeds and rank grass in other parts of Africa (e.g. Benson et al. 1973). Reeds and rank grass are rare in Tsavo, but thickets are present. There are, however, many other species of warbler and bush-shrike, Malaconotinae, which occur in thickets, but few in trees.

Summary of differences

a) African species

	<u>S.b.</u>	<u>C.s.</u>	<u>A.f.</u>	<u>S.r.</u>	<u>C.n.</u>	<u>C.c.</u>
<u>S. brachyura</u>	-	-	-	-	-	-
<u>C. simplex</u>	F	-	-	-	-	-
<u>A. flavida</u>	F	F	-	-	-	-
<u>S. rufifrons</u>	F	F	H	-	-	-
<u>C. nana</u>	F	F	F	FH	-	-
<u>C. cinereola</u>	F	H	H	H	HF	-
<u>C. aridula</u>	F	H	H	H	H	H

b) Palaearctic species

	<u>H.p.</u>	<u>H.l.</u>	<u>S.c.</u>	<u>S.n.</u>	<u>A.p.</u>
<u>H. pallida</u>	-	-	-	-	-
<u>H. languida</u>	F(O)	-	-	-	-
<u>S. communis</u>	F	O(F)	-	-	-
<u>S. nisoria</u>	HF	F(O)	F?	-	-
<u>A. palustris</u>	?	HO	F	F?	-
<u>P. trochilus</u>	HF	FO	F	F	H

The Palaearctic species are separate from

C. simplex by F (though less certainly from S. communis)

S. brachyura by F

C. cinereola by H

C. nana by F and

A. flavida by O

5.3.35 Muscicapidae (Muscicapinae, Platysteirinae, Monarchinae) - Flycatchers

Data from Tsavo - Ten species have been recorded but there are only two records of Myioparus plumbeus (though it was formerly fairly common) and Muscicapa caerulescens, and only three of Melaenornis pammelaina. The status of Bradornis pallidus is uncertain. It was certainly recorded formerly, and two people have positively identified it within the last five years. But I thought that all Bradornis that I saw were B. microrhynchus.

Of the Muscicapinae, B. microrhynchus is an uncommon resident ($R/N = 0.18$, $N = 95$, $0.01 < P < 0.05$), preferring thicker habitats ($X^2 = 7.1$, $df\ 1$, $P < 0.01$) especially Woodland, but it was not seen in Riverine. Muscicapa striata is a Palaearctic migrant occurring commonly in all habitats with trees (489 of 500 seen in censuses) and is particularly common in Riverine. It is common from November till the end of March, and most leave in the first half of April ($2R^2/N = 410$, $N = 500$, $P < 0.001$, peak Jan 2). The feeding behaviour of this and B. microrhynchus is rather different (Table 5.12). B. microrhynchus feeds mainly by pouncing to the ground and M. striata mainly takes insects in the air clear of, but often fairly close to, the vegetation.

The three Platysteirinae are all in the genus Batis, and all are probably resident although slight seasonal patterns are evident in two species. B. minor ($R/N = 0.30$, $N = 39$, $0.01 < P < 0.05$) is almost restricted to Riverine (37 of 39 seen in censuses) where it is fairly common. It was also seen occasionally in Woodland and along smaller watercourses.

B. molitor ($R/N = 0.19$, $N = 32$, N.S.) is regular in Woodland but very rare outside this. B. perkeo ($R/N = 0.40$, $N = 30$, $0.01 < P < 0.05$) occurs rarely in all habitats with trees, except Riverine. A very few were seen in Bushland. Hence the only potential competition is between B. molitor and B. perkeo in Woodland. The usual feeding behaviour of all three species is to make short flights within a tree taking insects mainly from the vegetation. Some data on the feeding behaviour are given in Table 5.13. All are similar.

The one species in the Monarchinae, Terpsiphone viridis, is an uncommon visitor to Woodland and Riverine from November to May ($R/N = 0.67$, $N = 20$, $P < 0.01$, peak Jan 2) though there are fewer present in the dry season. It is also regular in gardens and occasional in other habitats. Males of both the white and chestnut-tailed forms occur. It feeds in a similar fashion to both M. striata and the Batis species (50 per cent of 16 items from the air, 37 per cent from the vegetation, 13 per cent from the ground). It is a much larger bird than the latter despite being only 50 per cent heavier, and subjectively it remains in the cover of the vegetation much more than the former.

Summary of differences

	<u>M.s.</u>	<u>Br.m.</u>	<u>Ba.mi.</u>	<u>Ba.mo.</u>	<u>B.p.</u>
<u>M. striata</u>	-	-	-	-	-
<u>B. microrhynchus</u>	F	-	-	-	-
<u>B. minor</u>	F	FH	-	-	-
<u>B. molitor</u>	F	F	H	-	-
<u>B. perkeo</u>	F	F	H	H-?	-
<u>T. viridis</u>	F?	F	FS	FS	FS

Table 5.12 Feeding behaviour of two flycatchers Muscicapidae
(Muscicapinae) in Tsavo

	<u>M. striata</u>	<u>B. microrhynchus</u>
No. of items	373	73
% in air	74	15
% off twigs	4	7
% off leaves	9	7
% off ground	11	71
% taken with bird in flight	89	25
% pounce	6	69

Table 5.13 Feeding behaviour of three flycatchers Batis in Tsavo

	<u>B. minor</u>	<u>B. molitor</u>	<u>B. perkeo</u>
No. of items	45	49	49
% in air	24	14	14
% off leaves	53	69 ^a	55
% off twig/stem	18	14	31
% taken with bird in flight	91	100	100
% inside the vegetation	29 (of 17 birds)	81 (of 16 birds)	50 (of 14 birds)
% just inside	53	13	21
% at the edge	18	6	29
Height of feeding (m) ^b	9.8 $\pm$ 0.9 (n = 20)	4.8 $\pm$ 0.5 (n = 20)	3.4 $\pm$ 0.6 (n = 15)

Notes:

a) 62% of these were recorded as from the underside, 3% from the upper and 35% were not specified.

b) Height is quoted as mean $\pm$ standard error with sample size in brackets.

5.3.36 Paridae - Tits

Data from Tsavo - All three species recorded are rare. Parus afer occurs in the thicker habitats, especially in Woodland and in the northern area. Parus albiventris has only certainly been recorded around Voi, where it was seen fairly often between 1969 and 1972, but I only saw it three times. Finally Anthoscopus musculus, like P. afer, occurs rarely in thick habitats especially in the northern area.

I have no data on their feeding habits.

Data from the literature - Both Parus species are similar to tits in other parts of the world feeding mainly on insects while climbing about in trees. A. musculus too is similar but more warbler-like.

5.3.37 Nectariniidae - Sunbirds

Data from Tsavo - Eleven species are recorded but six are very rare. Formerly the situation was much more complicated because Nectarinia olivacea, N. venusta, N. marquensis, N. pulchella and N. nectarinioides all occurred, in varying numbers, mostly in Woodland and/or the Voi River forest. Of these, there is one recent record of N. venusta, there are one or two N. nectarinioides seen each year, and no recent records of the others. There is also on probable record of N. kilimensis.

Of the remainder, two are Anthreptes and three Nectarinia. A. collaris occurs rarely in riverine forest and in gardens around Park HQ. A. orientalis, a resident ($R/N = 0.32$, $N = 40$, $0.01 < P < 0.05$), by contrast is commonest in Woodland, but it also occurs in other thick habitats (χ^2 for the difference = 57, df 2, $P < 0.001$, 70 per cent due to W). The latter does not occur in the Voi River forest, but I did see it in the large Acacia elatior trees along the Tiva River where I did not see A. collaris. Nectarinia amethystina occurs rarely in Riverine and occasionally in gardens and Woodland. N. bifasciata is a fairly common resident ($R/N = 0.02$, $N = 146$, N.S.) in Woodland and occurs rarely in other thick habitats, especially

in the northern area. N. hunteri is the most widespread species. It is commonest in Woodland but occurs regularly in all other habitats except Grassland. Some are present all the year but more were seen in the dry season ($2R^2/N=40$, $N=421$, $P<0.001$, peak Jul 2).

All five species feed on both nectar and insects but in different proportions. These figures should be treated with some caution, as I think nectar-feeding is more conspicuous than insect-feeding. However, this should not affect the relative amount between species. These and other feeding data are shown in Table 5.14.

The table shows that, apart from the nectar, the two Anthreptes and N. amethystina are very like warblers except for taking more food in flight. Delonix elata flowers are shown to be predominant among the nectar taken by the two long-billed Nectarinia species, whereas N. bifasciata, on the whole, takes from other, usually smaller flowers. This last species too is much more of a flycatcher than the other species.

Summary of differences

	<u>A.o.</u>	<u>A.c.</u>	<u>N.b.</u>	<u>N.h.</u>
<u>A. orientalis</u>	-	-	-	-
<u>A. collaris</u>	HT	-	-	-
<u>N. bifasciata</u>	F(T)	HT	-	-
<u>N. amethystina</u>	H-S	T(S)	H-FS	-
<u>N. hunteri</u>	F-S	TF	F(S)	(H)-?

5.3.38 Zosteropidae - White-eyes

Data from Tsavo - The one species recorded, Zosterops abyssinica, occurs rarely in any area with large trees. It is usually seen in small groups and I saw it in trees behaving like a warbler.

Data from the literature - It is mainly insectivorous but eats some fruit and nectar.

Table 5.14 Feeding behaviour of five sunbirds Nectariniidae in Tsavo.

Bill		<u>Anthreptes</u> <u>orientalis</u>	<u>Anthreptes</u> <u>collaris</u>	<u>Nectarinia</u> <u>bifasciata</u>	<u>Nectarinia</u> <u>amethystina</u>	<u>Nectarinia</u> <u>hunteri</u>
		short straight short straight short curved			long curved	
Number of items		94	38	178	81	422 ^a
<u>Nectar</u>	Percentage of total	54	13	82	63	77
% of nectar from <u>Delonix elata</u>		-	-	10	41	35
% of nectar from other tree species		51	100	52	20	37
% of nectar from bushes		49	-	38	39	28
<u>Insect</u>	Percentage of total	46	87	18	37	21
% of insect off leaf		88	67	31	67	43
off twigs		-	15	-	33	36
in air		12	15	69	-	21
taken with bird in flight		14	52	69	33	34

Notes:
a) includes 10 feeds on Commiphora fruit

5.3.39 Emberizidae - Buntings

Data from Tsavo - Two species are recorded. Emberiza tahapisi occurs rarely usually near water. E. poliopleura is a common resident ($2R^2/N = 5$, $N = 353$, N.S.) in Bushland and Wooded Bushland with a few in other habitats where there are thick bushes, but not Riverine. It feeds while walking about on the ground very like a lark (130 items recorded but not identified).

Data from the literature - E. poliopleura eats both seeds and insects.

5.3.40 Fringillidae - Finches

Data from Tsavo - Four, possibly five, species are recorded but all are rare. The only one which has recently been seen more than three times is Serinus atrogularis which is a rare visitor in small flocks mostly to near water. The others recorded are: S. mozambicus (one probable record but occurred formerly around houses in the Park), S. dorsostriatus (three recent records but was formerly fairly common in Woodland), S. donaldsoni (two records) and S. sulphuratus (two records of small flocks that were probably this species in August 1970 and 1975).

5.3.41 Estrildidae - Waxbills

Data from Tsavo - Fifteen species are recorded but seven are very rare: Hypargos niveoguttatus (1 record), Pytilia afra (was formerly seen in Voi), Estrilda astrild (1 recent record and occurred formerly), E. erythronotos (3 recent records but formerly common), Uraeginthus cyanocephalus (rare visitor at any season), Lagonosticta sp. or spp. (rare visitor in the wet season), and Ortygospiza atricollis (1 record). Another three species are uncommon: Uraeginthus ianthinogaster occurs in Woodland, and other thick habitats in the northern area; Lonchura malabarica occurs occasionally near water and L. cucullata occurs mainly around houses.

This leaves five species but none, even of these, is very common. Pytilia melba occurs in all areas with thick bushes but is rarely seen due to its skulking habits. It is present all the year but more were seen in the dry season ($R/N = 0.29$, $N = 85$, $P < 0.01$, peak Jul 2). Uraeginthus bengalus, a resident ($R/N = 0.23$, $N = 59$, N.S.) is restricted to Riverine and gardens, but is there fairly common. Estrilda rhodopyga occurs rarely from December to March. It is almost always found near rivers or other damp places. Lonchura griseicapilla is an uncommon visitor to any area with records in January, March and April. Finally, Amadina fasciata is a visitor in very variable numbers mainly to open habitats (87 per cent of 702 seen in censuses) and mainly December to June, especially January to March ($2R^2/N = 858$, $N = 702$, $P < 0.001$, peak Feb 3).

I have very few data on their feeding, so the following are mainly subjective impressions. E. rhodopyga and L. griseicapilla mainly take seeds directly from the grass stem (and both occur in Tsavo only when this is most available). The other three seem to take seeds from the ground although P. melba at least takes some termites as well (the contents of the stomach analysed by Lack & Quicke (1978) contained 93 termites and 26 seeds). Further P. melba usually stays close to or under bushes while U. bengalus and A. fasciata are mainly further out in the open.

Data from the literature - All these species feed largely if not entirely on seeds.

Summary of differences

	<u>P.m.</u>	<u>U.b.</u>	<u>E.r.</u>	<u>L.g.</u>
<u>P. melba</u>	-	-	-	-
<u>U. bengalus</u>	H-F	-	-	-
<u>E. rhodopyga</u>	F(0)	F(0)	-	-
<u>L. griseicapilla</u>	F(0)	F(0)	?	-
<u>A. fasciata</u>	H	H	(H)	?

5.3.42 Ploceidae - Weavers, sparrows, etc.

Twenty six species in five subfamilies have been recorded and the species will be considered in these groups.

a) Viduinae

Data from Tsavo - Of the five Viduinae recorded there is only one record of Vidua hypocherina, and V. fischeri is an irregular rare visitor to any area with trees. Hypochera sp. (the taxonomy of this species group is very complicated and without collecting it is almost impossible to determine which species is involved) occurs rarely in Riverine in the wet seasons. V. macroura is also rare although regular occurring mainly during and soon after the wet seasons. It is almost restricted to Riverine. I have no records of it breeding and its main host in other places, Estrilda astrild is very rare in Tsavo. However males that were seen, were often displaying. V. paradisaea is the commonest of these species though it too is only a visitor, occurring soon after the rains especially January and February ($2R^2/N = 490$, $N = 312$, $P < 0.001$, peak Jan 4). It comes, usually in flocks, mostly to Riverine and to parts of Wooded and Bushed Grassland where there are large trees. Occasional individuals of unidentified Vidua sp. (they are not in breeding plumage then) occur at any time of year.

All seen feeding were on the ground.

Data from the literature - All species feed almost entirely on seeds on the ground.

b) Ploceinae

Data from Tsavo - Of the fourteen species five are very rare or have not been recorded recently: Amblyospiza albifrons formerly occurred in Voi Swamp, Ploceus velatus is a rare visitor to Woodland in the wet seasons, P. ocularis formerly occurred in the Voi River forest, Euplectes

hordeaceus appeared in some numbers on the Galana Ranch after the 1961 floods but has not been recorded since, and Anomalospiza imberbis has been seen once in Voi.

Of the others, two are resident. Ploceus nigricollis (R/N = 0.31, N = 39, N.S.) is fairly common in Woodland, and was only seen in other habitats in the northern area. Malimbus rubriceps (R/N = 0.33, N = 19, N.S.) is uncommon in Woodland and Riverine, but is fairly common around Park HQ where it often nests close to or even in buildings. The remaining seven species are visitors in the wet seasons. Many of them come in to breed, although not necessarily doing so every year. All occur between December and February, but it is only the commoner ones that re-appear, in smaller numbers, in April and May. Ploceus subaureus (not seen in censuses) was only seen around its nest-sites, particularly in reeds along the Galana River near Sala Gate; and there is sometimes a colony in Voi. P. intermedius (R/N = 0.57, N = 46, $P < 0.01$, peak Jan 1) occurs fairly commonly in Woodland and less so in other thick habitats. P. cucullatus nigriceps (R/N = 0.45, N = 32, $P < 0.01$, peak Mar 2—due to occurrence in both wet seasons), is almost restricted to the Voi area, with a very active colony at Voi Safari Lodge, where some individuals remain throughout the year. P. rubiginosus (R/N = 0.67, N = 183, $P < 0.01$, peak Dec 4) occurs especially in Woodland but may be found rarely in any habitat. Quelea quelea, ($2R^2/N = 9625$, N = 8053, $P < 0.001$, peak Jan 4) when it is present, is the most abundant bird in the Park, and it may occur in very large flocks. It is commonest in open habitats and along rivers but is commonly seen in all. A few may be seen in all months but large flocks are restricted to January and February, and it sometimes breeds then e.g. January 1972. Euplectes albonotatus (R/N = 0.98, N = 39, $P < 0.01$, peak Jan 1) was only recorded in December and January. It was seen mainly in damper areas especially near the Voi River. E. diadematus is common from December to February

($2R^2/N = 141$, $N = 353$, $P < 0.001$, peak Feb 1) but much less so after that.

It occurs in any habitat though it does not usually stop in Grassland (none in censuses). Finally, E. nigroventris is a rare though regular visitor to riverside habitats (only 2 in censuses).

I have very few feeding data for these species. The visiting species were only seen taking grass seeds. The two resident species, however, are primarily insectivorous taking insects mostly from leaves (all 16 insects of P. nigricollis, and 69 per cent of 42 insects of M. rubriceps (but see below)). My data suggest that P. nigricollis feeds mainly in the bushes (mean height of feeding ($\pm$ S.E.) $= 1.4 \pm 0.6$ m ($n = 4$), and that M. rubriceps feeds mainly in the trees (mean height similarly $= 7.9 \pm 1.3$ m ($n = 9$)) (for the difference, $d = 4.5$, $df = 11$, $P < 0.001$). (The figure for M. rubriceps excludes two birds seen catching flying termites in the air from bushes). I also have a few records of both species eating fruit when it is available (5 P. nigricollis, 2 M. rubriceps).

Data from the literature - The visiting species are all primarily granivores, although most, if not all, will take some insects when breeding.

Where these species spend the remainder of the year is largely unknown, except for Q. quelea which migrates between Somalia and southern Tanzania following the movements of the rain belt, with a dry season refuge in northern Tanzania (Ward 1971). I think that some of the other species in this group will be found to be similar, except, for example E. diadematus, which has hardly been recorded south of Tsavo (Hall & Moreau 1970). However, this and several other species are very difficult to distinguish when they are not in breeding plumage, and hence a species could be overlooked unless it is very common.

Summary of differences

	<u>P.s.</u>	<u>P.i.</u>	<u>P.r.</u>	<u>P.c.n.</u>	<u>P.n.</u>	<u>M.r.</u>	<u>Q.q.</u>	<u>E.a.</u>	<u>E.d.</u>
<u>P. subaureus</u>	-	-	-	-	-	-	-	-	-
<u>P. intermedius</u>	H	-	-	-	-	-	-	-	-
<u>P. rubiginosus</u>	H	?	-	-	-	-	-	-	-
<u>P.c. nigriceps</u>	H	S?	?	-	-	-	-	-	-
<u>P. nigricollis</u>	H	THF	THF	TH	-	-	-	-	-
<u>M. rubriceps</u>	H	THF	TH	HF	F	-	-	-	-
<u>Q. quelea</u>	H	?	TF	H	TH	TH	-	-	-
<u>E. albonotatus</u>	H	H	H	(H)	TH	TH	?	-	-
<u>E. diadematus</u>	H	?	S?	H	TH	TH	?	H	-
<u>E. nigroventris</u>	?	H	H	?	TH	TH	H	?	H

c) Bubalornithinae

Data from Tsavo - Both species, Bubalornis niger and Dinemellia dinemelli, are common and widespread. Their habitat preferences (Fig.5.23) overlap extensively but are statistically different ($X^2 = 99$, df 5, $P < 0.001$, 30 per cent due to WBG, 25 per cent to R). Both occur commonly throughout the year but show seasonal patterns of occurrence which are in part complementary (Fig. 5.24). B. niger is commonest in the wet seasons ($2R^2/N = 200$, $N = 1530$, $P < 0.001$, peak Mar 1 - caused by high numbers in both January and April), and occurs more often in flocks than. D. dinemelli is at its relatively most scarce around the end of the year, being commonest from June to August ($2R^2/N = 37$, $N = 799$, $P < 0.001$, peak July 1).

Both species feed primarily on the ground, and were seen to take both seeds and insects but as for other such species the proportion of each is unknown. Both species, too, eat some fruit but I do not think that the seasonal peak of D. dinemelli is because of Commiphora or Salvadora persica fruits, indeed it was not seen to eat any fruit in trees. There is no very obvious reason for the different seasonal patterns of occurrence.

Data from the literature - Both species eat both seeds and insects. For summary of differences see after Passerinae.

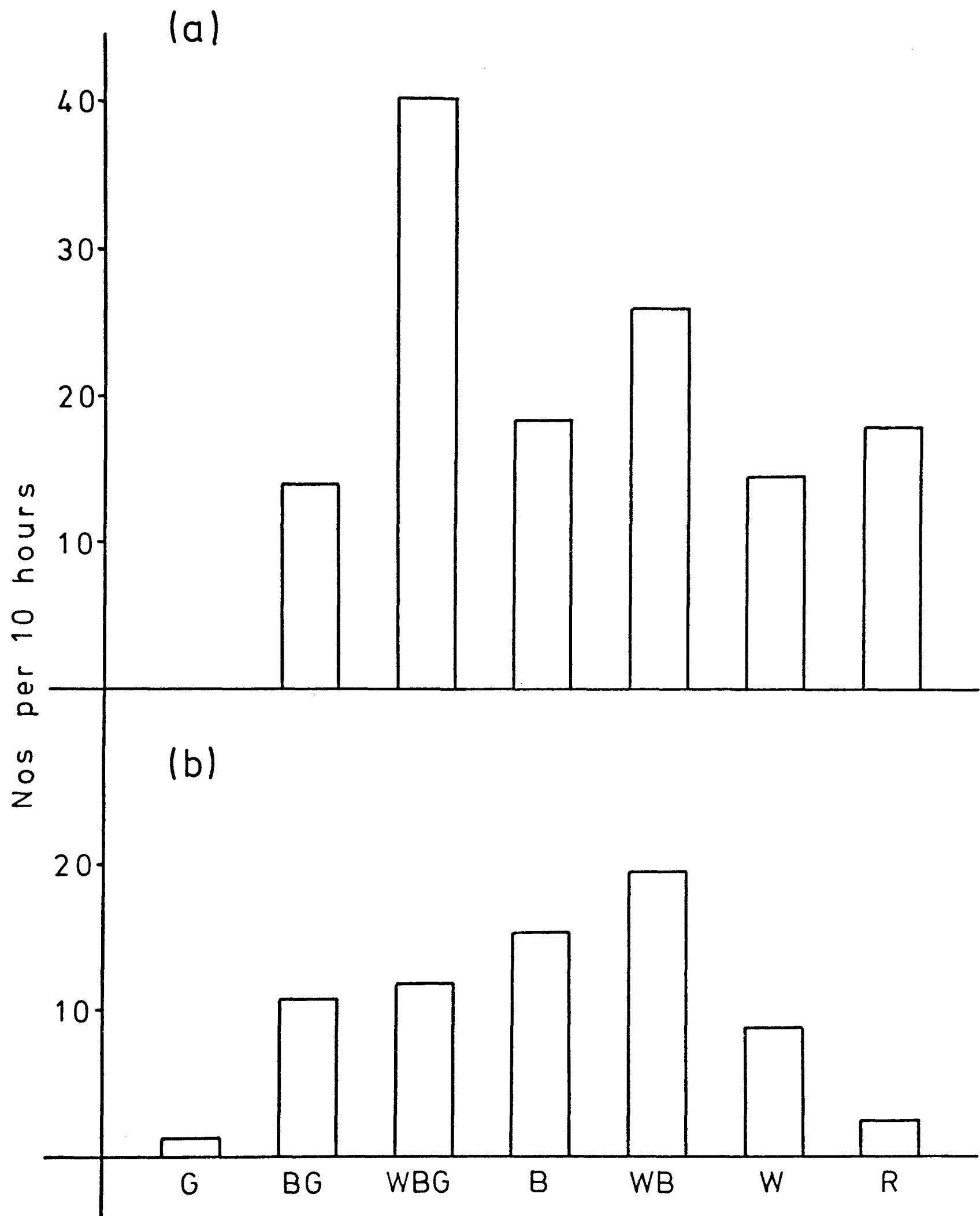


Fig. 5.23 The habitat preferences in Tsavo of two weavers; a) *Bubalornis niger*, b) *Dinemellia dinemelli*.

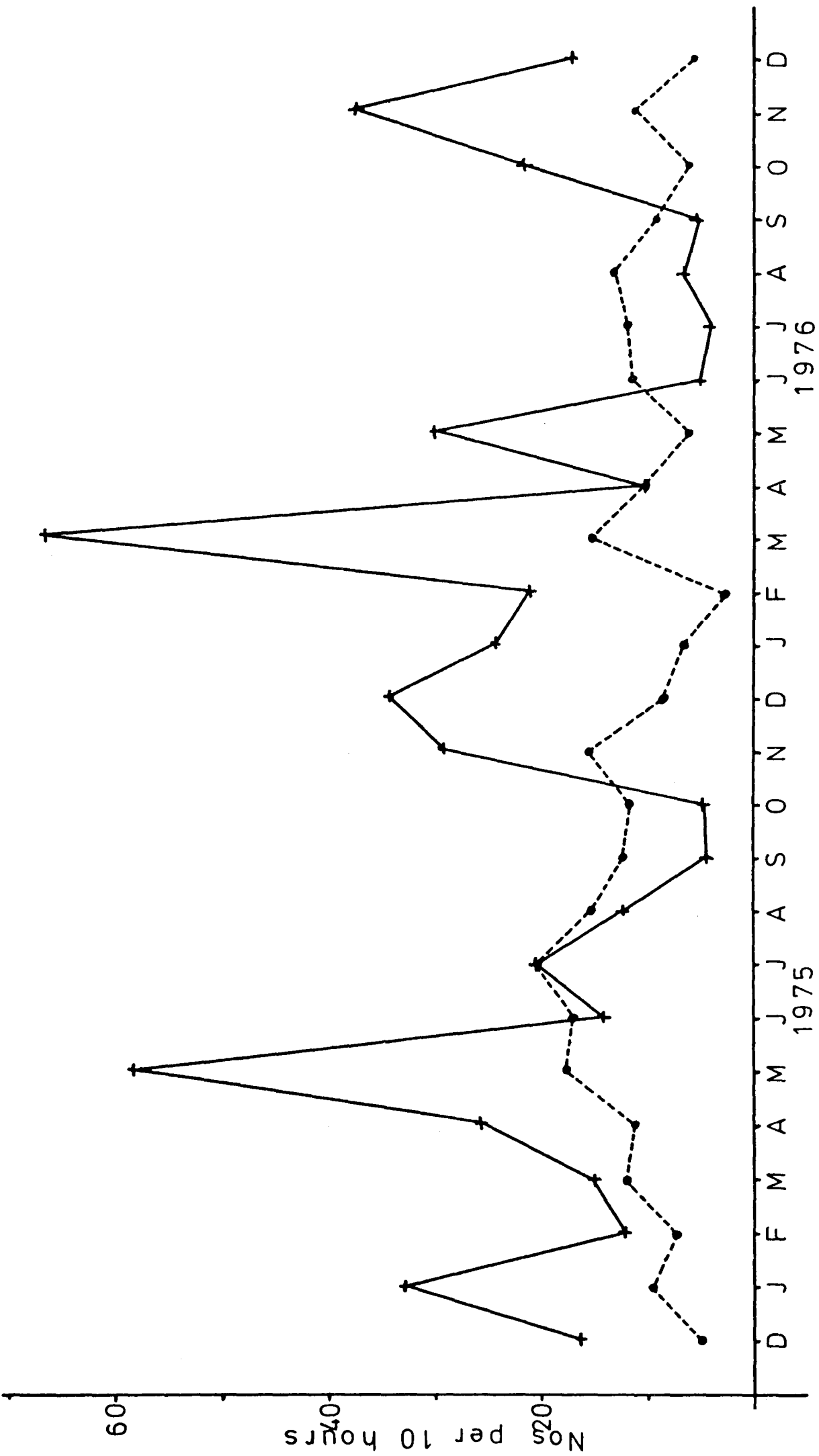


Fig. 5.24 The seasonal pattern of occurrence in Tsavo of two weavers; +---+ Bubalornis niger,
•---• Dinemellia dinemelli.

d) Plocepasserinae

Data from Tsavo - Two of the three species are rare: Pseudonigrita cabanisi is a rare visitor to thick habitats in the west of the Park, and P. arnaudi was formerly seen in small numbers, but none have been seen recently. Plocepasser mahali, however, is a fairly common resident ($R/N = 0.27$, $N = 63$, $0.01 < P < 0.05$) in all riverine fringes near water but it does not occur in riverine forest. It is also common around the gardens at Park HQ. All seen feeding were on the ground.

Data from the literature - P. mahali eats both seeds and insects.

e) Passerinae - Sparrows

Data from Tsavo - The two species Passer gongonensis and Petronia pyrgita, are very common and both are resident in some numbers. Both, however, show a slight increase in numbers in the dry season (P. gongonensis $2R^2/N = 19$, $N = 836$, $P < 0.001$, peak Jul 3; P. pyrgita $2R^2/N = 26$, $N = 937$, $P < 0.001$, peak Jul 4). But if the P. gongonensis seen in the northern area in July 1976 are excluded this seasonal pattern reduces considerably ($2R^2/N = 7.4$, $N = 784$, $0.01 < P < 0.05$, peak Jul 4). The habitat preferences of the two species (Fig 5.25) overlap extensively but are different ($X^2 = 170$, $df\ 6$, $P < 0.001$, 50 per cent due to W, 40 per cent to R).

P. gongonensis feeds primarily on the ground (95 per cent of 345 items) but in most cases it was unknown whether the birds were taking seeds or insects. P. pyrgita has a very varied diet; of 158 items taken 43 (27 per cent) were fruits, in both trees and bushes; 43 (27 per cent) were certainly insects (29 off leaves, 3 off twigs, 1 off a bud (mean height of these 33 ($\pm$ S.E.) = 4.7 ± 1.1 m ($n = 15$ birds), 1 in air, 5 off ground and 4 from unknown site); 21 (13 per cent) were certainly seeds (all but 5 from the ground); and 51 items (32 per cent) were taken from the ground, but it was undetermined whether the bird was eating seeds or insects.

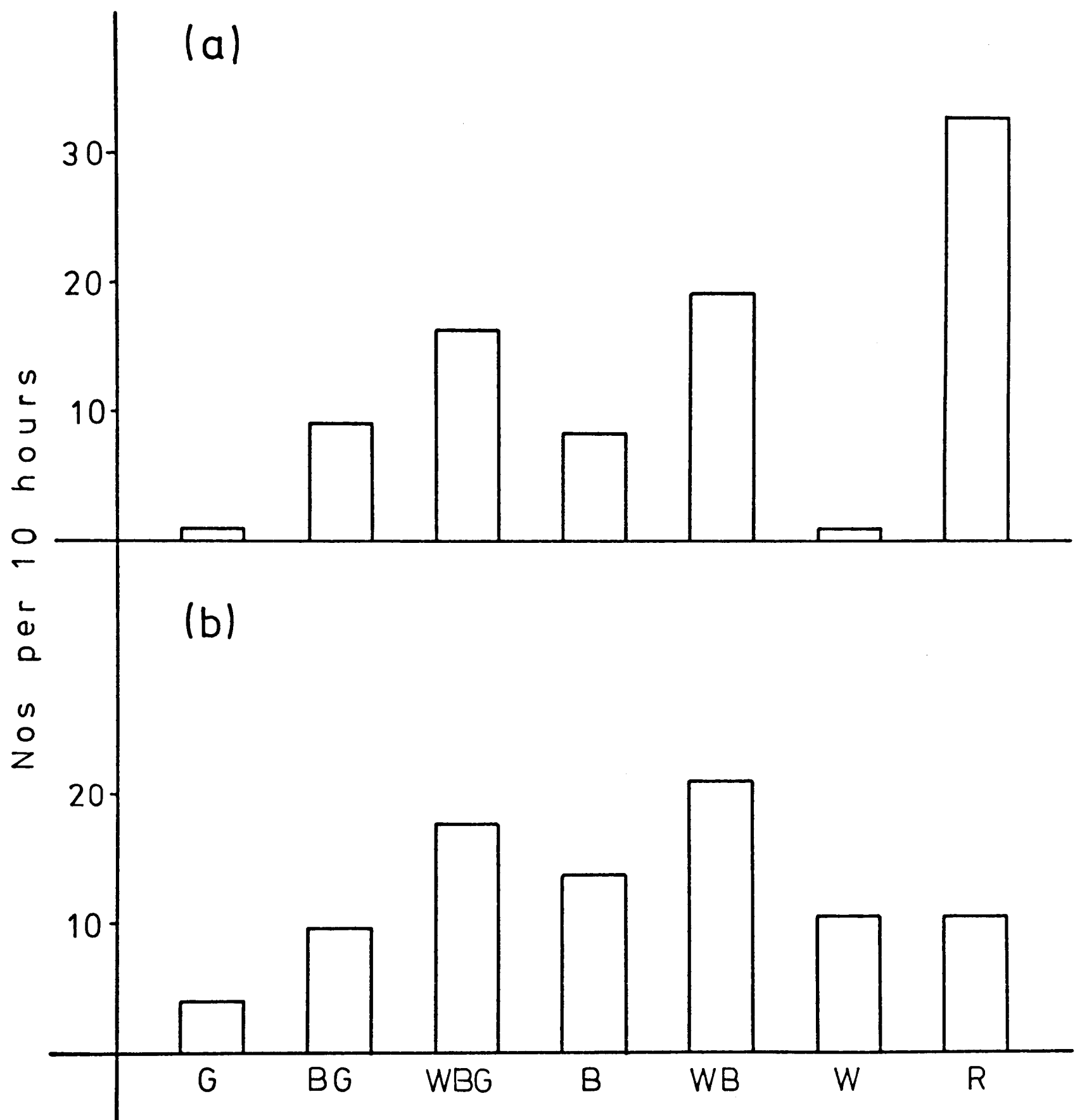


Fig. 5.25 The habitat preferences in Tsavo of two sparrows; a) *Passer gongonensis*, b) *Petronia pyrgita*.

Data from the literature - P. gongonensis eats both seeds and insects.

Summary of differences between species in Bubalornithinae, Plocepasserinae and Passerinae

	<u>B.n.</u>	<u>D.d.</u>	<u>P.m.</u>	<u>P.g.</u>
<u>B. niger</u>	-	-	-	-
<u>D. dinemelli</u>	O(H)?	-	-	-
<u>P. mahali</u>	H	H	-	-
<u>P. gongonensis</u>	H	S?	?	-
<u>P. pyrgita</u>	S	S?	H	(H)

Summarising the Ploceidae, it can be seen that most feed on the ground, and most eat seeds at least as a major part of the diet. The resident species seem to be more insectivorous than the visitors which may be entirely granivorous. The ecological relationships will have to await further study, but it appears that many of the closely related species are ecologically separate in some measurable way. There is further discussion of this in ch 5.4.4.

5.3.43 Sturnidae - Starlings

Data from Tsavo - Twelve species are recorded, and although six are uncommon, none are very rare. Onychognathus morio is the rarest. When it occurs inside the Park it is near rocky hills. There is usually a resident pair at Voi Safari Lodge; and there was an influx to one area of Woodland in August and September 1975, apparently in response to the abundance of Commiphora fruit at the time. Lamprotornis purpuropterus is fairly common along the Tiva River and in some other parts of the northern area. It is rare south of the Galana River inside the Park - indeed I never saw it there. The two birds I saw feeding were eating insects from the ground. Cinnyricinclus leucogaster is a rare visitor, mostly to Woodland, between late-March and September. Speculipastor bicolor is a sporadic visitor in flocks to thicker habitats especially

in the northern area. There were, however, several flocks well south of the Voi River in November and December 1976. Spreo hildebrandti is a sporadic visitor to any area. The 12 birds I saw feeding were behaving like other Spreos taking insects from the ground. S. shelleyi is an uncommon visitor, though it is often in fairly large flocks when it does occur. It may be a resident in parts of the northern area, where it is much commoner than south of the Galana River.

From an ecological point of view the remaining six species recorded in Tsavo can be divided into three singles and a group of three.

Lamprotornis chalybaeus is present all the year although shows a slight seasonal pattern of occurrence ($R/N = 0.38$, $N = 46$, $P < 0.01$, peak Jan 1). It occurs in Riverine and I hardly ever saw it outside this. It feeds both in typical starling fashion for insects on the ground (67 per cent of 21 items recorded) and on fruit when this is available (all seen were eating Salvadora persica fruits). Creatophora cinerea is a wide-ranging visitor to Tsavo which becomes fairly common in the wet seasons (Fig. 5.26), often occurring in quite large flocks ($2R^2/N = 295$, $N = 667$, $P < 0.001$, peak Feb 4). It occurs mainly where there are trees ($X^2 = 14$,

df 1, $P < 0.001$) although less common in Woodland than elsewhere. It is one of the few species which has an equally well-marked peak of numbers in the April wet season despite the low rainfall in 1975 and 1976, although the trough in March is not quite statistically significant (excluding December 1976, the difference Dec-Jan-Feb: March $d = 2.4$, df 6, $P < 0.10$; March: Apr-May $d = 2.6$ df 4, $P < 0.10$). The lack of birds in December 1976 is chance, due to the small amount of time spent censusing. There were many birds in the area then and 166 per ten hours were seen flying over. It feeds like other starlings on the ground for insects (61 per cent of 167 items recorded) and on fruit (39 per cent).

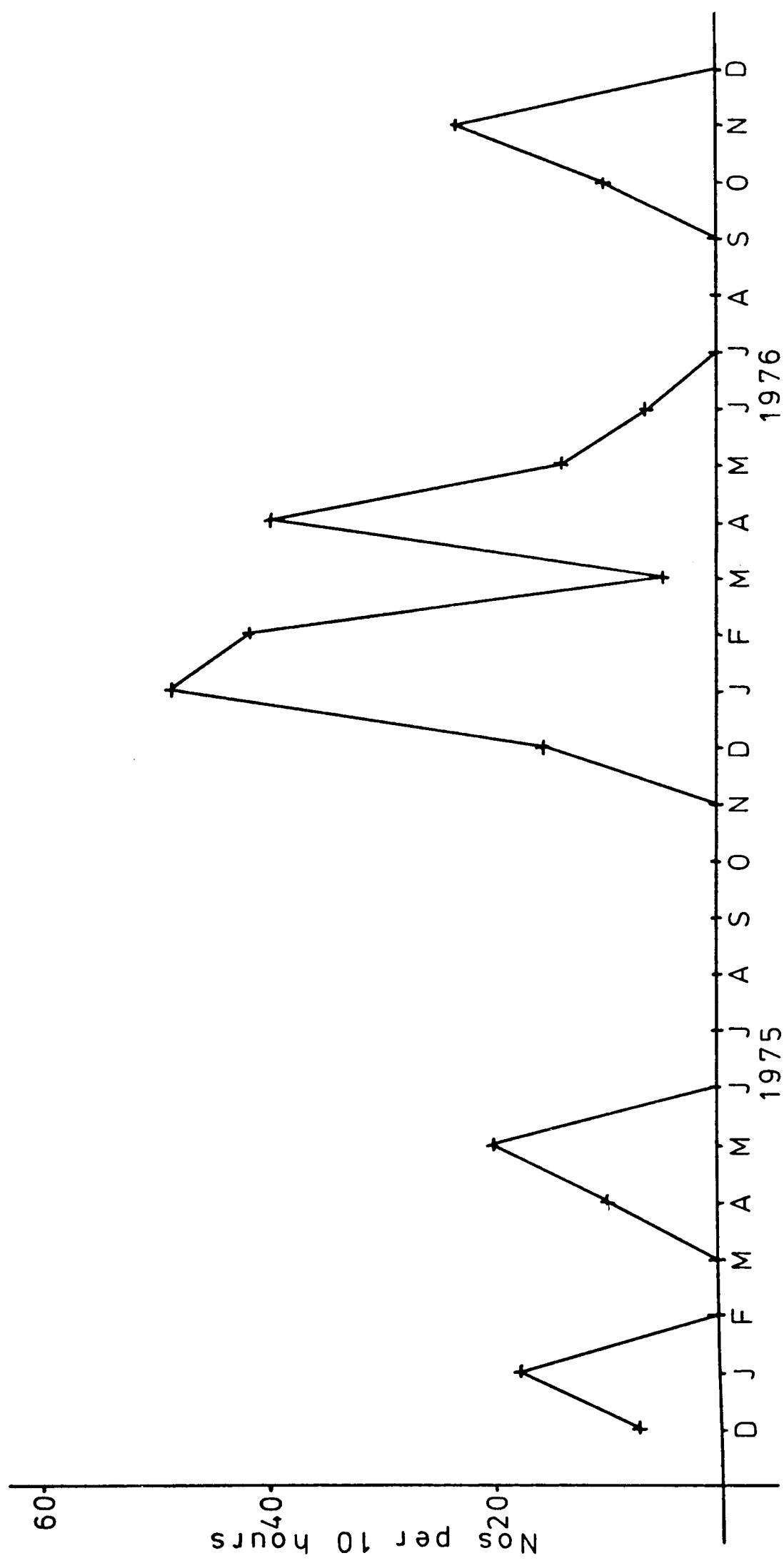


Fig. 5.26 The seasonal pattern of occurrence in Tsavo of a starling; Creatophora cinerea.

The final single bird is Buphagus erythrorhynchus, which is in a separate subfamily. This is unlike all other birds in Tsavo East N.P. though in other areas, including parts of Tsavo West N.P., its congener B. africanus is similar. It feeds almost entirely on the ectoparasites, and in some cases the sores, of large mammals and its distribution is largely determined by the latter (see Cobb 1976). Subjectively, its favourite species of mammal in Tsavo seem to be Buffalo, Rhino and Giraffe Giraffa camelopardalis, though I also recorded it on many antelopes (Antelopinae), Warthog, Phacochoerus aethiopicus, and even on domestic goats. Because of regular dipping, ectoparasites are now uncommon on domestic species of mammal and, as a result, B. erythrorhynchus was uncommon in the Woodland I worked in. It is a fairly common resident ($2R^2/N = 2$, $N = 223$, N.S.), however, in all the habitats in the Park.

The group of three are two Spreos, S. superbus and S. fischeri, and Cosmopsarus regius; and this last has been included in Spreo by some authors, e.g. White (1962). They are all similar in body weight but C. regius is much slimmer and has a long tail. The habitat preferences of the three species are shown in Fig. 5.27. S. superbus and S. fischeri are both commonest in the Park savanna habitats with trees, but S. superbus is commoner than S. fischeri in those without trees, and S. fischeri is commoner in Woodland (X^2 for the difference = 235, df 5, $P < 0.001$, 50 per cent due to W). C. regius is much commoner than either in Woodland and Riverine (difference with S. superbus $X^2 = 384$, df 5, $P < 0.001$, 70 per cent due to W; with S. fischeri $X^2 = 166$, df 5, $P < 0.001$, 45 per cent due to WBG, 30 per cent to B). A further difference is that S. superbus and C. regius were usually seen in groups of 6-10 birds, and groups of both species seemed to be larger in thicker habitats. S. fischeri, by contrast, usually occurs in flocks of up to 40 birds. Fig. 5.28 shows the seasonal pattern of occurrence in Tsavo of the three species, and,

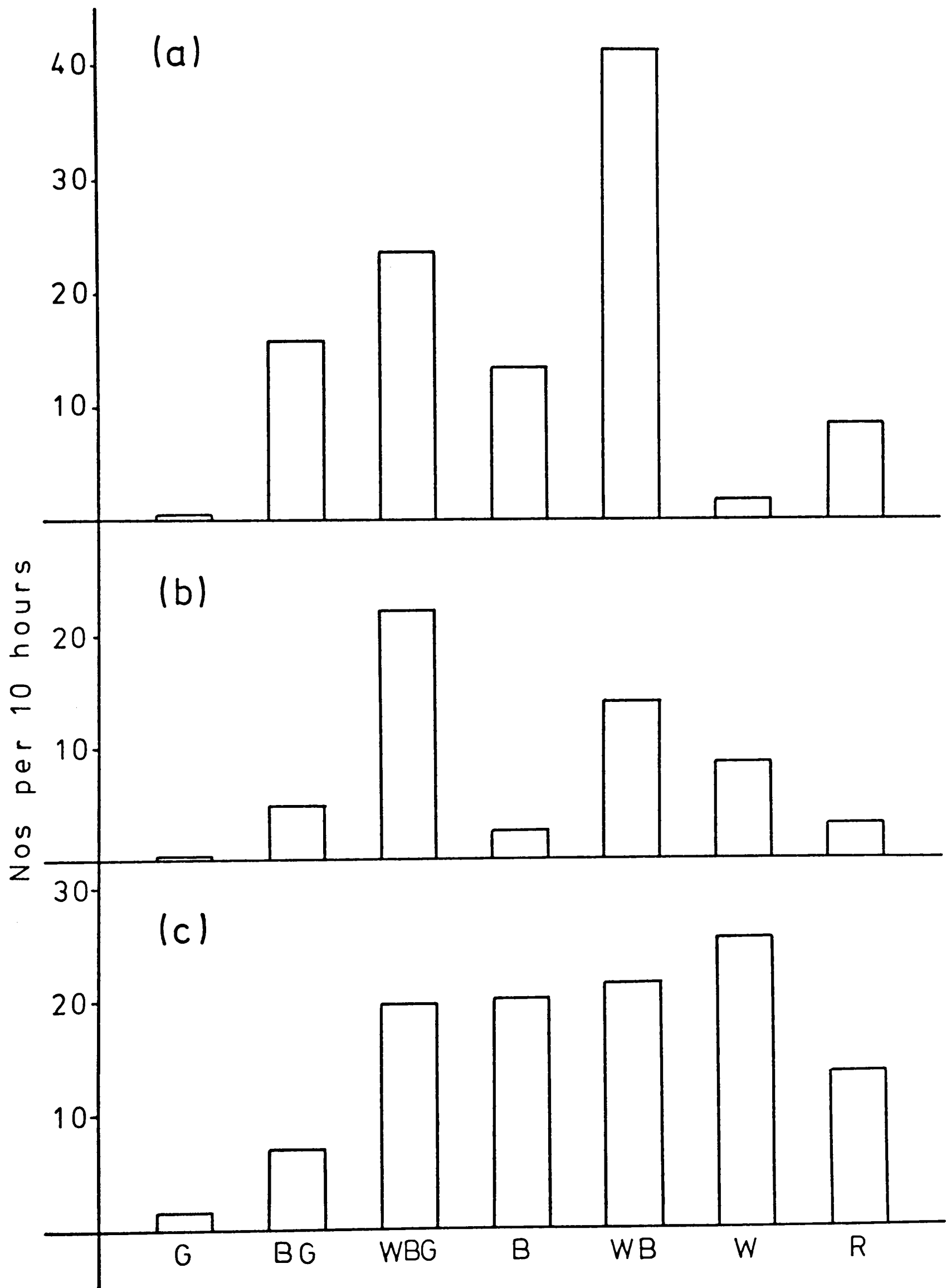


Fig. 5.27 The habitat preferences in Tsavo of three starlings; a) *Spreo superbus*, b) *S. fischeri*, c) *Cosmopsarus regius*.

as with the hornbills (ch 5.3.22, Figs 5.7 and 5.8) a three month running mean has been calculated. All three species are resident in some numbers but all show some seasonal variation with slight peaks between late May and August. (C. regius $2R^2/N = 29$, $N = 1177$, $P < 0.001$, peak Aug 2; S. fischeri $2R^2/N = 24$, $N = 713$, $P < 0.001$, peak Jan 4; S. superbus $2R^2/N = 69$, $N = 1163$, $P < 0.001$, peak May 4). The dotted line of Fig 5.28 in part of 1976 for the last species is the total but the lower line excludes birds seen on extended visits to the northern area of the Park in March, April and July 1976. If these are excluded and seasonal peak reduces in importance ($2R^2/N = 31$, $N = 997$, $P < 0.001$, peak Jun 1). The peaks are difficult to identify with season especially for the two Spreo species which are both purely insectivorous, yet have their lowest numbers coincident with peak insect abundance. All three species are very conspicuous so it is unlikely to be an artificial peak. Perhaps it is competition from other species?

All three species feed mainly on the ground, usually in bare patches, and when on the ground they are insectivorous (C. regius 76 per cent of 394 items were insect (97 per cent from the ground); S. fischeri 99 per cent of 292 were insect (all from ground); S. superbus 87 per cent of 597 items were insect (all from ground). They all eat large numbers of termites. I recorded all three species eating fruit - S. fischeri only once (1 per cent of items), S. superbus 8 birds (10 per cent of items) (3 birds (3 per cent items) were on Acacia flowers), and C. regius 18 birds (24 per cent items). This is related to their habitat preferences, as six of the 18 C. regius were eating Commiphora spp. (i.e. Woodland) and another four were on Dobera glabra (i.e. Riverine).

Data from the literature - In areas where Buphagus africanus occurs in addition to B. erythrorhynchus, the two have been shown to divide the resources, and they feed largely on different species of mammal, with B. africanus mainly on Buffalo and B. erythrorhynchus on other species (Buskirk 1975).

