AN ANALYSIS OF THE AVIFAUNA OF THE SOUTHERN KALAHARI GEMSBOK NATIONAL PARK

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INTRODUCTION

Most of the published work on the birds of the Kalahari Gemsbok National Park has been based on more or less incidental observations over relatively short periods of a few days at a time, and takes the form of species lists with, in some cases, only a very general attempt at relating the birds to specific habitats (Broekhuysen *et al.* 1968; de Villiers 1958; Labuschagne 1959; Macleod and Morris 1966; Prozesky and Haagner 1962). Similar, but rather more comprehensive works have appeared on the birds of areas adjacent to the Gemsbok Park (Hoesch 1955; Hoesch and Niethammer 1940; Maclean 1960, 1965; Smithers 1959, 1964).

The present paper is the result of a 19-month study in the Gemsbok Park from early October, 1964, to the end of April, 1966. The topography, geology and vegetation of the region have already been described (Leistner 1959a, b; Labuschagne 1959; Louw 1964; Maclean 1967, 1968, 1969; Smit 1964).

STUDY AREA AND METHODS

The study area consisted of the Nossob River from Twee Rivieren to a point 25 miles (40 km) upstream and the adjacent strip of country in Botswana along the east bank of the river; the Auob River from Twee Rivieren to Houmoed, ten miles north, the adjacent dune areas along the west bank and the dune triangle formed by the Auob and Nossob Rivers from their confluence to a line drawn from Houmoed to Leeudril; and an area of dunes on either side of the Nossob River within a three-mile radius of Twee Rivieren. These localities appear in Fig. 1.

All three of these parts of the study area were covered approximately twice weekly, the Auob and Nossob sections by Land Rover and the area around Twee Rivieren on foot. On each field trip complete counts of every bird seen were made; these counts were accurate for all but the most abundant species for which estimates were made. The number of field trips per month for all three parts of the study area varied from seven to 25, except for December, 1965 (five trips), and April, 1966 (two trips). The results from these two months have been disregarded in the analyses as being inadequate; instead mean figures for the preceding and succeeding months have been used. No counts are available for September, 1965, when I was absent from the Gemsbok Park and the mean between the August and October, 1965, counts has been used instead.

Usually the same route was followed in each of the three parts of the study area on each field trip, but the duration of each trip varied according to whatever other work was being done at the time. The incidental nature of these counts must be stressed; they were secondary