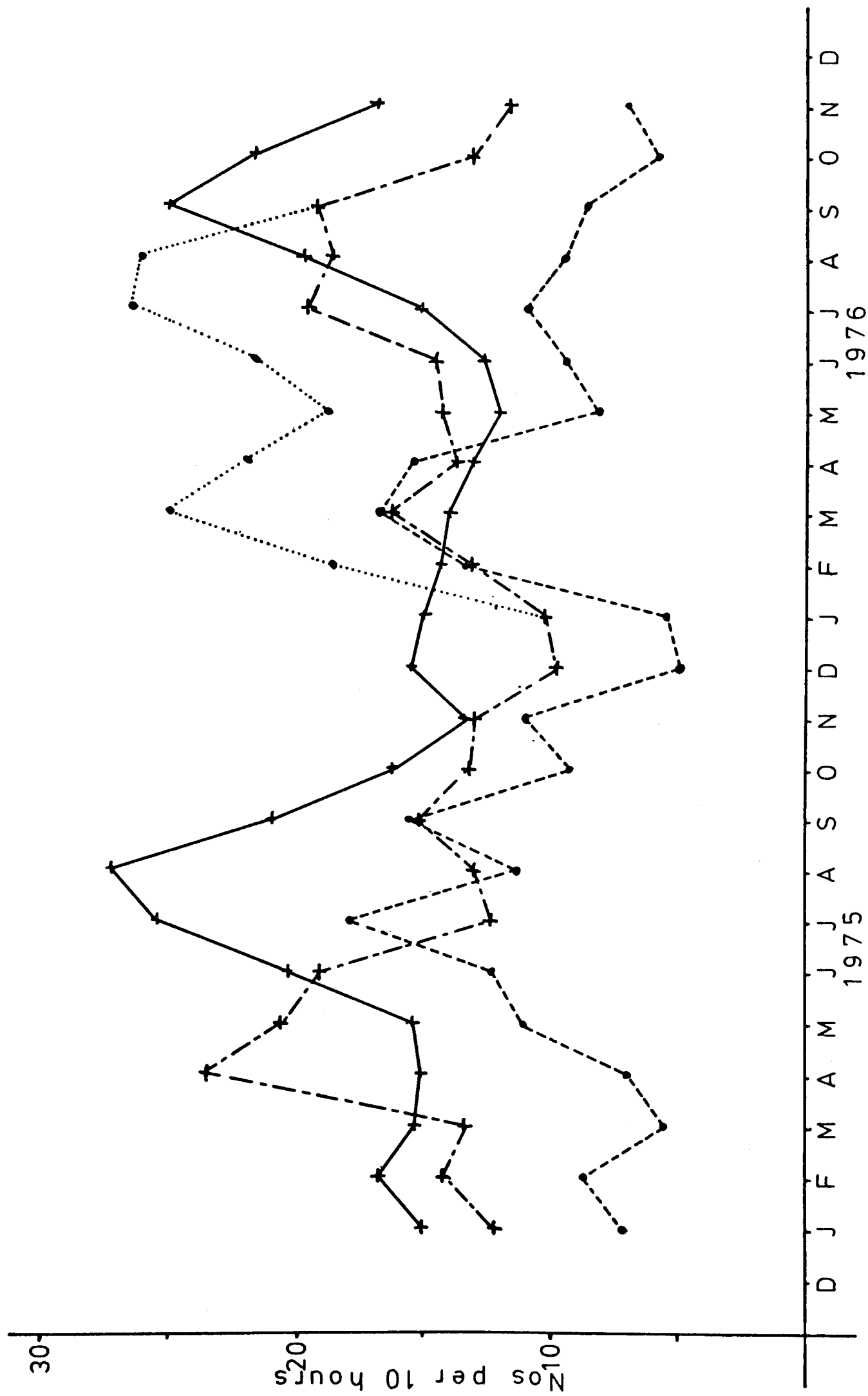


Fig. 5.28 The seasonal pattern of occurrence of three starlings; — *Cosmopsarus regius*, +---+ *Spreo superbus* (•.....• *S. superbus* including extended visits to the northern area of the Park - see text), •---• *S. fischeri*.
Three-month running means have been calculated as in Fig. 5.7.

Summary of differences

	<u>L.c.</u>	<u>C.c.</u>	<u>C.r.</u>	<u>S.f.</u>	<u>S.s.</u>
<u>L. chalybaeus</u>	-	-	-	-	-
<u>C. cinerea</u>	H(0)	-	-	-	-
<u>C. regius</u>	H-?	H	-	-	-
<u>S. fischeri</u>	H	TOF	TH	-	-
<u>S. superbus</u>	H	TOF	TH	H?	-
<u>B. erythrorhynchus</u>	F	F	F	F	F

5.3.44 Oriolidae - Orioles

Data from Tsavo - Three species are recorded but Oriolus auratus has only been seen three times. O. larvatus is a resident ($R/N=0.05$, $N=129$, N.S.) mainly in Riverine and Woodland, though it does occur elsewhere with trees. O. oriolus has very similar habitat preferences but is commoner in Wooded and Bushed Grassland ($X^2=12$ df 3, $P<0.01$, 80 per cent due to WBG with BG). It is a Palaearctic migrant occurring from October to April, and is one of the few of these to arrive before the rains; (others are the chat Oenanthe oenanthe and warbler Phylloscopus trochilus).

Both species were seen to eat both fruit and insects and almost entirely in trees. Table 5.15 gives some data on their feeding behaviour and shows there is almost no difference.

Summary of difference

	<u>O.o.</u>
<u>O. oriolus</u>	-
<u>O. larvatus</u>	H?-0?

5.3.45 Dicruridae - Drongos

Data from Tsavo - The only species Dicrurus adsimilis is one of the most widespread birds in the Tsavo area. It is a resident ($2R^2/N=5.6$, $N=919$, N.S.), commonest in Woodland but is common in all habitats with trees and only a little rarer in Bushland. It is uncommon in Bushed Grassland and Grassland.

Table 5.15 Feeding behaviour of two orioles Oriolus in Tsavo.

	<u>O. oriolus</u>	<u>O. larvatus</u>
No. of items	59	41
% insects ^a	25	37
% of insects taken off leaves	93	80
% of total food items taken with bird in flight	12	24
Height of feeding (m) ^b	8.8 $\pm$ 0.8 (18)	6.8 $\pm$ 1.0 (15)

Notes:

- a) All items that were not insect were fruit
- b) Height is quoted as mean $\pm$ standard error with the sample size in brackets.
The difference between the two species is not significant; $t = 1.56$ with
df 31, N.S.

It is an insectivore and mainly a flycatcher taking 71 per cent (of 363 items) in the air, with 20 per cent off the ground, and 8 per cent off leaves in bushes and tress. It often follows large mammals, and takes the insects disturbed by them.

5.3.46 Corvidae - Crows

Data from Tsavo - Three species have been recorded but none are important to the ecology of the area. Corvus splendens was only seen at Mtito Andei in March and April 1977, a record which significantly increases its range inland from where it was introduced on the coast (National Museum newsletter no.13). C. albus is a fairly common resident in and around Voi town, and some occur along the main Nairobi-Mombasa road, but they hardly even reach the Park boundary. C. albicollis is similar but a little more widespread and extends further into the Park.

Both these species were seen feeding mostly on rubbish etc left by man. But I also saw them eating from carcasses of animals killed on the main road. The vultures (in Accipitridae), are the main carrion eaters inside the Park, but carcasses on the main road are left to these two crows, and the kite Milvus migrans, which has a very similar distribution.

5.3.47. Other land-birds

Data from Tsavo and the literature - There is one major and one minor group of land-birds which have not yet been mentioned. The major group are the birds of prey Accipitridae, Falconidae and Sagittariidae. C. Smeenk has made a general survey of these in Tsavo East N.P. (Smeenk 1974, pp. 7-24 and Appendices 2 and 3) and he made some detailed studies on the larger eagles (Smeenk 1974, especially pp. 24-64) and on Melierax poliopterus and M. gabar (Smeenk & Smeenk-Enserink 1976). My methods were unsuited to studying such wide-ranging species, but what data I have largely agree with Smeenk.

The large species are known to feed mainly on vertebrates and/or carrion and therefore do not compete to a major extent with other bird species, except the two eagle owls Bubo lacteus and B. africanus (ch 5.3.12) but these latter are nocturnal. Some of the smaller birds of prey certainly feed on insects in addition and some may be dependent on them, but only two occur in comparable numbers with other land-birds, and neither of them is common. Polihierax semitorquatus occurs in all habitats in Tsavo especially where there are some open areas with some prominent perches. It feeds in a similar way to the shrikes Lanius spp., and the rollers Coracias spp., by pouncing to the ground from a perch. It is also known to chase small birds. The other, Falco tinnunculus, is a Palaearctic migrant and, in Tsavo, is usually seen hovering over open grassy areas and hence is probably taking a separate food to other species.

The minor group are a few storks Ciconiidae and some other large water-birds which at times feed on land. Flocks (sometimes several hundred individuals) of the Palaearctic Ciconia ciconia, and the intra-African migrant C. adhimii were seen a few times stalking prey, probably mainly grasshoppers, through long grass soon after the rains. Other species included the stork Anastomus lamelligerus and ibis Threskiornis aethiopicus but in no case can these species have an important effect on the terrestrial ecology of Tsavo.

5.4 General discussion of the species 'common' in Tsavo

5.4.1 Introduction

In the category of 'common' species I have included all species which had a total relative abundance value greater than 0.5 per 10 hours which is equivalent to having seen 35 or more in censuses (Type I).

Such an arbitrary criterion is obviously biassed against species which are only present in Tsavo for some of the year. However with smaller samples it becomes increasingly more difficult to define accurately the status, and other features of the ecology of the species concerned.

This criterion of 'common' includes 122 species, but seven will not be discussed further: the waxbill Lonchura griseicapilla, the weavers Pseudonigrita cabanisi and Euplectes albonotatus, and starlings Speculipastor bicolor, Spreo hildebrandti and Spreo shelleyi, which only reach the 35 seen by virtue of occurring inflocks - if only the number of flocks is scored, they are all well below the limit - and the ostrich Struthio camelus whose ecology, as said in ch 5.3.1 is more similar to that of the large herbivorous mammals.

Each of the remaining 115 species has been assigned to two categories one for its major food type, determined from my own data and the literature, and the other for its status in Tsavo East N.P.. Appendix 1.1 contains the details for each species. In very few cases was there any difficulty assigning a species to a category. Species will eat the 'wrong' food type at times, and this is particularly true of some granivores eating fallen fruit and/or insects, and a variety of species which take advantage of temporary superabundances of fruit. To avoid having two extra groups each with only one species, the dove Streptopelia semitorquata has been assigned to the 'seed' category, and the sparrow Petronia pyrgita to the 'insect plus seed' category, despite the former probably, and the latter certainly eating fruit on more than an opportunist basis. There are similarly a few arbitrary decisions in the status category, for example the cuckoo Cuculus canorus has been classed as a Palaearctic migrant although some are certainly the African race C.c. gularis; the cuckoo Clamator jacobinus is classed as an African visitor although some, if not

most, are probably migrants from the Indian subcontinent; and the several species that are partial migrants, but have a fairly large resident population, are classed as residents. The number of species in each category is shown in Table 5.16.

5.4.2 Frugivorous birds

As might be expected from the habitat distribution of fruits, all 20 species which eat fruit are most common in Woodland (8), Riverine (9) or about equally so in both (3). And only two, the starlings Cosmopsarus regius and Creatophora cinerea, neither of which is purely frugivorous, are as common in any other habitat. What is more surprising in view of the apparent scarcity of fruit, except for Commiphora, is that 18, including all six purely frugivorous species, are residents. Commiphora fruit, of course, is so abundant in Woodland from July to September that three of the resident species increase substantially in numbers there at this time - the hornbills Tockus deckeni and T. erythrorhynchus (but see ch 5.3.22), and starling C. regius - and in 1975 a few species which were otherwise hardly recorded came into the area, e.g. the starling Onychognathus morio. Evidently fruit is not as scarce as it appears at first sight.

Five of the six purely frugivorous species are almost restricted to one habitat, three to Woodland and two to Riverine; and the sixth species the mousebird Colius macrourus is much commoner in Riverine than elsewhere. All three woodland species eat Commiphora fruit but the two larger ones, the turaco Corythaixoides leucogaster, and especially the parrot Poicephalus rufiventris, also take larger fruits, and the latter harder ones, which the third species, the small barbet^t Lybius melanocephalus, does not take. C. leucogaster also eats flowers and leaves at times. Hence all have partially separate diets.

Table 5.16 The number of 'common' species in each food and status category.

Food category	Status			TOTAL
	Resident	Visitor	Palaearctic	
Insect only	37	8	18	63
Seeds only	7	8	-	15
Fruit only	6	-	-	6
Insect seed	11	3	-	14
Insect fruit	12	1	1	14
Insect nectar	3	-	-	3

All insectivores	63	12	19	94
All granivores	18	11	-	29
All frugivores	18	1	1	20
All nectarivores	3	-	-	3

TOTAL	76	20	19	115

The riverine species too are probably separate from each other, although all three are the same size. The two mousebirds C. macrourus and C. striatus are bush-living species (and see ch 5.3.15), and the barbet Lybius melanopterus is a tree-living species especially in Ficus spp.

All but three of the 14 partially frugivorous species seem to take whatever fruit is most available at the time, in particular Commiphora spp., Salvadora persica, and Ficus spp., and not to feed on other species. The three odd species are the two bulbuls Pycnonotus barbatus and Andropadus importunus and the barbet Trachyphonus darnaudii. These tend to stay in the bushes rather than the trees, even when Commiphora or Ficus are abundant (but see ch 5.3.23 for T. darnaudii), and presumably eat mainly other fruits.

As for the fruit they eat, most of these partially frugivorous species seem to take only the most available insects. When feeding on insects only six of the 14 species remain in the woody vegetation; the rest take their insects from the ground where all, even the largest, the hornbills Tockus spp., feed to a great extent on termites, which are probably the most abundantly available insect food in Tsavo. For those taking insects in the vegetation I have rather few data but none seem to be specialists on any one part of the vegetation, or one group of prey species. How much these species depend on such superabundant foods, and/or being complete generalists, and how much they do have separate niches will have to await further study. Obviously the larger species can take larger prey and they do take some, but whether this is a sufficient difference for full ecological separation is unknown.

Several other species take advantage of seasonally abundant fruit on an opportunist basis, especially the Commiphora in July to September. For some it may be very important. A few of the Palaearctic chats and warblers, notably the two warblers Sylvia communis and S. nisoria and chat Irania gutturalis, take quite large amounts of fruit, especially Premna

spp., in April when they are fattening for their northward migration to Europe. Recent experimental work by Berthold (1976) has shown that similar species preferred animal food at migration times and the intake of vegetable food was actually decreased then. This does not seem to apply in Tsavo. The birds were commoner, and Premna fruit was freely available in December, yet I have no records of these birds eating the fruit then. Further, many seemed to be only passing through even in December, but they did not require so much fat at that time as they were not going so far.

To summarise, fruit is relatively unimportant as a food source except in Woodland and Riverine where it supports a few resident species of frugivore, and the numbers of these are augmented in times of fruit abundance. The purely frugivorous species are ecologically separate from each other and eat a variety of fruits in addition to the most abundant ones. The partially frugivorous species eat mainly the most abundant fruits (and many eat mainly the most abundant insects as well). They therefore differ from the specialist species, but it is not clear how they divide the food resources between themselves.

5.4.3 Nectarivorous birds

The only species which take nectar regularly are the sunbirds Nectariniidae, and all of them eat insects as well. Differences between the species are summarised in ch 5.3.37. Very few other species were seen to probe flowers and some were probably taking insects rather than the nectar. A few species e.g. the turaco Corythaixoides leucogaster were seen to eat whole flowers and not just the nectar.

That birds are important pollinators in Tsavo I rather doubt as no sunbird species is common except Nectarinia hunteri, or possibly N. bifasciata in Woodland. There appear to be no "sunbird-flowers" in South Africa (assumed after Skead 1967 pp. 62-65) like the "hummingbird-flowers" in the New World, and only few of the flowers fed from by sunbirds

in Tsavo were red, which is the commonest for the hummingbird-pollinated species (e.g. Greenewalt 1960).

5.4.4 Granivorous birds

The 'common' purely granivorous species form a continuous gradation in size from the large sandgrouse Pterocles decoratus and dove Streptopelia semitorquata, to the waxbill Uraeginthus bengalus, but there is a concentration of numbers at the small end of the scale. How much this difference is projected onto the size of seeds taken is unknown. The large species are mostly doves which have weak bills, and cannot tackle large hard seeds, indeed three weavers Quelea quelea, Euplectes diadematus, and Vidua paradisaea may be capable of taking larger and harder seeds. All species seem to take predominately grass seeds and, subjectively, there was little difference between species.

The 15 species are in two groups. There are seven residents, including the lark Eremopterix signata, and eight species which are visitors (or almost entirely so) to the area only during the period of peak seed abundance at the end of each wet season. The seven resident species all have slightly different ecology. The four Columbiforms feed mainly on open bare ground though it may be under trees. They separate from each other as shown in ch 5.3.8. E. signata is the only one of the resident granivores occurring in Grassland, and it occurs much further from woody vegetation than the others when in other habitats; and the two waxbills Pytilia melba and U. bengalus are usually close to, or in the case of the former, even under, thick bushes and often among grass (see ch 5.3.41).

Five of the visitors, the three weavers above, waxbill Amadina fasciata, and the quail Coturnix delegorguei are different from the residents in preferring areas with a higher grass cover, and the first four

at least take many of their seeds direct from the stem. Two others, the doves Streptopelia senegalensis and Oena capensis, are very similar in their feeding ecology to other doves; but they are almost exactly in the middle of gaps in the size range of resident species: S. senegalensis between S. capicola and Turtur chalcospilos, and O. capensis between the latter and the waxbills with E. signata. Perhaps there is some separation with size of seeds. The final species the lark Eremopterix leucotis is very similar to E. signata with no obvious differences (ch 5.3.26).

The first five of these visitors are mainly in a niche which is only temporarily available and does not seem to be used by residents. The other three appear to be competing for the same resources as the residents, and the five appear to be competing among themselves. Seeds are very abundant at the times the visitors are in Tsavo, perhaps super-abundant, and hence there is no need of ecological separation. However there is a little evidence for it: the size of the two doves noted above, and the difference in the habitat preferences of S. senegalensis and S. capicola which were more different from each other when the former was commonest in January than at other times (see ch 5.3.8).

The species classed as eating both seeds and insects, like the partially frugivorous species, seem to be complete generalists. In addition to seeds and insects, most will probably eat any fruit that has fallen to the ground, and some were rarely recorded eating fruit in the woody vegetation. All species take their seeds from the ground rather than the stem and all remain on the ground when eating insects, except for the sparrow Petronia pyrgita and two weavers Ploceus intermedius and P. rubiginosus which also take some insects in the trees. As mentioned above, it was often impossible to see what was being eaten when the birds were feeding on the ground. Sometimes I disturbed birds from a feeding

site and searched the ground myself but I very often found neither seeds nor insects (nor fallen fruit). Whether and how these birds do keep separate I cannot tell. They are a very important group to the ecology of Tsavo as they include some of the most abundant birds in the area e.g. the lark Mirafrapa poecilosterna and sparrow P. pyrgita, and the most abundant "very large" species, the bustard Eupodotis ruficrista.

To summarise, the resident granivores are separate from each other. The visitors, although some use a separate niche may simply be taking advantage of a temporarily superabundant food-supply. However there is a little circumstantial evidence that there is nevertheless separation. Those eating seeds and insects all seem to be generalists feeding on the ground, and I have too few data, due partly to the difficulties of identifying their food, to say how they might separate from each other.

5.4.5 Insectivorous birds

In the proportion of residents, the purely insectivorous species fall between the granivores and the frugivores, but 18 of the Palaearctic migrants are purely insectivorous and the only other one is partially so. This is probably because of characteristics of the Palaearctic rather than Tsavo - it is a predominant feature of all Palaearctic migrants which winter in Africa (Moreau 1972).

There are three major sources of insect food; the air, the ground and the vegetation and there are only few species which regularly feed from more than one of these. A fourth source is used solely by one species, the large mammals by the starling Buphagus erythrorhynchus. Those using each of the other sources can be divided into two groups. Those taking in the air either do so by sallying from a perch to individual items, or take insects without using perches at all, a niche filled mainly by the swifts Apodidae, the swallows Hirundinidae and, at night, by the

nightjars Caprimulgidae. The ground feeders can be divided into those that pounce to the ground from an elevated perch, and those that stay on the ground and run between items. Finally the vegetation feeders can be divided into those feeding mainly from green vegetation, and the specialists on twigs or branches. Table 5.17 shows the number of purely insectivorous species in each category. Table 5.18 is the same but includes the 14 species eating insects and seeds, 14 eating insects and fruit, and 3 eating insects and nectar.

a) Aerial feeders

Of the eight (seven purely insectivorous) species, four are bee-eaters Meropidae, and all are likely to take larger prey than the drongo Dicrurus adsimilis despite three of them being lighter than this species. The prey of the bee-eaters was often seen to be fairly large and they almost invariably banged it vigorously on a perch before swallowing it. This behaviour occurs in other species but not so commonly. Of the others, the chat Oenanthe pleschanka takes 60% of its food from the ground (Table 5.9), and the sunbird Nectarinia bifasciata takes 30% of its insect food from the vegetation and, although the figure is likely to be high (see ch 5.3.28) it was recorded as taking 82% nectar (Table 5.14). D. adsimilis has similar habitat preferences to the Palearctic flycatcher Muscicapa striata, and feeds in a similar fashion but it is nearly three times the weight and, perhaps related, travels much further out to food items (mean ($\pm$ S.E.) = 9.3 ± 0.8 m ($n = 109$) cf 5.4 ± 0.7 m ($n = 75$) for M. striata; $d = 3.6$, $df = 181$, $P < 0.001$). Hence all separate from each other.

Also feeding in the air are the swifts and swallows, and, at night, the nightjars. They are not included in Table 5.17 but in a few areas they may be fairly common. The commoner species in the two diurnal families seem to have differences in habitat preferences among themselves

Table 5.17 The number of 'common' purely insectivorous species
in each status category and feeding guild

Feeding guild	Status			TOTAL
	Resident	Visitor	Palaearctic	
Air: hawking from perch	3	2	2 ^c	6 + 1
Ground: pounce	5	1	7 ^{c,d}	10+3
Ground: glean	14 ^a	3 ^b	5 ^{d,e}	15+7
Vegetation: green	10 ^a	3 ^b	8 ^e	16+5
Vegetation: twigs	7	-	-	7
Animal	1	-	-	1
TOTAL	37	8	18	63

Notes:

1) The following species are scored in both categories marked above.

a) Chatterer Turdoides aylmeri, and warblers Camaroptera simplex and Cisticola cinereola

b) Cuckoo Centropus superciliosus

c) Chat Oenanthe pleschanka

d) Thrush Monticola saxatilis and chat Oenanthe oenanthe

e) Chat Irania gutturalis

Table 5.18 The number of 'common' insectivorous species
 (including those also eating fruit, seeds or
 nectar) in each category.

Feeding guild	Status			TOTAL
	Resident	Visitor	Palaearctic	
Air: hawking from perch	4 ^a	2	2	6 + 2
Ground: pounce	5	1	7	10 + 3
Ground: glean	32 ^b	7 ^c	5	34 + 10
Vegetation: green	19 ^{a,b}	5 ^c	9	24 + 9
Vegetation: twig	7	-	-	7
Animal	1	-	-	1
	63	12	19	94

Notes:

- 1) the purely insectivorous species are included in more than one category as in Table 5.17. In addition here are:
- a) sunbird Nectarinia bifasciata
- b) sparrow Petronia pyrgita
- c) weavers Ploceus intermedius and P. rubiginosus

(see chs 5.3.14 and 5.3.27), and the differences are paralleled in each family. One species of each family nests mainly in buildings, one in culverts, and one by water; and there are two extra swallow species. The two waterside species are separate, with the swallow Hirundo smithii feeding near the water surface, and the swift Cypsiurus parvus higher in the air, and often near the palms. Hirundo rustica is separate by occurring well away from any rocks, buildings or water. But how the other two pairs, and the swallow Hirundo fuligula, may keep apart from each other is unknown; and all five may occur together at times e.g. at Voi Safari Lodge.

At night the swifts and swallows are replaced by the nightjars, at least for part of the year (see ch 5.3.13) but nightjars are considerably larger, and probably take larger insects so it is not simple ecological replacement.

A few other species notably the larger bee-eaters may feed by this method at times. But these are much larger than the swifts and swallows.

b) Ground-feeders; pouncing

The species that pounce for only part of their prey behave differently from the specialist pouncers, in that they usually fly out and eat several small items, rather than a single large one before returning to, or going on to another, elevated perch. This is related, as might be expected, to beak morphology, the specialists having stronger, and often hooked, beaks.

No species which also eats fruits or seeds is a pouncing species, which suggests that it is a technique requiring specific adaptations. The bird has to be fairly strong to overpower large prey items and fairly manoeuvrable to catch them. They and the aerial feeders must expend considerably more energy per food item than species using other feeding methods, so there may be a relatively high lower limit to the size of

prey worth taking. Most aerial feeders have had to sacrifice some of their beak strength for a wide gape to catch fast-moving prey. Hence they probably take more and smaller prey than the pouncers, and this may explain why there are relatively few large aerial feeders or small pouncers. The mean weight of the six specialist aerial feeders is about half that of the ten specialist pouncers (see Table 6.7).

There are some differences in habitat preferences among the ten specialist pouncers but most are commonest where there is open ground with some prominent perches. They fall into three size classes:

a) the two rollers Coracias garrulus and C. caudata; b) the three shrikes Lanius dorsalis, L. minor and Eurocephalus rueppelli with the two kingfishers Halcyon leucocephala and H. chelicuti; and c) the two shrikes Lanius c. collurio and L. c. isabellinus with the flycatcher Bradornis microrhynchus. Unfortunately I have no quantitative data on the size of prey items, except that I often noted it as "quite large". However, three measures might be related; height of perch, distance flown out to food items, and feeding rate. The correlation coefficient between each of these and the size (weight) of the ten species is shown in Table 5.19. Kingfishers have a very different beak shape to the other eight species, and Table 5.19 also shows the correlation coefficients if these two species are excluded. There is a significant relation with two of the three feeding variables, and in two there is an increase in the significance of the correlation coefficient when the two kingfishers are excluded. (In the other, distance flown, the probability is approximately equal to 0.05 in both cases.) This shows that beak shape may be as important as body size in determining what prey can be tackled. The two kingfishers perch higher, fly a little further and feed less often than one would expect from their weight in relation to the other species, and hence may be taking larger prey.

Table 5.19. Correlation coefficients between size of bird (weight) and three feeding characteristics of specialist pouncing species

Feeding characteristic	All 10 species (df 8)		Without 2 kingfishers (df 6)	
	r	Significance	r	Significance
Height of perch	0.33	N.S.	0.60	N.S.
Distance flown to food	0.63	P < 0.05	0.69	P < 0.10
Feeding rate	-0.55	P < 0.10	-0.76	P < 0.05

Note:
The probability level for 'distance flown to food' is approximately equal to 0.05 in both cases.

The three species which pounce for only part of their prey are all Palaearctic chats. One, Oenanthe pleschanka has already been mentioned with the aerial feeders. It takes more single items than the other two, much as if the prey were in the air. The other two, Oenanthe oenanthe and Monticola saxatilis are mainly ground gleaners, but search for feeding sites both from the ground and from an elevated perch. Both species eat many termites, as do many other ground gleaners.

c) Ground-feeders; gleaning

This and the next group contain the greatest number of species and they are the most complex. Four divisions can be broadly defined, and the species in each are shown in Table 5.20.

As will be apparent the divisions are largely reflections of habitat preferences, with those in the first two columns being open country species, those in the third being thick bush species, and those in the fourth two species confined to areas with a high grass cover. Apart from this division there are few differences between the species. Size is a possibility but most, if not all, species feed to a large extent on termites, and as explained earlier I think size is likely to be less important as a means of isolation when the major food is abundant small items. A further piece of evidence suggests that termites may be superabundant for at least some of the year. Of the five Palaearctic migrant species in Table 5.20, three remain fairly common throughout the winter, which is a higher proportion than among Palaearctic migrants as a whole ($8/19 = 42\%$), and particularly of those feeding in the vegetation ($0/8$) (Fisher exact probability test $P = 0.03$). Further four of the five species are bare ground species where one might expect termites to be easiest to find.

Table 5.20. The feeding substrate of 'common' purely insectivorous ground gleaning species
x = primary substrate, (x) = secondary substrate

	Bare ground	Sparse or short grass	litter, often near bushes	thick grass
<u>Ground glean only</u>				
plover <u>V. tectus</u>	x	-	-	-
<u>V. coronatus</u>	x	-	-	-
courser <u>C. cinctus</u>	x (nocturnal)-		-	-
hoopoe <u>U.e. africana</u>	x (and digs)		(x)	-
barbet <u>T. erythrocephalus</u>	-	-	x	-
pipit <u>T. tenellus</u>	-	x	-	-
<u>M. aurantiigula</u>	-	-	-	x
shrike <u>R. cruentus</u>	-	x	-	-
thrush <u>T. tephronotus</u>	-	-	x	-
chat <u>C. leucophrys</u>	-	-	x	-
<u>C. galactotes</u>	x	-	(x)	-
<u>O. isabellina</u>	x	(x)	-	-
warbler <u>C. nana</u>	-	x	-	-
starling <u>S. fischeri</u>	x	-	-	-
<u>S. superbus</u>	x	-	-	-
<u>Ground glean and pounce</u>				
thrush <u>M. saxatilis</u>	x	-	-	-
chat <u>O. oenanthe</u>	x	(x)	-	-
<u>Ground glean and vegetation glean</u>				
cuckoo <u>C. superciliosus</u>	-	-	x	-
chat <u>I. gutturalis</u>	-	-	x	-
chatterer <u>T. aylmeri</u>	-	-	x	-
warbler <u>C. simplex</u>	-	-	x	-
<u>C. cinereaola</u>	-	-	-	x
No. of species	10	3(+2)	7(+2)	2

Only one of the species which eats seeds or fruit as well, the starling Cosmopsarus regius, comes into the bare ground category, and only two, the larks Mirafra hypermetra and M. cantillans, are added to the thick grass category. The remaining nineteen, three of which also feed in the vegetation, are added to the middle columns and several can be classified in both categories. This falls into line with their position as complete food generalists and being very adaptable to whatever conditions are available.

d) Vegetation gleaners; green vegetation

In this group I have included all species taking insects in the woody vegetation except those specialising on twigs (next section). Nevertheless, some may take some of their food from twigs, often of necessity e.g. the warblers Hippolais languida and Camaroptera simplex. The 21 purely insectivorous species can be divided into those feeding in trees, and those in bushes, with six of the latter also feeding on the ground (Table 5.21).

All seven tree-feeding species are ecologically separate. Four are commonest in Riverine probably due to the higher proportion of ever-green trees, and four are Palaearctic migrants, three of which only occur when the trees are in leaf. All three African species are resident. The shrike Nilaus afer is in Wooded and Bushed Grassland and Wooded Bushland and the other two in Riverine. There the shrike Dryoscopus cubla takes food mainly from perches inside the trees, and the flycatcher Batis minor takes it mainly while in flight and near the edge. Of the four Palaearctic migrants the cuckoo Cuculus canorus is nearly ten times the size of the three warblers and these are discussed in ch 5.3.34.

The 14 bush feeders are more similar to each other, and nine are resident. Three stand out as separate. The warbler Cisticola cinereola is commonest in the very open habitats, the cuckoo Centropus superciliosus

Table 5.21 Feeding positions of the 'common' purely insectivorous
vegetation-gleaning species

Tree-feeders	Bush-feeders	Bush and ground-feeders
cuckoo <u>C. canorus</u>	cuckoo <u>C. jacobinus</u>	cuckoo <u>C. superciliosus</u>
shrike <u>D. cubla</u>	<u>C. caprius</u>	chat <u>I. gutturalis</u>
<u>N. afer</u>	bulbul <u>P. strepitans</u>	chatterer <u>T. aylmeri</u>
warbler <u>H. pallida</u>	shrike <u>T. jamesi</u>	warbler <u>C. simplex</u>
<u>A. palustris</u>	<u>L. funebris</u>	<u>C. cinereola</u>
<u>P. trochilus</u>	warbler <u>H. languida</u>	
flycatcher <u>B. minor</u>	<u>S. communis</u>	
	<u>S. nisoria</u>	
	weaver <u>P. nigricollis</u>	

is much larger, and the cuckoo Clamator jacobinus is at least twice the size of all the others except the shrike Laniarius funebris and chatterer Turdoides aylmeri. The remainder, and these last two, are medium-sized to small species, occurring in the thick habitats and feeding in thick bushes often in the middle of them and out of sight. How they separate I do not know, but only few are very common.

Only four of the vegetation gleaners can be considered very common and widespread and all four are visitors, one African - the cuckoo Chrysococcyx caprius - and three Palaearctic warblers Hippolais pallida, Sylvia communis and Phylloscopus trochilus. One or two others are, however, common in one habitat e.g. the shrike L. funebris in Woodland and shrike D. cubla in Riverine. This suggests that insects are rather scarce in the woody vegetation in the dry season. This is in complete contrast to the ground-feeders of which several are common widespread residents. I do not have the data to show it, but it is likely that insects in the woody vegetation are more seasonal than those on the ground as Morel (1968) found in Senegal (see ch 4.4.4).

Those species also eating fruit can be similarly divided into four tree-feeders and two bush-feeders. The former are all commonest in Riverine (one is equally common in Woodland). The two orioles are considerably larger than the other tree-feeding species in Riverine, and these and the barbet Lybius lacrymosus feed nearer the edge and more often in flight than the largest pure insectivore, the shrike D. cubla. The barbet Pogoniulus pusillus is similar to the warblers except for a much stronger beak. The two bush-feeding species the bulbuls Pycnonotus barbatus and Andropadus importunus seem in no way different to other bush-feeding species.

The three also eating seeds are two weavers and a sparrow, all of which take some of their insects from the ground. The two weavers,

Ploceus intermedius and P. rubiginosus, are visitors for the wet season only, and when feeding in the woody vegetation all three prefer trees, as do the three nectar-feeding sunbirds. The former three are complete generalists and the latter three in addition are very different morphologically so they seem unlikely to be serious competitors with other species in this category.

e) Vegetation-feeders; twigs/branches

This is a group of seven specialists. The warbler Sylvietta brachyura (ch 5.3.34) is much the smallest, and picks insects off horizontal branches and twigs. The two helmet-shrikes Prionops plumata and P. retzii (ch 5.3.31a) take fairly large insects off the surface of trunks and branches, many of them while in flight which suggests that at least some of the insects may be faster-moving ones. The two woodhoopoes Phoeniculus purpureus and P. minor (ch 5.3.21) pick, probe and to some extent excavate mainly on horizontal branches, and the woodpeckers Campethera nubica and Dendropicos fuscescens (ch 5.3.25) are similar, except they search by picking and hammering, and mainly on vertical branches. Hence all seven species are probably separate from each other.

f) Animals

The starling Buphagus erythrorhynchus has this niche to itself. However the swallow Hirundo rustica, drongo Dicrurus adsimilis and a few other species especially nightjars, Caprimulgidae, often follow mammals and take disturbed insects, but none of these birds are dependent on the mammals to disturb their food.

CHAPTER 6 The Bird Communities

6.1. Introduction

Chapter 5 was concerned with individual species and their ecological relationships with each other. In this chapter I consider the bird community in each habitat, both as a whole and divided into ecological groups.

Each species, including now the less common ones omitted from ch 5.4, has been assigned to a status category (resident, African visitor, or Palaearctic migrant), and a feeding guild: firstly by food type ('insect', fruit, seed, nectar or a combination of two of these), and secondly, if it is in the 'insect' guild, to feeding station (air, pounce to ground, ground glean, (green) vegetation glean, twig specialist, large mammal, or a combination of two of these). Details for each species are in Appendix 1.1.

Densities are calculated from Type II censuses. Biomasses are calculated by multiplying each individual by its mean weight (see Appendix 1.1) and then summing. In all cases birds of prey, owls, ostriches and any individuals only seen flying over are excluded. For species in two feeding guilds half the total has been assigned to each for these calculations. In a few cases, large flocks of small birds or a few individual large birds were recorded on sample plots. Where these make a substantial difference to a density or biomass estimate they are recorded as a separate item.

6.2. Structure of the communities and seasonal variations

6.2.1. Results

Table 6.1 shows the percentage composition of numbers of birds in each primary food guild in each habitat summed over the 24 months of the study. The most obvious feature of this table is that in all the Park

TABLE 6.1. Percentage composition (of numbers of individuals) in each primary food guild in each habitat in Tsavo

Food Guild	Habitat							PSH	TOTAL
	G	BG	WBG	B	WB	W	R		
Insect	44	29	24	22	19	39	24	24	26
Fruit	-	1	1	1	1	14	5	1	3
Seed	36	46	56	50	58	10	55	52	48
Insect + Fruit	-	5	4	5	6	25	9	5	14
Insect + Seed	20	19	15	23	16	5	6	17	8
Insect + Nectar	-	x	x	x	1	7	1	x	1

All insect	54	41	33	36	31	58	32	36	37
All fruit	-	3	3	3	4	26	9	3	7
All seed	46	56	64	61	65	12	58	61	55
All nectar	-	x	x	x	x	4	1	x	1

Total numbers	1078	2491	4836	2906	4133	2463	4865	15444	22772

Notes:

- 1) The numbers in each habitat are the total over the 24 months of the study.
- 2) Percentages are rounded to the nearest whole number.
- 3) x means less than 0.5%.
- 4) Habitat abbreviations in this and subsequent tables in this chapter as in ch. 2.5.
PSH is a combined figure for the Park savanna habitats (G, BG, WBG, B, and WB).

savanna habitats there is a very low proportion of frugivorous birds and high of granivorous, and in the Woodland a fair proportion of frugivorous and relatively low of granivorous birds. Riverine has an intermediate proportion of frugivores but still has a high granivorous population. Insectivores are progressively less important from Grassland to Wooded Bushland. The high proportion in Grassland is due mainly to plovers Charadriidae, in particular the Palaearctic Charadrius asiaticus. Woodland, too, has a high proportion of insectivores, and this habitat also has the highest proportion of polyphagous species (insect and fruit, insect and seed, insect and nectar).

Figures 6.1 to 6.7 show the total density, and the densities of all insectivores, all frugivores, all granivores and all nectarivores in each habitat over the two years. The statistics of the significance of the seasonal patterns are given in Table 6.2. There are similarities between several of the habitats particularly, as one might expect from the above, between the five Park savanna habitats (Figs 6.1 to 6.5). These five all show a peak in total abundance in December and January, and all have a trough between about May and October. Looking at the breakdown into food guilds, one can see that in these habitats the insectivores, granivores and frugivores all follow this pattern, although the contribution of the last to the total is minimal. The seasonal pattern is significant in each case, however. The contribution of the insectivores is to a large degree caused by the Palaearctic migrants and not Ethiopian region species. When they are excluded the significance of the seasonal pattern is reduced in all habitats although only actually lost in Bushland and Riverine (Table 6.2). The granivores are mainly responsible for the seasonal variation in the total.

Woodland (Fig 6.6), in contrast, shows a different pattern, although some of the elements of Figs 6.1 to 6.5 are still present. The total density shows much less variation through the year than in the Park savanna

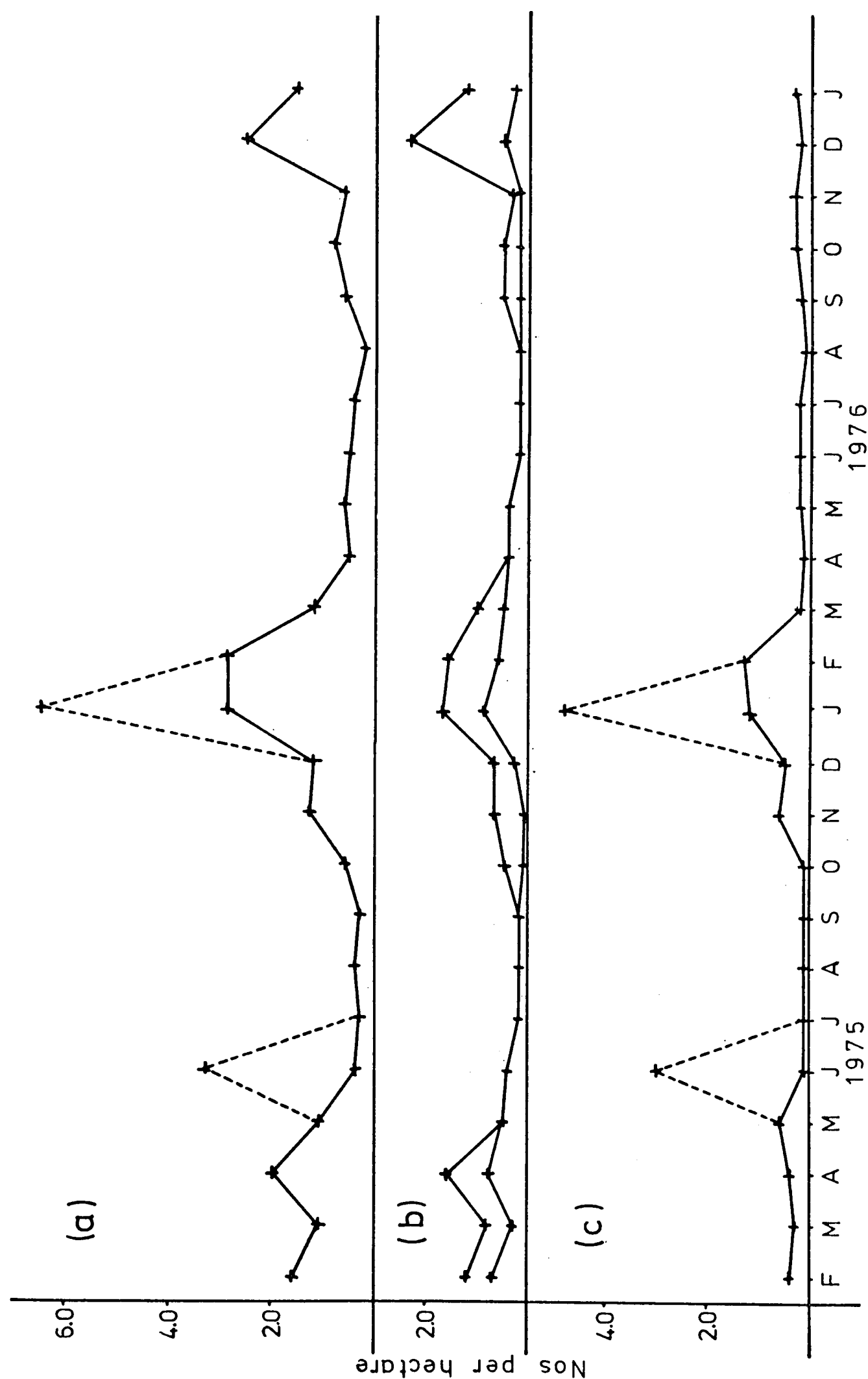


Fig. 6.1 The density of birds in Grassland in each month; a) total density, b) insectivores - the lower line excludes Palaeartic migrants, c) granivores. Dotted lines include large flocks as in Table 6.5. For the significance of the seasonal patterns see Table 6.2.

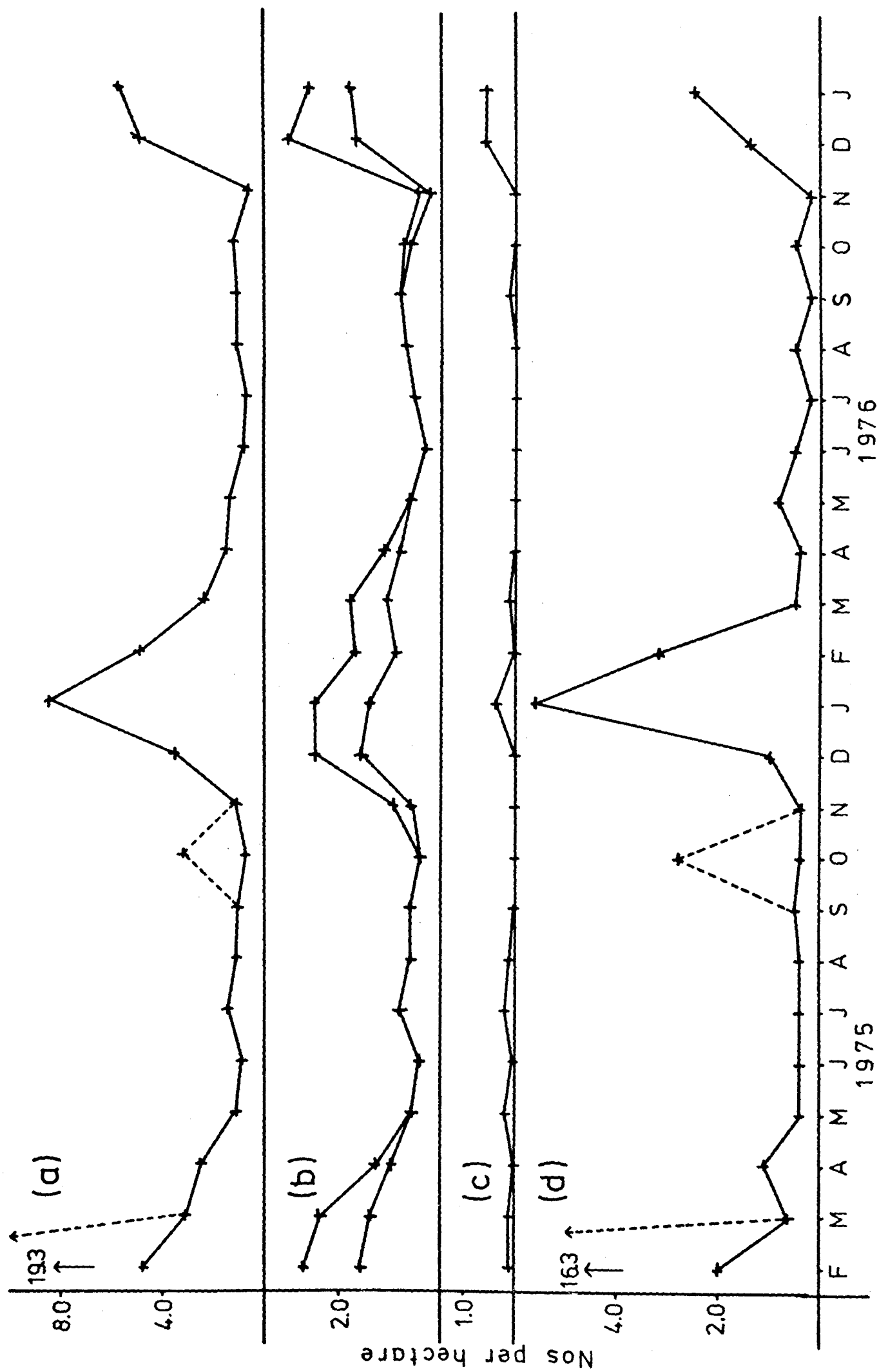


Fig. 6.2 The density of birds in Bushed Grassland in each month; a) total density, b) insectivores - the lower line excludes Palaearctic migrants, c) frugivores, d) granivores. Dotted lines include large flocks as in Table 6.5. For the significance of the seasonal patterns see Table 6.2.

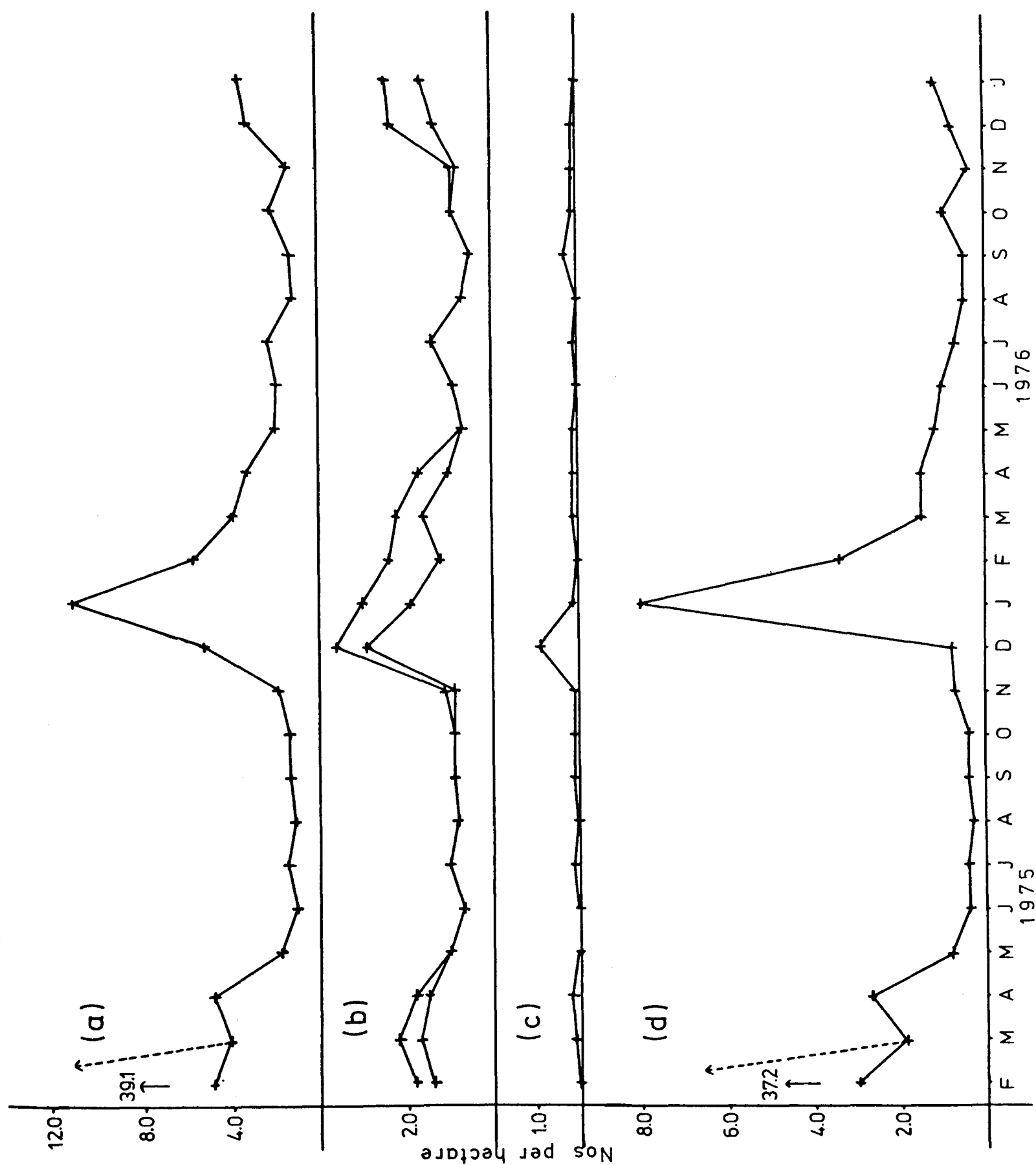


Fig. 6.3 The density of birds in Wooded and Bushed Grassland in each month; a) total density, b) insectivores - the lower line excludes Palaearctic migrants, c) frugivores, d) granivores. Dotted lines include large flocks as in Table 6.5. For the significance of the seasonal patterns see Table 6.2.