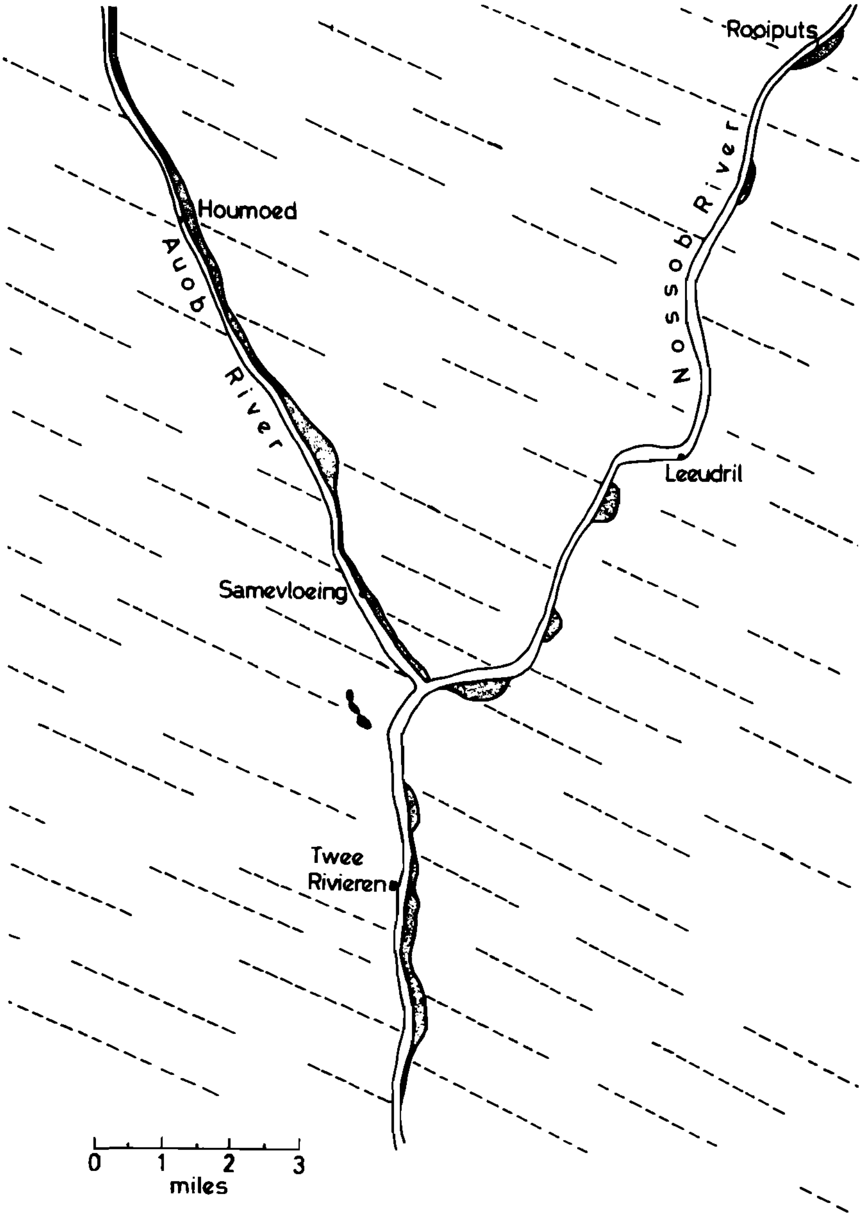


FIGURE 1
Map of the study area in the southern Gemsbok Park. The diagonal broken lines indicate the extent and direction of the sand dunes; the shaded areas on the east banks of the two rivers are exposed calcrete flats.

to all other projects in the study area, but were nevertheless meticulously made. Only the birds seen on the outward journey were counted, unless the return journey was by a different route. Furthermore, no birds were counted during long stops *en route* (for purposes of mist-netting, nest examination, etc.), unless they were species not hitherto included on the list for that trip. Further than this, I make no claim for standardised counts. Although Yapp (1956) has shown the need for standardisation in line transects, it was not possible under the conditions of the present study, but it would be over-cautious to disregard the figures completely for this reason.

The figures for all three parts of the study area have been pooled in the following analysis. Two criticisms are valid in this connection. Firstly, it may be considered a questionable practice to pool primary results made from a motor vehicle over 25 miles on the one hand with those made on foot over only five miles on the other. However, since I am dealing with trends and not with absolute numerical values, this should not be so important. In order to show that the trends in population fluctuations are similar, regardless of the method employed, I have chosen three species of birds at random—one resident (*Serinus flaviventris*), one breeding migrant (*Oenanthe pileata*) and one nomad (*Eremopterix verticalis*)—and, by the methods described below, analysed their populations in the Nossob River (counts made from a motor vehicle) and at Twee Rivieren (counts made on foot). The results appear in Figs. 2–4, which show that the trends in both regions are broadly similar.

I may add here that no serious discrepancy in trends is likely in an area like the Kalahari where visibility is good in nearly all habitats, and where vehicle speed did not exceed 25 m.p.h. and was usually very much less because of the rough terrain.

The second criticism is that the analyses which follow cut across a number of different ecological areas within the study area. This is true. This paper is not, however, an ecological study. It is an analysis of the population fluctuations of the birds of the whole study area and not of individual parts of it. The ecological requirements of most of the birds were fairly clear when viewed subjectively, but the complexity of the sub-habitats within what is otherwise a rather uniform piece of sandveld makes a much closer study than I was able to do, imperative. The size of the study area was also too great to subject it to a systematic ecological study in the limited time at my disposal. For this reason, too, it was impossible to make an accurate count of all the individuals of any one species in the area for comparison with the transect counts. This would be desirable, but in view of the fact that the analyses show similar trends in different areas using different sampling methods, it is not absolutely necessary.

The avifauna in the study area can be divided into five categories on the basis of their occurrence (Table 1). The resident birds form the largest category in terms of species numbers. Each category is dealt with separately in the following analysis.

The numerical data from the field counts were treated as follows:

The daily field counts for each month were summed to give a monthly total for each species (= M);

The total number of field trips per month = F;

The number of species per category of occurrence per month = S;

An "abundance index" (= A) for each species was derived from the formula $A = \frac{\Sigma M}{16}$,

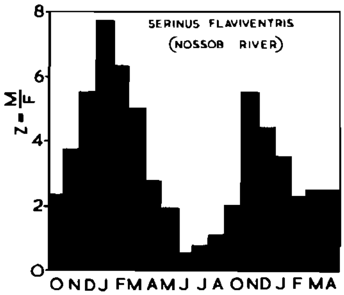


Fig. 2(a)

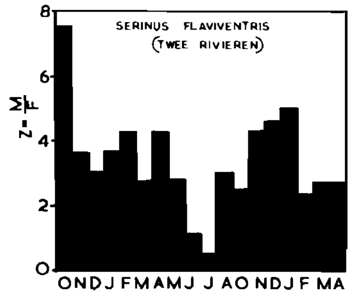


Fig. 2(b)

FIGURE 2

Monthly populations of *Serinus flaviventris* (a resident species) determined by counts (*a*) from a motor vehicle in the Nossob River and (*b*) on foot in the dunes around Twee Rivieren. Both (*a*) and (*b*) show similar high densities in summer and low densities in midwinter (June and July). There is also a similar drop in population in the second February. For an explanation of the derivation of "Z" (the monthly index), see text. The month of September 1965 has been omitted from Figs. 2, 3 and 4 for lack of data.

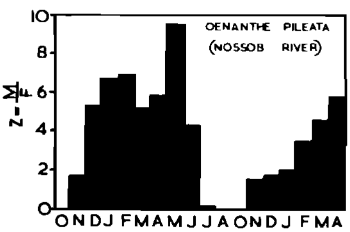


Fig. 3(a)

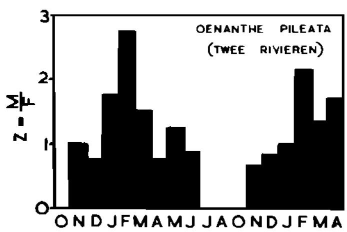


Fig. 3(b)

FIGURE 3

Monthly populations of *Oenanthe pileata* (a breeding migrant) determined by counts (*a*) from a motor vehicle in the Nossob River and (*b*) on foot in the dunes around Twee Rivieren. The similarity in trends between (*a*) and (*b*) is obvious.

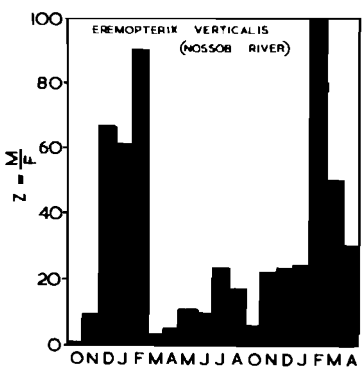


Fig. 4(a)

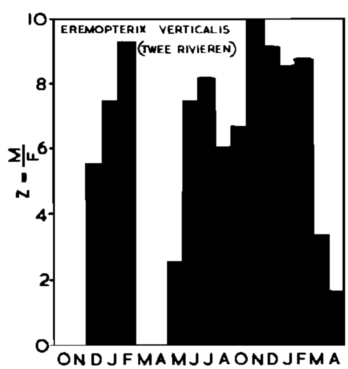


Fig. 4(b)

FIGURE 4

Monthly populations of *Eremopterix verticalis* (a nomadic species) determined by counts (*a*) from a motor vehicle in the Nossob River and (*b*) on foot in the dunes around Twee Rivieren. In both (*a*) and (*b*) it is possible to see an increase in population in December 1964, a decrease in the following March and April, an increase to a peak in July, a decrease again in August-October and peaks again in the following November and February followed by a final decrease in March and April. Differences in the proportions of increase and decrease in the populations of the two regions may be ascribed to habitat differences and possibly also differences in the rainfall.

where the figure 16 is the number of months in the study period excluding September and December, 1965, and April, 1966;

A "monthly index" (= Z) for each category of occurrence was derived from the formula $Z_x = \frac{\Sigma M_x}{S_x F}$, where x is the category concerned (values of Z could, of course, also be derived for a single species or for the whole avifauna each month).

A number of resident species has been omitted entirely from the numerical analyses because of different sampling methods (*Pterocles namaqua* and *P. burchelli*), difficulty of estimating numbers with reasonable accuracy (*Streptopelia capicola* and *Philetairus socius*, both abundant residents), or because they occur in small numbers at all times only around human habitations, so that counts would be biased too highly in their favour (*Hirundo fuligula* and *Passer domesticus*).

RAINFALL DURING THE STUDY PERIOD

Daily weather data were obtainable at Twee Rivieren. The mean annual rainfall at Twee Rivieren from 1960 to 1966 was 226·0 mm, with the main peaks in February and April, preceded by a smaller peak in November (Fig. 5). There were three rainy seasons during the study period—a small one in December, 1964, and larger ones in April, 1965, and late January, 1966 (Fig. 6). These three rainy seasons illustrate the general trend of rainfall in the south-western Kalahari. Fig. 5 shows that rainfall is to some extent sporadic, but largely a summer occurrence.

AVIFAUNAL ANALYSES

The entire avifauna of 148 species in the study area was divided into five categories of abundance according to the value of A for each species (Table 2).

1. *Resident species*

Apart from the six exceptions already mentioned, the resident species of birds are listed in Table 3, along with their abundance indices. *Pterocles namaqua*, *P. burchelli*, *Streptopelia capicola* and *Philetairus socius* would certainly fall into the "abundant" category with values of A well over 100. The position of *Passer domesticus* is difficult to assess. It is a common species around all human habitations, but these are so widely scattered that the species may not have an A value of more than 6 or 7 (= "fairly common"). *P. domesticus* is very seldom seen out in the veld and is at such times more than likely in transit from one settlement to another.