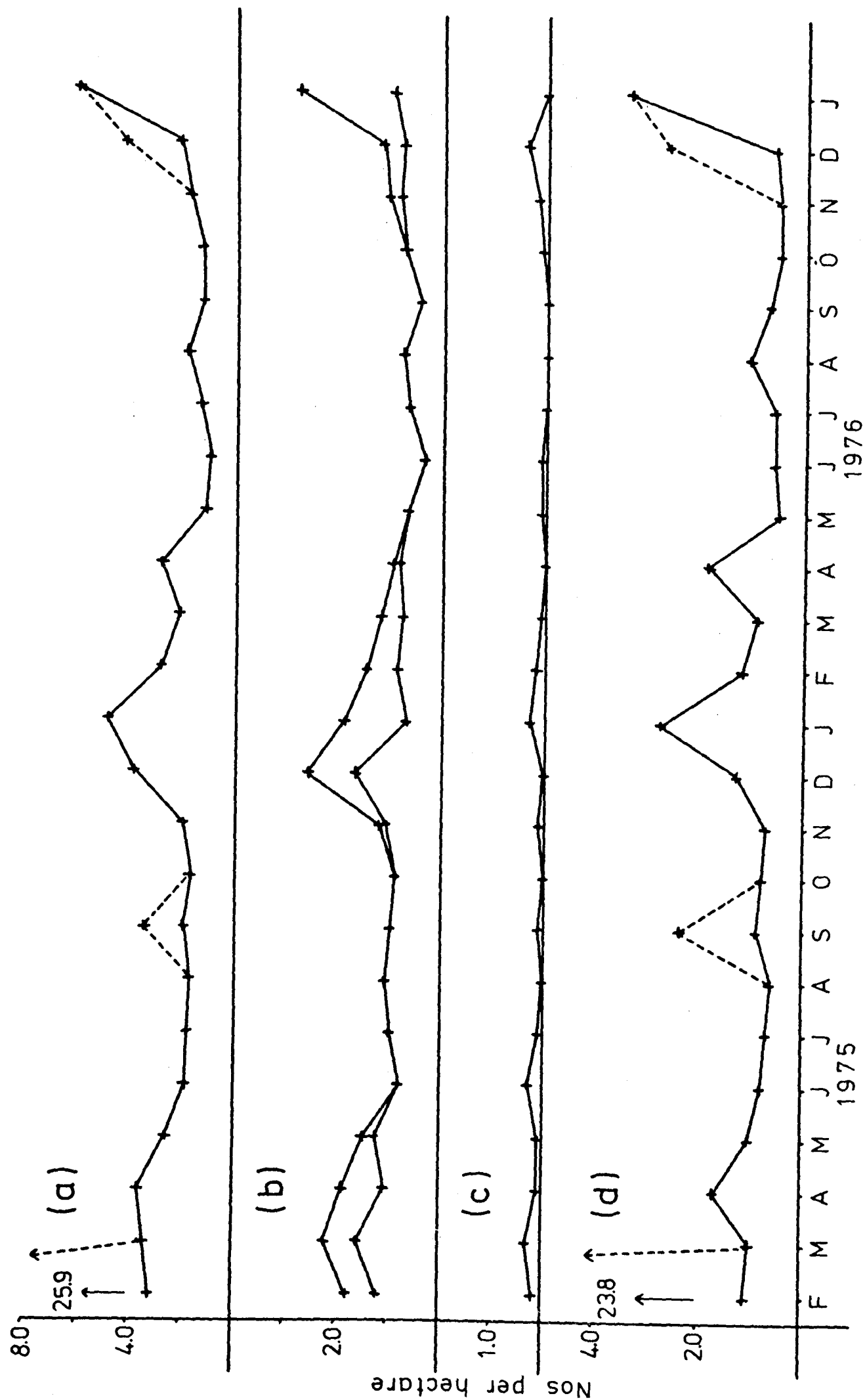


Fig. 6.4 The density of birds in Bushland in each month; a) total density, b) insectivores - the lower line excludes Palaearctic migrants, c) frugivores, d) granivores. Dotted lines include large flocks as in Table 6.5. For the significance of the seasonal patterns see Table 6.2.

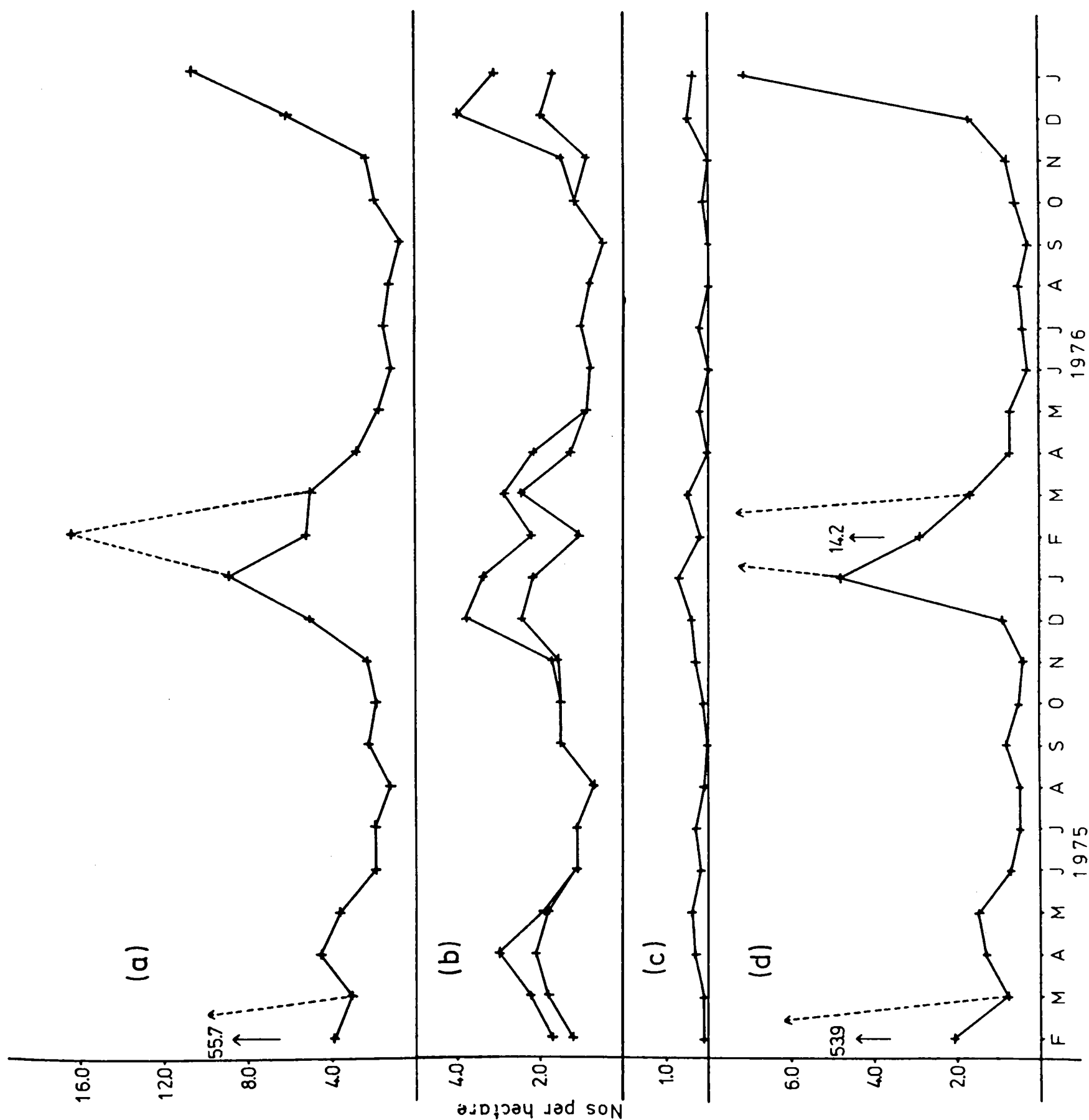


Fig. 6.5 The density of birds in Wooded Bushland in each month; a) total density, b) insectivores - the lower line excludes Palaearctic migrants, c) frugivores, d) granivores. Dotted lines include large flocks as in Table 6.5. For the significance of the seasonal patterns see Table 6.2.

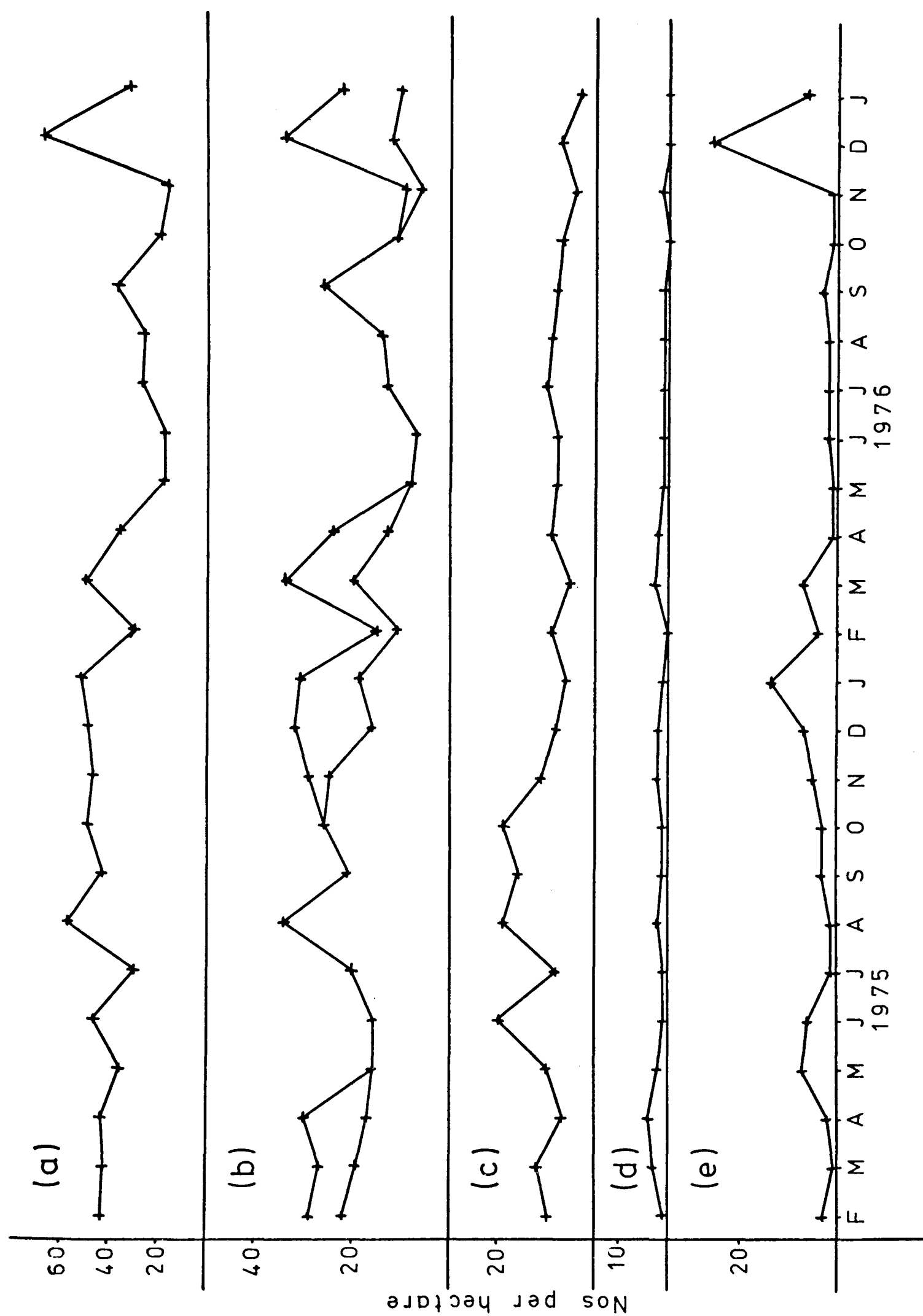


Fig. 6.6 The density of birds in Woodland in each month; a) total density, b) insectivores, - the lower line excludes Palaearctic migrants, c) frugivores, d) nectarivores, e) granivores. For the significance of the seasonal patterns see Table 6.2.

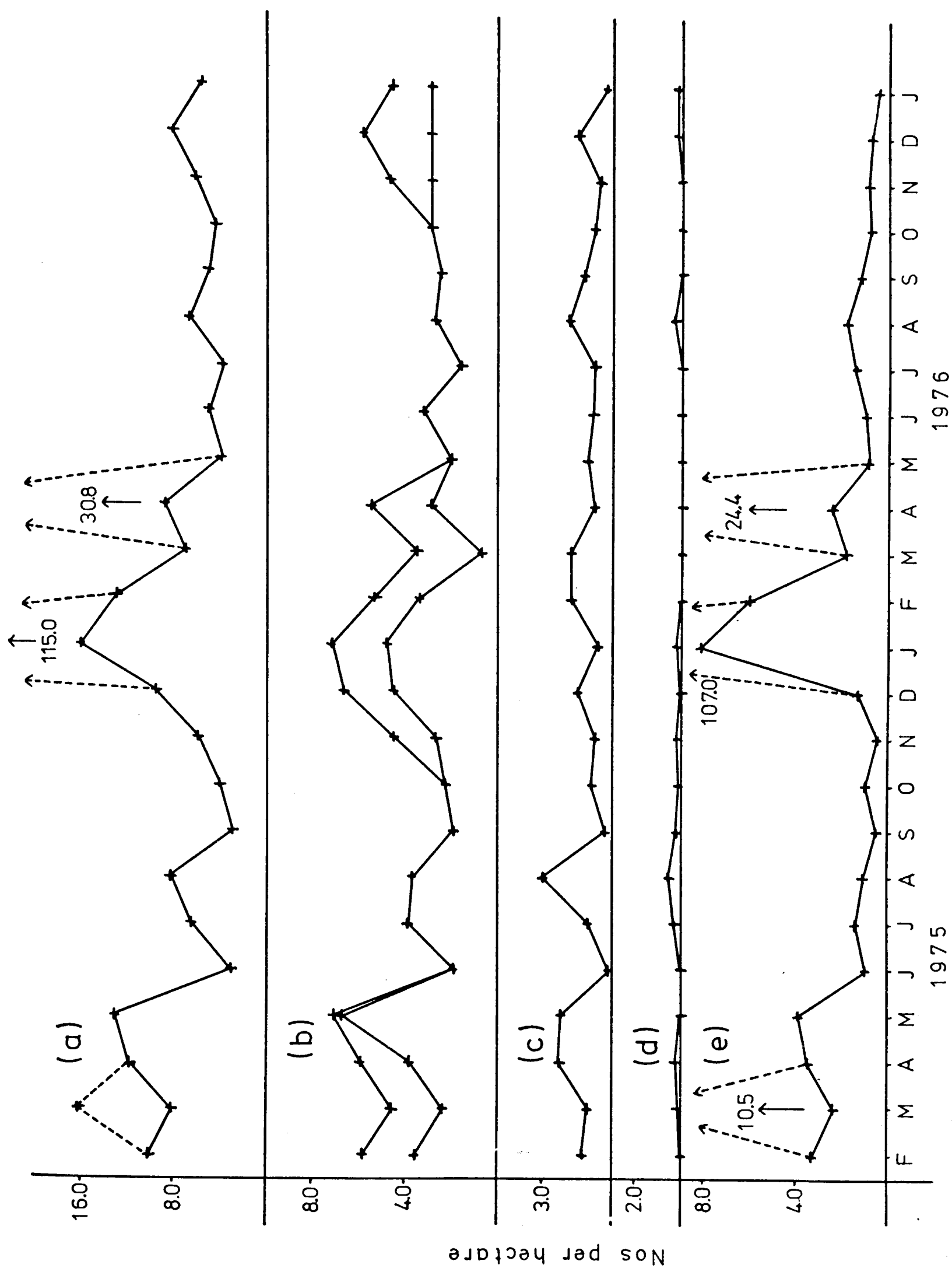


Fig. 6.7 The density of birds in Riverine in each month; a) total density, b) insectivores - the lower line excludes Palaearctic migrants, c) frugivores, d) nectarivores, e) granivores. Dotted lines include large flocks as in Table 6.5. For the significance of the seasonal patterns see Table 6.2.

TABLE 6.2. Statistics of seasonal patterns of density in each habitat

a) Grassland

Guild ^a	Insect	excl. Pal.	Seed	+flocks	TOTAL	+flocks
N	585	289	278	499	863	1084
R/N	0.43	0.31	0.39	0.32	0.42	0.38
2R ² /N	217	57	83	101	300	307
Significance	***	**	**	***	***	***
Peak week	Jan 3	Feb 4	Jan 3	Feb 1	Jan 3	Jan 4

b) Bushed Grassland

Guild	Insect	excl. Pal.	Fruit	Seed	+flocks	Nectar	TOTAL	+flocks
N	1019	717	83	820	1385	4	1926	2491
R/N	0.41	0.27	0.53	0.53	0.64	0.69	0.47	0.54
2R ² /N	346	104	47	457	1122	3.8	833	1447
Significance	***	***	**	***	***		***	***
Peak week	Jan 3	Jan 2	Jan 1	Jan 3	Jan 3		Jan 3	Jan 3

c) Wooded and Bushed Grassland

Guild	Insect	excl. Pal.	Fruit	Seed	+flocks	Nectar	TOTAL	+flocks
N	1620	1274	131	1359	3076	9	3059	4836
R/N	0.29	0.17	0.28	0.45	0.73	0.18	0.36	0.56
2R ² /N	280	75	21	556	3288	0.6	791	3032
Significance	***	**	**	***	***		***	***
Peak week	Jan 3	Jan 3	Apr 4	Feb 1	Feb 1		Feb 1	Jan 4

d) Bushland

Guild	Insect	excl. Pal.	Fruit	Seed	+flocks	Nectar	TOTAL	+flocks
N	1016	749	92	880	1172	6	2014	2906
R/N	0.24	0.06	0.30	0.25	0.56	0.34	0.25	0.44
2R ² /N	118	5.4	16	107	1094	1.5	254	1115
Significance	***		**	***	***		***	***
Peak week	Jan 3		Jan 4	Jan 4	Jan 4		Jan 4	Jan 4

e) Wooded Bushland

Guild	Insect	excl. Pal.	Fruit	Seed	+flocks	Nectar	TOTAL	+flocks
N	1262	952	147	921	2707	18	2348	4134
R/N	0.31	0.18	0.34	0.51	0.83	0.33	0.39	0.65
2R ² /N	241	64	34	470	3699	3.9	704	3452
Significance	***	**	**	***	***		***	***
Peak week	Jan 3	Jan 3	Jan 4	Jan 3	Feb 1		Jan 3	Jan 4

f) Woodland

Guild	Insect	excl. Pal.	Fruit	Seed	Nectar	TOTAL
N	1423	1081	635	294	91	2445
R/N	0.13	0.09	0.15	0.38	0.19	0.08
2R ² /N	47	17	27	85	6.2	33
Significance	**	**	**	**	*	**
Peak week	Dec 4	Sep 2	Aug 1	Dec 4	Apr 4	Dec 3

g) Riverine

Guild	Insect	excl. Pal	Fruit	Seed	+flocks	Nectar	TOTAL	+flocks
N	1609	1182	461	708	2820	33	2801	4913
R/N	0.20	0.04	0.08	0.31	0.69	0.49	0.19	0.46
2R ² /N	126	4.3	6.5	134	2660	16	193	2055
Significance	***		*	***	***	**	***	***
Peak week	Jan 4		May 1	Feb 4	Jan 4	Jan 4	Feb 2	Jan 4

Notes:

- 1) The statistics are explained in ch 5.2.5. Significance levels ~~xxx~~ = very significant $2R^2/N > 100$; ~~xx~~ = $P < 0.01$ but $2R^2/N < 100$; ~~x~~ = $0.01 < P < 0.05$; blank = not significant. Peak week is only given if there is a significant seasonal pattern.
- a) The 'insect' guild includes all insectivores and 'seed' includes all granivores etc. as in Figs 6.1 to 6.7. For insectivores a figure which excludes the Palaearctic migrants is also given (the lower dotted line in part b of Figs 6.1 to 6.7). For granivores and the total a second figure including the flocks shown by dotted lines on Figs 6.1 to 6.7 is also given.

habitats, and the most obvious feature is that there was a lower density in 1976 than in 1975 (see next section). The insectivores still show a peak in abundance from December to April, although this is now almost wholly due to the Palaearctic migrants, indeed if they are excluded the date of peak numbers moves to September (Table 6.2). Granivores too show a similar cycle to what they show in the Park savanna habitats. Frugivores, as shown above, are much more prominent. The small December and January peak, seen in the Park savanna habitats, is not present, indeed the lowest numbers are present for this period, but there is a significant peak of numbers from about June to October. This peak is paralleled by the African insectivores as noted above.

The seasonal variation of density in Riverine (Fig 6.7) largely follows the Park savanna habitats with major peaks in December and January resulting mainly from increases of insectivores and granivores. Frugivores are, however, more prominent (Table 6.1) than in the Park savanna habitats, and, in addition to a slight peak in December and January, there is a slight peak in August, again paralleled by the insectivores. The statistics show a barely significant peak in May, due to this being an average of the two actual periods of high numbers.

Nectarivores occur only very rarely in the Park savanna habitats. In Woodland and Riverine there are small numbers and they show barely significant seasonal patterns of variation.

One can see from Figs 6.1 to 6.7 that, at some times of year, Palaearctic migrants are an important component of the numbers of birds in all habitats. Table 6.3 shows the percentage in each habitat in each month. The proportion is highest in Grassland, with a slight decrease progressively to Wooded Bushland; Woodland has a high proportion and Riverine about average, altogether a pattern very similar to insectivores as a whole. In all habitats except Grassland the main increase in numbers of Palaearctic migrants occurs in November. Numbers reach a peak in

TABLE 6. 3. The percentage (of number of individuals) of Palaearctic migrant in each habitat in each month

		Habitat								
Month		G	BG	WBG	B	WB	W	R	PSH	TOTAL
1975	Feb	51	6(24)	1(9)	2(17)	1(12)	17	21	2(16)	3(17)
	Mar	43	33	11	18	12	19	13(27)	19	17(20)
	Apr	38	13	6	23	20	30	18	17	19
	May	-	-	1	8	2	-	1	3	2
	Jun	-	-	-	-	-	-	-	-	-
	Jul	-	-	-	-	-	-	-	-	-
	Aug	-	-	-	-	-	-	-	-	-
	Sep	-	-	-	-	-	-	-	-	-
	Oct	63	-	-	-	-	1	-	4	3
	Nov	43	21	12	7	6	8	31	15	16
	Dec	31	24	13	23	26	33	23	21	23
1976	Jan	12(27)	13	10	24	14	23	2(15)	13	8(16)
	Feb	34	16	21	22	7(21)	16	14	15(22)	15(21)
	Mar	45	31	16	16	7	29	39	18	23
	Apr	6	19	21	2	30	31	8(29)	17	14(22)
	May	-	2	1	-	-	-	-	1	1
	Jun	-	-	-	-	-	-	-	-	-
	Jul	-	-	-	-	-	-	-	-	-
	Aug	-	-	-	-	-	-	-	-	-
	Sep	50	-	-	-	-	-	-	6	3
	Oct	36	5	-	-	-	2	-	4	3
	Nov	16	40	9	10	26	17	28	18	20
	Dec	73	26	31	8(16)	32	33	37	30	32(36)
1977	Jan	62	13	21	30	14	37	30	21	23
Total		27(35)	12(16)	7(11)	9(13)	8(13)	14	8(15)	10(15)	10(15)
Total										
Nov to Apr		34(41)	15(20)	9(16)	12(19)	9(18)	25	11(24)	12(20)	13(21)

Notes:
1) Percentages are rounded to the nearest whole number
2) The figures in brackets show the percentage if large flocks are excluded from the total numbers seen. See text.

December in the middle of the rains, and there is then a decrease in the subsequent dry season. Numbers increase again slightly in March and/or April, the spring passage, and this coincides with the second wet season. Grassland is different from the others with a high proportion in October and, in 1976, September as well. This is entirely due to the plover C. asiaticus which passes through at that time (see ch 5.3.5).

6.2.2. Discussion

Increases in numbers could be caused by two factors: reproduction and immigration. Of these, immigration is far the more important in this study. Peaks of insectivores and granivores in the wet season are caused largely by species not present for the rest of the year, and the numbers increase within a week or two of the onset of the rains, before they have had time to produce young in Tsavo. Moreau (1950) said that in semi-arid areas many species start to breed before the wet season and hence young would be produced early in the wet season, but in Tsavo most species breed in the wet season only (see ch 7). The mid dry season peak in Woodland and Riverine is composed more of increased numbers of 'resident' species but I have no evidence of a great increase in juveniles rather than adults and, as most species breed in wet seasons, one would expect, if reproduction is the cause, for the increase to occur in May or June and not July or August.

Explanations for many of the similarities and differences between habitats in both the structure of the bird communities, and seasonal variations, can be found if one compares the data with those of food availability in ch 4. The birds in the different food guilds are therefore discussed below in turn.

a) Frugivores

There are no frugivores in Grassland and only very few, mostly of

species which eat both fruit and insects, in the other Park savanna habitats. This is because of the paucity of fruit-bearing trees and bushes in these habitats, indeed Premna spp. are the only significant producers. The seasonal fruiting of Premna spp. (Fig 4.1a) is sufficient, however, to cause a slight increase in the number of frugivores in December and January, although the small April peak of Premna fruiting does not produce a visible increase in the number of frugivorous birds.

There is much more fruit available in Woodland and Riverine, and both habitats have sizeable resident populations of frugivores, both obligate ones, and those eating both fruit and insects. The June to October peak in numbers of birds in Woodland coincides with the peak of Commiphora fruit (Fig 4.2), and the main contributors are species eating both fruit and insects, in particular the two hornbills Tockus erythrorhynchus and T. deckeni. The small August peak in Riverine coincides with the fruiting of Salvadora persica (Table 4.1). Here, however, it is two species of obligate frugivores which are the main contributors, the mousebirds Colius macrourus and C. striatus, although other species were seen to be taking advantage of the temporary food supply.

b) Nectarivores

Nectarivores only make a significant contribution to the numbers of birds in Woodland, though they occur at intervals in Riverine. There are three common species in the Woodland but only Nectarinia hunteri shows any seasonal pattern of occurrence and this species has as individual peak in July (ch 5.3.37). Sunbirds do not seem to increase in the Park savanna habitats with the short flowering season of Platycelyphium voense in late March (Fig 4.3a). There is, however, only the one species, again N. hunteri which is widespread in these habitats and it is never abundant. Further, the sunbirds may be really only dependent on the insects, taking nectar as a sideline only when it is available.

c) Granivores

The granivores show a very similar seasonal pattern of occurrence in each habitat. The only difference between habitats is the relative contribution they make to the total in each, high in the Park savanna habitats and low in Woodland. This follows the amount of grass seed available (ch 4.3.3).

The peaks in numbers are largely caused by the immigrants of two species, the dove Streptopelia senegalensis and weaver Quelea quelea, both of which seem to be entirely granivorous when in Tsavo, although the latter certainly eats many insects while breeding (Jones & Ward 1976). Q. quelea breeds in Tsavo but not every year and, presumably, the need for a plentiful supply of insects would not affect the species' arrival as insects show a peak in abundance at about the same time.

d) Insectivores

The main peak in numbers of insectivores, December to February, coincides with the peak insect abundance (ch 4.3.4). Ignoring the Palaearctic migrants for the present, the peak is partly due to additional species coming in but a proportion of the change occurs within the apparently resident species. In Woodland there is also a peak in the abundance of insectivores between July and October which does not coincide with a peak of insect abundance. Fig 6.8 shows that this is due almost entirely to those eating insects and fruit so it is presumably due to the fruiting of Commiphora spp. then (Fig 4.2 and see above). The peak of abundance coincides with the trough in the Park savanna habitats but, although it may occur to a limited extent, I consider migration between Woodland and the Park savanna habitats is less important than migration into and out of the Tsavo area as a whole. There are two reasons for this. In Woodland the insectivores show a sharp drop in

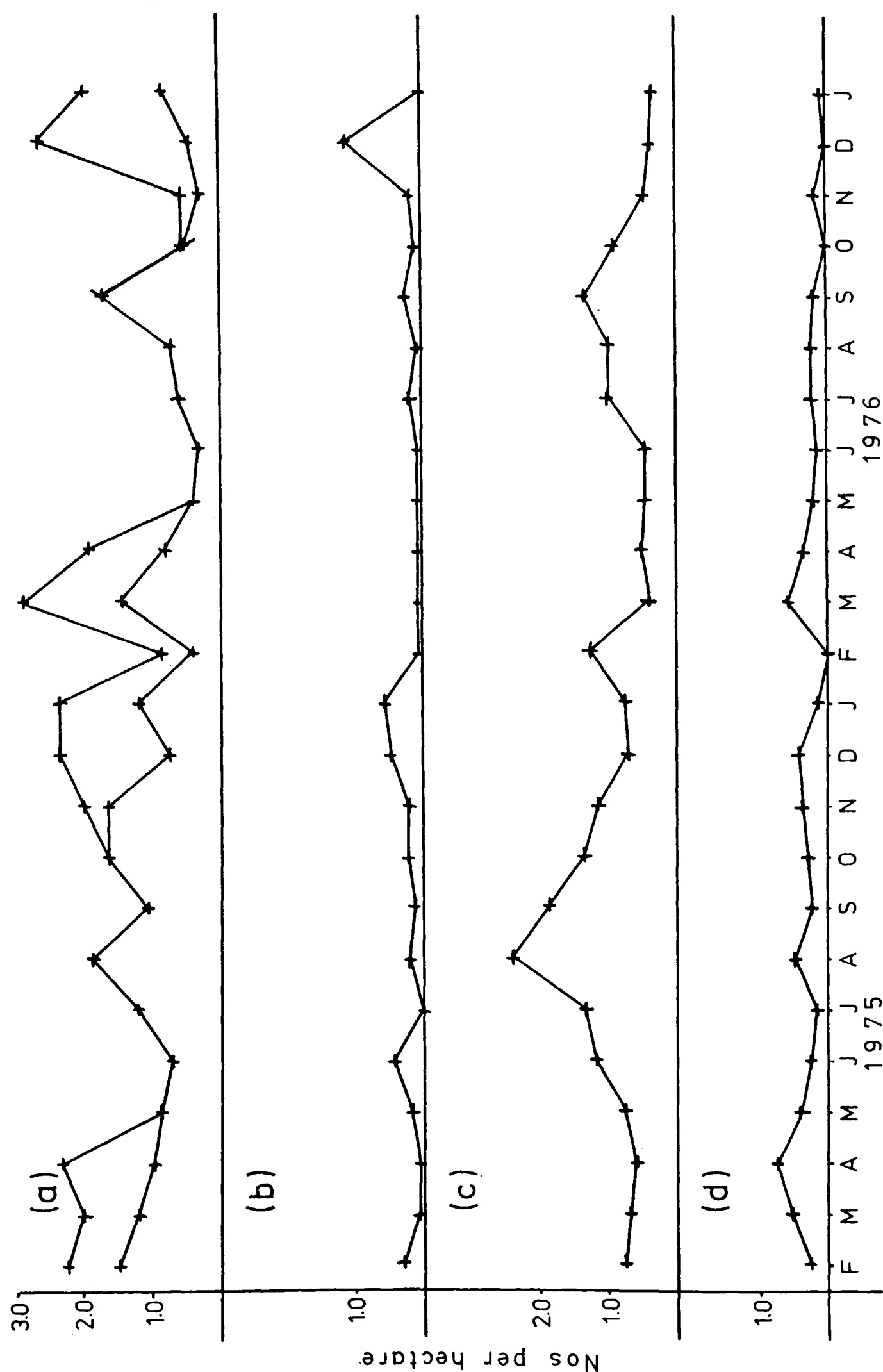


Fig. 6.8 The density of insectivorous birds in Woodland in each month;
 a) those eating only insects ($2R^2/N=100$, $N=972$, $P<0.001$, peak Jan 2),
 - the lower line excludes Palaearctic migrants ($2R^2/N=4.7$, $N=630$, N.S.),
 b) those eating insects and seeds ($2R^2/N=30$, $N=137$, $P<0.001$, peak
 Nov 3),
 c) those eating insects and fruit ($2R^2/N=69$, $N=594$, $P<0.001$, peak
 Aug 3),
 d) those eating insects and nectar ($2R^2/N=12$, $N=182$, $P<0.001$, peak
 Apr 4).

numbers after the peak, especially noticed in 1976, which is not matched by an increase in the Park savanna habitats. Secondly the Park savanna habitats have a higher proportion of insect-and-seed eaters and lower of insect-and-fruit eaters than Woodland (Table 6.1). And even within the purely insect eaters there are different proportions in each of the secondary guilds (Table 6.4).

Table 6.4 The percentage of numbers of purely insectivorous birds using each feeding method in the Park savanna habitats and Woodland.

	Air	Pounce	Percentage using		Twig	Animal	Total
			Ground Glean	Green Vegetation			Numbers
Park Savanna Habitats	13	23	42	8	12	2	1715
Woodland	17	12	18	21	32	-	577

The insectivores in Riverine remain in fairly constant numbers through the seasons. There is a small peak in numbers from December to February as there is elsewhere, and a very slight but not significant one coinciding with, and perhaps due to, the August fruiting peak.

The high proportion of Palaearctic migrants in Grassland is, as mentioned above, due almost entirely to the plover C. asiaticus. The relatively high proportion in Woodland to other Park savanna habitats, especially in the wet seasons, can be explained by the differing proportions of vegetation and ground gleaners in the respective habitats (Table 6.4). Most of the Palaearctic migrants which are vegetation gleaners are present only in the wet seasons, and, on the whole, such species feed more from small and young leaves such as Commiphora and Acacia, than on the thicker, larger, especially evergreen ones, because the insects in turn prefer them (Feeny 1970). These small-leaved plants are especially dominant in Woodland.

e) Polyphagous species

Table 6.1 showed Woodland to have a higher proportion of polyphagous species than other habitats. This is partly due to the three species of sunbird but it is still true if these are excluded. The high polyphagous proportion is correlated with the lesser seasonal variation and resultant higher resident population. Many of the common residents are polyphagous because of the harsh conditions in the dry season making a catholic diet advantageous (see ch 7.2).

6.3. Density, biomass and energy requirements

6.3.1. Results

Figures of bird density in each habitat can be read off Figs 6.1 to 6.7, but for convenience the totals are given in Table 6.5 with the breakdown into food guilds in Appendix 4.1. Figures for biomass are given similarly in Table 6.6 and Appendix 4.2. The proportion in each guild and the seasonal cycles have already been discussed in terms of density. Biomass, in general, follows the same patterns although the relative proportion of the birds in each guild is slightly different because of different average weights. Table 6.7 gives the range, mean, and because of the often very skewed distributions, the median weight of various groupings of the 115 'common' species. In particular it should be noted that insectivores are small and frugivores large. Within the former, species which feed on the ground (pouncers and gleaners) are larger than those which feed in the vegetation (vegetation gleaners and twig specialists), and the latter are larger than those which feed in the air. Palaearctic migrants are small.

Tables 6.5 and 6.6 show that there is a higher density and biomass with increased complexity of vegetation. Grassland has particularly low,

TABLE 6.5. The density of birds in each habitat in each month

Month	Habitat					
	G	BG	WBG	B	WB	W
1975	Feb	1.6	4.8(+14.3) ^b	4.9(+34.2) ^b	3.2(+22.7) ^b	4.3
	Mar	1.1	3.1	4.2	3.4	4.2
	Apr	2.0	2.5	4.8	3.6	4.3
	May	1.1	1.1	1.8	2.6	3.6
	Jun	0.4(+2.9) ^a	0.9	1.1	1.9	4.6
	Jul	0.3	1.5	1.5	1.8	3.0
	Aug	0.4	1.1	1.1	1.7	6.6
	Sep	0.3	1.1	1.4	2.0(+1.5) ^c	8.3
	Oct	0.6	0.8(+2.4) ^a	1.4	1.7	2.9
	Nov	1.3	1.2	1.9	2.0	4.1
	Dec	1.2	3.6	5.3	3.9	5.9
	1976 Jan	2.9(+3.6) ^b	8.5	11.1	4.9	9.6
	Feb	2.9	4.9	5.8	2.9	5.2
	Mar	1.2	2.4	3.9	5.3(+11.3) ^b	13.1
	Apr	0.5	1.5	3.3	2.2	7.1
	May	0.6	1.4	2.0	2.9	8.9(+21.9) ^b
	Jun	0.5	0.8	1.9	1.2	4.0
	Jul	0.4	0.7	2.3	1.0	5.1
	Aug	0.2	1.1	1.2	1.4	3.9
	Sep	0.6	1.1	1.3	1.9	6.8
	Oct	0.8	1.2	2.1	1.3	5.1
	Nov	0.6	0.6	1.4	0.8	4.5
	Dec	2.5	4.9	3.2	2.0	6.2
	1977 Jan	1.5	5.7	3.6	2.2(+2.1) ^b	8.1
						5.6
Average						7.4
Average incl.						
large flocks						12.8

Notes:

1) The figures in the table are the number of individuals per hectare

2) The figures in brackets are single large flocks identified by superscript a) lark Eremopterix signata b) weaver Quelea quelea c) weaver Pseudonigritya cabanisi

TABLE 6.6 . The biomass of birds in each habitat in each month

Habitat

Month	G	BG	WBG	B	WB	W	R
1975 Feb	53	259(+243) ^b	255(+582) ^b	155(+386) ^b	156(+880) ^b	240	572
Mar	35	134	224	111	134	224	315(+138) ^b
Apr	128	111	193	166	189	213	540
May	37	59	139	122	172	252(+74) ^d	625
Jun	29(+44) ^a	79	92	188	142	398(+429) ^e	197
Jul	14	89	71	138	118	231	451(+406) ^f
Aug	47	54	81	124	58	478	474
Sep	42	75	78	113(+28) ^c	91	392	206
Oct	34	37(+35) ^a	68	107	81	456	230
Nov	82	95	117	136	100	355	244
Dec	53	171	273	203	223	229	545
1976 Jan	134(+61) ^b	457	495	280	523	242	866(+1679) ^b
Feb	110	181	254	141	210(+193) ^b	201	647
Mar	48	127	124	239	303	198	391
Apr	30	97	139	166	194	247(+37) ^d	387(+372) ^b
May	30	66	104	70	113	184	349
Jun	26	92	119	114	53	192	400
Jul	23	53	182	93	69	218(+74) ^d	278
Aug	17	74	81	84	103	175	368
Sep	42	55	67	78	23	213	312
Oct	41	50	114	70	117	173	313
Nov	49	17	72	77	165	132	357
Dec	136	263	171	155(+36) ^b	272	242	352
1977 Jan	75	336	179	345	626	156	269
Average	55	126	154	145	176	252	404
Average incl. large flocks/ large birds	59	138	178	164	221	277	495

Notes:

1) The figures in the table are in grams per hectare

2) The figures in brackets are single large flocks or large birds identified by superscript a) lark Eremopterix signata

b) weaver Quelea quelea c) weaver Pseudonigrita cabanisi d) crow Corvus albicollis e) guinea-fowl Numida meleagris

f) hornbill Bucorvus cafer

Table 6.7. The average weight of groups of the 115 'common' species

Feeding guild	No. of species	Weight (g)		
		Lowest	Highest	Mean
Fruit only	6	21	225	87
Fruit and insects	14	10	260	88
All frugivores	20	10	260	87
Seeds only	15	9	185	59
Seeds and insects	14	16	690	135
All granivores	29	9	690	95
All nectarivores	3	7	13	11
Insects only ^a				
Aerial hawk	7	14	43	24
Pounce	13	18	120	47
Ground glean	22	5	170	54
Vegetation glean	21	9	145	33
Twigs	7	7	70	38
TOTAL	63	5	170	42
All insectivores ^a				
Aerial hawk	8	7	43	22
Pounce	13	18	170	47
Ground glean	44	5	690	93
Vegetation glean	33	7	145	31
Twigs	7	7	70	38
TOTAL	94	5	690	62
Residents	76	5	690	74
African visitors	20	15	145	43
Palaearctic migrants	19	9	120	39
TOTAL	115	5	690	62

Notes:

a) Species in more than one feeding guild among insectivores are included in the figures for both guilds.

and Riverine particularly high figures for both. The others are relatively much more similar to each other although Woodland has a higher biomass than the others due to the increase of frugivores over granivores.

Density and biomass are the simplest figures to use for comparing avifaunas. However, if one wishes to compare the avifauna with the other elements of the fauna, especially if these are of markedly different size, it is better to compare their energy requirements. Table 6.8 shows the total energy requirements of the birds in each habitat in each month, and Appendix 4.3 the breakdown into food guilds. The figures given are for Basal Metabolic Rate, in kilojoules per hectare per day, and have been calculated using the formulae given by Lasiewski & Dawson (1967) which are:

for non-passerines

$$\log M = 78.3 + 0.723 \log W$$

and for passerines

$$\log M = 129 + 0.724 \log W$$

where W = weight of bird in kg, and M is the Basal Metabolic Rate in kilo-calories per day. The figure of M for each species has been multiplied by 4.1868, to convert calories to joules, and by the density of each species, and these have been summed to give the total for each habitat in each month.

The main effect of these calculations is to reduce the effect of large individuals on the total.

6.3.2. Discussion

The relation of increasing density and biomass, and hence energy requirements, with increasing complexity of vegetation is what one might expect intuitively, but it is perhaps surprising within the Park savanna habitats if one considers how few species are dependent on the woody vegetation for their food in these habitats, whether the food is insects or

TABLE 6.8. The energy requirements of the birds in each habitat in each month

Month	Habitat					
	G	BG	WBG	B	WB	W
1975	Feb	67	248(+406) ^b	231(+975) ^b	146(+646) ^b	157(+1474) ^b
	Mar	50	137	209	127	141
	Apr	88	111	207	152	180
	May	44	53	145	112	190(+40) ^d
	Jun	23(+76) ^a	54	71	127	263(+123) ^e
	Jul	17	77	82	112	180
	Aug	26	53	61	94	377
	Sep	24	63	77	94(+45) ^c	282
	Oct	29	38(+61) ^a	73	84	289
	Nov	58	77	103	102	261
	Dec	60	164	296	183	213
	1976 Jan	124(+101) ^b	395	477	226	235
1976	Feb	112	189	248	125	217(+323) ^b
	Mar	51	116	159	144	176
	Apr	30	85	138	136	200
	May	27	62	91	61	187(+20) ^d
	Jun	23	58	99	69	116
	Jul	19	46	138	75	121
	Aug	15	70	66	91	154(+40) ^d
	Sep	33	66	60	61	145
	Oct	39	56	100	70	187
	Nov	32	24	70	79	129
	Dec	113	258	157	130(+59) ^b	92
	1977 Jan	101	294	172	271	262
Average		50	116	147	120	166
Average incl.						199
large flocks/						
large birds		58	136	188	151	208

Notes:

- 1) The figures in the table are of Basal Metabolic Rate in kilojoules per hectare per day. For the formulae used see text
- 2) The figures in brackets are single large flocks or large birds identified by superscript a) lark Eremopterix signata
- b) weaver Quelea quelea c) Pseudonigrita cabanisi d) crow Corvus albicollis e) guinea-fowl Numida meleagris
- f) hornbill Bucorvus cafer

fruit. The woody vegetation perhaps acts as a refuge from predators, or even as shade from the sun, but there is likely to be more food, both insects and seeds, on the ground in these habitats. In very open habitats, seeds, ground-living insects and other debris are easily blown along the ground. Where there are bushes and trees it has been shown that there is a lower wind-speed, increased humidity and less fluctuation in temperature at the soil surface (Coe 1972, Griffiths 1976). The first of these means that fewer items will be carried away and the latter ensures that the microclimate is more conducive to insects and other small animals.

The two main points to note in the figures for density and biomass are firstly, that the figures for the dry season in the Park savanna habitats are very low indeed and, secondly, that the difference between these and the peak figures is a factor of about five, which is very high. Discussion of these points is postponed to ch 6.5 when comparing Tsavo to other areas that have been studied in Africa.

In 1976 there was a generally lower density and biomass than in 1975. 1976 was a dry year following a series of dry ones, and the food supplies are likely to have been reduced, but I do not have any direct evidence for this. The numbers of birds in Tsavo are also dependent on conditions elsewhere and without data from any of these one cannot speculate further.

6.4. The number of species and species diversity

6.4.1. Results

The number of species on each plot in each month of the study is given in Appendix 4.4. Table 6.9 gives the mean number of species for each habitat in each month, the mean cumulative total for each plot, and the total number of species seen on plots in that habitat. For Woodland

TABLE 6. 9. The number of species in each habitat: the average number of species on a census plot in each month, the average cumulative total on a census plot, and the total number recorded on census plots

		Habitat					
Month		G	BG	WBG	B	WB	W ^a R ^a
1975	Feb	4	10	10	8	11	17 14
	Mar	3	8	8	9	9	19 12
	Apr	5	6	7	8	14	20 17
	May	3	4	5	8	6	15 13
	Jun	2	2	4	5	6	15 6
	Jul	1	4	4	4	5	13 9
	Aug	1	4	3	5	3	17 9
	Sep	2	3	4	5	5	14 5
	Oct	1	3	5	4	5	20 7
	Nov	2	3	5	7	7	21 8
	Dec	3	9	10	11	17	21 15
1976	Jan	5	12	13	10	14	22 14
	Feb	4	8	9	7	10	11 10
	Mar	4	7	9	7	9	18 9
	Apr	2	5	8	5	9	17 13
	May	2	3	5	4	6	9 7
	Jun	2	2	5	3	4	9 6
	Jul	1	3	7	5	4	10 6
	Aug	1	3	3	3	4	13 8
	Sep	1	2	3	3	3	17 7
	Oct	2	3	5	5	7	9 8
	Nov	2	2	6	5	9	10 11
	Dec	3	9	9	6	16	18 12
1977	Jan	3	10	9	12	14	16 9
Average Cumulative Total per plot		18	39	45	46	56	80 68
Total recorded on plots ^b		42	81	94	90	88	105 118

Notes:
1) All figures are rounded to the nearest whole number
2) Details for each census plot are in Appendix 4.3
a) An average figure is not strictly valid due to census plots being different sizes (see text)
b) The figures in the last row are not directly comparable because different total areas were censused in each habitat (see text)

and Riverine this is not strictly a valid procedure, because the individual plots are of different sizes, and similarly the figures in the last ^{row} are not strictly comparable because of different total areas covered in each habitat. The figures do, however, give an indication of the trends present.

Of the five Park savanna habitats, Wooded Bushland is shown to have the greatest number of species, Grassland much the lowest, and with the other three having much the same number as each other in between. Woodland has a consistently greater number than any of these. This is partly due to the larger size of the plots but plot A in Woodland on its own which is the same size as the plots in the Park savanna habitats has a high total. Individual Riverine plots are very variable but the figures suggest that there will be fewer species per small unit area than in the Woodland, but more than in any of the Park savanna habitats. The last ^{row} of the table shows that despite sampling over a smaller total area, both Woodland and especially Riverine show a higher total recorded on the plots than in any other habitat.

A better idea of the number of regular species in each habitat is obtained from the relative abundance censuses. I have scored species as 'Abundant' if more than 1.0 individual per hour's censusing was seen in that habitat, and as 'Present' if 0.05 to 1.0 individuals per hour's censusing was seen. Before designating the categories of the 'common' (ch 5.4.1) African visitors and Palaearctic migrants the numbers of them have been multiplied by a correction factor calculated for each species to allow for its absence from Tsavo for some of the year. This factor has been calculated by scoring one for each month in which more than 10% of the total number recorded in censuses were seen, and a half for each month in which 1 - 10% of the total recorded were seen. The sum (M) can be taken as the number of months the species was present in Tsavo and

hence the correction factor is $12/M$. The months when each is present are shown in Table 7.3 (African visitors) and 7.4 (Palearctic migrants) and the correction factors are quoted in Appendix 1.2 by the relevant species name. (The numbers of those species which do not reach the 'common' category have not been corrected. They are relatively unimportant ecologically, and because of the low sample size there is a difficulty in determining accurately their period of occurrence.)

Using these definitions, the number of species 'Abundant' and 'Present' in each habitat is shown in Table 6.10. Obviously it shows a similar pattern to Table 6.9 but here, all figures are directly comparable. There is an increase in the number of species in a habitat as the vegetation becomes more complex, except that Riverine has only the same number as Woodland. Grassland supports only about half the number of species of any other habitat.

An important point that does not emerge from these figures is that the species in the more open habitats are not simply a subset of those in the thicker ones. As will be more fully discussed in ch 6.6 many do occur in all habitats but some are only in the more open ones and some only in the thicker ones. All the Park savanna habitats have a broadly similar species composition, but it is different in many important respects from that in Woodland, and Riverine is different again.

A simple figure for the number of species is only one component of the diversity of birds in a sample. For example, take two samples both containing five species, even the same five. In the first, each species contains 20% of the individuals; in the second 95% of the individuals are of one species and the remaining 5% is divided among the other four species. Have these two samples the same diversity? In terms of number of species obviously yes, but a small group of individuals from the first sample is likely to contain more species than a similar group from the second, and

TABLE 6.10. The number of species in each habitat: regular species - data from relative abundance censuses (Type I).