Although *Hirundo fuligula* could be seen every day at Twee Rivieren, it was hardly ever recorded anywhere else. The largest number seen near Twee Rivieren in one day was three, but usually only a mated pair was present. If this is the only pair, or even one of two or three pairs, in the Gemsbok Park, it must be considered "very rare" with an A value of much less than 1·00.

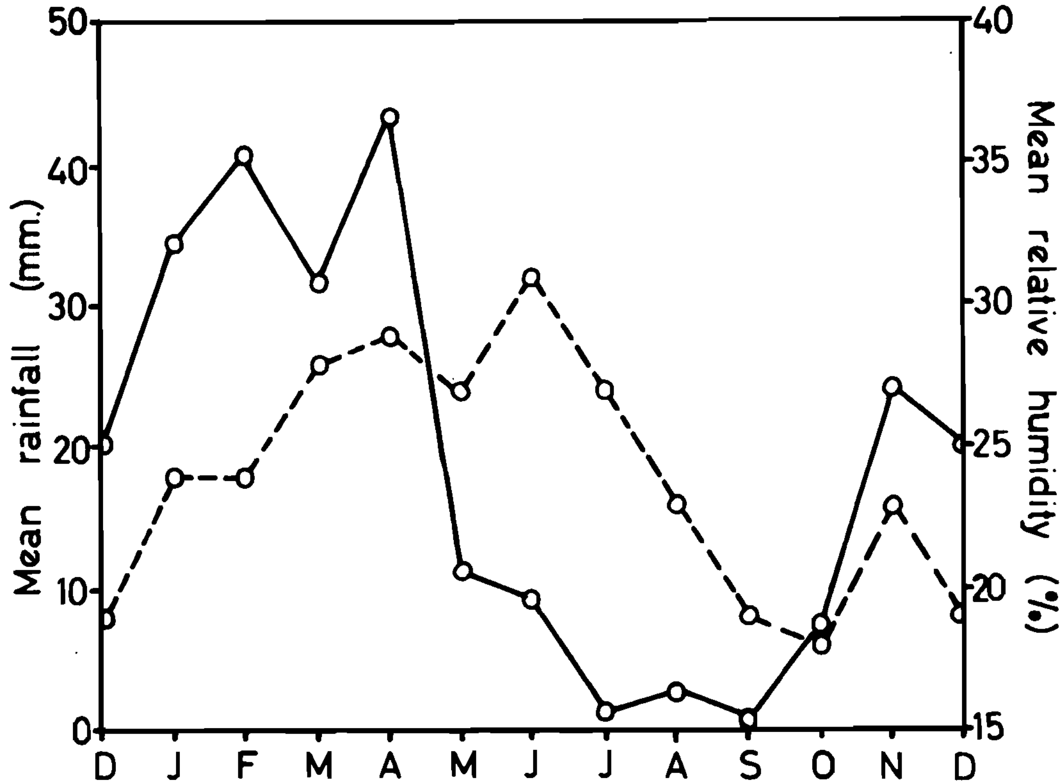


FIGURE 5
Graph showing the mean monthly rainfall (solid line) and mean monthly relative humidity (broken line) at Twee Rivieren from September 1960 to February 1966.

Incorporating these six species into Table 3 would give a final result of five abundant species (7·9%), three very common (4·8%), 21 common (33·3%), ten fairly common (16·0%), 13 uncommon (20·6%), six rare (9·5%) and five very rare (7·9%). There is little doubt about the status of any of these species except perhaps *Sporopipes squamifrons* which is to some extent nomadic. There are also considerable population fluctuations of *Rhinoptilus africanus*, although breeding birds are present throughout the year (Maclean 1967).

The reasons for the rarity (A = <4·00) of as many as 38·0% of the resident species are varied. Most of these species are on the periphery of their ranges and are more characteristic of *Acacia* savanna than of the open Kalahari sandveld that comprises most of the study area. Savanna occurs marginally in the extreme north-eastern part of the study area as far south as Rooiputs, the southern limit of most of these species. It is, therefore, not surprising to find five species of hole-nesting birds in this group (*Coracias caudata*, *Upupa africana*, *Rhinopomastus cyanomelas*, *Tockus flavirostris* and *Dendropicos fuscescens*), as well as a number of larger raptors, whose nesting habits require larger trees.

The status of *Falco biarmicus* is not clear. There appear to be no breeding records of this species for the Park, although immature Lanners are a common sight, especially in midsummer. I have assumed, therefore, that it is a resident breeding species. Other species classed as "resident" occur in the study area only after good rains (e.g. *Torgos tracheliotus* and *Streptopelia senegalensis*) and have not been recorded breeding there, but they do breed just beyond the northern limits of the study area and are regarded as resident and not occasional, since few, if any, of the occasional species breed anywhere in the Gemsbok Park.