	Habitat							
	G	BG	WBG	B	WB	W	R	TOTAL
Abundant ^a	15	20	28	19	27	26	23	29
Present ^a	30	52	63	69	71	78	83	92
Total	45	72	91	88	98	104	106	121 ^b
Total recorded	58	115	136	116	134	140	126	211
Number of hours censusing	42	146	170	71	87	129	53	698

Notes:

a) Abundant means more than 1 bird seen per hour's censusing (Type I censuses)
 Present means 0.05 to 1.0 birds seen per hour's censusing (Type I censuses) (see text)

b) Includes the six species mentioned in ch 5.4.1 as being 'common' only by virtue of occurring in flocks

therefore intuitively it is thought of as having a higher diversity. Hence a measure of the species diversity of a sample ought to combine both the number of species (species richness is preferred as a term because it is almost impossible to ascertain the total number of species in an open system (Peet 1974)), and the relative abundance of each (usually known as the equitability or evenness). Increasing either the species richness or the evenness must result in an increase of the species diversity index. Ecologists have devised a variety of indices which combine the two components, and many are reviewed by Peet (1974), who calls them 'heterogeneity indices' to distinguish them from indices of the two components individually - 'species richness indices' and 'equitability indices'. This is partly necessary because there has been a great deal of confusion over the definition of the terms used in the literature especially the term 'species diversity'.

These heterogeneity indices, now almost universally known as species diversity indices, are of two broad types (Peat 1974):

Type I - those which are most sensitive to changes in the abundance of rare species. The commonest of these, indeed the most commonly used of all such species diversity indices, is the Shannon-Wiener function based on an analogy with information theory: species diversity $H' = -\sum p_i \log p_i$, where p_i is the proportion of the total number of individuals in the population in the i th species.

Type II - those which are most sensitive to changes in the abundance of the common species. The commonest of these is Simpson's index $\lambda = \sum p_i^2$ (or some derivative of it e.g. $(1 - \sum p_i^2)$ or $1/\sum p_i^2$) where p_i is as before. In both cases, because the real proportion of individuals in each species is usually unknown, p_i is estimated by N_i/N where N_i is the number of individuals in the i th species in the sample and N is the total number in the sample.

It must be pointed out, though, that although the Type I indices are most sensitive to changes in the abundance of rare species, a species will contribute a maximum amount to the index when its relative abundance $(p_i) = 1/e$ (when using natural logarithms) (Peet 1974). So, in other words, the distinction between the Types is that a Type I index is affected more by a small absolute change in the abundance of a rare species than by the same small change in the abundance of a common species; and a Type II index is affected more by the change in the abundance of the common species.

As said above, the most commonly used of all indices of species diversity is the Shannon-Wiener function. It has the advantage of not being overly dismissive of rare species and yet it does not give equal weight to the very rare as the very common. Hence it is a compromise. The argument has been summarised in simple, but not strictly mathematical terms, by Alatalo & Alatalo (in press): species richness is the number of all species, the exponential of the Shannon-Wiener H' is the number of 'abundant' species, and the reciprocal of Simpson's λ is the number of 'very abundant' species (the exponential and reciprocal are required to convert the indices into comparable figures). The Shannon-Wiener function has also been shown to be relatively stable in incomplete bird censuses (Jarvinen & Sammalisto 1973), and hence relatively independent of sample size (see analysis of Merikallio's (1946) data in Jarvinen & Vaisanen 1973).

The evenness component of the species diversity indices has also received some attention in the recent literature. The most commonly used indices of evenness are simple heterogeneity indices scaled by some maximum or minimum value of such with a given species richness, e.g.

$J' = H'/H'_{\max}$ where H' is the Shannon-Wiener function (see above) and $H'_{\max} = \log S$ where S is the number of species in the sample. It is now clear

though that these should not be used (and incidentally nor should the variance of H' often given) unless the number of species in the whole population is known, not simply the number in the sample, a situation which is very rare. There is also a, purely mathematical, positive correlation between indices such as J' and species richness (see Alatalo & Alatalo (in press), de Benedictis 1973).

A different method of calculating the evenness component was suggested by Hill (1973), and Peet (1974) has recommended its use. Hill's (1973) numbers are those defined by Alatalo & Alatalo (in press) as the number of species (N_0) the number of abundant species $N_1 (= \exp H')$ and the number of very abundant species $N_2 (= 1/\lambda)$ and Hill (1973) suggested a ratio of N_1/N_0 or better (because of less dependence on the number of species and hence sample size) N_2/N_1 as an index of evenness. Peet (1974) noted a difficulty in interpreting this ratio (he actually used N_1/N_2 but the difficulty is the same) when species diversity is near unity, because in any community the minimum of Hill's numbers is 1.0. The difficulty may be avoided by adopting a modified Hill's ratio $(N_2 - 1)/(N_1 - 1)$ (Alatalo & Alatalo in press). However even with this index there are difficulties. The number of rare species in a sample is a function of sample size. So small samples will contain fewer rare species and they will therefore have a higher evenness (Peet 1974).

(There is also a completely different set of diversity indices which have been proposed, based on a statistic of a mathematical distribution e.g. log series, log normal. Use of one of these indices does, however, assume that the underlying distribution of relative abundance follows one of these mathematical distributions and, especially with widely variable sample sizes, this is not likely to hold throughout in studies such as this.)

I have calculated the Shannon-Wiener function H' and the modified Hill's ratio $(N_2 - 1)/(N_1 - 1)$ for each of my plots in each month. These are given in Appendix 4.5 (species diversity) and 4.6 (modified Hill's ratio). Tables 6.11 and 6.12 respectively give the means for each habitat of these two indices although again this is not strictly valid for Woodland and Riverine because of different sizes of individual plots, although both indices are much less dependent on sample size than the number of species in Table 6.9 (see above). Plots with either no birds seen, or individuals of only one species, cause some difficulties. The species diversity is zero in both cases and they are included in the calculation of a mean value. Obviously the evenness index is also zero but here the interpretation is much more difficult, and they are left out of the calculation of mean values.

The figures for species diversity are on the whole correlated with the number of species in Table 6.9. There is a higher species diversity in the more complex habitats and Grassland again shows particularly low figures. All the Park savanna habitats show a low figure in the long dry season and higher in the wet seasons, although in most cases there are slight, although not statistically significant, reductions in February. These are due to large flocks of single species, particularly granivores. Woodland shows more constant figures through the year despite the number of species being higher in the wet seasons. Riverine has a lower average species diversity than Woodland ($d = 6.46$, $df\ 45$, $P < 0.001$). This is partly a consequence of smaller plots, but even the plot of most similar size (Plot C) has an average species diversity of 2.2 which is lower than the Woodland figure although not quite significantly so ($d = 1.8$, $df\ 23$, $P < 0.10$).

The figures for evenness show an approximately inverse correlation with the number of species although the average in all the habitats is about the same. All habitats show an approximately similar seasonal pattern

TABLE 6.11. The species diversity in each habitat: the average species diversity on a census plot in each month.

Month	Habitat						R ^a
	B	WB	BG	G	WG	W	
1975 Feb	1.4	1.3	1.4	1.2	1.3	2.6	2.2
Mar	2.0	1.7	1.7	1.0	1.7	2.8	1.9
Apr	1.8	1.5	1.5	1.3	1.5	2.8	2.5
May	1.9	1.3	1.2	1.0	1.3	2.5	2.1
Jun	1.2	1.2	0.6	0.4	1.2	2.3	1.6
Jul	1.2	1.1	1.1	0.4	1.1	2.2	1.7
Aug	1.4	0.8	1.0	0.4	0.8	2.5	1.7
Sep	1.2	1.0	0.8	0.4	1.0	2.3	1.4
Oct	1.2	1.2	0.7	0.3	1.2	2.8	1.5
Nov	1.8	1.3	0.9	0.2	1.3	2.8	1.9
Dec	2.2	1.8	2.0	0.9	1.8	2.8	2.4
1976 Jan	1.7	1.9	2.0	0.9	1.9	2.7	1.5
Feb	1.6	1.7	1.7	1.0	1.7	1.9	1.8
Mar	1.6	1.7	1.7	1.1	1.7	2.6	1.9
Apr	1.3	1.4	1.5	0.7	1.4	2.6	1.8
May	1.2	1.0	0.9	0.5	1.0	2.0	1.9
Jun	0.8	1.3	0.5	0.6	1.3	2.0	1.6
Jul	1.3	1.5	0.8	0.5	1.5	2.0	1.6
Aug	0.7	0.7	0.7	0.3	0.7	2.4	1.8
Sep	0.9	0.6	0.5	0.2	0.6	2.6	1.7
Oct	1.4	1.3	1.3	0.4	1.3	1.9	1.9
Nov	1.4	1.5	0.8	0.7	1.5	2.1	2.2
Dec	1.3	1.9	1.9	0.8	1.9	2.4	2.2
1977 Jan	2.0	1.9	1.8	0.9	1.9	2.6	2.0
Average	1.4	1.4	1.2	0.7	1.4	2.4	1.9

Notes:

- 1) The figures are the mean species diversity for a census plot. Species diversity was calculated by the Shannon-Wiener formula $H' = -\sum p_i \log_e p_i$. See text.
- 2) Details for each plot are in Appendix 4.5.
- a) An average figure is not strictly valid due to census plots being different sizes. See text.

TABLE 6.12. The evenness (as a percentage) of the distribution of numbers over the species in each habitat: the average evenness on a census plot in each month.

		Habitat					
		G	BG	WBG	B	WB	W ^a
							R ^a
1975	Feb	88	61	59	72	64	81
	Mar	92	84	76	81	84	77
	Apr	90	82	77	79	83	90
	May	90	92	84	91	83	81
	Jun	83	87	94	82	86	75
	Jul	95	91	82	85	84	80
	Aug	91	93	88	85	88	75
	Sep	100	84	85	83	82	78
	Oct	85	74	87	88	82	82
	Nov	58	81	90	88	88	84
	Dec	88	80	74	79	83	77
1976	Jan	66	69	71	75	70	74
	Feb	83	78	76	84	77	71
	Mar	86	86	69	89	82	82
	Apr	96	94	80	79	89	87
	May	92	85	79	90	90	85
	Jun	91	95	80	86	91	88
	Jul	96	90	86	93	92	91
	Aug	93	73	84	80	91	83
	Sep	88	87	89	94	93	83
	Oct	83	91	90	92	86	75
	Nov	91	89	91	82	92	86
	Dec	76	79	82	74	81	68
1977	Jan	84	74	79	70	54	86
Average		87	83	81	83	83	81

- Notes:
- 1) The figures are the mean evenness for a census plot (converted to a percentage). The evenness was calculated from a modified Hill's (1977) ratio $(1/\sum p_i^2 - 1)/(\exp(-\sum p_i \log p_i) - 1)$. Plots with zero evenness (no species or only one species seen) are excluded - see text.
 - 2) Details for each plot are given in Appendix 4.6.
 - a) An average figure is not strictly valid due to the census plots being of different sizes - see text.

with higher figures in the long dry season and low in January and February, this latter again due mainly to large flocks of granivores. As for species diversity, Woodland shows more constant figures through the year, which is correlated with the relative lack of granivorous flocking species.

All these figures have been calculated from each individual plot of 5.7 ha. A different figure is produced if one treats the sum of all small plots in each habitat as one plot. Comparing the figures produced in this way with Tables 6.9, 6.11 and 6.12 one can get an idea of the variability between the small plots. In order to make the habitats comparable I have considered the three Woodland plots combined to be the same area as five plots of each of the Park savanna habitats and for each of these habitats I have chosen five plots at random before doing the calculations. The comparison between the dry season average (August and September of both years), wet season average (December and January) and the total average of these new figures with those calculated on the basis of the small plots is shown in Table 6.13. Details of the figures for the large plots are given in Appendix 4.7 (number of species), 4.8 (evenness) and 4.9 (species diversity). The number of species on a large plot is two to four times that on a small and the more complex habitats show a slightly smaller difference factor suggesting that in the more complex habitats the plots are slightly more similar to each other. Species diversity also increases substantially with increase in plot size, but there is no evidence of an increased difference factor in the simpler habitats. The evenness component on the other hand decreases with the increase in plot size and the wet season figures are all lower than the corresponding dry season ones. This may well be partly an artefact of the index used, because, as mentioned earlier, evenness is likely to be higher in smaller samples.

6.4.2. Discussion

Tramer (1969) has shown for bird populations that the Shannon-Wiener

Table 6.13. The number of species, evenness and species diversity in each habitat. A comparison of small plots and large plots

Habitat Plot size ^a		Dry Season ^b			Wet Season ^c			Total	
		No. species	Even	Sp. div.	No. sp.	Even	Sp. div.	Even	Sp. div
G	small	1	93	0.3	4	79	0.9	87	0.7
	large	5	83	1.3	11	59	1.6	73	1.6
BG	small	3	84	0.7	10	76	1.9	83	1.2
	large	10	71	1.9	27	67	2.1	72	2.2
WBG	small	3	87	0.8	10	77	1.9	81	1.4
	large	11	78	2.1	33	57	2.8	69	2.5
B	small	4	86	1.1	10	75	1.8	83	1.4
	large	13	59	1.9	29	58	2.6	65	2.3
WB	small	4	89	1.0	15	72	2.3	83	1.6
	large	13	75	2.2	41	59	3.0	69	2.6
W	small	15	80	2.5	19	76	2.6	81	2.4
	large	27	76	3.1	39	67	3.2	74	3.1
R ^d	small	7	78	1.7	13	77	2.0	79	1.9
	large	26	68	2.8	37	60	2.6	66	2.8

Notes:

- a) Small plots are the figures for 5.7 ha plots. The figures are taken from averages in Tables 6.9, 6.11 and 6.12.
 Large plots are the equivalent of 28.5 ha plots - adding 5 of the small plots together. See text. Details in Appendices 4.7, 4.8 and 4.9.
- b) The dry season figure is the average of August and September figures
- c) The wet season figure is the average of December and January figures
- d) The large plot for Riverine is all plots summed - a total of 16 ha

species diversity index is highly correlated with the species richness component while the evenness (in this case J' as defined earlier) remains fairly constant and high. He was, however, only concerned with breeding season censuses, and Kricher (1972) found that, outside the breeding season, especially in harsher and less predictable environments the evenness component (he also used J') would be lower and become a more important factor in the species diversity index. Kricher (1972) further suggested that low evenness might be a general characteristic of early successional areas or of ecosystems containing opportunistic species. In Tsavo the Park savanna habitats can be considered equivalent to earlier stages in the succession to Woodland and the second half of the long dry season must be considered the harshest season. Therefore Kricher (1972) would predict that the Park savanna habitats would have a lower species diversity and evenness than Woodland and that both would be lowest in the long dry season. My data on species diversity (Table 6.11) agree with this, but that on evenness (Table 6.12) show if anything the opposite. Kricher (1972) was working in temperate habitats where the highest densities and number of species occurred in the breeding season (summer), during which time most species were territorial and fairly evenly spread over the ground (therefore high evenness). Flocks of opportunist species, which were one of the main causes of low evenness figures (and were so in Tsavo too), only occurred outside the breeding season. In Tsavo the situation is very different. Birds breed mainly in the wet season (see ch 7) when some are territorial, but the wet season is also the season when flocks of opportunists occur, hence the lowest evenness. The situation has been reversed possibly due to the extreme harshness of the Tsavo dry season, which prevents all but the hardiest species from surviving at all and forcing these to spread out relatively evenly. It must be remembered though that Kricher (1972) was using J' as a measure of

evenness and hence his variations may be a purely mathematical artefact because of the correlation with number of species (see above).

Alatalo & Alatalo (in press) working in Finland found that evenness, using the same index as here, remained fairly constant through the year, with, if anything, a slight increase in the winter over the breeding season. However, they also showed that, in each census, a sample 20 individuals gave a higher evenness than the whole sample, with the smallest difference outside the breeding season when the effect of sample size was counteracted by flocking. Table 6.13 shows a similar effect to this, with lower evenness when considering larger plots, and it is possible that all the variations in evenness found both in this study and in others (most are based on small sample plots) are really only caused by differences in sample sizes, and that when considering whole communities, as opposed to samples, all will be found to have about the same evenness. The same area sampled at different seasons could still show spurious evenness variations if the densities in the two seasons are very different, as the evenness seems to be dependent on the number of individuals rather than the size of a census unit per se (Alatalo & Alatalo in press). More work on suitable measures of evenness and particularly their dependence on sample size needs to be done. Samples of any size seem to be much less satisfactory for studying evenness than for studying species diversity, and it may be only when samples covering whole populations are studied that any reliable and meaningful results about evenness will be obtained.

As expected Table 6.13 also shows that the number of species and species diversity are also both partially dependent on sample size. Comparison of the figures for five plots with those for all plots, in Grassland, Bushed Grassland, Wooded and Bushed Grassland and Bushland (compare parts a and b of Appendices 4.7 and 4.9) shows that the increase of both is beginning to level off at a plot size of about 30 ha which

should perhaps therefore be considered a minimum for future studies.

Many studies have shown that within a general habitat type (especially forest areas) bird species diversity (BSD) is closely correlated with vegetation structure. These correlations are again based almost entirely on breeding pairs of birds. The measure that has most often been used for vegetation structure is Foliage Height Diversity (FHD) (e.g. MacArthur 1965, Recher 1969). I do not have the data to calculate FHD but I have calculated two other measures of the diversity of vegetation structure - diversity indices (Shannon-Wiener) of canopy cover and of vegetation volume in each of three layers (grass, bush, tree). Details of the calculations are in Appendix 2. I have plotted these two measures of vegetation diversity against the BSD for each habitat (measured on both small and large plots) in Fig. 6.9. This shows that there is a significant linear relationship between canopy cover diversity and BSD and, contrary to what one might expect from MacArthur's (1965) findings there is no significant relation of BSD with volume diversity. The regression is significant with the volume diversity, however, for the Park savanna habitats alone i.e. taking out the Woodland point.

(BSD on small plots = $0.8 \text{ Volume Diversity} + 0.7$, $t = 3.5$, $P < 0.05$);

BSD on large plots = $1.0 \text{ Volume Diversity} + 1.6$, $t = 3.9$, $P < 0.05$).

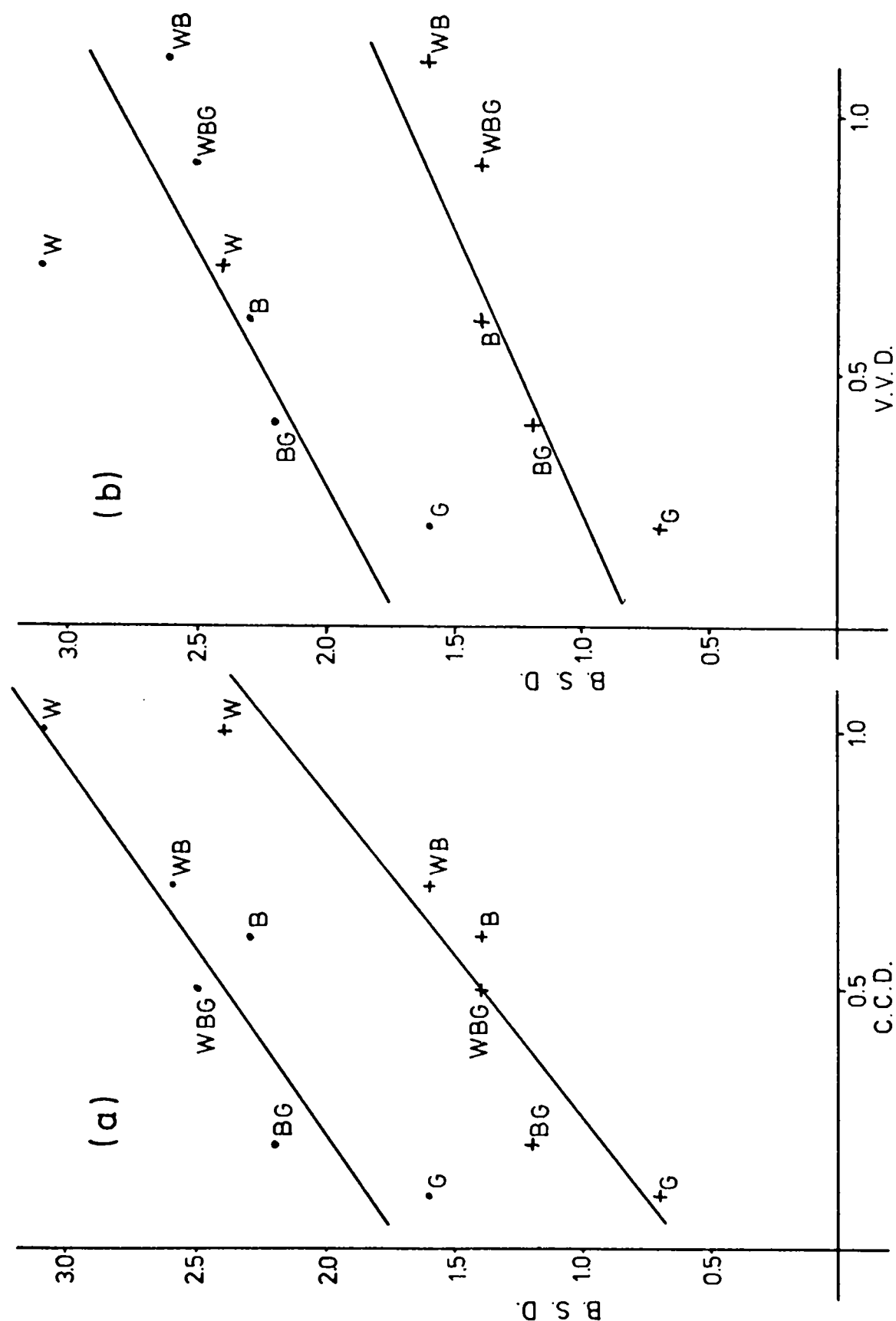


Fig. 6.9 The relation between Bird Species Diversity and a) Canopy Cover Diversity and b) Vegetation Volume Diversity. In each case the dots and the upper line refer to the BSD calculated for large plots, the crosses and the lower line refer to the small plots. For the BSD figures see Table 6.11. For the vegetation figures see Appendix 2. The regression equations are: a) $\text{BSD on large plots} = 1.4 \text{ CCD} + 1.7$ ($t = 5.0$, $P < 0.01$); $\text{BSD on small plots} = 1.6 \text{ CCD} + 0.6$ ($t = 5.9$, $P < 0.01$); b) $\text{BSD on large plots} = 1.1 \text{ VVD} + 1.7$ ($t = 1.9$, N.S.); $\text{BSD on small plots} = 0.9 \text{ VVD} + 0.8$ ($t = 1.3$, N.S.).

Karr & Roth (1971) found a sigmoid relation between per cent canopy cover and BSD, with the greatest rate of increase between a total canopy cover of between 100% and 150%. The canopy cover in the Tsavo habitats hardly reaches this except in Woodland and Riverine, but the effect is shown at lower canopy covers. Karr & Roth's (1971) 100 - 150% corresponded with the first shrubs and trees coming in to open grassland. The greatest increase in Tsavo occurs between Grassland and Bushed Grassland which is the equivalent stage in the succession, the only difference being that the total grass cover is much lower^{in Tsavo}/. My data within Grassland are not sensitive enough to detect any differences in diversity between zero and twenty-five per cent. Leading on from this, Willson (1974) found that the addition of the tree layer in a successional series had a disproportionate effect on the addition of species. The addition of trees does have an effect on the birds in this study - compare Wooded Bushland with Bushland, and Wooded and Bushed Grassland with Bushed Grassland - but the effect is not disproportionate. Wooded and Bushed Grassland and Bushland can both be considered as 'the next stage' after Bushed Grassland yet the increase in number of species is about the same to each, as also are the density, biomass, energy requirements and species diversity.

Riverine is not included in Fig. 6.9 because I do not have any critical vegetation data. It is a specialised habitat and not as closely related to the others as the others are to each other. Structurally it appears the most complex habitat in Tsavo East and, as such, might be considered the climax in the area. It does show one feature of climax communities over a penultimate stage of succession that of a slight reduction in species diversity, This has been found by Karr (1968) in bird populations and occurs in plants and a variety of other

organisms (Margalef 1968). This is probably part of the cause in this instance but, as said above, the species diversity in the Tsavo riverine may be artificially low due to the small size of the plots. Furthermore, there is probably an 'island effect' as the Voi River forest is both limited in total area and is now an isolated patch of such forest. The more extensive area of riverine forest along the Bura River near the Taita Hills holds many extra species which do not occur in the Voi River forest.

6.5. General Discussion

6.5.1. Comparison with other areas

East Africa

Angwin's (1968) study in riverine Acacia woodland was mainly qualitative in terms of community structure although she collected some detailed data on the feeding ecology of individual species. The only community parameter that can be compared with my data is the number of species. She had an average of 44 species on a day's visit with a total of 169 species recorded on her 2 acre plot during the year's study. The seasonal pattern was, however, similar ^{to my data} with peaks in the number of species in November and April which are the wet seasons, and she thought the reason was an increase in the number of insects although she did not measure these.

Beals's (1970) study in Ethiopia is also difficult to compare with my data in a quantitative manner. He found a density of between 50 and 250 birds per hectare (his Table 4), but this is artificially high as he seems to have counted all individual birds seen on the 2 ha plot during a 48 hour visit, and not only those on it at any particular moment. However, what is interesting is that the peak density occurred in the dry season (November to February), and the lowest in the wet season (June to August). Most of the dry season increase was due to Palaearctic migrants and African

wanderers, the latter being mainly insectivores. The reversal of seasonal patterns compared with my study is the more interesting, as the total rainfall is very similar (maximum 500 mm per annum). The rain is however more evenly spread, and the area is at an altitude of about 1800 m a.s.l., so the climate is likely to be milder and probably more predictable. As such it might act as a dry season refuge area for birds from the lowlands.

The other East African studies are concerned with the relative abundance of Palaearctic migrants. Ulfstrand (1973) gives the proportion of numbers in several habitats including some in Tsavo East N.P.. His identifications of several species in Tsavo East, though, are almost certainly incorrect e.g. he recorded the pipit Anthus similis as dominant in Tsavo East, this is almost certainly the lark Mirafraga poecilosterna; his records of the warblers Apalis flavida and Eremomela icteropygialis similarly seem unlikely in view of my records. He found a slightly lower proportion of Palaearctic migrants than in my data at the same time of year but, because of the above, all the figures in his paper should be treated with caution.

Britton (1974) showed that, in thicket and Acacia savanna, Palaearctic migrants were about 50 - 60% of the numbers of non-granivorous passerines (45 - 50% of the biomass) in October and November and reduced to 20 - 25% of numbers (10 - 25% biomass) in December and January. In cultivation the proportions were lower and in papyrus only 4%, but because there are very few resident species, 30% of the species in papyrus were Palaearctic. The proportion in the thicket and Acacia savanna study sites are approximately the same as in my study, and my data show a similar 'autumn passage', although in Tsavo this occurs in December rather than October - November.

West Africa

The two plots studied in Senegal by the Morels - at Keur Mor Ibra (Morel & Bourlière 1962, Morel 1968) and the International Biological

Programme plot at Fété Olé (Morel & Morel 1972, 1974, in press) have a very similar climate to Tsavo. These were two 25 ha plots in the Sahel savanna and both seem, on my habitat classification, to be Woodland, although more open than most Woodland in my study and with a slightly lower canopy. The plant species composition is broadly similar to Tsavo with many of the same genera. The most important difference is that in Senegal there was no, or very little Commiphora spp.

Table 2 of Morel (1968) provides detailed census data for the Keur Mor Ibra plot, and so a full comparison with my data is possible. In Fig. 6.10 I have presented these data, but I have reanalysed them to compare directly with mine. To do this I have left out his 'predator' category and have subdivided his 'vegetarian' category into 'fruit' and 'seeds' and his 'polyphage' category into 'fruit and insects', 'seeds and insects' and 'nectar and insects' on the basis of my knowledge of the species concerned. This caused few difficulties because, as with the plants, many genera and some of the species are the same as in Tsavo. Further, some of the published figures in the Table are incorrect and I have used a corrected version supplied by Morel (pers. comm.). Details of my subdivision of his food categories and the corrections to the Table are in Appendix 3.

The data show a very similar community structure and seasonal pattern to the thicker Park savanna habitats in Tsavo. For the statistics of the seasonal patterns see table 6.14a. The single wet season in Senegal is July to September and there is a sharp increase in numbers, especially of insectivores and granivores coinciding with it. African frugivores show no regular seasonal fluctuations in numbers. There is also a high population of Palaearctic migrants through the whole northern winter, and these have been the subject of much discussion by Morel (1968), and further by Morel (1973) and Moreau (1972). Total density and biomass are also very similar to my Tsavo data. Morel (1968) considers the dry season carrying capacity of the Keur Mor Ibra plot to be about 1 bird (equivalent to about

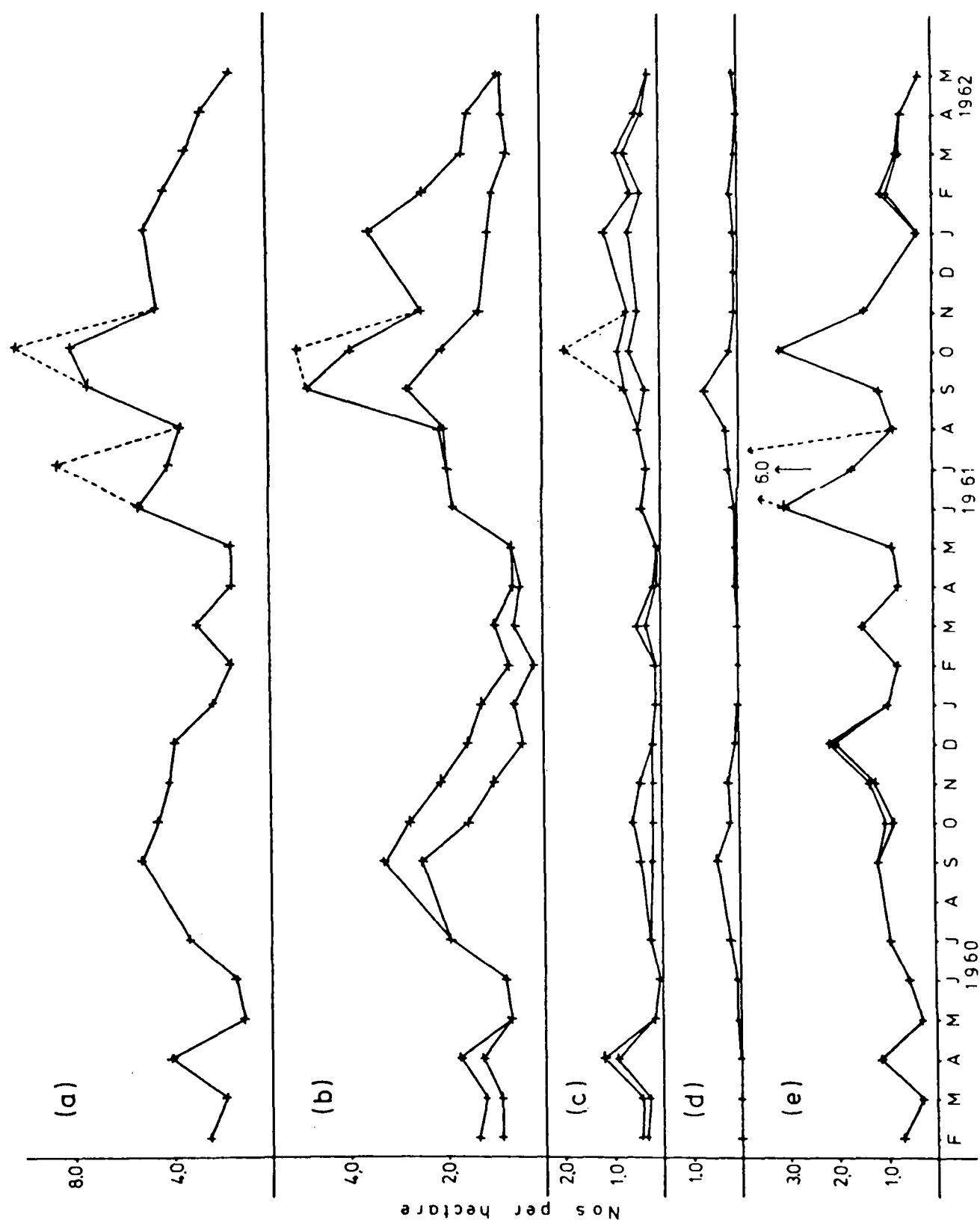


Fig. 6.10 The density of birds in Sahel savanna in Senegal; a) total density, b) insectivores, c) frugivores, d) nectarivores, e) granivores. In each case the lower line excludes Palaeartic migrants. Dotted lines include large flocks of single species. Data re-analysed from Morel (1968) - see text and Appendix 3. For the significance of the seasonal patterns see Table 6.14a.

TABLE 6.14. Statistics of seasonal patterns of density of birds in Senegal.

a) Savanna

Guild: Status	Insect			Fruit			Seed			Nectar		TOTAL		
	Afr.	Pal.	TOT.	Afr.	Pal.	TOT.	Afr.	Pal.	TOT.	Afr.	Pal.	Afr.	Pal.	TOT.
N	804	446	1250	225	96	321	812	13	825	80		1921	555	2476
R/N	0.33	0.52	0.28	0.12	0.42	0.19	0.20	0.66	0.20	0.59		0.26	0.50	0.23
2R ² /N	167	219	177	5.9	30	20	63	11	62	55		248	257	251
Significance	~~***~~	~~***~~	~~***~~	~~***~~	~~***~~	~~***~~	~~***~~	~~*~~	~~***~~	~~***~~		~~***~~	~~***~~	~~***~~
Peak week	Aug 4	Nov 4	Oct 1	Nov 4	Nov 4	Nov 1	Sep 1	Nov 1	Sep 1	Sep 2		Aug 4	Nov 4	Sep 3

b) Gallery Forest

Guild Status	Insect			Fruit			Seed			Nectar		TOTAL		
	Afr.	Pal.	TOT.	Afr.	Pal.	TOT.	Afr.	Pal.	TOT.	Afr.	Pal.	Afr.	Pal.	TOT.
N	1727	957	2684	612	486	1098	6697	179	9215	179		1443		10658
R/N	0.07	0.32	0.08	0.17	0.17	0.11	0.12	0.47	0.07	0.26		0.09		
2R ² /N	73	765	131	130	118	109	727	325	391	805		672		
Significance	~~**~~	~~***~~	~~***~~	~~***~~	~~***~~	~~***~~	~~***~~	~~***~~	~~***~~	~~***~~		~~***~~	~~***~~	~~***~~
Peak week	Jul 4	Dec 3	Nov 4	Apr 2	Jan 2	Mar 2	Feb 3	Oct 3	Feb 3	Dec 4		Feb 1		

Notes:

- 1) Data in Figs 6.10 (savanna) and 6.11 (gallery forest) from Morel (1968)
- 2) Statistics and conventions as in Table 6.2. In addition the birds are divided into African species and Palaearctic species where appropriate.

100 g) per hectare and this multiplies by about five times in the wet season peak abundance.

The community of Ethiopian region species on the Fété Olé plot has a similar structure and follows a similar seasonal pattern to the Keur Mor Ibra one, but the actual density and biomass average a little higher, and there is a smaller difference between wet and dry seasons - the mean is about 3 birds (about 200 g) per hectare in the dry season rising to about 7 birds (about 410 g) in the wet season (Morel & Morel in press). Here, however, there are very few Palaearctic migrants. Morel & Morel (1972) attribute both this, and the lesser seasonal variation than in the Keur Mor Ibra plot, to a richer flora with fewer Acacia spp. and Balanites aegyptiaca. They have studied this plot now for seven years and have found considerable variation from year to year, and there is a high correlation between the numbers of birds and the rainfall (Morel & Morel 1974, in press). This is probably also the case in Tsavo but with only two years data it is difficult to be sure.

Despite all these similarities, there are two major differences between my study and those of the Morels. Firstly, in Senegal, birds are ^{wild} one of the most important components of the/vertebrate fauna both in density and biomass terms. In the past there was a wild fauna of large mammals but these have now been hunted out by man, and domestic cattle are now common (Poulet 1972). How much ecological replacement has taken place is uncertain. The fact that the two areas nevertheless have a very similar community of birds helps to confirm that, as expected, there is little direct interaction between the birds and the large mammals, and that the two communities can largely be considered separate entities.

The second major difference between Tsavo and Senegal concerns the birds themselves. As has been seen, there is considerable movement out of the savanna in the dry season in both areas. The difference lies in where

the birds go. In Senegal many, if not all, simply move into the gallery forest along rivers/. Fig. 6.11 shows similar data to Fig. 6.10 and is taken from Table 13 of Morel (1968). The data are again divided up and corrected as before (see Appendix 3 for details)/. and the statistics are given in Table 6.14b. It shows that the highest density of birds occurs in mid to late dry season, at the period of lowest density in savanna, and that the total may be up to 90 birds (about 6000 to 7000 g) per hectare at this time. Woodland may act as a refuge for a few birds in my study but the majority move away altogether. The difference is related to the environments around the two study areas. There is almost nowhere within 1000 km of the Senegal plots which is any improvement on the prevailing savanna conditions except the gallery forest. There is no such gallery forest in Tsavo, and birds have only to fly 200 to 300 km to reach areas with considerably higher rainfall, and which may have a different rainfall regime as well. The Sagalla and Taita Hills, the nearest such areas, although they have largely been taken over by agriculture did not, however, show a major increase of either of the two most obvious visitors to Tsavo, the dove Streptopelia senegalensis and weaver Quelea quelea. The latter is known to have extensive migrations (Ward 1971 and see ch. 5.3.42).

One problem which Morel (1968) does not consider with this situation is that if the gallery forest can hold this density and biomass of birds in the dry season, which appears to be the leanest season, why can it not hold them in the wet season as well, when the resources are presumably more abundant. There are no indigenous species endemic to the gallery forest, so the answer must be that the savanna birds are so much more efficient at exploiting the resources than any specialist in the forest could be that the latter could not survive. The savanna birds simply disperse out into the savanna when they are able to. This problem does not arise among the birds in Tsavo because the visiting species in eastern Africa seem to be moving from one source of food abundance to another, and do not need to

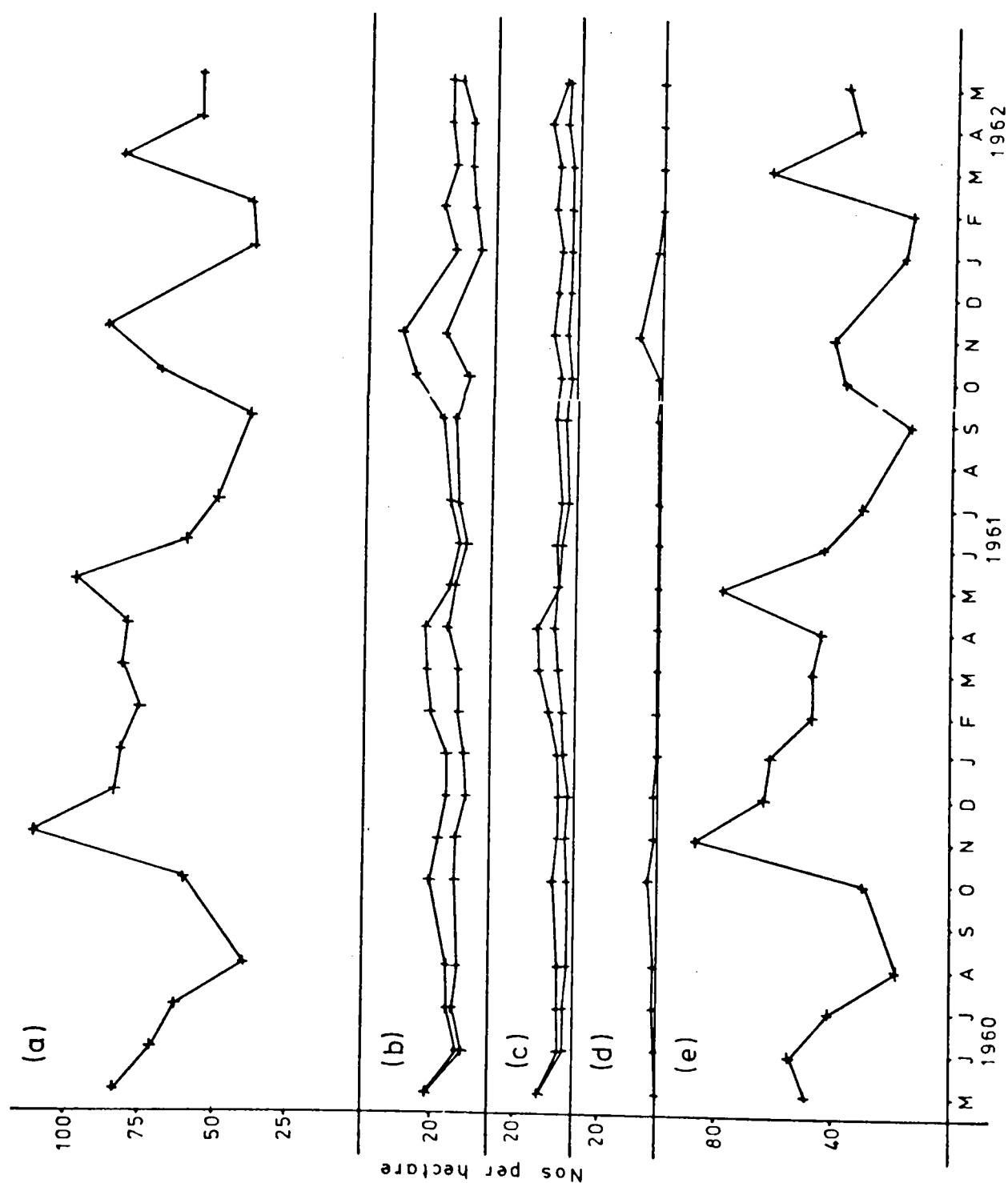


Fig. 6.11 The density of birds in gallery forest in Senegal; a) total density, b) insectivores, c) frugivores, d) nectarivores, e) granivores. In each case the lower line excludes Palearctic migrants. Data re-analysed from Morel (1968) - see text and Appendix 3. For the significance of the seasonal patterns see Table 6.14b.

exploit resources which may be already hard-pressed by resident species. The large mammals in Tsavo are, however, in a similar situation. The distribution of several is restricted in the dry season by water availability and they disperse out from dry season concentrations in the wet seasons. The same arguments for efficiency at using resources must apply but one would have to know the actual availability of the various foods at the relevant seasons before one can speculate further on what is happening.

The other two main ecological studies in West Africa were both in areas of higher rainfall than Tsavo. De Greling (1972) studied small plots in three habitats in the Sudan savanna of northern Cameroun a) dry savanna woodland, b) wet, seasonally flooded, very open lacustrine savanna, and c) very dense savanna thickets, for periods of eight, sixteen (except the wet season when impossible) and ten months respectively. The density and biomass of birds in each was considerably higher than in Tsavo in equivalent seasons, and although the full range of variation over the year was not, or could not be studied, the difference between wet and dry seasons was a factor of two or three and not five or six as in Tsavo. There was also a higher proportion of vegetarian than insectivorous species in the latter two study areas over the dry savanna woodland, and the Palaearctic element in all three was very small.

Thiollay's (1971) area was a mosaic of guinea savanna and riverine forest with higher rainfall still (c 1200 mm per annum). Here the seasonal cycle was much more constant with the density of birds varying from about 9 to 12 birds (about 800 to 1200 g) per hectare. The main peak of numbers coincided with the highest rain (July and August) but there was a secondary peak after the fires went through in the middle of the dry season (March and April), due to both insects and seeds becoming more visible and hence available. Where the influxes came from was not known. The insectivore population was considerably higher than the vegetarian, but the granivores

contributed a major proportion of the biomass. The Palaearctic element was again very small.

It is more difficult to compare the number of species in these studies due to differences in the size of plots. However, Morel's two plots both had about the same number of species each year as my Woodland plots combined (about the same area is involved) although a greater proportion was Palaearctic and less Ethiopian than in Tsavo. All of de Greling's and Thiollay's plots had higher numbers.

South Africa

Much of the South African data has been summarised by Winterbottom (1972a). Most habitats of the 'wooded savanna' type show an average annual density of 3 - 10 birds per hectare with seasonal differences being a factor of about two. Here, however, the main seasonal change is between summer and winter, and not between wet and dry seasons; and the annual cycle of most species is geared more to this than the amount of rain per se. Exceptions exist, notably in arid areas such as the Kalahari (MacLean 1969, 1970) but the data in these two papers are largely qualitative, so direct comparisons cannot be made.

Conclusions

My figures from Tsavo, given the aridity and climatic unpredictability more or less agree with data from other areas. Coe, Cumming & Phillipson (1976) have constructed a regression line of large mammal biomass on rainfall. Such a calculation cannot easily be made for bird populations because they are much more dependent on minutiae of habitat structure, and show considerably greater seasonal variations and migrations. Further, most studies have been on single small plots, and one cannot know how representative of an area these are - note the variation between my plots, and between those of the Morels. However, when considering the data that are available a few

generalisations can be made. In savanna, with a higher rainfall and/or richer vegetation, structurally and probably floristically, there will be a change within the vegetarian species from seed-eating to fruit-eating although the ratio of vegetarian to insectivorous birds will probably remain more or less the same, there will be a higher average density and biomass of birds, there will be more species per unit area, and there will be less seasonal variation in numbers. This means that the species composition will change from generalists and opportunists towards specialists (a change from r-selected species to K-selected species), and that there will be a higher proportion of residents than migrants, either Palaearctic or intra-African. Most of these generalisations can be extended from savanna into forest.

The density of birds in African savannas is generally fairly low but the total number of species in a large area is usually very high, often similar to that in forests. This is probably due to a high degree of patchiness and habitat heterogeneity. The number of species in an area is also increased by the birds' mobility and their ability to move in from a wide area to take advantage of temporary abundances of food.

6.5.2. The role of birds in the Tsavo ecosystem

a) Role in relation to other vertebrates and potential competitors

The other component of the vertebrate fauna of Tsavo that has been studied is the large mammals, by Cobb (1976). Small mammals and lizards have not been studied in Tsavo, but some data from South Turkana, an area of similar climate and vegetation, are available in Coe (1972) (small mammals) and Western (1974) (lizards). Table 6.15 gives a comparison of density, standing crop biomass and energy requirements for the birds, large mammals, small mammals and lizards. There is a considerable difference in Tsavo between wet and dry seasons, so the figures for the birds and large mammals are presented separately for the two seasons. Coe (1972) and Western (1974)

do not distinguish the seasons so the same average figure is used for both. Large mammal biomass in South Turkana is about the same as in Tsavo (Watson 1969), but unfortunately there were no estimates of bird numbers made. Western (1974) suggested that, in view of there being over 160 species recorded, the biomass would be higher than either lizards or small mammals but ^{my} Tsavo data suggest that this is unlikely. There are no data for snakes but Western (1974) thought that their biomass in South Turkana was likely to be similar to the lizards. Amphibians occur commonly in Tsavo but there are no estimates of numbers or biomass available. They are active all the year round only in damper parts such as along rivers, but in the wet seasons many come out of aestivation around waterholes and thus in the open dry savannas generally they are probably only important in the wet season.

Table 6.15 shows that birds are insignificant in biomass terms compared with the large mammals and, assuming the figures are at least the right order of magnitude, are only about 2 - 6% of the small mammal biomass and 12 - 29% of the lizard biomass. In density terms, though, they are many times more important than large mammals, but still less than either small mammals or lizards. The most significant figures for the ecosystem in comparing these groups are those of energy requirements. Here it is shown that the birds have about the same effect on the system as the lizards and although it is less than either group of mammals it is 10 - 20% of each of these. Further the figures in the Table are of Basal Metabolic Rate only. Active birds' energy requirements are higher than mammals because of flying, so the total effect on the system of birds is likely to be higher still in relation to the mammal figures.

Comparative data from other parts of Africa are few. Poulet (1972) gives a biomass figure for Taterillus pygargus, the commonest rodent, as about 150 - 200 g per hectare for the area near the Fété Olé IBP plot in

Table 6.15. Average bird density, biomass and energy requirements in each habitat in wet and dry seasons, compared to other vertebrate groups

Habitat	Density (nos./ha)		Biomass (g/ha)		Energy requirements (kJ/ha/day)	
	Wet	Dry	Wet	Dry	Wet	Dry
G	2.9(2.0)	0.4	115(100)	37	125(100)	25
BG	5.7	1.1	307	65	278	63
WBG	5.8	1.3	280	77	276	66
B	4.8(4.3)	2.1(1.7)	255(246)	107(100)	217(202)	96(85)
WB	7.8	1.4	411	69	369	73
W	5.0	4.1	217	315	213	248
R	34.6(9.9)	5.8	928(508)	340	1135(432)	283
Average Southern Area	5.6	1.2	284	71	265	65
Whole Park	5.8	1.9	290	121	269	104

Ostrich	7×10^{-4}	4×10^{-4}	80	46	7	4
Birds of prey	0.1	0.1	50	50	4	4

Large mammals	0.03	0.05	25kg/ha	20kg/ha	1264	1120
Small mammals	19.9		5 kg/ha		1422	
Lizards	189.0		1.01 kg/ha		90	

Notes:

- 1) For the birds the Wet Season figure is the average of December and January figures of both years, and the Dry Season figure is the average of the August and September figures for both years (from Tables 6.3, 6.4 and 6.6).
- 2) The figures in brackets are excluding the large flocks.
- 3) The average figures for the southern area of the Park are calculated by weighting those for each habitat in the proportion 10% G, 35% BG, 35% WBG, 10% B, and 10% WB.
- 4) The average figures for the whole Park are calculated by weighting those for each habitat in the proportion 5%G, 25% BG, 20% WBG, 10% B, 20% WB and 20% W.