Finally, the rarity of certain species is undoubtedly more a reflection of their secretive habits than of actual scarcity (e.g. *Burhinus capensis*, *Mirafra apiata*, *Laniarius atrococcineus*, *Malaconotus zeylonus* and *Nilaus afer*). All of these species have loud and characteristic songs by which, more often than not, they betray their presence and are recorded at all.

Although populations of resident species fluctuated, they did so within narrow limits ($Z = 0 \cdot 79$ to $2 \cdot 11$) as shown in Fig. 7. The population decrease to March, 1965, was due to increasingly dry conditions accompanied by intense heat before the rains. After the March-April, 1965, rains there was a slight increase, possibly the result of immigration. The population build-up to a peak in November, 1965, is almost certainly the result of continuous breeding activity throughout the winter as a consequence of the March-April rains (Maclean in preparation). The subsequent fall-off was the result of dispersal as the population levelled off towards the mean value of $Z = 1 \cdot 20$.

2. *Occasional species*

The occasional species with their A values appear in Table 4. Only one species, *Apus barbatus*, falls into the "abundant" category. It occurred only in summer and only after rain. Its status is open to question, since it may better be classed as a non-breeding migrant. However, if its identification is correct (and I am going on the inclusion of this species in Prozesky and Haagner's check list (1962) which presupposes that it is not *Apus apus*, a non-breeding migrant from the Palaearctic) then it must breed in neighbouring regions where there are suitable cliffs. It cannot, therefore, be classed strictly as a non-breeding migrant even though it definitely does not breed in the Gemsbok Park.

Another species of doubtful status is *Corvus capensis*. It may breed in the more northerly parts of the Park and may, therefore, better be considered a resident, but it is certainly only occasional in the study area. The breeding status of *Falco tinnunculus* is uncertain; it is considered occasional in the absence of further information.

Excluding the three species just mentioned, the remaining 47 occasional species are rare or very rare and none has been found breeding in the Park. I have, however, seen immatures of *Elanus caeruleus* on one or two occasions, even as far south as Twee Rivieren, but until their origin has been established it is convenient to class *E. caeruleus* as occasional. Further breeding information is needed for the migratory *Merops apiaster*, *Cecropis cucullata*, *Petrochelidon spilodera* (which has been found breeding in South West Africa (Clancey 1966)), *Acrocephalus baeticatus*, *Hirundo albigularis* and *H. dimidiata*, all of which are almost certainly only birds of passage in the Kalahari sandveld.

Seventeen of the occasional species are "water birds" and are usually found only after rain. This accounts for the high Z values for occasional species in April, 1965, and March,

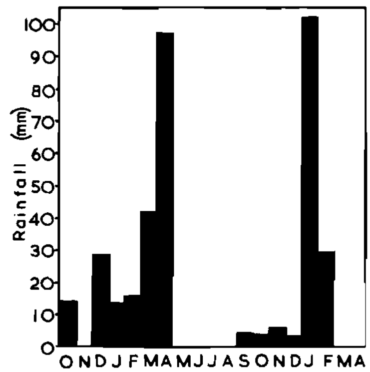


Fig. 6

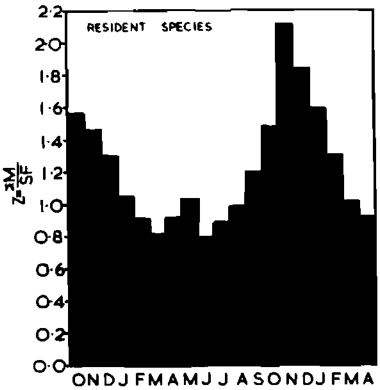


Fig. 7

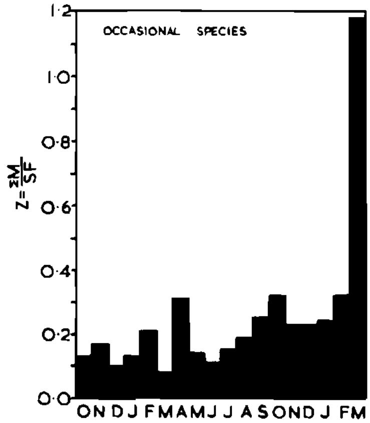


Fig. 8

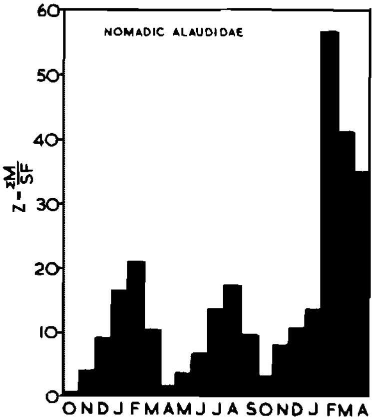


Fig. 9

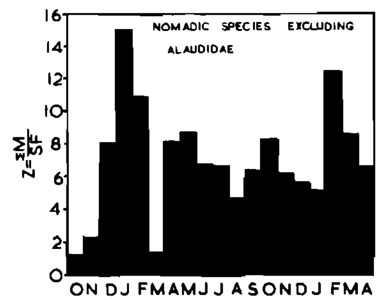


Fig. 10

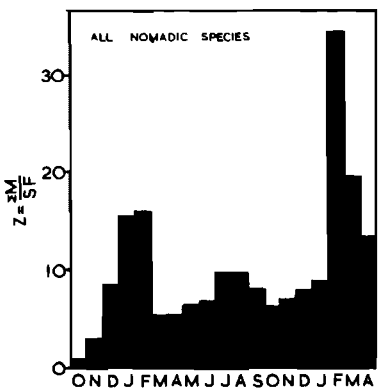


Fig. 11

FIGURES 6 TO 11

Fig. 6. The rainfall during the study period (October 1964 to April 1966).

Figs. 7 to 11. Monthly populations in the study area throughout the study period of: Fig. 7—resident birds, Fig. 8—occasional birds, Fig. 9—nomadic larks (Alaudidae), Fig. 10—nomadic birds other than larks, Fig. 11—all nomadic birds. (For an explanation of the formula $Z = \frac{\Sigma M}{SF}$, see text.)

1966 (Fig. 8). There are no breeding water birds in the south-western Kalahari sandveld. That the occurrence of most of the water birds in the study area was accidental was clearly shown by their weakness and poor nutritional state. Some individuals of *Phalacrocorax africanus*, *Ixobrychus minutus*, *Porphyrio porphyrio* and *Calidris minuta* died shortly after they were discovered near Twee Rivieren. Another *Ixobrychus minutus* was caught by hand and ringed, even though it seemed outwardly in good condition.

Most of the remaining species in the "occasional" category are incidental wanderers from the very edge of their ranges. The sandveld is notably poor in frugivorous and nectar-feeding birds and the only three species (*Lybius leucomelas*, *Pycnonotus nigricans* and *Nectarinia fusca*) are all occasional usually after rain. All three are rare in the study area.

The number of occasional species in the study area was never more than 13 in any one month and the Z values for this category were usually little more than 0·30, with the sole exception of March, 1966. Even so the March, 1966, value of Z = 1·18 is a comparatively small figure (Fig. 8).

It is possible that a few species included in the occasional list mey yet be found breeding in the Gemsbok Park. A special watch should be kept for *Falco tinnunculus*, *F. chiquera*, *Elanus caeruleus*, *Buteo rufofuscus*, *Circaëtus cinereus*, *Oenanthe monticola*.

3. *Nomadic breeding species*

The nomadic breeding species and their A values are listed in Table 5. The ecology and breeding biology of the nomadic larks have already been treated in some detail (Maclean 1969). These larks most clearly illustrate the effect of rain upon the movements of nomadic birds in the Kalahari sandveld (compare Fig. 6 with Fig. 9). The situation is rather less clearly shown in the case of the remaining nomads, but similar trends are evident (Fig. 10). A combination of the data for all the nomads (Fig. 11) still shows the three population peaks following the three main rainy seasons. The effect of midsummer rains, however poor, is more marked than late summer rains, but the better the summer rain, the greater the influx of nomadic species.

Table 5 shows that most nomadic species have high A values, despite the fact that certain species may be entirely absent from the region for months at a time. This reflects the dramatic increase in numbers when conditions are suitable. Sometimes many thousands of nomads move into an area from one day to the next and they may disappear just as suddenly, although the reduction in population at the end of a good season is usually not as rapid as the initial increase.

The status of the last two species in Table 5 is not well defined. *Cursorius rufus* usually occurs in small non-breeding groups of four to ten birds, but is included in the nomadic category on the basis of a single breeding record in August, 1965. I have never found *Coturnix coturnix* breeding in the sandveld, but the presence of males in full song after the rains leads me to believe that the species may breed in the long grass of the dunes where it is usually to be found.

4. *Migratory breeding species*

Oenanthe pileata is the only common breeding migrant in the study area (Table 6). The other four species are rare to very rare and are more commonly found in the *Acacia* savanna to the north.

It seems not to be generally recognised that *Oenanthe pileata* is migratory. McLachlan and Liversidge (1957) state that it is a "common resident except in the south-eastern coastal areas where it is uncommon during the colder months." I first recorded *O. pileata* in the Gemsbok Park on 19 November, 1964, in the first summer and on 1 November, 1965, in the second summer. The last recorded date of occurrence at the end of the first season was 9 July, 1965, but I left the region before the end of the second season and so have no last date. The species was, therefore, absent from the study area for just under four months; it arrived at least a month later than most migrants and departed at least two months later than most. It appears that *O. pileata* may be migratory over more of its range than is at present recognised, although it probably does not move very far north in winter.