5) The figures for the Ostrich Struthio camelus are taken from Cobb (1976) and are the average figures for the season in question from "Inside Tsavo East". Energy requirements have been calculated assuming a weight of 114 kg and the non-passerine formula of Lasiewski & Dawson (1967) (see text).

6) The figures for the birds of prey are a very rough estimate from my own data and from information in Smeenk (1974). Energy requirements were calculated assuming an average weight of 1000 g and the non-passerine formula used above.

7) The figures for the large mammals are taken from Cobb (1976) as for the Ostrich. Their energy requirements are calculated from the weights used by Cobb (1976) and the formula $\log M = \log 70 + 0.75 \log W$ (Kleiber 1947).

8) The figures for small mammals are for South Turkana from Coe (1972). The basis is his Table VIII. In the text he corrects the average biomass to 500 kg/km², from the 4320.6 kg/km² in the Table. The figure of 500 kg/km² is used above. Density is calculated from his table and multiplied by 500/4320.6 (= 0.116). Energy requirements are calculated using Kleiber's (1947) formula on the weights in Coe's table, and the total again multiplied by 0.116.

9) The figures for lizards are for South Turkana from Western (1974), and are the average figures he gives for the area excluding lava desert. Energy requirements are calculated from $\log M = \log 7 + 0.75 \log W$ (quoted by Poczopko (1971) as an average for poikilotherms).

Senegal (cf 200 g in the dry season and 410 g per ha in the wet season for birds (Morel & Morel in press)). Thiollay (1973) shows that his bird biomass in the Guinea Savanna of Ivory Coast is about the same as for small mammals (data in Bellier 1967) and higher than the amphibian and reptile biomass (data in Barbault 1967, 1970).

Hence the trophic impact of birds in savanna ecosystems in Africa is probably always less than the large mammals at least where these have not been hunted out, and probably less than or perhaps equal to the small mammals. For amphibians and reptiles the relationship probably depends on the rainfall. Amphibians increase steadily with higher rainfall as do the birds in savanna, but lizards have higher populations in the more arid areas.

Large herbivorous mammals do not compete with birds for food and most of the large predatory mammals feed almost exclusively on other mammals and not birds. The large mammals may, however, affect the birds considerably by having substantial effects on the structure of the vegetation; and their products i.e. dung and carcasses provide habitats for insects which are used by many birds as food. (Some birds of course eat from the carcasses themselves). Small mammals and lizards both feed on insects and the former on seeds, especially in the ground layer, and hence probably do compete directly and substantially with birds for these.. Coe (1972) gives some analysis of stomach contents from a few of the mammals he studied but he does not give a full breakdown into trophic categories so one cannot tell the relative importance to each of these food types. Lizards are insectivorous so it seems likely that there is, in total, greater potential competition for insects than seeds but this must remain an open question. Fallen fruit is available to ground living animals, and is likely to be eaten by small mammals just as it surely is by birds normally feeding on seeds and/or insects on the ground. Fruits in the trees are probably mainly taken by birds although fruit bats and other small mammals will take some of the

larger ones. There are, however, very few fruit bats in Tsavo, but I saw both baboons Papio sp. and Vervet Monkeys Cercopithecus aethiops eating figs Ficus spp..

The other potential competitors about which almost nothing is known are the invertebrates. Sinclair (1975) estimated that grasshoppers took 40% of the grass production taken by the ungulates in the long grass plains, 12% in the short grass plains and nearly 400% in the kopjes. Invertebrates also eat seeds, fruit and other invertebrates and they must exert a considerable pressure on the available resources in competition with the vertebrates for these foods.

b) Role of birds in relation to food supplies

As can be seen from Figs 6.1 to 6.7 and Appendices 4.1 to 4.3, the effects and impact of birds on the various food types depends on the habitat and the season. Birds eating a food type increase in numbers, and often very quickly, in response to an increase in the food supply but apparently not in direct proportion. Hence, as is usually the case with birds as 'predators'. they are acting as a weak inverse density dependent mortality factor on their prey populations. There seems to be a great excess of each food type present (except perhaps insects) when each is at its peak abundance, although it is not necessarily all available to birds. Yet in the lean seasons, many birds migrate away which is likely to be because of a food shortage.

Fruit-eating by birds and other animals has a rather different effect to either seed or insect-eating on the population of 'prey'. Fleshy fruits have been evolved to be eaten, so their seeds are dispersed, and for the fruits considered in this study birds seem to be the most important dispersers. So, despite probably only taking a relatively small proportion of the total amount of fruit available, birds play a vital part in the life of their food population.

Only two studies in Africa to my knowledge, have attempted to estimate the amount of a food type taken by birds. Smeenk (1974) did so for large eagles in Tsavo and estimated they were taking about half the population of Kirk's Dik-dik Rhynchotragus kirkii each year. Morel & Morel (1972) estimated that granivores consumed up to 10% of the biomass production of seeds and that the doves, Columbidae, were responsible for about half of this. As the climate and vegetation of the area were similar the proportion is likely to be similar in Tsavo.

6.5.3. The effects of the habitat changes on the bird populations

The habitats inside Tsavo East have changed from, predominantly, a Woodland scrub to a range from Grassland to Wooded Bushland. More specifically, the number of trees, especially Commiphora spp., has decreased considerably; the dominant bushes are no longer Grewia spp. but Premna spp., and the amount of grass has increased.

The main effects on the bird populations are shown by a comparison of the birds in the Park today (i.e. in the Park savanna habitats) with those present in areas of Woodland outside the Park. The effects on the whole population can be gleaned from Figs 6.1 to 6.8 and Tables 6.1 to 6.12. They can be summarised:

1. the average density and biomass and hence energy requirements of birds over the year has decreased.
2. the average proportion of frugivorous birds has decreased, and the seasonal cycle of abundance of these has changed in response to the different seasonal availability of fruit.
3. the average proportion of granivorous birds has increased, although their seasonal cycle of abundance has remained more or less the same.
4. the average proportion and seasonal cycle of abundance of insectivorous birds has remained more or less the same.

5. the different proportions of granivorous and frugivorous birds have resulted in a change in the overall cycle of seasonal abundance. In the Woodland there is a peak^{of} abundance in the middle of the long dry season (July to September). Inside the Park the peak is during and shortly after the short rains (December to January).
6. the number of species of bird that can be seen on a small unit area has decreased but, because there is still some Woodland in the area as a whole, the total number of species in the area has increased.
7. the greater proportion of granivorous species has meant an increase in the numbers of birds occurring in flocks. These occur mainly in the wet season.
8. the average species diversity has decreased. In the Woodland, species diversity is more or less constant through the year, but, inside the Park, there is a decrease in the dry season, and the increase in large flocks in January and February causes a slight decrease then as well.

Some discussion of these changes has been presented earlier in this chapter under the appropriate headings. Here I am concerned with the changes in the species composition that have occurred. The analysis and discussion are restricted to the 115 'common' species discussed in ch 5.4. The species are designated as in Forbes-Watson (1971) with the exception that the two races of shrike Lanius collurio are both included separately (see ch 5.3.3lc). Table 6.16 shows the number of these 115 species in each habitat that are 'Abundant' and 'Present' ('Abundant' and 'Present' as defined in ch 6.4 and with the correction factors applied to the numbers of African visitors and Palaearctic migrants). For the total in these categories in each habitat see Table 6.10.

Of the 115 species, seven are confined to Riverine. They are three insectivores (two vegetation gleaners and one twig specialist), one frugivore, one granivore, and two eating fruit and insects (one vegetation gleaner and one ground gleaner). A further species, the kingfisher Halcyon

TABLE 6.16. The number of the 115 'common' species in each habitat

	Habitat								
	G	BG	WBG	B	WB	W	R	PSH	TOTAL
Abundant	15	20	27	19	27	28	23	27	29
Present	22	47	57	63	61	58	55	63	86
TOTAL	37	67	84	82	88	86	78	90	115

Notes:

- 1) Abundant is more than 1.0 individuals seen per hour's censusing (Type I);
Present is 0.05 to 1.0 individuals seen per hour's censusing (Type I).
See text.

leucocephala (a pouncer), was 'Abundant' in Riverine but was not common enough to be included as 'Present' in Woodland or the Park savanna habitats, but it was 'Present' in Wooded Bushland, Wooded and Bushed Grassland and Bushed Grassland. These eight species are a cross section of the guilds that occur in the Tsavo area, and all are likely to be lost from the area if the Riverine vegetation disappears from the Park. Riverine is a very small total area, and was being heavily used and changed by elephants so it is possible that it will be destroyed.

A different situation exists in the remaining habitats as none is currently in imminent danger of disappearance in the area as a whole, although Woodland has already disappeared from the southern area of the Park, and Bushland and Wooded Bushland must be considered vulnerable as their total areas are relatively small. The Woodland (W) and the Park savanna habitats (PSH) have a similar total number of species (86 and 90 respectively) but the composition is rather different. Only 68 species are common to both and only 42 of these are equally common in each (10 'Abundant' and 32 'Present'). Tables 6.17 a to f show the distribution over feeding guilds of all these 107 species. Tables 6.17 a and b are the 42 species which have been more or less unaffected by the habitat changes and can be seen fairly commonly everywhere. As do those confined to Riverine, they represent a cross section of the guilds occurring in the area. The species in Tables 6.17 c and e are those which have decreased in numbers, and the species in Tables 6.17d and f are those that have increased in numbers as a result of the habitat changes. Here some generalisations can be made. Five (of the total of six) obligate frugivores are in Table 6.17. All are in W and four are 'Abundant' there. Only two are 'Present' in PSH, the mousebird Colius macrourus and parrot Poicephalus rufiventris, and there is no insect and fruit eater more common in the PSH than in W. Two obligate granivores, the doves Streptopelia semitorquata and Turtur chalcospilos are 'Present' in W (and Riverine) but not the PSH, and only one, the weaver Ploceus rubiginosus, which also eats

Table 6.17. A comparison of Woodland (W) and the Park savanna habitats (PSH). The number of 'common' species occurring in each feeding guild.

a) 'Abundant' in W, 'Abundant' in the PSH

Feeding guild	A	P	G	V	T	Total
I only	-	2	1	1	-	4
I + F	-	-	1	-	-	1
I + S	-	-	1.5	0.5	-	2
I + N	-	-	-	-	-	-
All I	-	2	3.5	1.5	-	7
All F						1
All S						<u>5</u>
Total						10

b) 'Present' in W, 'Present' in the PSH

Feeding guild	A	P	G	V	T	Total
I only	1	4.5	5.5	8	5	25 ^a
I + F	-	-	1	1	-	2
I + S	-	-	3.5	0.5	-	4
I + N	-	-	-	-	-	-
All I	1	4.5	10	9.5	5	31
All F						2
All S						<u>5</u>
Total						32

a) includes one on large mammals (starling Buphagus erythrorhynchus)

c) In W^a, not in the PSH

Feeding guild	A	P	G	V	T	Total
I only	-	-	3.5	3.5	-	7
I + F	-	-	1(1)	3	-	4(1)
I + S	-	-	-	-	-	-
I + N	0.5(0.5)	-	-	1.5(0.5)	-	2(1)
All I	0.5(0.5)	-	4.5(1)	8(0.5)	-	13(2)
All F						7(3)
All S						<u>2</u>
Total						20(4)

a) The figures given are the total (i.e. 'Present' + 'Abundant'). The number of 'Abundant' species is given in brackets.

d) Not in W, in the PSH^a

Feeding guild	A	P	G	V	T	Total
I only	3.5	3(1)	6.5(1)	1	-	14(2)
I + F	-	-	-	-	-	-
I + S	-	-	4	-	-	4
I + N	-	-	-	-	-	-
All I	3.5	3(1)	10.5(1)	1	-	18(2)
All F						-
All S						8(3)
Total						22(5)

a) The figures given are the total (i.e. 'Present' + 'Abundant').
The number of 'Abundant' species is given in brackets.

e) 'Abundant' in W, 'Present' in the PSH

Feeding guild	A	P	G	V	T	Total
I only	2	-	2	3	1	8
I + F	-	-	4	1	-	5
I + S	-	-	10.5	0.5	-	1
I + N	-	-	-	1	-	1
All I	2	-	6.5	5.5	1	15
All F						8
All S						-
Total						17

f) 'Present' in W, 'Abundant' in the PSH

Feeding guild	A	P	G	V	T	Total
I only	-	1	1	-	-	2
I + F	-	-	-	-	-	-
I + S	-	-	3	-	-	3
I + N	-	-	-	-	-	-
All I	-	1	4	-	-	5
All F						-
All S						7
Total						9

Notes:

- 1) I = Insect, F = Fruit, S = Seeds, N = Nectar, A = Aerial hawking, P = Pouncing, G = Ground-gleaning, V = (green) Vegetation-gleaning, T = Twig specialist
- 2) 'Abundant' is more than 1.0 individuals seen per hour's censusing (Type I). 'Present' is 0.05 to 1.0 individuals seen per hour's censusing (Type I). See ch 6.4.1.
- 3) Where a species is in two feeding guilds 0.5 has been scored in each

insects, is commoner in W than the PSH. But four granivores are in the PSH (three are 'Abundant') but not W, and another four are commoner in the PSH than in W. Among the insectivores, three pouncers are in the PSH (one is 'Abundant') but not W and another is commoner there; there are no pouncers commoner in W. In moving from W to the PSH there is a net loss of seven vegetation gleaners, and a net gain of six ground gleaners, with 5.5 more vegetation gleaners commoner in W, but 2.5 ground gleaners also commoner in W.

18 species occur in W but not the PSH, four of which are 'Abundant' there. Only three, however, the barbet Lybius melanocephalus, thrush Turdus tephronotus, and weaver Ploceus nigricollis are not 'Present' in either Riverine, or at least one of the individual PSH. Of the other 15 species, 10 are in Riverine, eight in Wooded Bushland, five in Bushland and one (uncommon) in Wooded and Bushed Grassland. The first three of these habitats are vulnerable to destruction, so, although the Park has so far lost only three species, it stands to lose 15 more if the destruction continues.

22 species, however, are in the PSH but not W, and have been gained, although nine occur in Riverine as well (two are Abundant there, the cuckoo Centropus superciliosus and the bee-eater Merops albicollis). There is obviously a great difference between W and the thickest of the PSH, Wooded Bushland (WB). Of the 22 species, 14 (64 %) are 'Present' in WB and one, the waxbill Amadina fasciata is 'Abundant'. Further, eight species are in all five of the PSH and none of these except A. fasciata and the roller Coracias caudata are in Riverine. They therefore represent new arrivals.

Looking through the sections of ch 5.3 it is clear that many other species have been lost from the area since the period 1959-60 when A.D. Forbes-Watson lived in Tsavo East but there are no quantitative data on them. For a few species there are early records which suggest that there really has been an immigration. Before 1960 the bee-eater Merops revoilii

was only seen north of the Galana River (A.D. Forbes-Watson pers. comm.). It is now fairly common south to the Voi River (pers. obs. and see Leuthold 1973). There is one record south of the Voi River (5 km) on 6.9.76 (pers. obs.) (see Lack et. al ¹⁹⁸⁰), and two records along the Tsavo River in Tsavo West N.P. in March 1976 (D.J. Pearson) and February 1979 (A.L. Archer) (records noted in Archer (1979) and editorial note after this). Another 'common' species, the lark Eremopterix signata, seems to have replaced E. leucopareia since about 1965 (see ch 5.3.26). Of the rarer species, or those not considered in detail in this study, the ostrich Struthio camelus molybdophanes (see ch 5.3.1), the button-quail Ortyxelos meiffrenii (see Lack 1975 and ch 5.3.3), and lark Mirafra pulpa (see Lack 1977 and ch 5.3.26) have also apparently moved in over the last twenty or thirty years. None of these was recorded in Woodland and, for all, the known geographic range is mainly to the north of Tsavo (Hall & Moreau 1970, Snow 1978). They/have been moving in in response to the general aridity and opening up of the habitat, which have made Tsavo more similar to the regions in northern Kenya and Somalia.

Summarising, the change from Woodland to the Park savanna habitats has meant a loss of frugivores and vegetation-gleaning insectivores, and a gain of granivores and ground-feeding insectivores (both pouncers and gleaners). These results can be deduced from the analyses of density and biomass presented earlier in this chapter but the differences here are more emphatic. They can of course be related directly to the availability of the different food types and feeding sites.

Postscript

Since I left Tsavo in early 1977, there has been a great deal of rain, even outside the normal wet seasons, and the elephant population has declined considerably perhaps as much as 50%. The result has been that the habitat is beginning to revert towards thicker bush. The effect of this

on the bird populations will be to maintain the present high diversity, and allow those species characteristic of thicker habitats to increase. Those characteristic of the more open habitats will still be present in substantial numbers for a long time yet, as their habitats are so widespread, except perhaps for those few largely confined to Grassland.

CHAPTER 7 Life cycles of birds in Tsavo East National Park

7.1. Introduction

I have divided the birds which occur in Tsavo into three groups: resident, African visitor, Palaearctic migrant. As explained in ch 5.4.1, in most cases a species was easily classified into one of these groups, although a few arbitrary decisions had to be made. Particularly difficult were those species with a resident population which was augmented from elsewhere at certain seasons. These have been classed as residents except for those species of which the vast majority move away and those few which remain often do so in a restricted habitat; for example the dove Streptopelia senegalensis (see ch 5.3.8). The annual cycle of these three groups can be considered in turn.

7.2. Residents

Just over 60% of the 'common' species in Tsavo East N.P. are classed as resident. The total number of individuals of resident species present, however, varies on a regular basis through the year; in most habitats the lowest numbers occurred in the dry season and peak numbers in December and January. Only a few of these species are sufficiently abundant to be shown individually to vary in numbers. Such species seem to move around both within and in and out of the area, either on a regular seasonal basis e.g. the hornbills Tockus erythrorhynchus and T. deckeni (ch 5.3.22) or on an irregular basis e.g. the lark Eremopterix signata (ch 5.3.26). However, for all resident species there is always a sizeable population present. It is likely that many other, if not most, resident species will be found to show some more or less local movement when more detailed data become available. Further, the number of individuals and number of species involved in such movements are likely to vary from year to year in response to local conditions.

In theory, breeding should occur around the time of peak food availability, both for the parent birds to be able to build up sufficient reserves to survive a breeding attempt, and for their young to have the greatest chance of survival when they first become independent. Table 7.1 shows, for each feeding guild, the number of breeding records that I noted each month. The records have been scored for the month in which eggs were laid (calculated from the age of the young if necessary). The table shows that all insectivorous species have a peak of breeding activity from November to January although not significant in some cases due to small sample sizes, but that those in the ground-gleaning guild also have a second, smaller and not significant peak in April and May. These periods coincide with peak food abundance. Sinclair (1978) found that ground-nesting, but not necessarily ground-gleaning, species had a peak of nesting in the long rains (April and May), and those nesting above ground a peak in January. My data for ground-nesting insectivores are too limited to know if the same is true in Tsavo (Fig. 7.1). Sinclair (1978) attributed the difference to the fact that ground-nesting species are larger and therefore need more time to build up condition. The ground-feeding species are larger than other insectivorous groups in Tsavo (Table 6.7) so the same could apply, but there will be a greater pressure in Tsavo for them to breed in the November-December rains if possible, and the main peak is then, because the April rains may not occur at all. In the Serengeti N.P., Tanzania, where Sinclair (1978) was working, the April rains are much more reliable, and the birds could therefore afford to wait. Another reason for breeding in April and May rather than December and January may be food availability. The grass cover in December and January may be so high that insects on the ground are hidden, and therefore less available than would appear from their abundance.

The purely granivorous species in Tsavo show two apparent peaks of breeding activity, in December-January and in May-June (the statistics identify a single peak between the two). And despite the lack of rain in April in both my study years, I have more breeding records in the second peak than the first.

TABLE 7.1. The number of breeding records of resident birds in each month(1975 and 1976 combined) in each feeding guild.

Feeding Guild	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	TOTAL (=N)	R/N	Signif.	Peak week
Insects																
Aerial hawking	-	-	-	1	2	4	1	-	-	-	-	1	9	0.69	**	Nov 4
Pouncing	-	-	2	2	4	6	6	3	1	2	1	-	27	0.58	**	Dec 3
Ground gleaning	-	1	2	6	8	18	3	-	1	7	4	2	52	0.41	**	Dec 1
Ground and vegetation gleaning	-	-	-	1	-	4	-	-	-	-	1	-	6			
Vegetation gleaning	-	-	-	3	3	1	1	2	1	-	-	-	11	0.64	*	Dec 1
Twig specialists	-	1	-	1	1	3	1	-	1	-	1	-	9	0.43	N.S.	
Insects and Ground gleaning																
Seeds	-	-	-	2	5	14	2	3	-	1	-	-	27	0.82	**	Dec 2
Insects and Ground gleaning																
Fruit	-	-	-	5	10	8	8	3	4	1	1	-	40	0.66	**	Dec 3
Vegetation gleaning	-	-	-	-	-	3	-	-	1	-	-	-	4			
Insects and Vegetation gleaning	-	-	-	2	2	5	2	1	-	-	-	-	12			
Nectar																
Aerial hawking and Vegetation gleaning	-	-	-	-	-	1	-	-	-	-	-	-	1	0.85	**	Dec 1
Seeds	1	-	-	-	-	2	4	1	-	2	4	5	19	0.45	*	Apr 3
Fruit	-	-	1	-	-	-	1	1	-	1	1	1	6	0.33	N.S.	Apr 3
TOTAL	1	2	5	23	35	69	29	14	9	14	13	9	223			

Notes:

- 1) The records are placed in the month in which eggs were laid (calculated back from age of young if necessary)
2) No records before 1st January 1975 or after 31st December 1976 are included.
3) The statistics are explained in ch 5.2.5. Significance levels ** P<0.01, *P<0.05, N.S. not significant. The peak is ²²₂ identified to the quarter month.

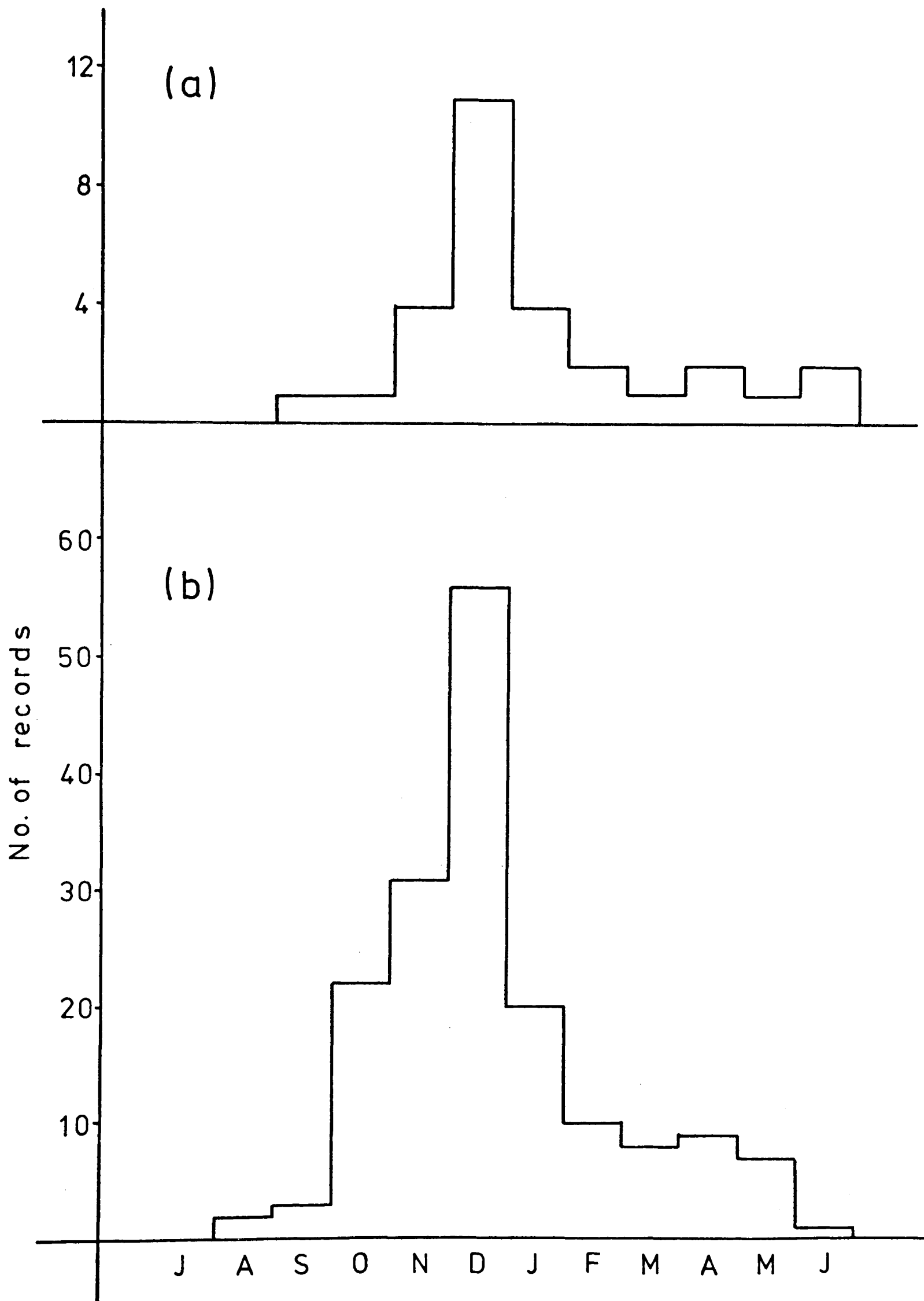


Fig. 7.1 The number of breeding records of a) ground-nesting birds; and b) above-ground-nesting birds in each month. Records are scored for the month in which eggs were laid.

Granivores do not breed at the start of the rains because seeds are likely to be at their lowest abundance then. The crop of seeds from the previous rains will have germinated and the new crop will not yet be ripe. The availability of the new crop is delayed still more for resident species of granivore because most take their seeds from the ground and not the stem (ch 5.4.4). They may breed preferentially in May and June rather than December and January because the young will then have a longer period before a severe food shortage occurs due to germination of the seeds in the next wet season. The six breeding records of purely frugivorous species are too scattered through the year to make any statements about their breeding regime. Sinclair (1978) found a relatively even spread of breeding among all vegetarian species and he attributed the lack of wet season peak of breeding to food shortage.

A few species in Tsavo breed in the dry season although there seems to be less such in Tsavo than in many areas, even semi-arid ones (see summaries in Moreau 1950). The most conspicuous of dry season breeders are several birds of prey (pers. obs. and see Smeenk (1974) and Smeenk & Smeenk-Enserink (1976)) and the Ostrich Struthio camelus (Leuthold 1977c). In the case of the birds of prey the reason is food availability (Smeenk 1974). Their prey is more easily visible in the dry season, due to less grass cover, even if it is less abundant in total then. For S. camelus Leuthold (1977c) argued for an extreme case of the size argument mentioned above. S. camelus lays its eggs in the middle of the long dry season, or occasionally in the short dry season, and Leuthold suggested that this is a compromise between the requirements of the adult (for egg production) and of the young (for growth and survival) in relation to the two wet seasons.

Some authors, e.g. Beals (1970), have found that closely related species stagger their breeding seasons, and have argued that this is one of the reasons why such a large number of species can coexist in tropical areas.

I found no evidence of this in Tsavo, perhaps because the dry season is too severe for most species to attempt to breed. Beals's (1970) study area in Ethiopia had a similar total rainfall to Tsavo, but the trees and bushes were in leaf between May and January which implies a much less severe dry season. The altitude, 1800 m above sea level, would also contribute to this. Hence the staggering of breeding that Beals found was possible in Ethiopia, and perhaps allowed even more species to coexist there than would otherwise have been able to.

If a bird is to be resident, one would expect that a catholic choice of food type would be advantageous. As seen in Table 5.16, 26 (34%) of the 'common' resident species are classified in polyphagous feeding guilds and a high proportion (84%) of all polyphagous species are resident. But this understates the importance of the polyphagous birds in the avifauna of Tsavo East N.P.. Table 6.1 has shown the proportion of each food guild in each habitat. Table 7.2 shows the proportion of polyphages in the Park savanna habitats combined, in Woodland and in Riverine in each month. The latter table shows that the proportion of polyphages is low in December and January, mainly as a result of the large number of visiting species (both African and Palaearctic). In all habitats, however, polyphages are a very important part of the fauna, especially in terms of their biomass, in the dry season when there are almost no visitors present.

Some residents are seen clearly to be dependent on less seasonally variable resources than visitors. The resident granivores take their seeds from the ground and not the stem (ch 5.4.4), and there is a higher proportion of residents among ground-gleaning insectivores than among vegetation-gleaning ones (Table 5.17) which follows predictions of insect availability (ch 4.4.4). This dependence of residents on less seasonally variable resources was found by Herrera (1978) on his Mediterranean study area, and in an intensive analysis, he was able to show that resident species had a narrower repertoire of foraging tactics than non-residents. He explained

TABLE 7.2. The percentage of polyphagous birds in each month in three habitat groups

		Park savanna habitats		Woodland		Riverine	
		Nos	Biomass	Nos	Biomass	Nos	Biomass
1975	F	3 (26)	9 (31)	30	40	16	21
	M	37	49	29	31	5	12
	A	32	41	33	32	24	38
	M	46	46	38	35	30	36
	J	35	40	37	29	29	15
	J	54	48	51	65	58	61
	A	59	49	53	76	41	48
	S	49	48	52	65	35	47
	O	41	34	38	48	30	35
	N	40	39	37	52	36	50
	D	39	43	33	38	29	32
1976	J	16	17	28	41	2 (13)	8 (25)
	F	12	19	45	53	27	36
	M	39	53	21	22	17	39
	A	28	37	26	27	5 (18)	14 (27)
	M	47	49	43	30	33	41
	J	30	17	41	41	53	58
	J	42	33	55	68	32	30
	A	45	47	51	59	35	44
	S	36	29	47	66	56	63
	O	51	50	54	60	38	33
	N	46	47	51	54	26	41
	D	27	32	24	47	22	33
1977	J	18	17	13	27	14	17

Notes: 1) The figures in brackets are the percentage if the large flocks are excluded.

this by saying that the less seasonally variable resources necessitated greater specialisation due to competition. I do not have sufficiently detailed data to show this for Tsavo, but there will be more of a conflict between this specialisation and the necessity to be a generalist in the harsher conditions.

There is a consistent significant relation, however, between residential status and habitat specialisation. I have scored each of the 115 'common' species as 'Present' or 'Absent' in each of the seven major habitat types. (A species was scored as 'Present' in a habitat if more than 0.05 individuals were seen per hour's censusing and the correction factors have again been applied to both visiting groups before designating their categories - see ch 6.4.1). A resident species ($n=76$) was found to be 'Present', on average, in 4.11 habitat types (S.E. = 0.21); an African visitor ($n=20$) 'Present' in 5.05 habitat types (S.E. = 0.34); and a Palaearctic migrant ($n=19$) in 5.68 habitat types (S.E. = 0.25). A visiting species (both latter groups combined) ($n=39$) was in 5.42 habitat types (S.E. = 0.21). The resident species have a significantly narrower habitat range than both the African visitors ($d=2.37$, $df\ 35$, $P<0.02$), and the Palaearctic migrants ($d=4.76$, $df\ 45$, $P<0.001$). (For residents: all visitors $d=4.14$, $df\ 98$, $P<0.001$.) The Palaearctic migrants also have a slightly broader but not significantly so, habitat range than the African visitors ($d=1.49$, $df\ 35$, N.S.). Hence residents would appear to be more habitat specialists than the visiting species, which agrees with Herrera's (1978) predictions.

So the resident species are perhaps more closely packed than the visitors but they seem to be doing the best they can in taking the most abundant foods and breeding at the best season; but it should be emphasised that it is doubtful whether any species is fully resident in the sense that all individuals stay within the confines of the Tsavo area throughout the year.

7.3 African visitors

Table 7.3 shows the months in which each of the 19 'common' visitors occur in Tsavo, and there are seen to be three main patterns of occurrence:

1. occurring from the short rains and through the subsequent dry season - 3 species e.g. the bee-eater Merops s. superciliosus;
2. occurring in the short rains only - 5 species e.g. the dove Streptopelia senegalensis;
3. occurring in or shortly after the short rains, not in at least the latter part of the short dry season, and reappearing in the long rains - 12 species e.g. the cuckoo Clamator jacobinus.

The hoopoe Upupa epops africana is slightly different because it is still fairly common into the long dry season and at least three of the second group, the quail Coturnix delegorguei, cuckoo Chrysoccyx caprius, and weaver Vidua paradisaea, may actually belong to group 3 whenever there is more rain in April/May than in 1975 and 1976.

None of these species are present in the middle to late part of the long dry season (except perhaps for a few individuals), and all are present in or very shortly after the short rains. Three of the four species which arrive earliest, in November, are at least partially insectivorous, and of the seven not arriving till January five are purely granivorous (cf. 12 of the total of 20 are at least partially insectivorous and 11 are at least partially granivorous (Table 5.16)). It is however correlated with food supplies. Grass seeds do not become abundant until about a month after the start of the rains, indeed the start of the rains is the leanest season. The reason some granivores are able to stay in Tsavo through this period is probably because the rain, especially at the start of the season, is very patchy in spatial distribution, so that sufficient seeds will remain in those areas which have not had rain, until the grasses in those which had the first rain have set seed. Some insects increase in numbers immediately the first rains fall, and as said previously, many of the arriving species,

TABLE 7.3. The months in which the 'common' African visitors occur

Species	J	A	S	O	N	D	J	F	M	A	M	J
Coturnix delegorguei(B)					-	x	x					
Streptopelia senegalensis(B)		-		-	-	xB	xB	-	-	-	-	-
Oena capensis(B)				-	-B	-	x	x	-	-	x	-
Chrysococcyx caprius				-	-	x	x	-	-	-	-	
Clamator jacobinus(B) ^a					-	x	x			x		
Centropus superciliosus(B)				-	-	xB	x	-	-	-	x	
Halcyon leucocephala	-	-			-	x	x	x	-	x	-	-
Merops s. superciliosus(B) ^b			-		-	x	x	x	x			
Merops albicollis					x	-	x	-	x	x		
Upupa epops africana	-				-	-	x	-	-	x	x	x
Mirafra cantillans (B)	-		-	-	-	x	xB	x	-	x	-	
Eremopterix leucotis							-	x		x	x	
Tmetothylacus tenellus(B)				-	xB	xB	x	x	x	-		
Vidua paradisaea						-	x	x		-		
Ploceus intermedius (B) ^c	(x)		-		x	x	-	-	-	x		
Ploceus rubiginosus(B)				x	-	x	-		x	x		
Quelea quelea(B)					-	-	x	x	-	-	-	
Euplectes diadematus(B)					x	xB	x	-		x	x	
Amadina fasciata(B)						-	x	x	x	x		
Creatophora cinerea(B)				-	-	-B	x	-	-	x	x	-
Total number of species	1	0	0	1	4	11	16	9	5	10	5	1
	+	+	+	+	+	+	+	+	+	+	+	+
	3	2	3	6	12	7	3	7	7	6	5	4

Notes: 1) x is those months in which more than 10% of the total numbers of individuals were seen; - is those months in which 1 - 10% of the total were seen.

2) B means there are breeding records for the area; b means there are records of probable breeding in the area.

a) many of the C. jacobinus are thought to be migrants from the Indian subcontinent; see text and ch 5.3.9.

b) this population of M. s. superciliosus probably does not breed; see text and ch 5.3.18.

c) the (x) in July is caused by one small flock which appeared to be simply passing through.

especially the pipit Tmetothylacus tenellus concentrate in those areas which have had rain.

The ecological relationships between these visiting species have been discussed in ch 5.4. There are, however, no general ecological characteristics of the species in each of the three groups mentioned at the start of this section. Some meet closely related residents e.g. the dove S. senegalensis and the kingfisher Halcyon leucocephala, others do not e.g. the hoopoe U. e. africana and quail C. delegorguei. How much direct competition there is between the visitors and residents is unknown but it is certain that many, if not most, of the visitors take their food from a different site or in a different way to residents. Further, the food they take is often only temporarily abundant (e.g. grass seeds on stem) which agrees fairly closely with Herrera's (1978) observations. He recorded visiting species at all seasons, though different ones at different seasons. All were generalists and were taking the foods that were most available at the time. The visitors to Tsavo certainly do the latter, but, at least in broad terms, seem to be less of food generalists than the residents although their habitat range was broader (see ch 7.2).

As can be seen from Table 7.3 a large proportion of these African visitors come into Tsavo to breed, although all will not do so every year. There is only one visitor which is almost certainly a non-breeder, the bee-eater Merops albicollis (see ch 5.3.18), but, as suggested in the species accounts, the population of the bee-eater M. s. superciliosus occurring between December and March is probably non-breeding (ch 5.3.18), and many of the cuckoo C. jacobinus are probably migrants from the Indian subcontinent (ch 5.3.9). The weaver V. paradisaea's main host is the waxbill Pytilia melba and, as this is uncommon in Tsavo, V. paradisaea too may not breed. In the November-December wet season, therefore, Tsavo has to support a great increase of birds in addition to the extra requirements of most for breeding.

Unfortunately very little is known about what these visiting species do at other seasons and where they go. Several species including the kingfisher H. leucocephala, and some species that I have classed as residents in Tsavo, were found by Tennent (1962) to disappear from Kitui township (about 250 km NNW of Voi) at the start of the rains in early November, and reappear there (some with young) in February or March. Kitui town is in a marked rain belt (average 1060 mm per annum), and the only true dry season is between May and October. Hence the climate is much less severe than in Tsavo and this presumably has an effect on the food supplies such that they are never so low. It seems likely therefore that some birds from Tsavo move north and west into these highlands in the dry seasons. Another likely place is towards the coast but there are no observations from there. Tennent (1962) also records several intra-African migrant species especially cuckoos e.g. C. caprius and C. jacobinus, as arriving at Kitui at the onset of the rains, so it is likely that these species at least travel much further, but how much this statement can be extended to other visiting species is unknown. Each species will have its own seasonal rhythm, and extent, of movement and the movement may be extensive. Most species in the African visitor category are fairly widespread in Eastern Africa and, as they are mostly opportunists, it is possible that some others will be found to follow a movement, and even breeding regime, similar to the weaver Quelea quelea (see Ward 1971 and ch 5.3.42).

7.4. Palaearctic migrants

The Palaearctic migrants are similar in many respects to the African Visitors but there are some important differences. Considerably more work has been done on their movements so a slightly clearer picture is available.

Moreau (1972) gives a summary of the state of knowledge of the Palaearctic migrants in Africa up to that date. One major fact that his book showed was that the concept of 'winter quarters' for most Palaearctic species would have to be modified, and this is confirmed by studies since

then. Most species will use at least two, and some three or four different areas, perhaps several hundred kilometers apart, over the course of the northern winter.

Table 7.4 shows, for the 19 'common' Palaearctic species, the months that each is present in Tsavo and it should be compared with Table 7.3 for the African visitors. Excluding the two Lanius which occur only or mainly in April the majority of the Palaearctic species arrive in November which is a month before the main arrival of the African species, but there are no granivorous Palaearctic migrants in Tsavo. The three Palaearctic species that do not arrive till December or January are all vegetation gleaners (one feeds on the ground as well) (Fisher exact probability $P=0.12$). Insects will not appear on the trees and shrubs until there are sufficient leaves, but on the ground there is usually some litter and the green grass responds very quickly indeed to the rain. Therefore insects are probably available earlier. A similar point emerges in considering the species which stay in Tsavo through the dry season compared with those that are only present in November/December and April (see ch 5.4.5c).

By the time that the Palaearctic migrants arrive in Tsavo they have already been in Africa south of the Sahara for about two months. They presumably spend this time to the north of Tsavo, just south of the desert. In September and October this area is green and food is at its most abundant. When the area starts to dry out and food supplies decrease, the intertropical front with its associated rain has moved south, and there is abundant food where there was very little in September. Some species probably move south slowly, feeding as they go, but some certainly undertake major movements which are typical of long distance migrations from and to Europe. The evidence for this has come particularly from observations at Ngulia in Tsavo West N.P.. Birds coming in to the lights included some carrying an appreciable amount of fat, and some in arrested moult. Most also seemed to

Table 7.4. The months in which the 'common' Palaearctic migrants occur

Species	J	A	S	O	N	D	J	F	M	A	M	J
Cuculus canorus canorus				-	x	x	-			x		
Coracias garrulus				-	x	x	x	x	x	-		
Monticola saxatilis				-	x	x	x	x	x	-		
Oenanthe oenanthe	-		-	x	x	x	x			-	-	
Oenanthe isabellina				-	x	x	x	x	x			
Oenanthe pleschanka				-	x	x	x	x	x	-		
Irania gutturalis					-	x	-	-	x	x		
Cercotrichas galactotes					x	x	x	x	x	-		
Hippolais pallida					x	x	x	x	x	x		
Hippolais languida						-	x	x	x	x		
Acrocephalus palustris					x	x	-	-		-		
Sylvia communis					x	x	x	-	-	x		
Sylvia nisoria					x	x	x	x	-	-		
Phylloscopus trochilus				-	-	x	-		x	x		
Muscicapa striata				-	x	x	x	x	x	-		
Lanius minor										x		
Lanius collurio collurio					-	-	-	-	-	x		
Lanius collurio isabellinus					x	x	x	x	x	-		
Oriolus oriolus				x	x	x		x	x	x		
Total number of species	0	0	0	2	14	16	12	11	12	9	0	0
	+	+	+	+	+	+	+	+	+	+	+	+
	1	0	1	7	3	2	6	5	3	9	1	0

Notes: 1) x and - as in Table 7.3.

move on quickly (Pearson & Backhurst 1976). The commonest species that were caught in the Ngulia study (warblers A. palustris, S. communis and chat Luscinia luscinia) are all among the eight species occurring in my study only in November/December (and, for some, April). This suggests that they are only passage migrants, with the birds going further south for the latter part of the winter and not staying in Tsavo. The maps of winter range in Moreau (1972) show all these species mainly to the south and west of Tsavo.

The only species that first arrives at the start of the dry season is the warbler Hippolais languida, although its congener H. pallida increases then as well (ch 5.3.34), and although both are regular in catches at Ngulia, neither species has been found there with large fat reserves, a situation paralleled in the chat Cercotrichas galactotes and suggesting that they are not going further south at least immediately.

By early April the species which have been present in Tsavo through the dry season are leaving rapidly, presumably northwards. This exodus coincides with an arrival of the same passage migrants which occurred in December and a shrike, Lanius minor. Apart from this last, its congener L.c. collurio and the warbler Phylloscopus trochilus, all these passage migrants are, however, less common in April and give the impression even more of simply passing through than they did in December. March to early May is the long rainy season in much of Kenya, and hence there is likely to be plenty of food available over a wide area, although the rains are unpredictable in space and exact timing in some of the more arid areas.

All birds seem to start moving north about the end of March and will presumably fatten for the desert crossing as far north as possible. Those spending the major part of the winter in Tsavo leave about this time and those species occurring in April are those that seem to have started moving north at the same time but from further south. There is, however, no evidence that the species which winter further north in Africa arrive in

Europe before (or after) those wintering further south. Birds must travel through Africa south of the desert at different speeds. They start moving slowly, feeding as they go and presumably where possible building up some reserves. At some point they will need to build up the necessary fat reserves for the major flight to Europe probably remaining in one "good patch" to do so. It has been shown that this process can be extremely rapid e.g. only about two weeks is necessary at Lake Chad (Fry, Ash & Ferguson-Lees 1970). In East Africa there do not appear to be any major concentrations of birds fattening up. One might expect Lake Turkana (Rudolf) to be such a concentrating place but the numbers recorded there by Fry, Britton, & Horne (1974) in spring do not support the idea. The birds must be able to fatten in any relatively good patch and Tsavo might be such a patch in years with plenty of rain; but it may be too far south.

Birds in eastern Africa face much less harsh conditions during the spring migration than those in West Africa. How the migrants there are able to fatten in such apparently harsh and adverse conditions has come to be known as Moreau's paradox (e.g. Morel 1973). Morel & Morel (1974) and Elgood, Fry & Dowsett (1973) suggest that the migrants are following local food superabundances such as at Lake Chad, as I suggest they do in eastern Africa. In West Africa however, the patches are likely to be fewer and therefore the birds more concentrated. They do concentrate at good patches but it is also certain that the birds are capable of surviving, and even fattening, in very adverse conditions. The conditions cannot be as bad as has often been thought.

Competition between Palaearctic migrants and African species seems to be relatively slight. Only four Palaearctic species meet congeners of similar size as themselves: the roller Coracias garrulus meets C. caudata (and very rarely C. naevia), the chat C. galactotes meets C. leucophrys, the shrike L. minor meets L. dorsalis but only in April, and the oriole Oriolus

oriolus meets O. larvatus. For distinctions between these pairs see the appropriate sections of ch 5.3. The chat Irania gutturalis meets several species with similar ecology, although not closely related ones even at subfamily level, but it is only a passage migrant in Tsavo. All passage migrants are, like the granivorous African visitors, taking food which is of seasonal occurrence, insects off leaves. The remainder of the Palaearctic migrants, however, are not creaming off an obviously seasonal surplus, but coming in to otherwise vacant niches. Competition appears to be more intense between themselves than between them and the local African species.

CHAPTER 8 Summary and Conclusions

In all habitats the supply of insects and grass seeds is at a maximum in and shortly after the November-December wet season. The supply of both foods decreases after January until about the end of March. The April rains bring a second increase, but in both years I was in Tsavo there was very little rain then and the increase was not marked. After May the supply of both seeds and insects decreases steadily until the onset of the rains in November. Some insects then increase immediately in abundance, but the first two weeks of the wet season are probably the period of lowest abundance of seeds due to germination. The supplies of fruit through the year vary with the habitat. In the Park savanna habitats fruit is only commonly available in the latter part of each wet season. In Woodland, some fruit is probably available all the year, but there is a major peak of abundance between July and September due to Commiphora spp. In Riverine, too, there is probably always some available, but there is a small peak in August.

The annual cycle of the birds in each habitat closely follows these cycles of food abundance. In the Park savanna habitats, densities are lowest in the long dry season when the average is 1.0 to 1.5 birds per hectare (equivalent to 70 to 75 g per hectare). With the onset of the rains there is an almost immediate increase in insectivorous birds, both of species moving in, to breed, from elsewhere in Africa and migrants from the Palaearctic. These latter, however, will have already been in Africa south of the Sahara for about two months. By a month after the onset of the rains granivorous birds are also moving in in very large numbers and these are all Ethiopian region birds, and none are Palaearctic migrants. Total numbers reach a peak density (about five times the lowest) during January, with the granivorous birds forming the majority. Many of the visitors disappear again after January, in particular the granivores and those

insectivores which feed in the woody vegetation. In April a few return and as a result there is a slight increase in numbers (both insectivores and granivores), but in 1975 and 1976 this was probably less than usual due to the relative failure of the rains. Frugivores play a very minor role in these habitats (3 - 4% of the total numbers).

Total numbers in Woodland remain much more constant through the year with a density of about 4.0 to 5.0 birds per hectare all through (equivalent to 200 to 300 g per hectare). Insectivores and granivores are still dominant in December and January but, compared with the Park savanna habitats frugivores are much more prominent at all seasons (about 25% of the total). These last show a peak in numbers in the long dry season and insectivores show a second peak then. In contrast to those responsible for the peak in December-January, the birds in the long dry season peak are mainly of species which have a resident population and not immigrant species. It is likely though that many of the individuals are immigrants from outside the Tsavo area and not simply moving out of the Park savanna habitats into the Woodland.

Riverine shows a peak abundance in December and January with granivores and insectivores mainly responsible. There is also a small peak in August due to frugivores and insectivores.

These different cycles in the different habitats are the more important because over the last 20 years the vegetation in the Park has changed from predominantly Woodland into the more open habitats (here referred to as the Park savanna habitats). The result is that there has been a decrease in the average density and biomass of birds in the Park and a change in the annual cycle of numbers. It has also meant a considerable change in bird species composition and, because there is still some of the original Woodland remaining in the area (though not in the southern area of the Park) the total diversity of birds in the area as a whole is considerably higher than it was when the Park was gazetted in 1948, and probably higher than it has ever been.

REFERENCES

- Abbott, I., Abbott, L.K. and Grant, P.R. 1977. Comparative ecology of Galapagos Ground Finches (Geospiza Gould): evaluation of the importance of floristic diversity and interspecific competition. *Ecol. Monogr.* 47:151-184.
- Agnew, A.D.Q. 1968. Observations on the changing vegetation of Tsavo National Park (East). *E. Afr. Wildl. J.* 6:75-80.
- Angwin, J. 1968. A preliminary study of the ecology of birds in riverine Acacia woodland. Unpublished M.Sc. thesis, University of Nairobi.
- Archer, A.L. 1979. Somali Bee-Eater Merops revoilii in Tsavo West. *Scopus* 3:58-59.
- Archer, G.F. and Godman, E.M. 1937-1961. Birds of British Somaliland and the Gulf of Aden. London: vols. 1 and 2, Gurney and Jackson; vols. 3 and 4, Oliver and Boyd.
- Ash, J.S. 1976. Bird ringing in Ethiopia: report no. 5. 1969-1975. US Naval Medical Research Unit Five. Ethiopia and Smithsonian Institution.
- Backhurst, G.C. and Pearson, D.J. 1977a. Southward migration at Ngulia 1976-77. *Scopus* 1:12-17.
- Backhurst, G.C. and Pearson, D.J. 1977b. Ethiopian region birds attracted to the lights of Ngulia Safari Lodge, Kenya. *Scopus* 1:98-103.
- Backhurst, G.C. and Pearson, D.J. 1979. Southward migration at Ngulia, Tsavo, Kenya 1978/79. *Scopus* 3:19-25.
- Barbault, R. 1967. Recherches écologiques dans la savane de Lamto (Côte d'Ivoire): le cycle annuel de la biomasse des amphibiens et des lézards. *Terre et Vie* 21:297-318.
- Barbault, R. 1970. Les traits quantitatifs du peuplement des Ophidiens. *Terre et Vie*. 24:94-107.
- Beals, E.W. 1970. Birds of a Euphorbia-Acacia woodland in Ethiopia: habitat and seasonal changes. *J. Anim. Ecol.* 39:277-297.
- Beesley, J.S.S. 1972. Birds of the Arusha National Park, Tanzania. *Jl. E. Afr. nat. Hist. Soc. natn. Mus. no.* 132:1-30.
- Bellier, L. 1967. Recherches écologiques dans la savane de Lamto (Côte d'Ivoire): densités et biomasses des petits mammifères. *Terre et Vie* 21:319-329.
- Benson, C.W. and Benson, F.M. 1977. The birds of Malawi. Limbe, Malawi: D.W.K. MacPherson (sponsor).
- Benson, C.W., Brooke, R.K., Dowsett, R.J. and Irwin, M.P.S. 1973. Birds of Zambia. 2nd edition. London: Collins.

- Berthold, P. 1976. Animalische und vegetabilische Ernährung omnivorer Singvogelarten: Nahrungsbevorzugung Jahresperiodik der Nahrungswahl, physiologische und ökologische Bedeutung. J. Ornithol. 117: 145-209.
- Britton, P.L. 1971. Some non-passerine bird weights from East Africa. Bull. Br. Orn. Club 90:142-144, 152-154.
- Britton, P.L. 1974. Relative biomass of Ethiopian and Palaearctic passerines in West Kenya habitats. Bull. Br. Orn. Club. 94:108-113.
- Britton, P.L. and Britton, H.A. 1977. An April fall of Palaearctic migrants at Ngulia. Scopus 1:109-111.
- Brown, L.H. 1966. Observations on some Kenya eagles. Ibis 108:531-572.
- Brown, L.H. and Brown, B.E. 1973. The relative numbers of migrant and resident rollers in eastern Kenya. Bull. Br. Orn. Club 93:126-130.
- Buskirk, W.H. 1975. Substrate choice of oxpeckers. Auk 92:604-606.
- Buxton, R.D. 1979. The role of termites in the ecology of Tsavo National Park, Kenya. Unpublished D. Phil. thesis, Oxford University.
- Cobb, S.M. 1976. The distribution and abundance of the large herbivore community of Tsavo National Park, Kenya. Unpublished D. Phil. thesis, Oxford University.
- Coe, M.J. 1972. Ecological studies of the small mammals of South Turkana. The South Turkana Expedition Scientific Papers IX. Geogr. J. 138:316-338.
- Coe, M.J., Cumming, D.H. and Phillipson, J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. Oecologia 22:341-354.
- Clancey, P.A. 1968. On Merops superciliosus Linnaeus from western South Africa. Ostrich 34:202.
- Corfield, M.M. 1974. Historical notes on Tsavo. Nairobi: Kenya National Parks. Duplicated MS.
- Corfield, T.F. 1973. Elephant mortality in Tsavo National Park, Kenya. E. Afr. Wildl. J. 11:339-368.
- Cornwallis, L. 1975. The comparative ecology of eleven species of wheatear (genus Oenanthe) in S.W. Iran. Unpublished D. Phil. thesis, Oxford University.
- Cottam, G. and Curtis, J.T. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.
- Cunningham van Someren, G.R. 1971. Breeding of White-throated Bee-Eaters Merops albicollis. EANHS Bull. 1971:162-163.
- de Greling, C. 1972. Sur les migrations et mouvements migratoires de l'avifaune éthiopienne, d'après les fluctuations saisonnières des densités de peuplement en savane soudanienne au nord Cameroun. Oiseau Revue fr. Orn. 42:1-27.

- Diamond, J.M. 1972. Avifauna of the eastern highlands of New Guinea
Cambridge, Mass.: Publs. Nuttall Orn. Club no. 12.
- Dingle, H. and Khamala, C.P.M. 1972. Seasonal changes in insect abundance
and biomass in an East African grassland with reference to breeding
and migration in birds. *Ardea* 60:216-221.
- Elgood, J.H., Fry, C.H. and Dowsett, R.J. 1973. African migrants in
Nigeria. *Ibis* 115:1-45, 375-411.
- Elliott, C.C.H. 1972. An ornithological survey of Kidepo National Park,
northern Uganda. *Jl;E. Afr. nat. Hist. Soc. natn. Mus. no.*
129:1-31.
- Emlen, J.T. 1971. Population densities of birds derived from transect
counts. *Auk* 88:323-342.
- Emlen, J.T. 1977. Estimating breeding season bird densities from transect
counts. *Auk* 94:455-468.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a
cause of spring feeding by winter moth caterpillars. *Ecology*
51:565-581.
- Forbes-Watson, A.D. 1967. Preliminary check list of the birds of Tsavo
(East) National Park. Nairobi: Kenya National Parks. Duplicated
MS.
- Forbes-Watson, A.D. 1971. Skeleton check list of East African birds.
Nairobi: National Museum. Duplicated MS.
- Friedmann, H. 1964. Evolutionary trends in the avian genus Clamator.
Smithsonian Miscellaneous Collections. Vol. 146 no. 4.
- Fry, C.H. 1969. The evolution and systematics of Bee-Eaters (Meropidae).
Ibis 111:557-592.
- Fry, C.H. 1972. The biology of African Bee-Eaters. *Living Bird* 11:75-112.
- Fry, C.H., Ash, J.S. and Ferguson-Lees, I.J. 1970. Spring weights of some
Palearctic migrants at Lake Chad. *Ibis* 112:58-82.
- Fry, C.H., Britton, P.L. and Horne, J.F.M. 1974. Lake Rudolf and the
Palearctic exodus from East Africa. *Ibis* 116:44-51.
- Goodwin, D. 1967. Pigeons and doves of the world. London: Trustees of
the British Museum (N.H.).
- Grant, P.R. 1968. Bill size, body size and the ecological adaptations of
bird species to competitive situations on islands. *Syst. Zool.*
17:319-333.
- Greenewalt, C.H. 1960. Hummingbirds. New York: American Museum of
Natural History.
- Greenway, P.J. 1969. A check list of plants recorded in Tsavo National
Park East. *Jl. E. Afr. nat. Hist. Soc. natn. Mus.* 27:169-209.

- Greenway, P.J. 1973. A classification of the vegetation of East Africa. *Kirkia* 9:1-68.
- Grimes, L.G. 1976. The occurrence of co-operative breeding behaviour in African birds. *Ostrich* 47:1-15.
- Hall, B.P. and Moreau, R.E. 1970. An atlas of speciation in African passerine birds. London: British Museum (Nat. Hist.).
- Hardin, G. 1960. The competitive exclusion principle. *Science* 131: 1292-1297.
- Herrera, C.M. 1978. Ecological correlates of residence and non-residence in a Mediterranean passerine bird community. *J. Anim. Ecol.* 47: 871-890.
- Hespenheide, H. 1971. Food preference and the extent of overlap in some insectivorous birds with special reference to the Tyrannidae. *Ibis* 113:59-72.
- Hespenheide, H. 1973. Ecological inferences from morphological data. *Ann. Rev. Ecol. Syst.* 4:213-229.
- Irving, N.S. and Beesley, J.S.S. 1976. Bird pest research project, Botswana. Final Report 1972-75. London: Centre for Overseas Pest Research.
- Jackson, F.J. 1938. The birds of Kenya Colony and the Uganda Protectorate. 3 vols. London: Gurney and Jackson.
- Janzen, D.H. 1967. Synchronisation of sexual reproduction of trees within the dry season in Central America. *Evolution* 21:620-637.
- Jones, P.J. and Ward, P. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea, Quelea quelea. *Ibis* 118: 547-574.
- Karr, J.R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. *Condor* 70:348-357.
- Karr, J.R. and Roth, R.R. 1971. Vegetation structure and avian diversity in several New World areas. *Amer. Nat.* 105:423-435.
- Kemp, A.C. 1973. Environmental factors affecting the onset of breeding in some southern African hornbills, Tockus spp. *J. Reprod. Fert.*, Suppl. 19:319-331.
- Kendeigh, S.C. 1944. Measurement of bird populations. *Ecol. Monogr.* 14:67-106.
- Kingston, T.J. 1977. Natural manuring by elephants in the Tsavo National Park, Kenya. Unpublished D. Phil. thesis, Oxford University.
- Kingston, T.J. and Coe, M.J. 1977. The biology of a giant dung-beetle (Helicoprion dilloni) (Coleoptera: Scarabaeidae). *J. Zool. Lond.* 181:243-263.

- Kleiber, M. 1947. Body size and metabolic rate. *Physiol. Rev.* 27: 511-541.
- Kricher, J.C. 1972. Bird species diversity: the effect of species richness and equitability on the diversity index. *Ecology* 53:278-282.
- Lack, D. 1971. *Ecological isolation in birds*. London: Blackwells Scientific Publications.
- Lack, D. 1976. *Island biology illustrated by the land-birds of Jamaica*. London: Blackwells Scientific Publications.
- Lack, P.C. 1975. Range expansion of the Quail Plover. *EANHS Bull.* 1975: 110.
- Lack, P.C. 1977. The status of Friedmann's Bush Lark, Mirafrapa pulpa. *Scopus* 1:34-39.
- Lack, P.C., Leuthold, W. and Smeenk, C. 1980. Check list of the birds of Tsavo East National Park, Kenya. *Jl. E. Afr. nat. Hist. Soc. natn. Mus.* no. 170:1-25.
- Lack, P.C. and Quicke, D.L.J. 1978. Dietary notes on some Kenyan birds. *Scopus* 2:86-91.
- Lasiewski, R.C. and Dawson, W.R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13-23.
- Laws, R.M. 1969. The Tsavo Research Project. *J. Reprod. Fert., Suppl.* 6:495-531.
- Leuthold, W. 1971. Studies on the food habits of lesser kudu in Tsavo National Park, Kenya. *E. Afr. Wildl. J.* 9:35-45.
- Leuthold, W. 1973. Is the Somali Bee-Eater extending its range? *EANHS Bull.* 1973:101.
- Leuthold, W. 1976a. Group size in elephants of Tsavo National Park and possible factors influencing it. *J. Anim. Ecol.* 45:425-439.
- Leuthold, W. 1976b. Age structure of elephants in Tsavo National Park, Kenya. *J. appl. Ecol.* 13:435-444.
- Leuthold, W. 1977a. Changes in tree populations of Tsavo East National Park, Kenya. *E. Afr. Wildl. J.* 15:61-69.
- Leuthold, W. 1977b. Spatial organisation and strategy of habitat utilisation of elephants in Tsavo National Park, Kenya. *Z. Saugetiertunde* 42:358-79.
- Leuthold, W. 1977c. Notes on the breeding biology of the Ostrich, Struthio camelus, in Tsavo East National Park, Kenya. *Ibis* 119:541-544.
- Leuthold, W. and Leuthold, B.M. 1975a. Patterns of social grouping in ungulates of Tsavo National Park. *J. Zool. Lond.* 175:405-420.
- Leuthold, W. and Leuthold, B.M. 1975b. Temporal patterns of reproduction in ungulates of Tsavo East National Park, Kenya. *E. Afr. Wildl. J.* 13:159-169.

- MacArthur, R.H. 1965. Patterns of bird species diversity. *Biol. Rev.* 40:510-533.
- Mackworth-Praed, C.W. and Grant, C.H.B. 1957-60. African handbook of birds. Series 1, 2 vols. Birds of eastern and north-eastern Africa. 2nd edition. London: Longmans, Green and Co.
- McLachlan, G.R. and Liversidge, R. 1977. Roberts' birds of South Africa. 4th edition. Cape Town: Trustees of the John Voelcker Bird Book Fund.
- Maclean, G.L. 1968. Field studies on the sandgrouse of the Kalahari Desert. *Living Bird* 7:209-235.
- Maclean, G.L. 1969. The breeding seasons of birds in the south-western Kalahari. *Ostrich Suppl.* 8:179-192.
- Maclean, G.L. 1970. An analysis of the avifauna of the southern Kalahari - Gemsbok National Park. *Zool. afr.* 5:249-273.
- Margalef, R. 1968. *Perspectives in Ecological Theory*. London; University of Chicago Press.
- May, R.M. 1975. Patterns of species abundance and diversity. pp. 81-120 in Cody, M.L. and Diamond, J.M. (ed.) *Ecology and evolution of communities*. Harvard University Press.
- Milon, P., Petter, J.-J., and Randrianasolo, G. 1973. Faune de Madagascar. vol. 35. Oiseaux. Tananarive: ORSTOM, and Paris: CNRS.
- Moreau, R.E. 1950. The breeding seasons of African birds. 1. Land birds. *Ibis* 92:223-267. 2. Sea birds. *Ibis* 92:419-433.
- Moreau, R.E. 1958. Some aspects of the Musophagidae. *Ibis* 100:67-112, 238-270.
- Moreau, R.E. 1966. *The bird faunas of Africa and its islands*. London; Academic Press.
- Moreau, R.E. 1972. *The Palaearctic-African bird migration systems*. London; Academic Press.
- Morel, G. 1968. Contribution à la synécologie des oiseaux du Sahel sénégalais. Thèse Doct. Etat. Mémoires ORSTOM no. 29.
- Morel, G. 1973. The Sahel zone as an environment for Palaearctic migrants. *Ibis* 115:413-417.
- Morel, G. and Bourlière, F. 1962. Relations écologiques des avifaunes sédentaires et migratrices dans une savane sahélienne du bas Senegal. *Terre et Vie* 4:371-393.
- Morel, G. and Morel, M.-Y. 1972. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Senegal: l'avifaune et son cycle annuel. *Terre et Vie* 26:410-439.

- Morel, G. and Morel, M.-Y. 1974. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Senegal. II. Influence de la sécheresse de l'année 1972/73 sur l'avifaune. *Terre et Vie* 28:95-123.
- Morel, G. and Morel, M.-Y. in press. Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Senegal. Étude d'une communauté avienne. *Cahiers de l'ORSTOM Biol. Animale*.
- Napier-Bax, P. and Sheldrick, D.L.W. 1963. Some preliminary observations on the food of elephant in the Tsavo Royal National Park (East) of Kenya. *E. Afr. Wildl. J.* 1:40-53.
- Owen, D.F. 1969a. The migration of the Yellow Wagtail from the equator. *Ardea* 57:77-85.
- Owen, D.F. 1969b. Species diversity and seasonal abundance in tropical Sphingidae (Lepidoptera). *Proc. R. Ent. Soc. London Ser. A.* 44:162-168.
- Pearson, D.J. 1972. Palaearctic migrants in Uganda. *Ibis* 114:43-60.
- Pearson, D.J. and Backhurst, G.C. 1976. The southward migration of Palaearctic birds over Ngulia, Kenya. *Ibis* 118:78-105.
- Pearson, D.J. and Backhurst, G.C. 1978. Southward migration at Ngulia, Tsavo, Kenya 1977/78. *Scopus* 2:42-47.
- Peters, J.L. and Loveridge, A. 1937. Scientific results of an expedition to rainforest regions in eastern Africa. IV Birds. *Bull. Mus. comp. Zool. Harvard* 79:128-205.
- Petter, A. 1975. Road transects for large scale surveying. *Bull. Nigerian Orn. Soc.* 11:2-18.
- Pianka, E.R. 1966. Latitudinal gradients in species diversity: a review of concepts. *Amer. Nat.* 100:33-46.
- Poczopko, P. 1971. Metabolic levels in adult homeotherms. *Acta. theriol.* 16:1-21.
- Poulet, A.R. 1972. Recherches ecologiques sur une savane sahelienne du Ferlo septentrional, Senegal: les mammiferes. *Terre et Vie* 26:440-472.
- Pratt, D.J., Greenway, P.J. and Gwynne, M.D. 1966. A classification of East African rangeland with an appendix on terminology. *J. appl. Ecol.* 3:369-382.
- Recher, H.F. 1969. Bird species diversity and habitat diversity in Australia and North America. *Amer. Nat.* 103:75-80.
- Sanders, L.D. 1963. Geology of the Voi-South Yatta area. Nairobi: Government Printer. Ministry of Commerce and Industry: Geological Survey of Kenya.
- Sheldrick, D. 1973. The Tsavo story. London: Collins.

- Short, L.L. 1971. Notes on South African woodpeckers. *Ostrich* 42:89-98.
- Sinclair, A.R.E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. *J. Anim. Ecol.* 44:497-520.
- Sinclair, A.R.E. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palaearctic migrants in a tropical African savanna. *Ibis* 120:480-497.
- Skead, C.J. 1967. Sunbirds of southern Africa: also Sugarbirds, White-eyes and Spotted Creeper. Cape Town and Amsterdam: A.A. Balkema (for South African Bird Book Fund).
- Smeenk, C. 1974. Comparative-ecological studies of some East African birds of prey. *Ardea* 62:1-97.
- Smeenk, C. and Smeenk-Enserink, N. 1976. Observations on the Pale Chanting Goshawk Melierax poliopterus, with comparative notes on the Gabar Goshawk Micronisus gabar. *Ardea* 63:93-115.
- Snow, D.W. (ed.) 1978. An atlas of speciation in African non-passerine birds. London: British Museum (Nat. Hist.).
- Stronach, B. 1966. The feeding habits of the Yellow-necked Spurfowl (Pternistes leucoscepus) in northern Tanzania. *E. Afr. Wildl. J.* 4:76-81.
- Swank, W.G. 1977. Food of three upland game-birds in the Selengei Area, Kajiado district, Kenya. *E. Afr. Wildl. J.* 15:99-105.
- Tennent, J.R.M. 1962. Notes on the migration and dispersal of birds at Kitui. *Jl. E. Afr. nat. Hist. Soc. natn. Mus.* 24:41-42.
- Thiollay, J.-M. 1971. L'avifaune de la région de Lanto (moyenne Côte d'Ivoire). *Ann. Univ. Abidjan Ser. E. (Ecol.)* 4:5-132.
- Thiollay, J.-M. 1973. Places des oiseaux dans les chaînes trophiques d'une zone préforestière en Côte d'Ivoire. *Alauda* 41:273-300.
- Tramer, E.J. 1969. Bird species diversity: components of Shannon's formula. *Ecology* 50:927-929.
- Trevor, S. and Lack, P.C. 1976. Great Spotted Cuckoo parasitising Superb Starling. *EANHS Bull.* 1976:50.
- Turner, D.A. 1977. A new host for the Black and White Cuckoo Clamator jacobinus. *Scopus* 1:51-52.
- Tyrell, J.G. and Coe, M.J. 1974. The rainfall regime of Tsavo National Park, Kenya and its phenological significance. *J. Biogeography* 1:187-192.
- Ulfstrand, S. 1973. Proportions of Palaearctic birds in some East African habitats. *Die Vogelwarte* 27:137-141.
- Voous, K.H. 1960. Atlas of European birds. London: Nelson.
- Ward, P. 1971. The migration patterns of Quelea quelea in Africa. *Ibis* 113:275-297.

- Watson, R.M. 1969. The South Turkana Expedition: Scientific Papers II. Geogr. J. 135:529-546.
- Western, D. 1974. The distribution, density and biomass density of lizards in a semi-arid environment of northern Kenya. E. Afr. Wildl. J. 12:49-62.
- White, C.M.N. 1962. A revised check list of African shrikes, orioles, drongos, starlings, crows, waxwings, cuckoo-shrikes, bulbuls, accentors, thrushes and babblers. Lusaka: Government Printer.
- White, C.M.N. 1965. A revised check list of African non-passerine birds. Lusaka: Department of Game and Fisheries.
- Williams, J.G. 1967. A field guide to the National Parks of East Africa. London: Collins.
- Williams, J.G. 1969. A field guide to the birds of east and central Africa. 2nd edition. London: Collins.
- Willson, M.F. 1974. Avian community organisation and habitat structure. Ecology 55:1017-1029.
- Winterbottom, J.M. 1972a. The ecological distribution of birds in southern Africa. Monog. Percy Fitzpatrick Institute of African Ornithology no. 1.
- Winterbottom, J.M. 1972b. Results of the garden bird counts organised by the Percy Fitzpatrick Institute of African Ornithology. Ostrich 43: 125-129.

ADDENDA

- Alatalo, R.V. & Alatalo, R.H. In press. Seasonal variation of evenness in forest bird communities. *Ornis. Scand.*
- Bailey, N.T.J. 1959. *Statistical Methods in Biology.* English Universities Press, London.
- Cody, M.L. 1974. *Competition and the structure of bird communities.* Princeton University Press.
- de Benedictis, P.A. 1973. On the correlation between certain diversity indices. *Amer. Nat.* 107:295-302.
- Griffiths, J.F. 1976. *Climate and the environment. The atmospheric impact on man.* Paul Elek, London.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427-432.
- Jarvinen, O. & Sammalisto, L. 1976. Regional trends in the avifauna of Finnish peatland bogs. *Am. Zool. Fenn.* 13:31-43.
- Jarvinen, O. & Vaisanen, R.A. 1973. Species diversity of Finnish birds, I: Zoogeographical zonation based on land-birds. *Ornis Fennica* 50:93-25.
- Merikallio, E. 1945. Über regionale Verbreitung und Anzahl der Landvögel in Süd - und Mittelfinnland, besonders in deren östlichen Teilen, im lichte von quantitativen Untersuchungen. I. Allgemeiner Teil. *Ann. Zool. Soc. 'Vanamo'* 12(1):1-140.
- Pearson, E.S. & Hartley, H.O. ed. 1972. *Biometrika tables for statisticians.* Vol. II. Cambridge University Press.
- Peet, R.K. 1974. The measurement of species diversity. *Ann. Rev. Ecol. Syst.* 5:285-307.

Appendix 1.1. The land-birds of Tsavo East National Park

1. All species of land-bird in the families considered in detail in this study are mentioned.
2. Scientific names follow Forbes-Watson (1971). The Mackworth-Praed & Grant (1957-60) number precedes each species.
3. "Common"; x = the species was seen more than 0.05 times per census hour (see ch 5.4.1).
4. "Breed"; x = breeding records exist; (x) = records of probable breeding exist.
5. Information is tabulated in the Food, Site, Status and Weight columns only if the species concerned occurred in censuses used for estimating density (Type II).
6. "Food"; I = Insect; F = Fruit; S = Seed; N = Nectar.
7. "Site"; A = Air; P = Pounce to ground; G = Ground glean V = Vegetation glean (green vegetation); T = Twig specialist. The "site" column is filled only for insectivorous species. All fruit is eaten in the woody vegetation, and all seeds on the ground.
8. "Status"; The 'common' species (ch. 5.4.1) are designated R = Resident; V = Visitor from elsewhere in Africa; M = Migrant from the Palaearctic. The remainder are designated X = Uncertain. Where necessary in analyses these are scored as residents, unless they are known to be Palaearctic migrants. These are designated X(M).
9. "Weight"; an average of sources which include data from ringing in Tsavo East N.P. of my own, museum skins, published material (especially Britton 1971), and the ringing schedules of the East Africa Natural History Society ringing scheme.
10. Also recorded are:
 Accipitridae, Falconidae, Sagittariidae - birds of prey 52 species;
 Strigidae, Tytonidae - owls 6 species;
 Caprimulgidae - nightjars 8 species;
 Apodidae - swifts 11 species;
 Hirundinidae - swallows 9 species.
11. Further details for the land-birds, except birds of prey, are in ch 5.3. The status of all birds recorded in Tsavo East N.P. and its immediate surrounds is noted in Lack, Leuthold & Smeenk (1980).

	Common?	Breed?	Food	Site	Status	Weight (g)
STRUTHIONIDAE - Ostriches						
1 Struthio camelus molybdophanes	-	x				
1 S.c. massaicus	-	-				
PHASIANIDAE - Game-birds						
195 Francolinus sephaena	x	x	IS	G	R	255
203 F. hildebrandtii	-	-				
210 F. leucoscepus	x	x	IS	G	R	540
212 Coturnix delegorguei	x	x	S		V	75
NUMIDIDAE - Guinea-fowl						
215 Numida meleagris	-	x	IS	G	X	1650
218 Guttera pucherani	-	-				
219 Acryllium vulturinum	-	x				
TURNICIDAE - Button-quails						
365 Turnix sylvatica	-	x	IS	G	X	45
367 Ortyxelos meiffrenii	-	-	S		X	18
OTIDIDAE - Bustards						
250 Otis kori	-	-				
252 Neotis heuglini	-	-				
257 Eupodotis ruficrista	x	(x)	IS	G	R	690
256 E. senegalensis	-	-	IS	G	X	950
259 E. hartlaubii	-	-	IS	G	X	1050
CHARADRIIDAE - Plovers (+ 9 waterside species)						
292 Vanellus tectus	x	x	I	G	R	115
282 V. lugubris	-	-				
281 V. coronatus	x	x	I	G	R	170
277 Charadrius asiaticus	-	-	I	G	X(M)	72
271 C. pecuarius (mainly waterside)-		x	I	G	X	32
BURHINIDAE - Thicknees (+ 1 waterside species)						
262 Burhinus capensis	-	-	I	G	X	410
GLAREOLIDAE - Coursers (+ 1 waterside species (Pratincole))						
325 Cursorius cursor	-	-				
326 C. temminckii	-	(x)	I	G		68
327 C. africanus	-	-				
328 C. cinctus	x	-	I	G	R	125
329 C. chalcopterus	-	-				
PTEROCLIDIDAE - Sandgrouse						
369 Pterocles exustus	-	-				
370 P. decoratus	x	x	S		R	185
COLUMBIDAE - Pigeons						
379 Columba guinea	-	-				
386 Streptopelia semitorquata	x	(x)	S		R	185
387 S. decipiens	-	-	S		R	135
388 S. capicola	x	x	S		R	125
392 S. senegalensis	x	x	S		V	90

	Common?	Breed?	Food	Site	Status	Weight (g)
393 <i>Oena capensis</i>	x	x	S		V	35
394 <i>Turtur tympanistria</i>	-	-				
397 <i>T. chalcospilos</i>	x	(x)	S		R	60
401 <i>Treron australis</i>	-	-				
PSITTACIDAE - Parrots						
448 <i>Poicephalus rufiventris</i>	x	x	F		R	120
MUSOPHAGIDAE - Turacos						
434 <i>Tauraco porphyreolophus</i>	-	-				
440 <i>Corythaixoides leucogaster</i>	x	-	F		R	225
CUCULIDAE - Cuckoos						
413 <i>Clamator glandarius</i>	-	x				
415 <i>C. jacobinus</i>	x	x	I	V	V	65
406 <i>Cuculus solitarius</i>	-	-				
407 <i>C. clamosus</i>	-	-				
404 <i>C. canorus canorus/gularis</i>	x	-	I	V	M	100
418 <i>Chrysococcyx klaas</i>	-	-				
417 <i>C. caprius</i>	x	-	I	V	V	30
416 <i>C. cupreus</i>	-	-	I	V	X	37
424 <i>Ceuthmochares aereus</i>	-	-				
423 <i>Centropus superciliosus</i>	x	x	I	GV	V	145
COLIIDAE - Mousebirds						
566 <i>Colius striatus</i>	x	-	F		R	52
567 <i>C. leucocephalus</i>	-	-				
568 <i>C. macrourus</i>	x	x	F		R	48
TROGONIDAE - Trogons						
570 <i>Apaloderma narina</i>	-	-				
CAPRIMULGIDAE - Nightjars						
<i>Caprimulgus</i> sp.	-	-	I	A	X	35
ALCEDINIDAE - Kingfishers (+ 2 waterside species)						
471 <i>Ceyx picta</i>	-	-				
479 <i>Halcyon chelicuti</i>	x	-	I	P	R	39
476 <i>H. albiventris</i>	-	-	I	P	X	55
477 <i>H. leucocephala</i>	x	-	I	P	V	47
MEROPIIDAE - Bee-Eaters						
481 <i>Merops apiaster</i>	-	-				
482a <i>M. superciliosus superciliosus</i>	x	x	I	A	V	43
482b <i>M. s. persicus</i>	-	-				
484 <i>M. nubicus</i>	-	-				
486 <i>M. albicollis</i>	x	-	I	A	V	25
488 <i>M. pusillus</i>	x	x	I	A	R	14
491 <i>M. revoilii</i>	x	-	I	A	R	14
CORACIIDAE - Rollers						
457 <i>Coracias garrulus</i>	x	-	I	P	M	120
460 <i>C. caudata</i>	x	x	I	P	R	110
461 <i>C. naevia</i>	-	(x)	I	P	X	170
463 <i>Eurystomus glaucurus</i>	-	(x)	I	A	X	115

	Common?	Breed?	Food	Site	Status	Weight (g)
UPUPIDAE - Hoopoes						
517 <i>Upupa epops senegalensis/epops</i>	-	-				
518 <i>U. e. africana</i>	x	-	I	G	V	57
PHOENICULIDAE - Wood-Hoopoes						
519 <i>Phoeniculus purpureus</i>	x	x	I	T	R	70
520 <i>P. granti</i>	-	-				
527 <i>P. minor</i>	x	x	I	T	R	24
526 <i>P. cyanomelas</i>	-	-				
BUCEROTIDAE - Hornbills						
504 <i>Tockus nasutus</i>	x	(x)	IF	G	R	140
505 <i>T. erythrorhynchus</i>	x	x	IF	G	R	170
507 <i>T. deckeni</i>	x	x	IF	G	R	M-205, F-150
506 <i>T. flavirostris</i>	x	x	IF	G	R	260
509 <i>T. alboterminatus</i>	-	-	IF	GV	X	230
501 <i>Bycanistes brevis</i>	-	-				
515 <i>Bucorvus cafer</i>	-	-	I	G	X	3250
CAPITONIDAE - Barbets						
580 <i>Lybius melanopterus</i>	x	-	F		R	54
576 <i>L. leucocephalus</i>	-	-				
575 <i>L. torquatus</i>	-	-				
583 <i>L. melanocephalus</i>	x	x	F		R	21
584 <i>L. lacrymosus</i>	x	x	IF	V	R	23
585 <i>L. leucomelas</i>	-	-				
594 <i>Pogoniulus pusillus</i>	x	-	IF	V	R	10
597 <i>P. bilineatus</i>	-	-				
603 <i>Trachyphonus darnaudii</i>	x	x	IF	G	R	32
601 <i>T. erythrocephalus</i>	x	x	I	G	R	59
INDICATORIDAE - Honeyguides						
606 <i>Indicator variegatus</i>	-	-				
605 <i>I. indicator</i>	-	x	I	V	X	52
608 <i>I. minor</i>	-	-	I	V	X	26
PICIDAE - Woodpeckers						
619 <i>Campethera nubica</i>	x	(x)	I	T	R	59
623 <i>Dendropicos fuscescens</i>	x	-	I	T	R	25
629 <i>Thripias namaquus</i>	-	-	I	T	X	82
ALAUDIDAE - Larks						
654 <i>Mirafra cantillans</i>	x	(x)	IS	G	V	20
- <i>M. pulpa</i>	-	-	IS	G	X	22
657 <i>M. hypermetra</i>	x	(x)	IS	G	R	55
660 <i>M. rufocinnamomea</i>	-	-				
665 <i>M. poecilosterna</i>	x	x	IS	G	R	24
682 <i>Eremopterix leucopareia</i>	-	-				
681 <i>E. signata</i>	x	x	S		R	15
679 <i>E. leucotis</i>	x	-	S		V	15

	Common?	Breed?	Food	Site	Status	Weight (g)
MOTACILLIDAE - Wagtails, Pipits						
695-701 Motacilla flava	-	-				
694 M. cinerea	-	-				
691 M. aguimp	-	-				
706 Anthus novaeseelandiae	-	-	I	G	X	24
705b A. leucophrys	-	-				
708 A. trivialis	-	-	I	G	X(M)	18
713 A. cervinus	-	-				
715 Tmetothylacus tenellus	x	x	I	G	V	20
720 Macronyx aurantiigula	x	x	I	G	R	41
CAMPEPHAGIDAE - Cuckoo-Shrikes						
1081 Campephaga flava	-	-	I	V	X	31
PYCNONOTIDAE - Bulbuls						
743 Pycnonotus barbatus dodsoni	x	x	IF	V	R	27
773 Andropadus importunus	x	x	IF	V	R	31
769 Chlorocichla flaviventris	-	-				
754 Phyllastrephus strepitans	x	x	I	V	R	24
1148 Nicator chloris	-	-				
LANIIDAE - Shrikes						
1097 Eurocephalus rueppelli	x	x	I	P	R	50
1090 Prionops plumata	x	(x)	I	T	R	34
1095 P. retzii	x	x	I	T	R	49
1098 Nilaus afer	x	x	I	V	R	20
1130 Dryoscopus pringlii	-	-	I	V	X	24
1128 D. cubla	x	(x)	I	V	R	29
1135 Tchagra jamesi	x	-	I	V	R	29
1134 T. australis	-	-				
1133 T. senegala	-	-	I	V	X	55
1147 Rhodophoneus cruentus	x	x	I	G	R	56
1126 Laniarius ruficeps	-	-				
1125 L. aethiopicus	-	-	I	V	X	52
1121 L. funebris	x	x	I	V	R	41
1138 Malaconotus sulfureopectus	-	-	I	V	X	28
1142 M. quadricolor	-	-				
1144 M. blanchoti	-	-	I	V	R	80
1112 Lanius collurio collurio	x	-	I	P	M	26
1114 L. c. isabellinus	x	-	I	P	M	26
1103 L. minor	x	-	I	P	M	44
1108 L. cabanisi	-	-	I	P	X	70
1107 L. dorsalis	x	x	I	P	R	46
MUSCICAPIDAE - Thrushes, Chats, Chatterers, Warblers, Flycatchers						
883 Saxicola rubetra	-	-				
854 Oenanthe oenanthe	x	-	I	PG	M	22
859 O. pleschanka	x	-	I	AP	M	18
855 O. isabellina	x	-	I	G	M	28
868 O. pileata	-	-	I	G	X	31
871 Cercomela familiaris	-	-				
876 Myrmecocichla cinnamomeiventris	-	-				
850 Monticola saxatilis	x	-	I	PG	M	46
934 Cercotrichas galactotes	x	-	I	G	M	22
911 C. leucophrys	x	x	I	G	R	18
913 C. quadrivirgata	-	-				
909 Cichladusa guttata	-	x	I	G	X	24
884 Cossypha heuglini	-	-				
848 Neocossyphus rufus	-	-				

	Common?	Breed?	Food	Site	Status	Weight (g)
921 <i>Luscinia megarhynchus</i>	-	-				
922 <i>L. luscinia</i>	-	-	I	GV	X(M)	25
920 <i>Irania gutturalis</i>	x	-	I	GV	M	22
843 <i>Turdus tephronotus</i>	x	-	I	G	R	47
732 <i>Turdoides rubiginosus</i>	-	x	I	GV	X	44
733 <i>T. aylmeri</i>	x	x	I	GV	R	37
940 <i>Locustella fluviatilis</i>	-	-				
947 <i>Acrocephalus schoenobaenus</i>	-	-	I	V	X(M)	12
945 <i>A. palustris</i>	x	-	I	V	M	11
944 <i>A. scirpaceus</i>	-	-				
942 <i>A. arundinaceus arundinaceus</i>	-	-				
943 <i>A. a. griseldis</i>	-	-	I	V	X(M)	16
955 <i>A. gracilirostris</i>	-	-				
1051 <i>Sphenoeacus mentalis</i>	-	-				
936 <i>Hippolais olivetorum</i>	-	-	I	V	X(M)	15
937 <i>H. languida</i>	x	-	I	V	M	13
938 <i>H. pallida</i>	x	-	I	V	M	10
933 <i>Sylvia nisoria</i>	x	-	I	V	M	23
925 <i>S. borin</i>	-	-	I	V	X(M)	19
924 <i>S. communis</i>	x	-	I	V	M	15
959 <i>Phylloscopus trochilus</i>	x	-	I	V	M	9
1024 <i>Cisticola chiniana</i>	-	-				
1033 <i>C. galactotes</i>	-	-	I	V	X	14
1042 <i>C. cinereola</i>	x	x	I	V	R	13
1041 <i>C. nana</i>	x	(x)	I	G	R	5
1018 <i>C. aridula</i>	-	-	I	V	X	7
1045 <i>Prinia subflava</i>	-	-				
1046 <i>P. somalica</i>	-	-				
979 <i>Apalis flavida</i>	-	-	I	V	X	8
987 <i>Spiloptila rufifrons</i>	-	-	I	V	X	7
995 <i>Phyllolais pulchella</i>	-	-				
1011 <i>Camaroptera brevicaudata</i>	-	-				
968 <i>C. simplex</i>	x	(x)	I	GV	R	12
1004 <i>Eremomela flavicrissalis</i>	-	x	I	V	X	5
996 <i>Sylvietta brachyura</i>	x	x	I	T	R	7
999 <i>S. isabellina</i>	-	x				
787 <i>Parisoma boehmi</i>	-	-				
778 <i>Muscicapa striata</i>	x	-	I	A	M	14
785 <i>M. caerulescens</i>	-	-				
788 <i>Myioparus plumbeus</i>	-	-				
799 <i>Melaenornis pammelaina</i>	-	-				
793 <i>Bradornis microrhynchus</i>	x	(x)	I	P	R	20
792 <i>B. pallidus</i>	-	-				
817 <i>Batis molitor</i>	-	x	I	V	X	10
819 <i>B. perkeo</i>	-	-	I	V	X	8
820 <i>B. minor</i>	x	-	I	V	R	11
832 <i>Terpsiphone viridis</i>		x	I	A	X	14
PARIDAE - Tits						
1151 <i>Parus afer</i>	-	-				
1155 <i>P. albiventris</i>	-	-				
1161 <i>Anthoscopus musculus</i>	-	-	I	V	X	5
NECTARINIIDAE - Sunbirds						
1274b <i>Anthreptes orientalis</i>	x	(x)	NI	V	R	13
1271 <i>A. collaris</i>	-	-	I	V	X	7
1269 <i>Nectarinia olivacea</i>	-	-				
1261 <i>N. amethystina</i>	-	x	NI	V	X	12
1264 <i>N. hunteri</i>	x	x	NI	V	R	12

	Common?	Breed?	Food	Site	Status	Weight (g)
1251 Nectarinia venusta	-	-				
1242 N. bifasciata	x	-	NI	AV	R	7
1245 N. mariquensis	-	-				
1233 N. pulchella	-	-				
1234 N. nectarinioides	-	-	NI	V	X	10
1230 N. kilimensis	-	-				
ZOSTEROPIDAE - White-eyes						
1219c Zosterops abyssinica	-	-	IF	V	X	10
EMBERIZIDAE - Buntings						
1470 Emberiza poliopleura	x	x	IS	G	R	16
1476 E. tahapisi	-	-	IS	G	X	15
FRINGILLIDAE - Finches						
1448 Serinus mozambicus	-	-				
1459 S. atrogularis	-	-	S		X	16
1449 S. dorsostriatus	-	-	S		X	16
1452 S. donaldsoni	-	-				
ESTRILDIDAE - Waxbills						
1406 Hypargos niveoguttatus	-	-				
1410 Pytilia melba	x	(x)	S		R	15
1409 P. afra	-	-				
1420 Estrilda rhodopyga	-	-	S		X	8
1418 E. astrild	-	-				
1427 E. erythronotos	-	-				
1433 Uraeginthus ianthinogaster	-	-	S		X	13
1431 U. bengalus	x	(x)	S		R	9
1432 U. cyanocephalus	-	-	S		X	11
1411 Lagonosticta sp.	-	-	S		X	9
1403 Ortygospiza atricollis	-	-				
1402 Amadina fasciata	x	x	S		V	15
1383 Lonchura malabarica	-	(x)	S		X	9
1384 L. griseicapilla	-	-	S		X	11
1379 L. cucullata	-	-	S		X	9
PLOCEIDAE - Weavers, Sparrows						
1441 Vidua macroura	-	-	S		X	14
1443 V. fischeri	-	-	S		X	11
1442 V. hypocherina	-	-				
1444 V. paradisea	x	-	S		V	22
1434-40 Hypochera sp.	-	-				
1358 Amblyospiza albifrons	-	-				
1341 Ploceus subaureus	-	-				
1319 P. intermedius	x	x	IS	GV	V	22
1321 P. velatus	-	-				
1313 P. cucullatus nigriceps	-	x	IS	V	X	35
1327 P. rubiginosus	x	x	IS	GV	V	28
1337 P. ocularis	-	-				
1336 P. nigricollis	x	x	I	V	R	25
1359 Malimbus rubriceps	-	x	I	V	R	24
1360 Quelea quelea	x	x	S		V	17
1373 Euplectes albonotatus	-	(x)	S		X	19
1368 E. diadematus	x	x	S		V	15
1365 E. hordeaceus	-	-				
1364 E. nigroventris	-	x	S		X	12
1405 Anomalospiza imberbis	-	-				

	Common?	Breed?	Food	Site	Status	Weight (g)
1285 Bubalornis niger	x	x	IS	G	R	70
1286 Dinemellia dinemelli	x	x	IS	G	R	69
1287 Plocepasser mahali	x	x	IS	G	R	38
1291 Pseudonigrita arnaudi	-	-				
1292 P. cabanisi	-	(x)	S		X	19
1303 Passer gongonensis	x	x	IS	G	R	41
1308 Petronia pyrgita	x	x	IS	GV	R	24
STURNIDAE - Starlings						
1203 Onychognathus morio	-	-	IF	GV	X	150
1188 Lamprotornis chalybaeus	x	x	IF	G	R	80
1196 L. purpuropterus	-	-				
1184 Cinnyricinclus leucogaster	-	-	IF	GV	X	45
1211 Spreeo fischeri	x	(x)	I	G	R	54
1214 S. hildebrandti	-	-	I	G	X	57
1215 S. shelleyi	-	-	I	G	X	53
1216 S. superbus	x	x	I	G	R	67
1198 Cosmopsarus regius	x	(x)	IF	G	R	63
1182 Creatophora cinerea	x	x	IF	G	V	76
1218 Buphagus erythrorhynchus	x	x	I	Animal	R	49
1187 Speculipastor bicolor	-	-	IF	G	X	53
ORIOOLIDAE - Orioles						
1164 Oriolus oriolus	x	-	IF	V	M	74
1165 O. auratus	-	-				
1167 O. larvatus	x	x	IF	V	R	62
DICRURIDAE - Drongos						
1088 Dicrurus adsimilis	x	x	I	A	R	39
CORVIDAE - Crows						
1174 Corvus splendens	-	-				
1172 C. albus	-	-				
1175 C. albicollis	-	-	all		X	1000

Appendix 1.2. The relative abundance of birds in each habitat.

1. Habitats are identified as G - Grassland, BG - Bushed Grassland, WBG - Wooded and Bushed Grassland, B - Bushland, WB - Wooded Bushland, W - Woodland, R - Riverine, PSH - Park savanna habitats (the sum of G, BG, WBG, B and WB) and Total (the sum of all habitats).
2. The figure given is the number of birds seen per ten hours censusing. x means less than 0.5 per ten hours. The number of hours censused in each habitat can be obtained from Table 5.1.
3. For the 'common' African visitors and Palaearctic migrants (see ch 5.4) a figure is placed in brackets after the species name. This is the factor that the relative abundance should be multiplied by to make the figures directly comparable with those of residents allowing for their absence from Tsavo for some of the year. See ch 6.4.1 and Tables 7.3 and 7.4.
4. For two Palaearctic chats Oenanthe spp. and warblers Hippolais spp. a figure is given for each species and one for the two combined. The last is those individuals which were not identified to species; see ch 5.3.32 (Oenanthe spp.) and 5.3.34 (Hippolais spp.).