Since the number of cuckoos and nightjars in the study area was so low, the population fluctuations in Fig. 12 apply mainly to *O. pileata*, although all the breeding migrants have been included in the histogram. I have no idea why populations in the first summer should have been so much higher than in the second, but it might have had something to do with conditions in neighbouring areas, for which I have no information. It may, therefore, be a reflection of the very local nature of rains in theKalahari.

5. *Non-breeding migratory species*

Table 7 lists the non-breeding migrants in the study area, along with their A values. Most of the species are very rare, having been recorded only once or twice during the study period. Six of them are water birds and, as with the occasional water birds in Table 4, were usually seen only after rain. Except for *Milvus migrans migrans*, *Lanius collurio*, *L. minor*, *Oriolus oriolus*, *Hieraaëtus pennatus* and perhaps the two species of *Circus*, most of the migrants were birds of passage. This is shown by the early and late summer peaks (Fig. 13) when the birds were passing southwards and northwards respectively, although the picture is somewhat obscured by the influx of some migrants after rain.

Milvus migrans migrans was especially affected by rainfall and moved into the study area in large flocks of up to 20 birds after a good fall. Where the birds came from was not determined.

The rarity of *Oriolus oriolus*, *Lanius minor* and *Hieraaëtus pennatus* is attributable to the paucity of trees south of Rooiputs. These birds were more plentiful in the northern part of the Park in the *Acacia* savanna.

My single record of *Oenanthe oenanthe* near Rooiputs on 29 October, 1965, is the first for the Gemsbok Park and probably constitutes the most southerly record for the species. Described as a "very rare migrant" by McLachlan and Liversidge (1957), this species was found in South West Africa in 1963 and a specimen collected (von Maltzahn 1964).

Table 8 lists first and last dates on which some of the better documented non-breeding migrants were sighted. The earliest date for any Palaearctic migrant was 1 October (*Tringa glareola*) and the latest date was 16 April (*Lanius minor*).

Fig. 12

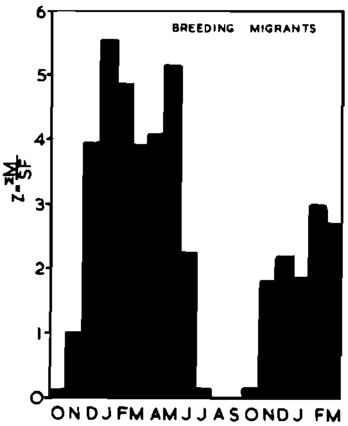


Fig. 13

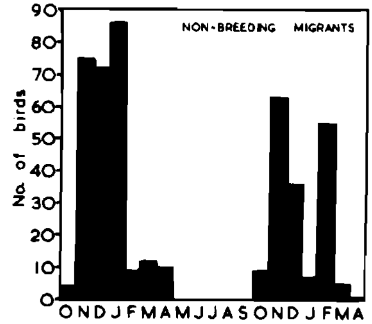


Fig. 14

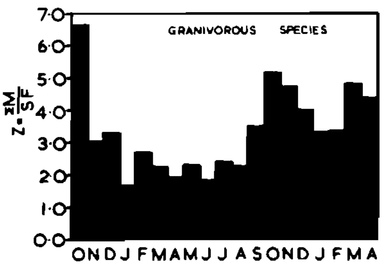


Fig. 15

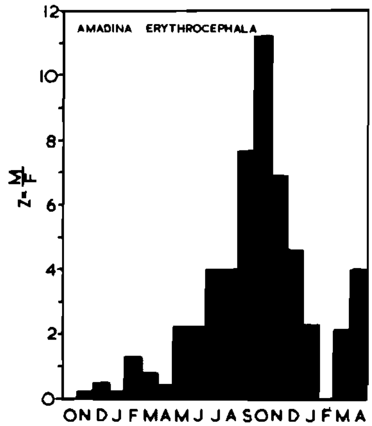


Fig. 16

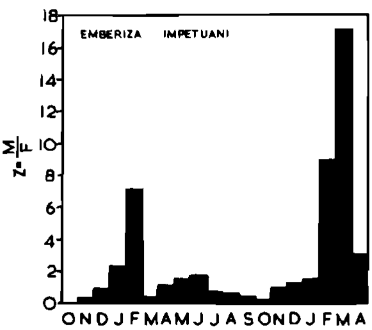
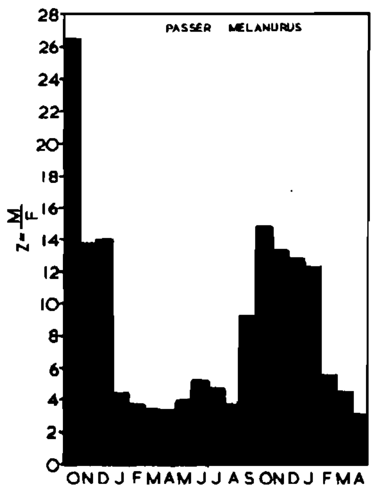