Species	G	BG	WBG	B	WB	W	R	PSH	TOTAL
Francolinus sephaena	-	-	x	2	2	4	1	1	1
F. leucoscepus	-	1	-	1	3	x	2	1	1
Coturnix delegorguei(x4.8)	6	8	12	7	6	1	2	8	7
Numida meleagris	-	-	-	x	-	1	x	x	x
Turnix sylvatica	-	x	x	-	x	-	-	x	x
Ortyxelos meiffrenii	1	x	x	1	x	-	-	x	x
Eupodotis ruficrista	x	2	3	4	2	1	-	2	2
E. senegalensis	1	x	x	x	x	-	-	x	x
E. hartlaubii	1	x	x	-	-	-	-	x	x
Vanellus tectus	-	4	5	6	4	x	1	4	3
V. lugubris	-	x	x	-	-	-	-	x	x
V. coronatus	3	5	1	1	-	-	-	2	2
Charadrius asiaticus	3	1	x	-	-	-	-	1	x
C. pecuarius	x	-	-	-	-	-	-	x	x
Burhinus capensis	-	x	x	1	-	-	-	x	x
Cursorius temminckii	x	x	x	x	-	-	-	x	x
C. cinctus	-	1	1	1	x	x	-	1	1
Pterocles exustus	1	2	-	-	-	-	-	1	x
P. decoratus	-	21	18	19	12	1	-	16	12
Streptopelia semitorquata	-	-	-	-	x	6	9	x	2
S. decipiens	-	x	-	-	-	-	x	x	x
S. capicola	3	9	17	11	17	15	22	13	14
S. senegalensis(x2.0)	15	16	21	16	21	12	39	19	19
Oena capensis(x2.2)	x	3	6	1	2	x	-	3	3
Turtur chalcospilos	-	-	x	1	1	6	6	x	2
Poicephalus rufiventris	-	x	x	1	6	12	4	1	4
Corythaixoides leucogaster	-	-	-	x	2	15	-	x	3
Clamator glandarius	-	-	x	-	x	x	-	x	x
C. jacobinus(x3.4)	-	x	1	x	1	2	x	1	1
Cuculus solitarius	-	-	-	-	-	x	-	-	x
C. clamosus	-	-	-	-	-	x	-	-	x
C. canorus(x3.0)	-	x	1	1	2	1	2	1	1
Chrysococcyx klaas	-	-	-	-	x	x	-	x	x
C. caprius(x2.4)	-	x	2	x	1	x	1	1	1
C. cupreus	-	-	-	-	-	-	x	-	x
Centropus superciliosus(x2.2)	-	-	1	x	1	x	6	x	1
Colius striatus	-	x	x	1	-	1	8	x	1
C. leucocephalus	-	-	-	-	-	x	-	-	x
C. macrourus	-	1	5	4	6	10	27	4	6
Caprimulgus spp.	-	x	x	x	-	x	1	x	x
Halcyon chelicuti	x	1	4	x	1	1	6	2	2
H. albiventris	-	-	-	-	-	-	2	-	x
H. leucocephala(x1.7)	-	x	x	-	x	x	28	x	2

Species	G	BG	WBG	B	WB	W	R	PSH	TOTAL
Merops apiaster	-	-	-	-	1	x	1	x	x
M. s. superciliosus(x2.4)	x	x	x	x	x	3	2	x	1
M. s. persicus	-	x	-	-	-	-	-	x	x
M. albicollis(x2.4)	2	1	1	-	-	-	9	1	1
M. pusillus	-	x	1	1	1	x	9	1	1
M. revoilii	-	1	1	1	2	-	-	1	1
Coracias garrulus(x2.0)	8	6	7	5	6	3	1	7	6
C. caudata	1	2	2	1	1	x	10	2	2
C. naevia	-	x	x	x	1	x	2	x	x
Eurystomus glaucurus	-	-	-	-	-	-	4	-	x
Upupa epops africana(x1.8)	-	x	1	1	3	5	1	1	2
Phoeniculus purpureus	-	-	1	-	1	1	9	1	1
P. minor	-	x	3	3	4	5	-	2	2
Tockus nasutus	x	1	2	x	x	3	7	1	2
T. erythrorhynchus	-	2	7	4	10	16	14	5	8
T. deckeni	-	x	2	1	6	35	6	2	8
T. flavirostris	-	x	x	1	1	13	1	x	3
T. alboterminatus	-	-	-	-	-	x	1	-	x
Bucorvus cafer	-	-	-	-	-	-	x	-	x
Lybius melanopterus	-	-	-	-	-	-	8	-	1
L. torquatus	-	-	-	-	-	-	x	-	x
L. melanocephalus	-	-	-	-	x	13	-	x	2
L. lacrymosus	-	-	x	-	-	x	8	x	1
Pogoniulus pusillus	-	-	-	-	-	2	2	-	1
Trachyphonus darnaudii	-	x	1	8	9	10	x	3	4
T. erythrocephalus	-	1	3	2	3	1	2	2	2
Indicator indicator	-	-	x	x	x	1	x	x	x
I. minor	-	-	-	-	x	1	2	x	x
Campethera nubica	x	1	1	1	3	3	4	1	2
Dendropicos fuscescens	-	x	2	1	2	4	1	1	2
Thripias namaquus	-	-	x	-	x	-	3	x	x
Mirafraga cantillans(x1.7)	5	3	x	1	-	-	-	1	1
M. pulpa	x	x	x	-	x	-	-	x	x
M. hypermetra	44	15	6	2	x	-	-	10	7
M. poecilosterna	15	55	46	58	40	9	-	47	36
M. rufocinnamomea	-	-	-	x	-	-	-	x	x
Eremopterix signata	77	52	43	4	7	-	-	37	27
E. leucotis(x3.4)	68	32	-	x	-	-	-	15	11
Motacilla aguimp	-	x	-	-	x	-	-	x	x
Anthus novaeseelandiae	1	-	-	-	-	-	x	x	x
A. trivialis	-	-	-	x	-	-	1	x	x
Tmetothylacus tenellus(x2.0)	4	20	22	16	10	2	x	17	13
Macronyx aurantiigula	11	4	2	2	x	-	2	3	2
Campephaga flava	-	-	x	-	x	1	2	x	x
Pycnonotus barbatus	-	x	1	1	1	15	5	1	4
Andropadus importunus	-	-	-	-	-	3	2	-	1
Phyllastrephus strepitans	-	-	-	-	-	4	3	-	1
Nicator chloris	-	-	-	-	-	x	-	-	x

Species	G	BG	WBG	B	WB	W	R	PSH	TOTAL
Eurocephalus rueppelli	x	7	11	10	19	18	9	10	12
Prionops plumata	-	x	1	1	8	22	1	2	5
P. retzii	-	-	-	-	-	-	17	-	1
Nilaus afer	-	x	2	x	2	1	-	1	1
Dryoscopus pringlii	-	-	-	x	x	x	-	x	x
D. cubla	-	-	-	-	-	-	8	-	1
Tchagra jamesi	x	1	1	3	3	3	x	1	2
T. senegala	-	-	-	-	-	1	x	-	x
Rhodophoneus cruentus	x	4	3	4	2	1	-	3	2
Laniarius aethiopicus	-	-	-	-	-	-	1	-	x
L. funebris	-	-	x	x	2	6	-	x	1
Malaconotus sulfureopectus	-	-	-	-	-	x	x	-	x
M. blanchoti	-	-	-	-	-	1	1	-	x
Lanius c. collurio(x3.4)	x	2	2	4	5	2	4	3	3
L. c. isabellinus(x2.2)	9	17	12	12	10	9	5	13	11
L. minor(x12.0)	1	1	x	1	1	x	-	1	1
L. cabanisi	-	x	x	1	1	-	x	x	x
L. dorsalis	18	24	11	10	3	-	-	14	10
Oenanthe oenanthe(x2.2)	x)16	2)12	2)3	1)1	1)1	-)	-)	2)6	1)4
O. isabellina(x2.2)	6)16	8)12	3)3	4)1	1)1	-)	-)	4)6	3)4
O. pleschanka(x2.0)	1	1	2	1	2	x	-	1	1
O. pileata	x	1	x	-	-	-	-	x	x
Monticola saxatilis(x2.0)	2	3	5	4	2	2	-	4	3
Cercotrichas galactotes(x2.2)	x	6	5	6	8	6	4	6	5
C. leucophrys	-	x	x	5	6	4	-	2	2
Cichladusa guttata	-	-	-	-	-	x	-	-	x
Luscinia luscinia	-	-	-	x	-	1	1	x	x
Irania gutturalis(x2.7)	-	-	x	-	x	2	x	x	1
Turdus tephronotus	-	-	-	-	x	3	-	x	1
Turdoides rubiginosus	-	-	-	-	-	-	1	-	x
T. aylmeri	-	-	-	1	1	5	-	x	1
Acrocephalus palustris(x3.4)	-	x	2	1	1	3	5	1	2
A. arundinaceus griseldis	-	-	x	-	-	-	x	x	x
A. schoenobaenus	-	-	x	-	-	-	1	x	x
Hippolais olivetorum	-	-	-	-	-	x	-	-	x
H. languida(x2.7)	-)1	x)1	1)2	1)2	x)2	1)7	-)10	x)1	1)3
H. pallida(x2.0)	-)1	x)1	x)2	-)2	x)2	6)7	10)10	x)1	2)3
Sylvia nisoria(x2.4)	-	1	2	1	2	2	2	1	1
S. borin	-	-	x	-	x	1	-	x	x
S. communis(x2.4)	1	2	5	4	8	7	1	4	4
Phylloscopus trochilus(x2.7)	-	1	2	1	3	4	1	2	2
Cisticola chiniana	-	-	x	x	-	-	-	x	x
C. galactotes	-	-	-	-	-	-	x	-	x
C. cinereola	10	3	1	1	x	-	-	2	2
C. nana	-	x	1	-	1	5	-	x	1
C. aridula	5	x	-	-	-	-	-	x	x
Prinia subflava	-	-	-	-	x	-	-	x	x
Apalis flava	-	-	-	x	x	x	-	x	x
Spiloptila rufifrons	-	-	-	1	x	-	x	x	x
Camaropectera brevicaudata	-	-	-	-	-	x	x	-	x
C. simplex	-	x	x	3	3	3	1	1	2
Eremomela flavicrissalis	-	-	x	-	-	1	-	x	x
Sylvietta brachyura	-	1	1	1	3	5	-	1	2
S. isabellina	-	-	-	x	-	-	-	x	x

Species	G	BG	WBG	B	WB	W	R	PSH	TOTAL
Muscicapa striata(x2.0)	-	x	5	1	3	14	38	2	7
Bradornis microrhynchus	-	x	2	1	1	4	-	1	1
Batis molitor	-	-	-	-	x	2	-	x	x
B. perkeo	-	-	1	x	1	1	-	x	x
B. minor	-	-	x	-	-	-	7	x	1
Terpsiphone viridis	-	-	x	-	-	1	1	x	x
Parus afer	-	-	x	-	x	1	-	x	x
Anthoscopus musculus	-	-	-	-	x	x	-	x	x
Anthreptes orientalis	-	-	x	1	x	2	-	x	1
A. collaris	-	-	-	-	-	-	3	-	x
Nectarinia amethystina	-	-	-	-	-	x	4	-	x
N. hunteri	-	2	3	5	11	13	8	4	6
N. bifasciata	-	x	-	-	1	10	1	x	1
N. nectarinioides	-	-	-	-	-	-	1	-	x
Zosterops abyssinica	-	-	1	x	x	x	1	x	x
Emberiza polioptera	-	2	5	15	12	3	-	6	5
E. tahapisi	-	x	x	x	-	x	-	x	x
Serinus atrogularis	-	-	-	-	-	1	x	-	x
S. dorsostriatus	-	-	x	-	-	-	-	x	x
Pytilia melba	-	1	1	2	3	1	1	1	1
Estrilda rhodopyga	-	-	1	-	-	-	2	x	x
E. astrild	-	-	-	-	-	-	x	-	x
Uraeginthus ianthinogaster	-	-	-	-	1	1	-	x	x
U. bengalus	-	-	x	-	x	x	10	x	1
U. cyanocephalus	-	-	-	-	x	x	-	x	x
Lagonosticta sp.	-	-	-	-	-	-	1	-	x
Amadina fasciata(x2.7)	8	8	27	2	8	-	1	14	10
Lonchura malabarica	-	1	-	-	-	-	-	x	x
L. griseicapilla	-	-	1	-	1	2	-	1	(1)
L. cucullata	-	-	-	-	-	-	1	-	x
Vidua macroura	-	-	-	-	-	-	2	-	x
V. fischeri	-	-	x	x	x	-	-	x	x
V. paradisaea(x4.8)	-	-	13	-	1	1	13	5	4
Hypochera sp.	-	-	-	-	-	-	1	-	x
Ploceus intermedius(x2.2)	-	x	x	2	x	2	x	x	1
P. velatus	-	-	-	x	-	x	-	x	x
P. cucullatus migriceps	-	x	x	-	2	-	1	1	x
P. rubiginosus(x2.4)	-	4	x	x	x	9	-	1	3
P. nigricollis	-	-	-	-	x	3	-	x	1
Malimbus rubriceps	-	-	x	-	x	1	2	x	x
Quelea quelea(x2.7)	46	80	144	11	88	19	594	90	115
Euplectes albonotatus	-	-	1	-	-	-	6	x	(1)
E. diadematus(x2.2)	-	4	4	12	6	4	8	5	5
E. nigricollis	-	-	-	-	-	-	x	-	x
Bubalornis niger	-	14	40	19	26	15	18	24	22
Dinemellia dinemelli	1	11	14	15	19	9	2	13	11
Plocepasser mahali	-	1	1	x	1	-	2	1	1
Pseudonigrita cabanisi	-	-	-	9	-	-	-	1	(1)
Passer gongonensis	1	9	17	8	20	1	33	13	12
Petronia pyrgita	4	10	18	14	21	10	11	14	13

Species	F	BG	WBG	B	WB	W	R	PSH	TOTAL
Onychognathus morio	-	-	-	-	-	2	-	-	x
Lamprotornis chalybaeus	-	-	-	-	x	-	8	x	1
L. purpuropterus	-	-	-	1	1	-	-	x	x
Cinnyricinclus leucogaster	-	-	-	-	-	2	-	-	x
Speculipastor bicolor	-	-	3	-	-	-	1	1	(1)
Spreo fischeri	x	5	22	3	16	7	3	12	10
S. hildebrandti	-	2	x	-	-	x	-	1	(1)
S. shelleyi	-	x	1	x	2	x	-	1	(1)
S. superbus	x	16	24	13	42	2	8	21	17
Cosmopsarus regius	1	7	20	20	22	25	14	15	17
Creatophora cinerea(x2.0)	6	10	11	3	17	2	19	11	10
Buphagus erythrorhynchus	1	4	3	2	5	1	6	3	3
Oriolus oriolus(x1.8)	-	x	1	-	1	3	7	x	1
O. larvatus	-	x	x	-	1	5	9	x	2
Dicrurus adsimilis	1	3	14	10	16	26	16	10	13
Corvus albicollis	-	x	-	-	-	x	-	x	x

Appendix 1.3 The relative abundance of birds in each month

1. The figure given is the number of birds seen per ten hours in all habitats combined and with both years combined. x means less than 0.5 birds per ten hours. The number of hours censused in each month can be obtained from Table 5.1.
2. The number in brackets after each species is the total number of individuals of that species counted in the relative abundance censuses.
3. For the chats Oenanthe oenanthe and O. isabellina and the warblers Hippolais languida and H. pallida only those individuals positively identified are given and for both, only those censuses after 1st July 1975 are used in the calculations (see ch 5.3.32 and 5.3.34).

Species (no. of individuals)	J	F	M	A	M	J	A	S	O	N	D
Francolinus sephaena (97)	1	4	1	1	2	-	2	2	x	1	2
F. leucoscepus (56)	2	x	1	1	1	1	1	x	-	x	1
Coturnix delegorguei (459)	31	x	x	x	x	-	-	-	1	2	41
Numida meleagris (19)	x	-	x	-	x	x	-	-	-	-	x
Turnix sylvatica (4)	x	-	-	x	-	-	-	-	-	-	x
Ortyxelos meiffrenii (24)	x	x	x	1	x	x	x	1	x	x	-
Eupodotis ruficrista (136)	1	3	1	5	1	2	1	3	1	2	1
E. senegalensis (14)	-	-	-	x	x	x	x	1	-	x	-
E. hartlaubii (9)	-	1	-	-	x	x	x	-	x	-	x
Vanellus tectus (232)	1	2	4	4	7	3	2	2	5	2	6
V. lugubris (9)	-	-	-	-	-	-	2	-	-	-	-
V. coronatus (112)	2	4	1	2	2	1	1	2	1	2	-
Charadrius asiaticus (27)	1	2	x	-	-	-	-	x	1	1	-
C. pecuarius (2)	-	-	-	x	-	-	-	-	-	-	-
Burhinus capensis (16)	-	-	x	x	-	x	-	-	x	x	-
Cursorius temminckii (10)	x	-	-	-	x	x	-	x	-	x	-
C. cinctus (44)	-	-	x	x	-	1	2	1	-	1	x
Pterocles exustus (27)	-	-	-	-	x	-	-	4	-	-	-
P. decoratus (859)	6	7	14	18	13	17	15	12	16	14	8
Streptopelia semitorquata (122)	2	1	1	3	2	2	x	2	1	1	4
S. decipiens (3)	-	-	-	x	-	-	-	-	x	-	-
S. capicola (955)	23	15	12	19	12	15	9	9	13	15	13
S. senegalensis (1318)	102	14	5	4	9	6	2	2	7	7	53
Oena capensis (177)	7	5	3	2	6	1	-	-	2	1	3
Turtur chalcospilos (117)	2	2	2	2	2	1	x	1	1	1	4
Poicephalus rufiventris (245)	2	3	5	5	4	5	5	2	3	3	4
Corythaixoides leucogaster (206)	3	3	4	3	5	4	3	3	4	2	1

Species (no. of individuals)	J	F	M	A	M	J	A	S	O	N	D
Clamator glandarius (14)	1	-	-	-	-	-	-	-	-	x	2
C. jacobinus (51)	1	-	-	1	-	-	-	-	-	x	6
Cuculus solitarius (2)	-	-	-	-	-	-	-	-	x	x	-
C. clamosus (1)	-	-	-	-	-	-	-	-	-	-	x
C. canorus (64)	x	-	-	4	-	-	-	-	1	3	2
Chrysococcyx kiaas (3)	-	-	-	-	-	x	-	-	-	x	-
C. caprius (54)	3	x	x	1	x	-	-	-	1	x	3
C. cupreus (1)	-	-	-	-	-	-	-	-	-	-	x
Centropus superciliosus (55)	3	1	x	1	1	-	-	-	x	x	3
Colius striatus (63)	2	1	1	x	2	1	2	-	x	x	2
C. leucocephalus (1)	-	-	-	-	x	-	-	-	-	-	-
C. macrourus (452)	3	2	7	5	6	11	11	3	8	8	10
Caprimulgus spp. (13).	-	-	-	x	-	x	-	-	x	x	-
Halcyon chelicuti (128)	3	2	1	2	2	1	2	1	1	1	3
H. albiventris (8)	x	-	x	x	x	-	-	-	-	-	x
H. leucocephala (160)	5	4	2	3	1	x	x	x	-	1	8
Merops apiaster (14)	-	-	-	-	-	-	-	-	-	x	2
M. s. superciliosus (65)	5	1	3	-	-	-	-	x	-	x	1
M. s. persicus (6)	-	-	-	-	-	-	-	-	-	1	-
M. albicollis (91)	6	x	2	1	-	-	-	-	-	4	1
M. pusillus (96)	2	3	x	1	3	1	1	1	1	x	1
M. revoillii (74)	1	1	2	1	1	1	1	1	1	1	1
Coracias garrulus (385)	17	9	8	2	-	-	-	-	1	7	18
C. caudata (147)	3	2	2	2	3	2	1	2	2	1	3
C. naevia (23)	-	x	x	x	2	x	-	-	x	x	-
Eurystomus glaucurus (19)	-	1	x	-	-	-	-	-	x	x	2
Upupa epops africana (108)	3	1	1	3	4	1	x	x	-	1	x
Phoeniculus purpureus (87)	2	1	1	x	2	1	3	2	1	x	2
P. minor (169)	2	3	2	4	2	2	2	2	2	3	1

Species (no. of individuals)	J	F	M	A	M	A	J	J	A	S	C	N	D
<i>Tockus nasutus</i> (120)	2	2	1	2	2	1	2	2	1	x	2	2	2
<i>T. erythrorhynchus</i> (548)	12	7	10	10	9	10	6	6	5	6	6	9	8
<i>T. deckeni</i> (580)	8	5	9	8	10	13	13	14	8	14	7	4	7
<i>T. flavirostris</i> (188)	3	2	6	3	2	5	5	1	3	1	2	1	2
<i>T. alboterminatus</i> (5)	x	-	-	-	-	x	x	-	-	-	-	-	x
<i>Bucorvus cafer</i> (2)	-	-	-	-	-	-	x	x	-	-	-	-	-
<i>Lybius melanopterus</i> (42)	x	1	1	1	1	1	2	2	1	1	x	x	x
<i>L. torquatus</i> (1)	-	-	-	-	-	-	-	-	-	-	-	-	x
<i>L. melanocephalus</i> (163)	3	3	2	2	1	2	2	3	4	3	1	1	3
<i>L. lacrymosus</i> (52)	1	1	x	-	2	2	2	-	-	x	1	1	2
<i>Pogoniulus pusillus</i> (35)	1	1	1	x	1	1	1	1	x	x	x	x	-
<i>Trachyphonus darnaudii</i> (288)	4	5	4	6	4	5	5	3	3	3	5	4	4
<i>T. erythrocephalus</i> (137)	1	5	2	2	2	2	3	3	3	2	2	x	1
<i>Indicator indicator</i> (13)	-	-	1	x	x	-	x	x	x	-	-	-	-
<i>I. minor</i> (18)	x	x	-	1	x	-	-	-	-	-	-	x	1
<i>Campethera nubica</i> (133)	2	2	1	3	1	2	2	3	2	3	2	2	2
<i>Dendropicos fuscescens</i> (114)	2	2	1	2	2	1	2	1	2	1	1	2	2
<i>Thripas namaquus</i> (18)	x	x	x	x	x	-	x	-	1	1	x	x	x
<i>Mirafra cantillans</i> (74)	4	2	1	1	1	1	x	x	-	x	1	x	2
<i>M. pulpa</i> (10)	-	1	-	-	-	-	-	-	-	-	-	-	1
<i>M. hypermetra</i> (512)	9	12	8	10	7	6	6	7	6	7	7	6	8
<i>M. poecilosterna</i> (2527)	23	38	37	52	29	32	34	49	34	49	51	47	23
<i>M. rufocinnamomea</i> (1)	-	-	-	x	-	-	-	-	-	-	-	-	-
<i>Eremopterix signata</i> (1903)	1	24	11	67	77	79	18	40	18	40	9	12	7
<i>E. leucotis</i> (756)	5	75	-	26	21	-	-	-	-	-	-	-	1
<i>Motacilla aguimp</i> (2)	-	x	-	-	x	-	-	-	-	-	-	-	-
<i>Anthus novaeseelandiae</i> (5)	x	x	-	-	-	-	-	-	-	-	-	-	x
<i>A. trivialis</i> (7)	-	-	1	-	-	-	-	-	-	-	-	-	-
<i>Tmetothylacus tenellus</i> (895)	22	26	22	13	x	x	1	1	1	1	3	20	39
<i>Macronyx aurantiigula</i> (165)	5	2	3	3	4	2	2	1	x	1	2	1	3
<i>Campephaga flavus</i> (30)	x	2	x	1	1	-	x	-	-	-	x	-	1

Species (no. of individuals)	J	F	M	A	M	J	A	S	O	N	D
Pycnonotus barbatus (275)	3	2	3	4	5	5	4	5	5	4	5
Andropadus importunus (49)	2	1	x	-	1	x	x	1	1	1	1
Phyllastrephus strepitans (65)	1	-	1	1	2	1	x	2	1	3	1
Nicator chloris (1)	x	-	-	-	-	-	-	-	-	-	-
Eurocephalus rueppelli (819)	10	11	12	16	14	16	18	9	9	9	10
Prionops plumata (382)	2	5	7	5	2	5	8	5	7	7	7
P. retzii (89)	2	2	-	-	1	1	3	1	1	1	3
Nilaus afer (67)	1	1	1	1	1	1	1	1	1	1	1
Dryoscopus pringlii (9)	-	-	-	-	-	x	x	-	x	-	-
D. cubla (45)	1	2	x	1	1	1	1	x	x	x	2
Tchagra jamesi (111)	2	3	1	2	1	1	1	1	1	2	2
T. senegala (16)	-	x.	x	-	x	-	-	1	x	1	x
Rhodophoneus cruentus (160)	2	4	2	3	2	3	1	1	5	2	2
Laniarius aethiopicus (3)	-	-	-	x	-	-	-	-	-	-	x
L. funebris (95)	1	1	3	x	2	1	2	1	1	1	2
Malaconotus sulfureopectus (5)	-	-	-	-	-	-	-	-	-	1	x
M. blanchoti (18)	x	-	x	x	-	-	x	1	x	x	x
Ianius c.collurio (184)	1	1	1	25	-	-	-	-	-	1	1
L. c. isabellinus (802)	28	29	23	3	-	-	-	-	x	16	33
L. minor (38)	-	-	-	6	-	-	-	-	-	-	-
L. cabanisi (21)	x	-	-	1	1	-	1	-	x	-	x
L. dorsalis (708)	8	14	12	11	11	10	8	15	11	11	6
Oenanthe oenanthe (85)	4	1	-	1	x	-	-	1	5	4	5
O. isabellina (226)	14	17	13	1	-	-	-	-	1	12	13
O. pleschanka (75)	2	2	1	x	-	-	-	-	1	3	2
O. pileata (15)	-	x	-	x	2	x	-	-	-	-	-
Monticola saxatilis (218)	9	5	5	1	-	-	-	-	1	7	7
Cercotrichas galactotes (381)	11	11	9	3	-	-	-	-	-	11	17
C. leucophrys (146)	2	2	2	3	2	1	4	3	1	2	1
Cicladusa guttata (3)	-	-	-	-	-	x	-	x	-	x	-
Luscinia luscinia (22)	x	-	-	1	-	-	-	-	-	1	2
Irania gutturalis (39)	x	x	2	1	-	-	-	-	-	x	2
Turdus tephronotus (48)	1	-	1	1	1	x	x	1	1	1	1
Turdoides rubiginosus (18)	1	-	-	x	-	-	-	-	1	1	-
T. aylmeri (74)	2	2	x	1	2	x	3	-	1	1	x

Species (no. of individuals)	J	F	M	A	M	A	J	A	S	O	N	D
Acrocephalus palustris (109)	2	1	x	1	-	-	-	-	-	-	3	11
A. arundinaceus griseldis (4)	-	-	-	-	-	-	-	-	-	-	-	1
A. schoenobaenus (4)	-	-	-	x	1	-	-	-	-	-	-	-
Hippolais olivetorum (1)	-	-	-	-	-	-	-	-	-	-	x	-
H. languida (36)	2	4	5	3	-	-	-	-	-	-	-	x
H. pallida (141)	11	14	7	5	-	-	-	-	-	x	-	13
Sylvia nisoria (96)	6	2	1	x	-	-	-	-	-	-	2	5
S. borin (16)	x	x	1	1	-	-	-	-	-	-	x	1
S. communis (309)	8	2	1	7	-	-	-	-	-	-	5	28
Phylloscopus trochilus (134)	1	x	6	9	-	-	-	-	-	2	x	4
Cisticola chiniana (3)	-	-	-	-	-	-	x	-	-	-	-	x
C. galactotes (1)	-	-	-	-	-	-	-	-	-	-	-	-
C. cinereola (105)	2	2	2	3	-	-	1	1	1	1	x	2
C. nana (83)	2	2	1	2	-	-	1	1	x	x	1	1
C. aridula (24)	1	1	x	x	-	-	x	-	-	-	-	x
Prinia subflava (3)	-	-	-	-	-	-	-	1	-	-	-	-
Apalis flavida (9)	-	-	-	-	-	-	x	x	x	x	-	-
Spiloptila rufifrons (10)	-	-	-	-	-	-	x	x	-	-	-	-
Camaroptera brevicaudata (2)	-	-	-	-	-	-	-	-	-	-	-	x
C. simplex (106)	2	1	2	1	-	-	3	2	x	1	1	4
Eremomela flavicrissalis (13)	-	x	x	x	-	-	x	x	1	-	x	-
Sylvietta brachyura (122)	x	3	3	1	-	-	1	2	3	3	2	1
S. isabellina (1)	-	-	-	x	-	-	-	-	-	-	-	-
Muscicapa striata (500)	12	13	14	6	-	-	-	-	-	2	17	18
Bradornis microrhynchus (95)	1	2	1	1	1	-	2	3	1	2	1	x
Batis molitor (32)	1	-	x	x	x	-	x	x	1	x	1	x
B. perkeo (30)	-	x	1	-	-	-	1	1	1	1	-	-
B. minor (39)	1	1	x	x	1	-	x	1	-	-	x	2
Terpsiphone viridis (20)	1	1	x	x	x	-	-	-	-	-	1	1
Parus afer (12)	x	x	1	-	-	-	1	-	-	-	-	-
Anthoscopus musculus (9)	-	x	x	x	-	-	x	-	-	-	-	-
Anthreptes orientalis (40)	-	x	x	1	x	-	2	x	2	1	x	1
A. collaris (17)	-	x	-	x	1	-	x	1	x	-	x	x
Nectarinia amethystina (25)	x	-	x	x	x	-	1	2	x	x	-	x
N. hunteri (421)	2	3	7	9	6	-	8	13	6	5	5	5
N. bifasciata (148)	2	1	2	2	1	-	2	3	2	1	1	4
N. nectarinioides (3)	-	-	-	-	-	-	-	-	-	-	-	1

Species (no. of individuals)	J	F	M	A	M	A	J	A	S	O	N	D
<i>Zosterops abyssinica</i> (24)	-	-	x	x	2	-	x	-	-	x	-	2
<i>Emberiza poliopleura</i> (353)	4	6	4	4	5	4	7	4	5	7	5	3
<i>E. tahapisi</i> (6)	x	x	-	-	-	-	-	-	-	-	-	x
<i>Serinus atrogularis</i> (17)	-	-	-	-	-	-	x	2	-	-	1	-
<i>S. dorsostriatus</i> (4)	-	-	1	-	-	-	-	-	-	-	-	-
<i>Pytilia melba</i> (85)	1	1	1	1	2	1	1	3	1	1	1	1
<i>Estrilda rhodopyga</i> (25)	1	-	x	-	-	-	-	-	-	-	-	3
<i>E. astrild</i> (2)	-	-	-	-	-	-	-	-	-	-	-	x
<i>Uraeginthus ianthinogaster</i> (21)	x	x	-	-	x	-	x	1	-	x	x	-
<i>U. bengalus</i> (59)	1	x	1	2	1	-	-	-	2	1	1	2
<i>U. cyanocephalus</i> (5)	-	-	-	x	-	-	-	-	-	-	-	x
<i>Lagonosticta</i> sp. (7)	-	x	x	x	-	-	-	-	-	-	-	x
<i>Amadina fasciata</i> (702)	33	22	41	12	1	1	-	1	-	-	x	2
<i>Lonchura malabarica</i> (8)	x	-	-	1	-	1	-	-	-	-	-	-
<i>L. griseicapilla</i> (56)	3	-	3	3	-	3	-	-	-	-	-	-
<i>L. cucullata</i> (5)	-	-	-	-	x	-	-	-	-	-	-	1
<i>Vidua macroura</i> (11)	x	x	x	x	-	x	-	-	-	-	-	x
<i>V. fischeri</i> (6)	-	x	1	-	-	-	-	-	-	-	-	-
<i>V. paradisaea</i> (312)	35	12	-	2	1	2	-	-	-	-	-	1
<i>Hypochoera</i> sp. (3)	-	-	-	x	-	x	-	-	-	-	-	-
<i>Ploceus intermedius</i> (47)	x	1	x	1	-	1	2	-	x	-	1	2
<i>P. velatus</i>	-	-	-	-	-	-	-	-	-	-	-	x
<i>P. cucullatus nigriceps</i> (32)	1	1	-	-	3	-	-	-	-	-	-	1
<i>P. rubiginosus</i> (183)	2	-	6	2	-	2	-	-	-	3	x	18
<i>P. nigricollis</i> (39)	x	-	x	1	1	1	1	1	1	1	x	1
<i>Malimbus rubriceps</i> (19)	x	x	x	-	x	-	x	-	-	1	-	1
<i>Quelea quelea</i> (8053)	800	134	98	98	32	98	x	5	x	9	41	73
<i>Euplectes albonotatus</i> (39)	5	-	-	-	-	-	-	-	-	-	-	2
<i>E. diadematus</i> (353)	15	4	x	6	15	6	-	-	-	-	6	13
<i>E. nigricollis</i> (2)	x	-	-	-	-	-	-	-	-	-	-	-
<i>Bubalornis niger</i> (1530)	30	15	43	22	46	22	12	10	5	12	33	22
<i>Dinemellia dinemelli</i> (799)	9	6	14	13	13	13	16	15	11	9	14	6
<i>Plocepasser mahali</i> (63)	1	1	1	1	x	1	4	-	x	x	x	-

Species (no. of individuals)	J	F	M	A	M	J	A	J	J	S	O	N	D
Pseudonigrita cabanisi (63)	2	-	-	-	-	-	-	8	-	-	1	-	-
Passer gongonensis (836)	11	8	12	12	11	12	13	20	11	11	13	12	10
Petronia pyrgita (937)	11	11	12	14	13	21	17	15	17	17	17	14	12
Onychognathus morio (31)	-	-	-	-	-	-	4	-	2	2	-	-	-
Lamprotornis chalybaeus (46)	1	-	-	1	x	-	2	-	1	1	1	1	2
L. purpuropterus (15)	-	-	-	x	1	-	x	1	-	-	-	-	-
Cinnyricinclus leucogaster (26)	-	-	1	-	2	1	-	-	-	-	-	-	-
Speculipastor bicolor (61)	-	-	-	-	-	-	-	-	-	-	1	8	1
Spreo fischeri (713)	7	5	22	6	7	19	20	8	6	6	14	5	9
S. hildebrandti (35)	-	-	4	-	-	x	-	-	1	1	-	x	1
S. shelleyi (44)	-	3	x	-	-	-	-	-	-	-	-	5	-
S. superbus (1163)	14	11	22	24	26	15	21	20	15	15	15	10	10
Cosmopsarus regius (1177)	15	17	16	15	15	16	29	20	25	15	15	15	12
Creatophora cinerea (667)	29	11	2	27	17	2	-	-	-	4	4	9	8
Buphagus erythrorhynchus (228)	3	3	x	6	6	2	4	3	2	2	6	2	4
Oriolus oriolus (91)	1	3	3	2	-	-	-	-	-	-	2	1	4
O. larvatus (129)	2	1	2	3	2	1	3	2	2	2	2	1	2
Dicrurus adsimilis (919)	13	11	10	15	14	16	13	13	16	16	14	14	12
Corvus albicollis (7)	-	-	-	x	x	-	x	x	-	-	-	-	-

Appendix 1.4. Table of critical values of R/N for different values of N for use with seasonal abundance statistics (from Table 56 of Pearson and Hartley 1972). See ch 5.2.5 for details of the calculation of R/N .

N	$P < 0.05$	$P < 0.01$
6	0.690	0.825
7	0.642	0.771
8	0.602	0.725
9	0.569	0.687
10	0.540	0.655
12	0.494	0.602
16	0.429	0.525
20	0.385	0.472
30	0.315	0.387
40	0.273	0.336
60	0.223	0.276
100	0.173	0.214
200	0.122	0.152

For $N \geq 200$ it has been found that with increasing accuracy as N increases $2R^2/N$ approximates to χ^2 with df 2 (see Pearson and Hartley 1972 p. 125).

The critical values are:

$$P < 0.05, \quad \chi^2 = 5.991$$

$$P < 0.01, \quad \chi^2 = 9.210$$

$$P < 0.001, \quad \chi^2 = 13.82$$

Appendix 2 The vegetation on census plots

types

A general description of the vegetation and the habitat/is given in ch 2.5. Here, the vegetation on each of the plots used for Type II censuses (to estimate the density of birds) is given in more detail.

For each plot except those in Riverine, the canopy cover of both bushes and, where appropriate, trees was estimated by the point-centre-quarter method of Cottam & Curtis (1956). For the five Park savanna habitats a standard regular grid of 18 points was used covering the whole plot. In the Woodland plots, measurements were taken at 10 points covering a representative sample of the strip. At each point the nearest bush and, in Wooded and Bushed Grassland and Wooded Bushland and Woodland, tree was measured in each quarter. Three measurements were taken: 1) distance to near side, 2) distance to far side, 3) height of canopy (top and bottom in the case of trees). The two distances were measured to the nearest half pace (1 pace approximately equalled 0.75 m), and the height was estimated in metres.

From these measurements the distance to the centre of the bush/tree was found ($= d$) and the density easily calculated ($= 1/(\text{mean of } d)^2$). Trees and bushes were assumed to have a circular perimeter, and canopy cover was calculated from the average basal area and the density. Vegetation volume was calculated by: average basal area (in m^2) $\times$ average height (in m) $\times$ number on 1 hectare. Bushes were assumed cylindrical. For trees only the canopy volume was included, and this too was assumed cylindrical.

Figures for canopy cover and volume of both bushes and trees on each plot are given in Table A2.1. The table also includes a figure for grass cover and volume. The figure for grass cover is the average over the year and was measured while estimating seed abundance (see ch 4.2.3). The figure includes all vegetation in the herb layer. For grass volume, grass was assumed to be 0.33 m high throughout.

Two measures of the diversity of the vegetation have been calculated. The Shannon-Wiener index of diversity has been calculated for each of canopy cover and vegetation volume on each plot, and the figures used in ch 6.4 are the averages of these for each habitat.

The plots are located in Fig. 3.2. Further specific details about the plots follow:

Grassland

- 3B - on black cotton soil which became waterlogged in the wet seasons.
- 5B - the few bushes were mostly Boscia coriacea, many of which were dead, and only reached 0.5 m in height.
- 5C - had a few dead logs and sticks on the ground.
- 5G - bushes were mostly Cordia gharaf and a few dead sticks. The grass cover was very patchy.
- 6D - bushes were almost entirely Sericocomopsis spp. None were more than 0.5 m in height which was hardly higher than the grass. The whole aspect was that of Grassland. Pratt, Greenway & Gwynne (1966) would have classified it as Dwarf Shrub Grassland but I did not recognise this as a distinct type.
- 6E - very similar to 3B but on brown soil.

Bushed Grassland

- 3A - similar to 5G but with more, although smaller, bushes.
- 3E - contained a Delonix elata tree in one corner.
- 4A - many of the bushes were the low (up to 1 m) evergreen Thylachium thomasii.
- 4D - on white stony soil on a gentle slope.
- 4E - had many logs and sticks lying on the ground.
- 5A - ground almost bare in the dry season but many annual grasses and herbs (especially Tribulus terrestris) germinated with good rains. 10% of the 72 bushes measured were the very thick Calyptrorhiza sp. (up to 3 m high).

Wooded and Bushed Grassland

- 4B - the trees were mostly Boscia coriacea (3 - 6 m high) with 4 large Delonix elata.
- 4C - the trees were mostly Platycelyphium voense.
- 5D - bushes mostly very small Strychnos decussata and B. coriacea. Trees were mostly P. voense, but one D. elata in the middle of the plot often had a concentration of birds.
- 5E - bushes and trees dominated by S. decussata and P. voense respectively.
- 5F - a very open area under P. voense trees. Bushes mainly small B. coriacea.
- 6A - dominated by the tree Melia volkensii. Two small thickets of bushes.
- 6B - similar to 6A but Premna spp. (26% of bushes measured) much more prevalent in the bush layer.
- 6C - a nearly exclusive stand of the tree P. voense and bush Sericocomopsis sp..

Bushland

- 1A - included a low (4.5 m) Acacia tortilis tree in one corner which often had a small concentration of birds.
- 1C - no special notes
- 1D - no special notes
- 2A - a very dense area dominated by Premna spp. (56% of bushes measured).
- 2D - a relatively open area, but with many logs and sticks on the ground.
- 3F - a fair amount of the climber/creeper Helinus integrifolius.

Wooded Bushland

- 1B - trees were mostly Boscia coriacea, with 3 Delonix elata and 1 Melia volkensii, bushes mainly Erythrochlamys spectabilis.
- 2B - bushes mainly Premna spp. and trees Platycelyphium voense.
- 2C - very similar to 2B.
- 3C - similar to 2B and 2C but Premna spp. especially prominent.
- 3D - Premna spp. still more dominant (67% of bushes measured); trees P. voense with a few M. volkensii.

Woodland

- A - Grewia bicolor nearly half the bushes measured (45%), and all but 5 trees were Commiphora spp. or Acacia spp.
- B - bushes mainly Grewia villosa.
- C - nearly a pure stand of Commiphora spp. with much smaller and fewer bushes than in plots A or B.

Riverine

- A - between Park HQ and Kanderi - a patch of thick evergreen bushes and tall (up to 20 m) trees; and a few large dead trunks.
- B - between Park HQ and Kanderi - similar to plot A but fewer large dead trees.
- C - Ndololo Camp Site - an open "park" area under trees, mostly Acacia elatior and Dobera glabra with a few large Ficus spp., surrounded by thick evergreen bushes especially Capparis sepiaria.
- D - near the first crossing of the Voi River east of Voi - a dense, nearly pure, stand of D. glabra with little bush layer. Many fallen logs and, after rain, very thick grass.
- E - near second crossing of the Voi River east of Voi - a fringe of trees on both banks of the river, mainly A. elatior, with some thick evergreen bushes underneath.

Table A2.1 Canopy cover, vegetation volume and vegetation diversity on each plot. For methods of calculation see text of Appendix 2.

Plot	Canopy cover (%)				Volume (m ³ on 1 ha)			
	Grass	Bush	Tree	Diversity	Grass	Bush	Tree	Diversity
3B	59	-	-	-	1960	-	-	-
5B	7	0.5	-	0.3	240	65	-	0.5
5C	4	-	-	-	130	-	-	-
5G	30	0.5	-	0.1	980	100	-	0.3
6D	61	3.5	-	0.2	2015	195	-	0.3
6E	54	-	-	-	1770	-	-	-
G Average	36	0.8	-	0.1	1185	60	-	0.2
3A	57	1.0	-	0.1	1870	70	-	0.2
3E	40	4.5	-	0.3	1330	445	-	0.6
4A	58	4.0	-	0.2	1925	325	-	0.4
4D	55	3.5	-	0.2	1800	230	-	0.4
4E	29	1.5	-	0.2	950	105	-	0.3
5A	20	2.0	-	0.3	655	195	-	0.5
BG Average	43	2.8	-	0.2	1420	230	-	0.4
4B	53	2.0	2.5	0.3	1750	165	620	0.8
4C	50	4.5	1.5	0.4	1635	415	1065	1.0
5D	10	0.5	1.0	0.5	340	40	520	0.8
5E	13	5.0	2.0	0.9	415	555	1215	1.0
5F	10	0.5	1.0	0.5	320	50	455	0.9
6A	43	1.5	3.0	0.4	1415	120	1730	0.8
6B	41	3.5	5.0	0.6	1365	380	3355	0.8
6C	44	3.0	4.0	0.5	1455	230	1655	0.9
WBG Average	33	2.5	2.5	0.5	1085	245	1325	0.9
1A	25	9.0	-	0.6	830	915	-	0.7
1C	20	15.5	-	0.7	660	1510	-	0.6
1D	26	13.0	-	0.6	860	1190	-	0.7
2A	19	22.5	-	0.7	620	2925	-	0.5
2D	35	7.0	-	0.5	1170	745	-	0.7
3F	45	18.5	-	0.6	1470	1715	-	0.7
B Average	28	14.5	-	0.6	935	1500	-	0.6
1B	27	17.0	1.0	0.8	885	1835	375	0.9
2B	32	9.5	1.5	0.7	1060	965	965	1.1
2C	29	12.5	2.0	0.8	960	1475	1385	1.1
3C	48	14.0	2.5	0.7	1580	1670	1540	1.1
3D	44	22.0	2.5	0.8	1450	2945	1445	1.0
WB Average	36	15.0	2.0	0.7	1185	1780	1140	1.1
A		49.0	36.0	1.1		8315	9760	0.8
B		63.0	48.0	1.0		9025	14265	0.8
C		29.0	93.5	0.9		4475	27975	0.5
W Average	25 ^a	47.0	59.0	1.0	825 ^a	7270	17335	0.7

a) This measure is an average of 3 counts by W. van Wijngaarden and it has been used for each plot.

Appendix 3 Data from Senegal (Morel 1968).

- 1) The tables which follow contain the data used in ch 6.5 (Figs 6.11 and 6.12).
- 2) The species names follow those used by Morel (1968).
- 3) The food guilds are those used in my re-analysis. The only changes from Morel's designations are that his "Vegetarian" has been divided into "Seeds" and "Fruit", and his "Polyphage" into "Insects + Seeds", "Insects + Fruit" and "Insects + Nectar". In a few cases he has considered a species to be in the "Polyphage" category which I have considered purely "Insect" in Tsavo, but his designations have been retained (with any necessary divisions) in all cases. I have excluded his "Predator" category.
Abbreviations used: I = Insect; S = Seed; F = Fruit; N = Nectar.
- 4) The figures in the body of the tables are the corrected versions supplied by Dr. Morel (in litt.).

Table A3.1. - the savanna plot - adapted from Table 2 in Morel (1968). There was no count in August 1960 or December 1961

Table A3.2. - the gallery forest plot - adapted from Table 13 in Morel (1968)
There was no count in September 1960, August 1961 or December 1961.

Table A3.1 - the savanna plot

Species	Food Guild	1960												1961												1962											
		F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M								
Ethiopian species																																					
Eremopterix leucotis	S	-	-	-	-	-	-	-	-	-	4	10	9	12	7	5	7	17	-	-	10	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Mirafra cantillans	IS	1	-	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	
Halcyon leucocephala	I	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Bubalornis albirostris	IS	-	-	-	-	-	25	-	14	9	-	-	-	-	-	-	-	-	10	2	3	17	18	-	1	10	2	7	-	-	-	-	-	-	-	-	
Tockus erythrorhynchus	IF	8	3	2	-	2	-	-	-	-	2	-	-	-	4	2	-	1	2	-	2	4	1	-	-	1	1	-	-	-	-	-	-	-	-	-	
Tockus nasutus	IF	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Oediconemus capensis	I	-	-	-	-	-	-	-	1	-	2	-	-	-	-	-	-	2	2	1	1	-	2	-	2	1	-	-	1	-	-	-	-	-	-	1	
Lybius vieilloti	F	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2	-	1	2	-	-	-	-	-	-	-	-	
Macrodipteryx longipennis	I	-	-	-	-	-	1	-	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Sarcophorus tectus	I	-	-	-	-	-	-	-	-	-	2	2	-	-	2	1	4	5	-	2	-	-	2	-	3	3	-	3	2	-	-	-	-	-	-	-	
Colius macrourus	F	-	-	-	-	-	-	-	-	2	-	-	-	-	1	-	-	-	2	-	-	8	8	-	14	1	8	-	-	-	-	-	-	-	-	-	-
Oena capensis	S	4	-	-	2	-	1	-	5	4	2	18	3	2	8	-	3	11	10	8	3	13	6	-	-	-	4	6	1	-	-	-	-	-	-	-	
Stigmatopelia senegalensis	S	-	-	-	-	-	4	-	2	1	4	3	-	-	1	-	-	4	5	3	3	1	6	-	-	-	-	-	-	-	-	-	-	-	-	-	
Streptopelia roseogrisea	S	1	1	1	3	-	3	-	4	5	5	2	-	4	4	4	9	11	1	4	2	8	-	-	5	7	4	7	2	-	-	-	-	-	-	-	-
Streptopelia vinacea	S	-	-	-	-	-	-	-	2	2	-	-	-	-	-	-	-	5	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Turtur abyssinica	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Coracias abyssinicus	I	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	2	2	2	3	4	1	-	4	-	1	-	3	-	-	-	-	-	-	-	
Clamator levaillanti	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Lampromorpha caprius	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Cursorius temminckii	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Rhinoptilus chalcopterus	I	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	7	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Tchagra senegala	I	1	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	
Laniarius barbarus	I	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Aerops albicollis	I	-	-	-	-	4	2	-	9	11	-	-	-	-	-	-	-	9	4	9	18	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Merops orientalis	I	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Hedydipna platyura	IN	1	-	1	1	-	-	-	-	-	3	2	-	-	1	1	-	-	-	-	-	-	-	-	-	4	2	1	2	-	-	-	-	-	-	-	
Nectarinia pulchella	IN	-	-	-	-	2	11	-	24	10	10	2	-	-	1	1	3	4	11	12	33	8	2	-	3	2	-	-	2	-	-	-	-	-	-	-	
Oriolus auratus	IF	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Ardeotis arabs	IS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	
Eupodotis senegalensis	IS	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Anthoscopus punctifrons	I	3	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	5	-	3	-	2	-	-	-	-	-	-	-	
Francolinus bicalcaratus	IS	3	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Phoeniculus senegalensis	I	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	
Scotopelia atterimus	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Campethera punctuligera	I	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Mesopicos goertae	I	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Amadina fasciata	S	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Euodice cantans	S	3	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	3	2	-	-	-	5	-	-	-	-	-	-	-	-	-	
Gymnonis pyrgita	S	-	-	-	-	-	-	-	-	2	-	2	-	-	1	-	-	3	-	-	-	-	5	-	-	-	2	-	-	-	-	-	-	-	-	-	
Passer griseus	IS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	
Passer luteus	S	2	-	11	-	6	-	-	-	-	-	-	-	1	-	-	-	23	11	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Ploceus vitellinus	S	3	6	2	1	1	-	-	8	2	2	7	8	-	14	2	1	1	5	1	2	12	5	-	-	-	2	-	3	-	-	-	-	-	-	-	
Pytilia melba	S	2	-	3	-	4	-	-	1	-	3	6	-	-	1	-	-	1	3	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Quelea quelea	S	-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	10	-	-	20	-	-	1	-	-	-	-	-	-	-	-	-	-	-	

Table A3.2 - the gallery forest plot

Species	Food Guild	1960												1961												1962											
		M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M											
Ethiopian species																																					
Halcyon leucocephala	I	-	-	2	1	-	-	4	-	-	-	-	-	-	2	-	-	-	1	1	-	-	-	-	-	-	-										
Halcyon senegalensis	I	-	-	6	4	-	6	-	-	-	-	-	-	-	5	-	1	3	-	-	-	-	-	-	-	-	-										
Ispidina picta	I	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-										
Tockus erythrorhynchus	IF	5	3	1	6	-	2	9	1	9	5	2	1	2	-	6	-	2	4	8	-	1	2	3	1	8	-										
Tockus nasutus	IF	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-										
Oedicnemus capensis	I	9	4	2	3	-	-	-	-	1	6	9	10	1	1	1	-	2	-	-	-	-	-	-	-	2	-										
Lybius vieilloti	F	-	-	-	-	-	4	3	-	-	2	2	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-										
Sarciophorus tectus	I	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-										
Colius macrourus	F	-	7	-	-	-	-	-	2	6	8	10	2	11	14	-	-	-	-	-	-	5	4	4	2	-	-										
Oena capensis	S	-	1	-	-	-	-	2	2	2	1	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-										
Stigmatopelia senegalensis	S	87	143	18	7	-	7	8	6	29	41	25	9	13	14	13	-	6	6	6	-	10	12	9	35	39	-										
Streptopelia decipiens	S	162	129	27	35	-	39	30	43	47	72	62	56	81	76	55	-	26	43	47	-	38	44	54	112	110	-										
Streptopelia roseogrisea	S	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-										
Streptopelia vinacea	S	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-										
Turtur abyssinica	S	11	14	11	11	-	18	20	32	31	19	20	18	33	18	17	-	9	17	9	-	6	7	15	12	18	-										
Coracias abyssinica	I	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-										
Centropus senegalensis	I	1	1	3	3	-	6	2	4	2	1	2	3	1	2	1	-	2	1	3	-	1	-	-	-	1	-										
Clamator levaillanti	I	-	-	1	2	-	-	-	-	-	-	-	-	-	-	1	-	4	1	3	-	-	-	-	-	-	-										
Lampromorpha caprius	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	1	1	1	-	-	-	-	-	-	-										
Lampromorpha klaasi	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	3	-	-	-	-	-	-	-										
Dicrurus adsimilis	I	-	3	1	2	-	-	1	2	-	-	-	1	1	2	3	-	4	-	-	-	-	-	3	1	2	-										
Scotornis climacurus	I	9	1	-	-	-	-	13	13	13	32	23	23	8	6	-	-	3	17	22	-	36	39	25	20	11	-										
Poliospiza leucopygia	S	-	-	-	-	-	-	-	-	-	1	-	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-										
Indicator indicator	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-										
Corvinella corvina	I	-	-	7	-	-	1	3	-	-	4	1	3	1	1	2	-	1	-	-	-	1	-	-	4	2	-										
Laniarius barbarus	I	11	2	11	9	-	14	12	12	12	11	8	7	6	12	10	-	12	10	14	-	3	10	9	4	10	-										
Nilaus afer	I	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	1	-	-	-										
Tchagra senegala	I	2	2	1	1	-	1	-	-	-	-	1	2	1	-	1	-	-	1	-	-	-	2	1	-	1	-										
Aerops albicollis	I	-	1	-	-	-	1	-	-	-	-	-	-	5	3	-	-	-	-	-	-	-	-	-	-	5	-										
Merops orientalis	I	-	-	-	-	-	-	2	-	-	2	2	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-										
Alseonax aquaticus	I	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	3	2	-										
Batis senegalensis	I	2	1	-	-	-	-	2	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2	2	-	-	-										
Tchitrea viridis	I	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-										
Crinifer piscator	F	5	9	7	2	-	1	4	3	4	5	3	5	3	8	1	-	1	8	4	-	3	1	3	3	-	-										
Nectarinia pulchella	IN	1	15	24	20	-	46	16	18	10	10	2	11	6	4	9	-	16	10	106	-	20	3	4	1	5	-										
Oriolus auratus	IF	-	-	-	-	-	1	4	-	-	-	-	1	-	-	4	-	4	1	-	-	-	-	-	-	1	-										
Fringilla bicalcaratus	IS	2	5	2	2	-	1	4	2	-	2	5	5	7	2	-	-	3	-	2	-	3	2	7	2	-	-										
Numida meleagris	IS	1	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	4	3	-	3	3	3	3	3	-										
Ptilopachus petrosus	IS	2	5	-	5	-	5	-	-	-	-	-	-	5	5	1	-	-	-	-	-	-	-	-	-	-	-										
Phoeniculus senegalensis	I	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-										
Scopelogadus aterrimus	I	2	-	-	4	-	-	2	-	2	-	1	2	2	-	4	-	-	1	-	-	-	-	-	1	-	-										
Campethera punctuligera	I	2	2	2	2	-	2	1	2	2	1	1	1	2	3	2	-	3	2	1	-	1	-	-	1	2	-										
Mesopodops goertae	I	3	2	1	2	-	4	3	1	3	4	-	3	1	-	-	-	1	4	1	-	-	2	-	1	-	-										
Estrilda troglodytes	S	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-										
Euodice cantans	S	20	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	6	-	-										
Hypochera chalybeata	S	-	2	-	-	-	-	2	2	1	-	-	2	6	17	2	-	-	-	1	-	-	-	3	-	-	-										
Lagonosticta senegalensis	S	33	56	91	43	-	88	155	144	112	58	73	65	92	103	78	-	57	89	111	-	35	20	54	26	37	-										
Passer griseus	IS	-	-	1	-	-	-	-	-	-	-	2	2	1	5	-	-	1	-	-	-	1	-	5	-	3	-										
Passer luteus	IS	-	-	-	-	-	1	-	-	-	-	-	6	12	11	-	-	-	-	-	-	-	3	-	-	-	-										
Ploceus capitalis	S	28	24	113	21	-	40	313	169	171	116	75	46	240	34	16	-	-	94	84	-	17	11	130	354	8	-										
Ploceus cucullatus	IS	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-										
Ploceus luteolus	S	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-										
Ploceus vitellinus	S	-	-	-	-	-	1	-	-	-	1	12	10	10	10	10	-	-	2	-	-	-	-	-	-	-	-										
Quelea quelea	S	-	-	11	4	-	-	71	25	9	1	34	85	34	2	-																					

Appendix 4.1 The density of birds in each habitat, divided into food guilds
All figures are numbers of birds per 10 ha. x = less than 0.5. Figures in brackets are large flocks of small birds or single large birds a) lark *Eremopterix signata* b) weaver *Quelea quelea* c) weaver *Pseudonigrita cabanisi* d) crow *Corvus albicollis* e) guinea-fowl *Numida meleagris* f) hornbill *Bucorvus cafer*
I = Insect F = Fruit S = Seed N = Nectar

Grassland				Bushed Grassland				Wooded and Bushed Grassland								
I S I+S				I F S				I+F I+S I+N			I F S			I+F I+S I+N		
1975	Feb	9	2	5	19	-	13(+143) ^b	2	14	-	15	-	27(+343) ^b	1	6	-
	Mar	6	1	4	19	-	1	1	10	-	16	-	14	3	10	x
	Apr	12	x	7	9	-	8	1	7	-	12	1	22	2	10	x
	May	3	4	4	4	2	1	-	4	-	6	-	4	1	7	-
	Jun	3	-(+29) ^a	1	3	-	3	-	2	-	4	-	1	-	6	-
	Jul	1	-	2	5	2	x	-	7	-	5	-	x	1	8	1
	Aug	1	-	2	2	-	1	1	6	x	6	-	1	-	4	-
	Sep	1	-	2	3	-	2	-	6	-	5	x	2	1	6	-
	Oct	4	-	2	2	-	1(+24) ^a	-	9	-	6	x	1	1	6	-
	Nov	6	6	1	7	-	2	-	4	x	6	-	3	2	7	x
	Dec	5	3	4	20	-	6	1	9	1	23	x	4	17	7	x
1976	Jan	13	9(+36) ^b	7	18	1	52	6	8	-	23	-	75	2	12	x
	Feb	16	12	1	14	-	30	-	5	x	19	-	30	1	8	x
	Mar	9	1	2	14	-	2	1	7	-	18	-	12	2	7	-
	Apr	2	-	3	10	-	2	-	3	-	13	-	12	2	6	-
	May	3	1	1	4	-	6	-	5	-	4	-	9	2	4	-
	Jun	2	2	1	1	-	4	x	3	-	8	-	8	x	3	-
	Jul	1	1	2	5	-	2	-	1	-	10	-	4	2	6	x
	Aug	1	-	1	4	-	2	-	6	-	4	-	2	x	6	-
	Sep	4	1	1	6	-	x	1	4	-	4	3	4	-	3	x
	Oct	4	2	2	4	-	2	-	6	x	4	x	7	1	7	x
	Nov	1	1	3	3	-	x	-	3	-	6	x	2	1	5	-
	Dec	22	1	2	22	-	12	11	4	x	18	-	4	2	7	-
1977	Jan	11	2	2	17	2	19	7	11	-	21	-	9	1	5	-

Bushland							Wooded Bushland									
I F S I+F I+S I+N							I F S I+F I+G I+N									
1975	Feb	13	1	7(+227) ^b	2	9	-	11	-	17(+518) ^b	2	8	1			
	Mar	15	2	4	2	11	x	14	x	1	2	14	1			
	Apr	12	-	11	1	11	-	20	-	6	6	12	x			
	May	8	-	5	2	11	x	9	1	8	6	13	-			
	Jun	2	1	4	4	7	x	5	-	3	4	8	x			
	Jul	6	-	3	2	7	-	6	2	2	2	7	1			
	Aug	6	-	1	x	9	-	2	-	1	-	8	-			
	Sep	4	-	4(+15) ^c	1	11	1	7	-	1	1	15	x			
	Oct	3	-	2	x	12	x	9	x	-	1	10	x			
	Nov	7	-	3	2	8	1	11	2	-	1	9	1			
	Dec	20	-	7	x	12	-	28	-	3	7	11	2			
1976	Jan	14	1	24	3	7	-	23	1	44	13	8	1			
	Feb	10	1	8	2	8	-	16	-	25(+113) ^b	4	8	1			
	Mar	7	1	4	1	9	-	13	x	6	10	20	1			
	Apr	6	-	16	1	7	1	16	-	2	1	10	-			
	May	2	-	1	1	8	-	2	1	1	1	12	x			
	Jun	1	x	4	1	4	-	6	-	1	1	4	-			
	Jul	4	-	4	1	6	-	5	x	1	3	6	x			
	Aug	6	-	9	-	5	-	4	-	1	-	8	-			
	Sep	3	-	6	1	4	x	2	-	x	-	6	-			
	Oct	3	-	2	2	6	1	6	-	2	3	9	1			
	Nov	5	-	1	3	9	-	12	-	6	x	6	1			
	Dec	6	1	4(+21) ^b	6	5	-	31	-	12	10	10	-			
1977	Jan	22	-	29	1	10	-	24	-	69	9	5	x			

Woodland							Riverine									
I F S I+F I+S I+N							I F S I+F I+S I+N									
1975	Feb	22	6	1	7	3	3	50	6	31	13	3	-			
	Mar	20	9	x	7	x	5	43	9	23(+81) ^b	4	2	1			
	Apr	23	4	1	6	1	7	44	11	34	23	3	4			
	May	9(+1) ^d	6	6	7	2	4	49	8	33	28	12	1			
	Jun	7	14	5	12	2(+3) ^e	3	14	-	7	2	6	1			
	Jul	12	1	1	13	x	2	20(+1) ^f	4	4	14	19	5			
	Aug	19	7	x	24	2	5	21	26	4	9	14	11			
	Sep	11	7	2	19	1	3	14	3	1	1	6	4			
	Oct	17	12	1	13	2	3	16	6	7	6	6	-			
	Nov	20	6	4	11	2	4	34	2	1	13	8	1			
	Dec	24	4	5	7	5	4	54	7	9	17	9	1			
1976	Jan	24	2	11	7	6	1	62	9	78(+988) ^b	10	9	1			

		Woodland		S	I+F	I+S	I+N	Riverine		S	I+F	I+S	I+N
		I	F					I	F				
1976	Feb	9	3	4	13	x	-	35	4	56	28	8	1
	Mar	29	3	7	4	1	6	29	14	16	8	4	1
	Apr	19(+x) ^d	7	1	5	x	4	48	4	22(+219) ^b	9	6	1
	May	4	6	x	5	1	2	14	6	8	10	3	-
	Jun	3	6	2	5	1	2	18	1	5	16	11	-
	Jul	6(+1) ^d	5	1	10	2	3	10	6	11	6	6	1
	Aug	7	4	2	10	1	3	15	13	16	13	4	7
	Sep	17	1	1	13	2	2	11	3	9	21	7	-
	Oct	6	3	1	9	1	-	21	2	5	12	5	1
	Nov	6	2	-	4	2	1	39	3	4	6	10	1
	Dec	26	4	20	4	11	x	51	9	4	11	6	1
1977	Jan	20	1	6	3	-	1	43	1	4	4	3	-

Appendix 4.2 The biomass of birds in each habitat, divided into food guilds
All figures are in grams per hectare (x = less than 0.5/ha)
Figures in brackets are large flocks of small birds or single large birds a) lark *Eremopterix signata*
b) weaver *Quelea quelea* c) weaver *Pseudonigrita cabanisi* d) crow *Corvus albicollis* e) guinea-fowl
Numida meleagris f) hornbill *Bucorvus cafer*
I = Insect F = Fruit S = Seed N = Nectar

		Grassland			Bushed Grassland			Wooded and Bushed Grassland								
		I	S	I+S	I	F	S	I+F	I+S	I+N	I	F	S	I+F	I+S	I+N
1975	Feb	28	7	19	74	-	99(+243) ^b	18	69	-	51	-	160(+582) ^b	9	36	-
	Mar	22	1	19	69	-	15	14	37	-	61	-	48	44	71	x
	Apr	65	2	61	32	-	38	6	35	-	44	6	77	16	48	1
	May	12	8	16	27	10	8	-	14	-	27	-	61	14	36	-
	Jun	26	-(+44) ^a	4	18	-	54	-	6	-	29	-	15	-	49	-
	Jul	4	-	10	23	11	4	-	51	-	25	-	7	10	28	1
	Aug	13	-	34	10	-	22	4	18	x	27	-	25	-	30	-
	Sep	3	-	39	19	-	36	-	19	-	22	2	27	8	19	-
	Oct	25	-	9	7	-	15(+35) ^a	-	16	-	31	2	14	4	17	-
	Nov	40	9	34	52	-	33	-	10	x	32	-	26	17	41	x
	Dec	14	18	21	57	-	46	4	63	1	79	2	42	125	25	1
1976	Jan	52	59(+61)	22	63	4	319	48	22	-	84	-	330	12	69	x
	Feb	82	22	6	56	-	108	-	16	x	75	-	114	10	56	x
	Mar	39	1	7	59	-	9	16	43	-	56	-	23	19	26	-
	Apr	17	-	13	51	-	38	-	8	-	45	-	29	27	38	-
	May	22	2	6	19	-	32	-	16	-	22	-	26	30	27	-
	Jun	10	12	4	20	-	63	2	7	-	33	-	75	1	11	-
	Jul	15	1	7	27	-	24	-	2	-	47	-	62	22	51	1
	Aug	13	-	5	26	-	26	-	22	-	20	-	25	3	32	-
	Sep	26	12	4	30	-	4	7	14	-	17	13	16	-	21	1
	Oct	27	3	11	26	-	3	-	20	x	24	2	26	8	53	1
	Nov	7	6	36	7	-	1	-	10	-	23	2	19	12	16	-
	Dec	122	4	10	65	-	105	84	9	x	74	-	41	8	49	-
1977	Jan	56	13	6	58	10	181	54	33	-	99	-	54	8	18	-

		Bushland			Wooded Bushland								
		I	F	S	I+F	I+S	I+N	I	F	S	I+F	I+S	I+N
1975	Feb	37	6	47(+386) ^b	17	48	-	36	-	52(+880) ^b	17	50	1
	Mar	43	9	7	6	46	x	47	4	7	8	66	1
	Apr	30	-	65	5	67	-	52	-	43	29	64	x
	May	24	-	40	9	48	x	29	3	26	45	70	-
	Jun	29	6	71	20	63	x	23	-	30	19	69	x
	Jul	31	-	56	8	42	-	28	14	22	11	41	2
	Aug	37	-	22	2	62	-	15	-	10	7	27	-
	Sep	15	-	29(+28) ^c	5	65	1	34	-	1	3	53	x
	Oct	18	-	42	1	46	x	45	4	-	9	23	-
	Nov	31	-	37	8	60	1	59	10	-	7	23	1
	Dec	70	-	91	4	38	-	86	-	36	52	47	2
1976	Jan	34	6	203	23	13	-	117	3	281	100	20	2
	Feb	23	3	67	12	36	-	46	-	100(+193) ^b	15	48	1
	Mar	21	7	63	7	140	-	56	4	46	110	85	1
	Apr	50	-	86	2	28	1	55	-	19	11	108	-
	May	8	-	16	5	41	-	11	17	22	6	57	x
	Jun	10	4	69	3	29	-	27	-	9	2	14	-
	Jul	15	-	59	4	16	-	18	2	17	11	20	x
	Aug	29	-	20	-	35	-	14	-	13	-	76	-
	Sep	35	-	30	3	9	x	4	-	1	-	18	-
	Oct	10	-	29	13	17	1	24	-	22	19	50	1
	Nov	23	-	16	17	22	-	46	-	52	2	65	1
	Dec	29	4	55(+36) ^b	33	33	-	84	-	85	70	34	-
1977	Jan	61	-	214	2	68	-	72	-	482	60	13	x

		Woodland			Riverine								
		I	F	S	I+F	I+S	I+N	I	F	S	I+F	I+S	I+N
1975	Feb	52	81	10	53	41	2	166	29	257	106	13	-
	Mar	52	103	1	60	3	6	143	43	75(+138) ^b	45	8	2
	Apr	55	73	17	54	5	8	143	68	126	188	11	4
	May	30(+74) ^d	103	32	63	21	3	209	53	137	175	50	1
	Jun	25	209	48	108	4(+428) ^e	3	48	-	120	4	24	1
	Jul	47	26	9	145	3	1	106(+406) ^f	20	51	102	166	6
	Aug	63	45	5	332	27	5	96	125	25	114	101	13
	Sep	36	75	25	214	38	2	74	16	19	4	88	5
	Oct	52	173	9	184	32	3	82	27	42	53	26	-
	Nov	61	82	25	151	31	4	107	14	1	90	29	2
	Dec	74	33	34	68	15	4	227	38	105	138	38	1
1976	Jan	63	35	44	62	37	1	205	18	429(+1679) ^b	77	135	2

		Woodland					Riverine						
		I	F	S	I+F	I+S	I+N	I	F	S	I+F	I+S	I+N
1976	Feb	25	47	22	96	9	-	113	20	279	206	28	1
	Mar	80	d,46	29	35	3	6	71	73	94	77	77	1
	Apr	55(+37)	104	21	59	3	4	185	18	80(+372) ^b	80	24	1
	May	13	114	2	50	2	2	87	29	91	131	12	-
	Jun	16	78	19	75	2	2	107	8	53	182	51	-
	Jul	22(+74) ^d	39	8	132	13	3	46	30	118	65	19	1
	Aug	25	28	18	100	2	2	81	76	49	106	49	8
	Sep	48	7	18	131	6	3	65	12	39	172	24	-
	Oct	20	35	14	100	4	-	136	10	63	84	19	1
	Nov	19	42	-	40	29	1	151	25	36	41	103	1
	Dec	52	27	49	38	75	x	148	46	43	95	20	1
1977	Jan	64	18	32	41	-	1	178	6	39	37	10	-

Appendix 4.3 The energy requirements of birds in each habitat, divided to food guilds
All figures are of Basal Metabolic Rate in kilojoules per hectare per day (x = less than 0.5 kJ/ha/day)
Figures in brackets are large flocks of small birds or single large birds a) lark *Eremopterix signata*
b) weaver *Quelea quelea* c) weaver *Pseudonigrita cabanisi* d) crow *Corvus albicollis* e) guinea-fowl
Numida meleagris f) hornbill *Bucorvus cafer*
I = Insect F = Fruit S = Seed N = Nectar

		Grassland			Bushed Grassland			Wooded and Bushed Grassland								
		I	S	I+S	I	F	S	I+F	I+S	I+N	I	F	S	I+F	I+S	I+N
1975	Feb	37	7	24	85	-	66(+406) ^b	15	83	-	62	-	123(+975) ^b	6	40	-
	Mar	25	2	23	83	-	9	10	37	-	74	-	48	25	62	x
	Apr	39	2	48	38	-	32	15	26	-	55	5	79	14	53	1
	May	12	12	20 ^a	22	8	5	-	19	-	31	-	34	9	72	-
	Jun	18	-(+76)	5	16	-	28	-	9	-	27	-	9	-	35	-
	Jul	5	-	12	25	9	2	-	41	-	29	-	4	10	37	2
	Aug	9	-	18	10	-	11	6	25	1	34	-	13	-	24	-
	Sep	4	-	20	18	-	19	-	26	-	26	2	14	10	26	-
	Oct	19	-	11	8	-	8(+61) ^b	-	22	-	34	2	9	5	24	-
	Nov	30	15	13	45	-	17	-	14	1	33	-	17	13	39	x
	Dec	20	14	27	76	-	30	4	52	2	98	2	26	25	33	1
1976	Jan	52	41(+101) ^b	31	69	3	239	54	31	-	91	-	291	13	81	x
	Feb	70	34	8	62	-	104	-	22	1	80	-	108	6	54	x
	Mar	40	2	10	61	-	8	10	38	-	74	-	35	17	34	-
	Apr	13	-	17	53	-	20	-	12	-	49	-	38	17	34	-
	May	16	3	8	15	-	24	-	22	-	18	-	31	20	22	-
	Jun	9	9	5	11	-	34	2	10	-	37	-	47	1	15	-
	Jul	8	2	9	29	-	14	-	3	-	47	-	33	18	39	1
	Aug	9	-	6	27	-	14	-	28	-	20	-	15	3	28	-
	Sep	20	8	5	37	-	21	9	18	-	21	10	14	-	14	1
	Oct	20	5	14	23	-	5	-	28	1	22	2	24	10	42	1
	Nov	7	4	20	10	-	x	-	13	-	26	2	11	9	22	-
	Dec	98	3	13	84	-	67	93	14	1	76	-	25	10	46	-
1977	Jan	83	9	8	70	8	112	60	44	-	100	-	42	7	24	-

		Bushland						Wooded Bushland					
		I	F	S	I+F	I+S	I+N	I	F	S	I+F	I+S	I+N
1975	Feb	49	4	34(+646) ^b	13	46	-	73	-	90(+2379) ^b	17	69	4
	Mar	58	7	11	5	46	1	93	4	7	12	108	2
	Apr	44	-	49	5	54	-	115	-	50	49	101	1
	May	28	-	26	10	48	1	54	4	46	80	135	-
	Jun	17	4	38	22	45	1	41	-	30	33	78	1
	Jul	36	-	30	9	37	-	52	14	21	20	54	5
	Aug	33	-	12	2	47	-	28	-	9	12	59	-
	Sep	18	-	25(+45) ^c	5	45	1	63	-	3	6	112	1
	Oct	13	-	22	1	47	1	83	4	-	12	55	-
	Nov	30	-	21	7	43	1	89	12	-	11	55	4
	Dec	78	-	53	2	52	-	167	-	34	72	87	6
1976	Jan	47	4	131	20	23	-	176	4	332	165	48	5
	Feb	34	2	44	13	32	-	61	-	97(+323) ^b	17	41	1
	Mar	25	4	35	8	72	-	60	3	32	77	107	2
	Apr	36	-	68	2	29	1	64	-	12	6	72	-
	May	11	-	8	5	37	-	12	10	12	6	55	1
	Jun	8	2	36	2	20	-	30	-	6	4	19	-
	Jul	17	-	32	4	22	-	21	1	9	11	28	1
	Aug	35	-	29	-	27	-	18	-	7	-	54	-
	Sep	19	-	25	3	14	1	7	-	1	-	25	-
	Oct	14	-	16	15	24	1	26	-	13	19	44	2
	Nov	20	-	9	18	32	-	56	-	33	3	39	2
	Dec	31	3	31(+59) ^b	55	11	-	113	-	59	73	45	-
1977	Jan	74	-	144	2	51	-	88	-	337	63	19	1

		Woodland						Riverine					
		I	F	S	I+F	I+S	I+N	I	F	S	I+F	I+S	I+N
1975	Feb	74	44	7	44	23	5	171	22	170	84	17	-
	Mar	70	57	1	44	3	11	152	33	75(+231) ^b	30	10	3
	Apr	74	38	10	37	6	14	146	48	121	185	14	7
	May	48(+40) ^d	54	26	40	15	7	226	37	122	140	56	1
	Jun	27	113	30	85	3(+123) ^e	5	53	-	64	6	32	1
	Jul	55	13	6	99	3	3	106(+23) ^f	15	30	83	130	10(+23)
	Aug	83	23	11	232	18	9	105	94	18	55	89	23
	Sep	44	38	21	156	18	4	68	12	10	4	40	8
	Oct	68	91	12	93	18	6	93	20	30	40	34	-
	Nov	81	44	18	92	18	7	131	9	2	72	39	3
	Dec	88	21	23	51	21	8	216	27	61	126	49	1
1976	Jan	83	18	42	47	42	2	195	12	335(+2811) ^b	67	73	3

		Woodland.					Riverine						
		I	F	S	I+F	I+S	I+N	I	F	S	I+F	I+S	I+N
1976	Feb	22	25	17	97	4	-	119	15	242	220	38	1
	Mar	112	25	24	24	4	11	82	54	72	67	38	1
	Apr	71(+20) ^d	54	11	39	3	8	186	14	81(+623) ^b	68	31	1
	May	17	58	2	33	3	4	64	22	53	78	16	-
	Jun	18	43	11	42	3	4	98	4	32	136	63	-
	Jul	26(+40) ^d	26	5	82	10	6	41	22	71	69	27	1
	Aug	33	18	11	76	3	4	77	54	53	96	33	15
	Sep	64	5	10	93	9	5	49	9	31	156	32	-
	Oct	25	20	7	71	5	-	124	7	36	83	26	1
	Nov	22	21	-	31	15	2	154	16	22	38	73	1
	Dec	80	18	81	30	52	1	165	35	25	82	27	3
1977	Jan	78	11	25	25	-	1	143	4	25	42	14	-

Appendix 4.4 The number of species on each census plot in each month
The figures are of the number of species recorded on each plot. N.C. = not censused

		Grassland					Bushed Grassland								
		3B	5B	5C	5G	6D	6E	3A	3E	4A	4D	4E	5A		
1975	Feb	2	3	6	6	5	2	5	6	5	15	16	10		
	Mar	3	N.C.	4	3	4	2	6	2	14	5	12	10		
	Apr	5	10	3	5	5	1	6	4	4	8	3	10		
	May	4	2	3	5	2	3	6	2	4	6	3	2		
	Jun	1	4	3	0	2	1	5	1	0	3	1	4		
	Jul	0	2	2	2	2	0	2	7	4	1	6	4		
	Aug	0	1	3	2	2	0	4	1	5	4	1	6		
	Sep	2	1	1	3	2	1	0	5	3	3	1	4		
	Oct	0	3	3	0	1	0	0	0	5	4	4	4		
	Nov	1	3	2	2	0	1	2	3	1	5	2	6		
	Dec	3	3	2	4	7	1	7	9	8	9	6	14		
	1976	Jan	5	4	3	1	11	6	8	13	19	14	9	9	
Feb		5	1	3	4	10	3	9	7	12	6	10	4		
Mar		5	2	2	3	9	2	5	11	6	3	7	10		
Apr		4	1	2	3	2	2	5	6	1	6	7	7		
May		0	1	5	3	2	0	4	1	3	5	2	4		
Jun		2	4	0	2	3	1	0	3	2	2	2	1		
Jul		0	3	0	3	2	0	1	2	6	2	3	2		
Aug		0	2	0	2	2	0	1	2	3	2	3	5		
Sep		0	1	0	1	4	1	3	1	1	2	1	5		
Oct		1	2	1	3	2	2	3	4	3	5	5	4		
Nov		1	5	2	0	4	2	2	0	3	3	2	4		
Dec		2	4	2	6	4	0	3	10	10	10	9	12		
1977	Jan	4	4	3	5	3	0	4	12	14	7	7	17		
Cumulative Total		14	15	20	20	24	12	23	50	46	36	34	46		
		Wooded and Bushed Grassland							Bushland						
		4B	4C	5D	5E	5F	6A	6B	6C	1A	1C	1D	2A	2D	3F
1975	Feb	10	19	11	10	3	6	13	7	10	11	8	4	7	9
	Mar	9	3	4	9	4	12	9	16	9	10	9	8	8	11
	Apr	5	12	6	6	1	11	7	10	6	10	8	11	9	6
	May	4	8	1	5	3	7	2	11	15	8	6	4	7	9
	Jun	4	7	4	5	4	4	2	2	8	7	4	3	1	6
	Jul	8	4	0	4	2	6	3	4	5	2	3	3	10	3
	Aug	2	5	2	1	4	0	5	3	8	5	3	4	3	8
	Sep	4	4	2	1	1	5	14	2	12	4	2	5	7	2
	Oct	4	7	4	8	1	2	7	3	2	3	6	5	3	4
	Nov	5	8	3	0	2	7	11	5	6	7	7	7	7	6
	Dec	11	16	2	10	5	13	7	17	14	7	10	8	13	16
	1976	Jan	16	10	5	10	2	25	22	11	9	20	11	2	9
Feb		8	20	0	5	9	15	10	8	6	12	13	1	7	4
Mar		3	8	9	11	3	15	13	12	6	17	4	3	5	4
Apr		4	10	1	7	1	10	23	8	9	5	4	5	7	2
May		0	6	1	4	1	4	13	9	4	3	2	4	3	6
Jun		2	3	0	8	4	8	10	7	7	4	2	1	2	2
Jul		9	6	1	13	2	5	8	9	12	3	3	3	6	2
Aug		0	6	1	5	2	1	3	4	5	2	1	3	4	2
Sep		2	2	3	1	0	2	5	5	1	3	4	1	6	3
Oct		4	1	5	8	0	6	10	8	3	3	4	6	5	8
Nov		7	4	1	6	2	11	6	10	5	4	3	2	8	4
Dec		7	11	6	8	5	14	13	4	11	6	7	7	7	5
1977	Jan	15	13	6	7	8	8	7	8	8	15	12	15	10	11
Cumulative Total		48	53	27	46	27	55	53	51	53	46	40	39	51	45
		Wooded Bushland			Woodland				Riverine						
		1B	2B	2C	3C	3D	A	B	C	A	B	C	D	E	
1975	Feb	11	16	16	6	5	16	23	12	7	9	27	13	N.C.	
	Mar	10	10	6	17	2	23	18	17	8	11	17	19	7	
	Apr	8	15	18	10	17	17	13	30	16	17	23	13	18	
	May	1	15	1	1	11	21	11	14	10	7	35	11	4	
	Jun	7	4	3	7	8	19	8	17	6	6	10	2	7	
	Jul	5	9	6	4	3	5	13	22	6	5	14	17	3	
	Aug	3	5	7	0	2	20	19	13	8	10	15	5	5	
	Sep	6	8	3	1	7	14	14	13	10	6	7	2	2	
	Oct	6	4	3	5	9	17	26	18	8	4	7	12	2	
	Nov	3	11	8	7	8	16	20	27	6	4	10	11	9	
	Dec	15	20	14	13	23	25	15	23	11	12	28	11	12	
	1976	Jan	15	7	11	23	12	11	26	29	11	12	28	9	12
Feb		9	2	10	15	15	13	12	17	10	6	18	9	9	
Mar		9	5	4	17	11	20	20	14	8	12	10	7	8	
Apr		3	9	4	10	18	14	12	24	12	20	15	9	11	
May		6	4	4	2	12	9	9	8	6	11	4	9	8	
Jun		4	3	2	6	5	6	10	10	6	4	6	5	11	
Jul		8	8	3	2	1	14	14	3	4	8	8	7	4	
Aug		1	9	2	4	2	12	17	11	11	6	12	6	6	
Sep		2	1	3	5	3	21	10	19	9	10	6	6	5	
Oct		3	12	11	1	6	5	11	12	4	10	7	8	11	
Nov		4	14	11	6	10	9	12	8	11	9	16	8	12	
Dec		15	21	13	10	19	17	21	16	10	11	22	5	12	
1977	Jan	10	20	13	13	15	14	23	11	6	9	N.C.	5	15	
Cumulative Total		44	61	54	58	63	79	82	80	63	73	87	57	62	

Appendix 4.5

Species diversity on each census plot in each month

The figures are of the species diversity (Shannon-Wiener index) on each plot. A dash is put if there were no birds recorded. A zero is put if there was one species. For the averages in Table 6.9 both have been included.

		Grassland					Bushed Grassland						
		3B	5B	5C	5G	6D	6E	3A	3E	4A	4D	4E	5A
1975	Feb	0.7	0.9	1.6	1.7	1.5	0.7	1.5	1.6	1.2	0.5	1.7	1.9
	Mar	1.0	N.C.	1.3	1.0	1.2	0.7	1.7	0.7	2.5	1.4	2.2	2.0
	Apr	1.6	2.0	1.0	1.6	1.5	0	1.7	1.2	1.1	1.7	1.0	2.1
	May	1.2	0.6	0.9	1.5	0.7	1.1	1.7	0.6	1.4	1.6	1.0	0.7
	Jun	0	1.4	0.2	-	0.7	0	1.5	0	-	0.8	0	1.3
	Jul	-	0.6	0.7	0.6	0.7	-	0.7	1.9	1.1	0	1.7	1.3
	Aug	-	0	1.0	0.6	0.6	-	1.4	0	1.4	1.3	0	1.7
	Sep	0.7	0	0	1.1	0.7	0	-	1.4	1.0	0.9	0	1.2
	Oct	-	0.8	1.0	-	0	-	-	-	1.5	1.3	0.2	1.2
	Nov	0	0.6	0.5	0.2	-	0	0.5	1.0	0	1.6	0.6	1.4
	Dec	1.0	1.0	0.5	1.3	1.7	0	1.7	2.1	1.9	1.9	1.7	2.3
	1976	Jan	1.1	1.1	0.8	0	1.0	1.5	1.5	2.0	2.4	2.0	1.7
Feb	1.3	0	0.9	1.4	1.6	1.0	1.5	1.8	1.9	1.6	2.2	1.3	
Mar	1.4	0.6	0.7	1.1	2.0	0.6	1.5	2.2	1.6	1.1	1.8	2.1	
Apr	1.3	0	0.6	1.1	0.7	0.7	1.6	1.7	0	1.7	1.8	1.9	
May	-	0	1.5	0.6	0.6	-	1.3	0	1.1	1.3	0.7	1.1	
Jun	0.6	1.3	-	0.6	1.0	0	-	1.0	0.6	0.7	0.7	0	
Jul	-	1.1	-	1.1	0.6	-	0	0.6	1.7	0.7	1.0	0.6	
Aug	-	0.6	-	0.6	0.7	-	0	0.3	0.9	0.4	1.1	1.4	
Sep	-	0	-	-	1.3	0	1.1	0	0	0.5	0	1.5	
Oct	0	0.6	0	0.8	0.6	0.6	1.1	1.3	1.0	1.5	1.5	1.3	
Nov	0	1.5	0.7	-	1.2	0.6	0.6	-	1.0	1.0	0.6	1.3	
Dec	0.7	1.0	0.1	1.5	1.3	-	1.0	2.1	2.0	2.2	2.1	1.7	
1977	Jan	1.2	0.8	0.8	1.6	1.1	-	1.2	2.1	2.2	1.8	1.6	2.1

		Wooded and Bushed Grassland						Bushland							
		4B	4C	5D	5E	5F	6A	6B	6C	1A	1C	1D	2A	2D	3F
1975	Feb	1.9	0.6	2.0	1.2	0.9	1.5	2.0	0.2	0.2	1.3	1.7	1.4	1.7	2.1
	Mar	1.9	0.7	1.3	2.1	0.6	2.2	2.1	2.4	2.0	2.1	2.1	2.0	1.7	2.1
	Apr	1.4	1.8	1.8	1.4	0	1.3	1.9	2.2	1.6	2.1	1.4	2.3	1.9	1.7
	May	1.3	1.9	0	1.5	1.0	1.7	0.6	2.1	2.5	2.0	1.7	1.3	1.8	2.1
	Jun	1.3	1.8	1.3	1.5	1.3	1.3	0.6	0.7	2.0	1.4	1.3	1.4	0	1.4
	Jul	1.7	1.0	-	1.4	0.7	1.7	0.8	1.3	1.4	0.6	1.0	0.8	2.1	1.0
	Aug	0.6	1.1	0.7	0	1.4	-	1.5	1.1	2.0	1.4	1.0	1.3	0.7	1.9
	Sep	1.3	1.1	0.7	0	0	1.6	2.5	0.6	1.3	1.3	0.7	1.6	1.6	0.7
	Oct	1.3	1.9	1.3	2.0	0	0.6	1.7	0.8	0.7	1.0	1.6	1.5	1.0	1.3
	Nov	1.5	1.9	1.1	-	0.7	1.7	2.3	1.5	1.7	1.7	1.9	1.8	1.9	1.7
	Dec	2.0	1.7	0.7	2.1	1.3	2.2	1.8	2.7	2.4	1.6	2.1	1.8	2.4	2.6
	1976	Jan	2.3	1.2	1.5	1.8	0.7	2.9	2.5	1.9	1.3	2.5	2.0	0.6	2.1
Feb	1.9	2.2	-	1.5	2.1	1.9	2.1	1.9	1.7	2.3	2.2	0	1.8	1.3	
Mar	0.4	1.8	2.1	2.3	1.0	2.0	2.0	1.8	1.7	2.5	1.3	1.1	1.5	1.3	
Apr	1.1	2.1	0	1.8	0	2.2	2.2	2.0	2.1	1.1	1.3	0.6	1.8	0.7	
May	-	1.7	0	1.3	0	1.3	1.8	2.0	1.3	1.0	0.7	1.4	0.8	1.7	
Jun	0.6	0.9	-	1.8	1.1	1.9	2.1	1.8	1.7	1.3	0.6	0	0.6	0.6	
Jul	2.1	1.7	0	2.3	0.6	1.4	2.0	2.0	2.4	1.0	1.0	1.0	1.6	0.7	
Aug	-	1.6	0	1.4	0.7	0	0.8	1.2	0.9	0.7	0	1.1	1.1	0.5	
Sep	0.5	0	1.1	0	-	0.6	1.4	1.3	0	1.1	1.4	0	1.7	1.1	
Oct	1.4	0	1.5	2.0	-	1.8	1.8	2.0	1.1	1.0	1.3	1.7	1.4	2.0	
Nov	1.8	1.2	0	1.7	0.7	2.4	1.8	2.2	1.3	1.3	1.1	1.8	2.0	1.0	
Dec	1.8	2.2	1.7	1.8	1.5	2.5	2.4	1.1	2.3	1.1	1.8	0.7	1.8	0.3	
1977	Jan	2.5	2.3	1.0	1.8	2.0	2.0	1.4	2.0	2.0	2.3	2.2	1.8	2.0	1.9

		Wooded Bushland					Woodland			Riverine				
		1B	2B	2C	3C	3D	A	B	C	A	B	C	D	E
1975	Feb	2.3	2.5	0.1	1.7	0.7	2.6	2.9	2.3	1.4	2.0	3.0	2.5	N.C.
	Mar	2.2	2.1	1.4	2.8	0.7	2.9	2.7	2.7	2.0	0.7	2.6	2.4	1.7
	Apr	1.8	2.5	2.8	2.2	2.6	2.8	2.4	3.3	2.7	2.4	2.8	2.4	2.3
	May	0	2.6	0	0	1.8	2.7	2.3	2.5	1.9	1.9	3.2	2.3	1.3
	Jun	1.8	1.4	0.9	1.8	1.8	2.7	1.7	2.5	1.6	1.7	2.3	0.7	1.9
	Jul	1.5	2.0	1.6	1.3	0.8	1.5	2.3	2.8	1.4	1.6	2.1	2.6	0.8
	Aug	0.9	1.5	1.8	-	0.7	2.8	2.7	2.0	1.7	2.0	2.4	0.7	1.5
	Sep	1.7	1.6	1.1	0	1.6	2.4	2.4	2.2	2.1	1.5	1.8	0.7	0.7
	Oct	1.6	1.2	1.1	1.6	1.6	2.7	2.8	2.8	1.7	1.3	1.8	2.3	0.5
	Nov	1.0	2.4	2.0	1.8	1.9	2.6	2.8	3.1	1.7	1.3	2.2	2.1	2.0
	Dec	2.7	2.8	2.6	2.2	3.0	2.9	2.5	2.9	2.2	2.4	3.0	2.1	2.4
	1976	Jan	2.4	1.8	2.2	2.4	1.6	2.2	2.7	3.2	1.7	1.8	0.4	1.6

		Wooded Bushland					Woodland			Riverine				
		1B	2B	2C	3C	3D	A	B	C	A	B	C	D	E
1976	Feb	2.1	0.6	2.2	2.0	0.5	1.6	2.3	1.9	2.1	1.0	2.0	2.1	2.0
	Mar	2.1	1.4	1.2	2.4	2.2	2.6	2.8	2.5	1.9	2.3	2.0	1.8	1.6
	Apr	1.1	2.1	1.3	2.1	2.7	2.5	2.4	3.0	1.5	0.6	2.5	2.1	2.1
	May	1.7	1.3	1.4	0.7	2.2	2.1	1.9	2.0	1.6	2.3	1.3	2.1	2.0
	Jun	1.4	1.0	0.7	1.7	1.5	1.6	2.2	2.2	1.6	1.3	1.6	1.5	2.2
	Jul	2.0	1.9	1.0	0.7	0	2.5	2.5	1.0	1.1	1.8	2.0	1.8	1.2
	Aug	0	2.1	0.7	1.3	0.5	2.2	2.7	2.3	1.9	1.4	2.4	1.7	1.5
	Sep	0.7	0	1.0	1.6	1.1	2.8	2.1	2.8	2.1	1.9	1.4	1.5	1.5
	Oct	0.8	2.3	2.3	0	1.7	1.5	2.1	2.2	1.3	2.2	1.8	2.0	2.1
	Nov	1.3	2.5	2.3	1.8	2.2	2.0	2.4	2.0	2.3	2.1	2.3	1.9	2.2
	Dec	2.5	2.9	2.4	2.2	2.5	1.9	2.6	2.7	2.2	2.2	2.8	1.4	2.4
1977	Jan	1.7	2.3	1.7	2.0	2.0	2.5	3.0	2.2	1.7	2.2	N.C.	1.5	2.7

Appendix 4.6 The evenness of the distribution of numbers (as a percentage) over the species on each census plot in each month. The figures are of the evenness of the distribution calculated as in ch. 6.4.1. Conventions of zero, dashes and figures in brackets as in Appendix 4.5.

		Grassland					Bushed Grassland						
		3B	5B	5C	5G	6D	6E	3A	3E	4A	4D	4E	5A
1975	Feb	100	71	79	89	89	100	89	80	63	29	40	65
	Mar	94	N.C.	93	94	79	100	86	100	90	84	66	78
	Apr	100	76	88	92	92	0	89	79	76	67	94	88
	May	79	89	86	88	100	100	94	89	97	76	94	100
	Jun	0	100	50	-	100	0	92	0	-	75	0	93
	Jul	-	89	100	89	100	-	100	95	86	0	83	93
	Aug	-	0	94	89	89	-	100	0	84	93	0	94
	Sep	100	0	0	100	100	0	-	88	81	87	0	79
	Oct	-	75	94	-	0	-	-	-	92	93	33	79
	Nov	0	56	67	50	-	0	67	94	0	92	88	63
	Dec	89	94	83	93	81	0	80	87	84	74	84	69
1976	Jan	63	76	73	0	41	78	68	61	69	60	59	95
	Feb	67	0	87	97	68	94	48	87	72	80	86	93
	Mar	73	89	90	95	78	89	86	83	83	95	91	79
	Apr	93	0	89	100	100	100	100	91	0	93	91	93
	May	-	0	88	100	89	-	93	0	95	72	90	76
	Jun	89	90	-	89	94	0	-	94	89	100	100	0
	Jul	-	100	-	100	89	-	0	89	89	100	81	89
	Aug	-	89	-	89	100	-	0	50	73	60	100	84
	Sep	-	0	-	0	88	0	100	0	0	71	0	89
	Oct	0	89	0	77	89	75	100	93	94	82	88	88
	Nov	0	95	100	-	80	89	89	-	94	94	75	93
Dec	100	71	50	72	88	-	94	78	78	74	88	61	
1977	Jan	79	62	77	100	100	-	80	76	71	91	74	51

		Wooded and Bushed Grassland					Bushland								
		4B	4C	5D	5E	5F	6A	6B	6C	1A	1C	1D	2A	2D	3F
1975	Feb	79	29	63	41	73	76	58	50	50	43	72	100	79	89
	Mar	71	64	93	93	50	80	90	68	79	77	87	90	72	82
	Apr	80	54	100	69	0	46	93	94	85	87	48	86	75	94
	May	85	84	0	92	81	88	75	85	91	90	91	93	91	87
	Jun	93	91	96	95	93	93	89	100	92	58	85	100	0	75
	Jul	66	67	-	100	100	89	67	88	79	88	95	67	85	94
	Aug	89	53	100	0	100	-	88	100	92	84	94	93	64	82
	Sep	85	73	100	0	0	95	83	75	40	88	100	95	76	100
	Oct	93	95	93	92	0	75	85	77	100	82	88	91	81	85
	Nov	92	80	95	-	100	81	94	86	91	73	93	86	93	94
	Dec	65	37	100	77	69	67	91	83	82	63	81	79	83	87
1976	Jan	72	48	95	46	100	75	66	67	44	58	67	89	93	96
	Feb	81	59	-	86	89	44	85	87	89	87	67	0	86	93
	Mar	50	75	95	92	94	46	52	49	91	70	88	100	89	93
	Apr	100	79	0	86	0	83	36	96	88	62	88	44	91	100
	May	-	84	0	93	0	93	51	72	93	94	100	97	67	88
	Jun	89	73	-	80	68	82	84	87	77	88	89	0	89	89
	Jul	88	93	0	74	89	84	94	82	93	94	95	94	82	100
	Aug	-	88	0	72	100	0	73	86	53	100	0	95	71	83
	Sep	83	100	95	0	-	89	88	78	0	95	97	-	89	95
	Oct	100	0	92	94	-	98	59	94	100	94	88	94	79	94
	Nov	80	80	0	88	100	100	100	90	67	88	95	91	88	64
Dec	86	79	91	71	86	85	90	71	90	50	91	100	87	25	
1977	Jan	84	79	50	86	92	92	57	89	88	65	68	57	73	68

		Wooded Bushland				Woodland			Riverine					
		1B	2B	2C	3C	3D	A	B	C	A	B	C	D	E
1975	Feb	90	68	30	94	40	82	79	83	57	87	78	91	N.C.
	Mar	86	80	62	93	100	70	76	85	95	30	82	63	71
	Apr	77	74	88	94	82	100	81	89	92	61	71	89	62
	May	0	90	0	0	75	68	85	89	60	96	73	93	88
	Jun	84	100	87	87	71	76	80	70	85	94	94	100	93
	Jul	88	83	83	93	75	95	70	74	84	97	58	89	75
	Aug	71	89	91	-	100	85	80	60	64	69	78	44	83
	Sep	88	59	100	0	79	83	81	69	88	68	86	100	90
	Oct	83	80	95	92	59	90	67	89	68	85	82	86	83
	Nov	94	96	87	81	84	84	81	86	89	88	89	80	84
	Dec	94	81	92	61	89	71	85	74	84	92	74	71	92
1976	Jan	74	91	76	55	55	84	54	83	50	51	20	53	63
	Feb	90	89	87	88	29	40	84	89	81	50	57	88	81
	Mar	92	78	80	72	86	73	85	89	84	81	83	64	61
	Apr	95	93	93	82	84	87	88	85	41	25	82	93	85
	May	91	88	100	100	71	90	72	92	85	87	93	87	92
	Jun	97	81	100	91	88	88	89	87	76	93	78	88	82
	Jul	92	80	94	100	0	87	91	94	68	81	94	91	88
	Aug	0	87	100	93	83	74	85	89	63	59	91	94	72
	Sep	90	0	94	92	95	80	79	91	87	85	75	76	82
	Oct	67	86	96	0	94	95	63	68	93	76	87	89	76
	Nov	93	87	90	100	90	80	91	87	90	95	67	81	70
Dec	85	84	85	89	64	46	69	89	91	82	76	76	91	
1977	Jan	61	44	42	68	55	89	84	84	89	100	N.C.	88	94

Appendix 4.7 The number of species in each habitat: the number of species on large plots (sum of small plots)

The figures in part a are the total number of species seen each month on the equivalent of a 28.3 ha plot. This is five plots in each of the Park savanna habitats, all three Woodland plots combined (a total of 27 ha). The figure for Riverine is for the 16 ha total.

The figures in part b are the total recorded on all plots in the four habitats where the total area exceeds 28.3 ha.

The plots left out in calculating the figures in part a were chosen at random and were: for Grassland 5E, Bushed Grassland 4E, Wooded and Bushed Grassland 5C, 5E and 6B, and for Bushland 2D.

a) The equivalent of 28.3 ha plots								b) All plots combined			
Habitat								Habitat			
	G	BG	WBG	B	WB	W	R	G	BG	WBG	B
1975 Feb	12	23	28	25	34	37	38	15	31	37	30
Mar	9	21	31	28	24	37	38	9	25	36	31
Apr	14	23	28	26	34	42	48	16	24	35	28
May	12	13	21	25	24	32	48	14	16	23	27
Jun	9	10	15	16	20	27	22	9	10	17	16
Jul	4	13	16	12	21	29	27	5	17	18	17
Aug	5	15	8	17	10	34	29	5	15	10	20
Sep	5	11	9	17	17	27	21	6	11	19	22
Oct	5	10	15	12	18	43	23	5	12	19	13
Nov	5	14	17	23	22	42	30	7	14	26	26
Dec	10	24	39	30	43	42	43	11	24	43	36
1976 Jan	16	30	41	32	40	44	44	16	30	49	33
Feb	13	24	34	20	31	25	34	14	28	37	22
Mar	13	22	27	24	27	33	26	14	25	34	25
Apr	6	17	27	17	33	33	38	7	20	40	21
May	8	12	16	10	17	19	25	9	14	25	12
Jun	7	6	18	10	16	18	24	8	7	22	10
Jul	4	10	23	16	15	25	24	4	10	27	18
Aug	3	8	15	9	14	26	26	4	10	18	12
Sep	6	8	11	10	9	32	26	7	8	14	13
Oct	7	12	18	16	21	20	30	9	13	23	16
Nov	11	17	21	16	27	21	36	11	7	23	20
Dec	6	24	27	22	42	36	36	10	26	35	25
1977 Jan	10	29	26	32	38	34	26	13	33	33	34
Average	8.3	16.1	22.1	19.4	24.9	31.6	31.8	9.5	17.9	27.6	22.0

Appendix 4.8 The evenness of the distribution of numbers over the species: the evenness on large plots. Conventions and explanation as in Appendix 4.7.

		a) The equivalent of 28.3 ha plots					b) All plots combined					
		G	BG	WBG	B	WB	W	R	G	BG	WBG	B
1975	Feb	80	32	28	28	26	82	73	78	29	20	27
	Mar	73	71	65	67	76	77	26	77	68	66	65
	Apr	68	69	54	65	74	76	66	68	69	54	66
	May	90	85	84	71	63	76	79	74	83	78	71
	Jun	33	80	78	58	79	76	69	33	71	77	79
	Jul	88	72	64	88	80	70	77	82	69	67	82
	Aug	78	75	64	74	87	75	50	72	79	75	60
	Sep	91	68	85	45	76	80	84	71	64	79	46
	Oct	67	72	78	73	65	73	80	67	38	68	68
	Nov	53	70	78	74	75	82	68	72	76	74	70
	Dec	72	60	43	75	78	78	79	73	61	45	72
	Jan	48	68	48	67	46	59	28	48	68	46	67
1976	Feb	76	63	60	83	28	50	55	77	65	62	82
	Mar	73	79	55	72	77	81	78	76	79	50	21
	Apr	76	76	81	46	78	79	25	74	78	43	48
	May	89	75	72	73	78	69	84	87	74	55	59
	Jun	91	87	80	76	87	81	82	90	87	81	68
	Jul	80	84	82	81	84	75	79	100	88	80	69
	Aug	95	80	84	53	64	72	71	100	75	68	56
	Sep	66	61	80	63	74	75	67	65	64	78	62
	Oct	71	72	80	68	77	72	82	78	77	68	68
	Nov	89	91	75	64	81	88	60	89	81	75	63
	Dec	56	67	64	42	71	51	69	52	67	76	41
	Jan	59	73	74	48	39	79	64	57	75	74	49
Average		73	72	69	65	69	74	66	73	70	65	63

Appendix 4.9 The species diversity in each habitat: the species diversity on large plots
Conventions and explanation as in Appendix 4.7

a) The equivalent of 28.3 ha plots								b) All plots combined			
Habitat								Habitat			
	G	BG	WBG	B	WB	W	R	G	BG	WBG	B
1975 Feb	2.3	1.1	0.5	0.6	0.4	3.4	3.3	2.5	1.3	0.7	0.7
Mar	1.9	2.6	3.0	2.9	2.9	3.3	2.1	1.9	2.7	3.1	3.0
Apr	2.2	2.7	2.6	2.8	3.1	3.5	3.4	2.3	2.8	2.8	2.9
May	2.2	2.4	2.8	2.9	2.6	3.2	3.6	2.3	2.6	2.8	2.9
Jun	0.6	2.1	2.5	2.5	2.7	2.9	2.7	0.6	2.0	2.5	2.5
Jul	1.3	2.1	2.3	2.3	2.8	3.0	3.0	1.5	2.5	2.5	2.6
Aug	1.4	2.4	1.6	2.5	2.2	3.2	2.7	1.4	2.4	2.0	2.6
Sep	1.5	1.9	2.0	1.9	2.4	3.0	2.9	1.6	1.9	2.7	2.2
Oct	1.1	2.1	2.5	2.0	2.3	3.4	2.9	1.1	1.1	2.6	2.0
Nov	0.9	2.2	2.6	2.8	2.8	3.5	3.0	1.3	2.2	2.9	2.9
Dec	1.9	2.7	2.9	3.1	3.5	3.4	3.5	2.0	2.7	3.1	3.2
1976 Jan	1.7	2.8	2.5	3.0	2.8	3.3	0.8	1.7	2.8	2.7	3.0
Feb	2.1	2.5	2.8	2.7	1.4	2.7	2.7	2.2	2.7	3.0	2.8
Mar	2.3	2.8	2.7	2.8	2.9	3.2	2.9	2.4	3.0	2.8	2.9
Apr	1.6	2.6	3.1	1.9	3.2	3.2	1.3	1.7	2.7	3.0	2.3
May	2.0	2.1	2.5	2.0	2.5	2.6	3.0	2.0	2.3	2.6	2.0
Jun	1.8	1.6	2.6	2.0	2.6	2.6	2.9	2.0	1.7	2.8	1.9
Jul	1.2	2.2	2.9	2.6	2.5	3.0	2.9	1.4	2.2	3.0	2.5
Aug	1.1	1.8	2.5	1.5	2.3	2.9	2.9	1.4	2.0	2.5	1.9
Sep	1.4	1.5	2.1	1.8	2.0	3.1	2.9	1.6	1.5	2.3	2.1
Oct	1.6	2.2	2.7	2.4	2.8	2.6	3.2	1.9	2.2	2.7	2.4
Nov	2.3	1.8	2.8	2.4	3.1	2.9	3.1	2.3	1.7	2.9	2.5
Dec	1.0	2.5	2.9	1.9	3.3	2.8	3.1	1.4	2.6	3.2	2.0
1977 Jan	1.7	2.9	2.9	2.6	2.5	3.3	2.9	1.9	3.0	3.1	2.7
Average	1.6	2.2	2.5	2.3	2.6	3.1	2.8	1.8	2.3	2.7	2.4