Fig. 17



FIGURES 12 TO 17

Monthly populations in the study area throughout the study period of: Fig. 12—breeding migrant birds, Fig. 13—non-breeding migrant birds (actual counts), Fig. 14—granivorous passerine birds Fig. 15—*Amadina erythrocephala*, an exclusively granivorous nomadic passerine, Fig. 16—*Emberiza impetuani*, an exclusively granivorous nomadic passerine, Fig. 17—*Passer melanurus*, a facultatively granivorous resident passerine. (For an explanation of the formula $Z = \frac{\Sigma M}{SF}$, see text.)

6. *Granivorous and insectivorous Passeriformes compared*

Ecologically one of the most important components of the passerine avifauna of the open sandveld is constituted by the three granivorous families Ploceidae, Estrildidae and Fringillidae. The omission of *Passer domesticus* and *Philetairus socius* from the analysis of this group probably makes little difference to the general picture since they are both so sedentary. Of the remaining 11 species (Table 9) six are resident and two nomadic; most of them are fairly common to abundant. *Vidua regia*, although resident, is on the periphery of its range in the Gemsbok Park and is uncommon. The remaining three species are too rare to make any impression upon a population analysis of the group.

Comparing Fig. 14 with Fig. 6, there seems to be a tendency towards an inverse population : rainfall ratio, albeit sometimes slight. This may seem curious, but the causes of this phenomenon are twofold.

Firstly, rain results both in pools of water scattered along the river beds and in the rapid appearance of food in the form of flowers (such as *Rhigozum trichotomum*) in the dunes resulting in a more widely scattered and less free-water-dependent seedeater population and, therefore, in smaller counts per field trip. Secondly, since the adults are at least partly dependent upon seeds in their diet, the influx of seedeaters might be expected to be delayed with respect to other species immediately after a rain, until just before the flowering plants have set seed. Hence, no doubt, the population increases in February, 1965 (after the December, 1964, rains), in October, 1965 (after the previous winter's flowering season initiated by the March-April, 1965, rains), and in March, 1966 (after the January, 1966, rains), as shown in Fig. 14. The October, 1965, increase would further have been augmented by the birds' reproductive activities of the previous winter (Maclean in preparation).

A separate examination of population fluctuations in two nomadic granivorous species, *Amadina erythrocephala* and *Emberiza impetuani*, and two resident granivorous species, *Passer melanurus* and *Serinus flaviventris* (Figs. 15-18), makes for an interesting series of comparisons. The histograms of the two nomadic species show to some extent the same three population peaks as do the nomadic larks (Fig. 9), but, especially in the case of *Amadina erythocephala*, the peaks of the granivorous species are somewhat delayed relative to those of the larks, with respect to rainfall. This is almost certainly a reflection of the fact that the exclusively granivorous species rely largely on seeds for feeding their young, while the larks rely mainly on insects (Maclean 1969). Insects appear to be most abundant very soon after rain, while seeds are set usually towards the end of a good season following rain.

Populations of the two resident granivorous birds (Figs. 17–18) show much less fluctuation than those of the nomads, but numbers of *Passer melanurus* and *Serinus flaviventris* are greatest in the summer months and both show an increase in October and November. This may be due to augmentation by a somewhat migratory or nomadic element that leaves the area in winter. However, there may be another contributory factor. A similar November population increase occurs in the resident insectivorous species (Figs. 19-22), even though the fluctuations in numbers within this group are generally rather small. It is, therefore, possible that the increase is due to the appearance of young birds resulting from the winter breeding season, at least in the second summer of the study period.

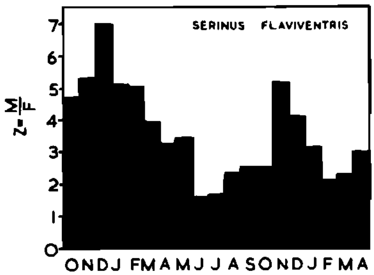


Fig. 18

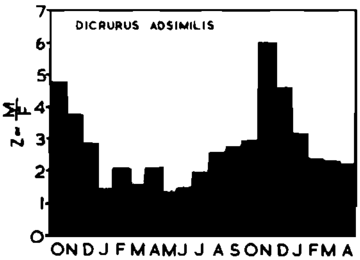


Fig. 19

Fig. 20

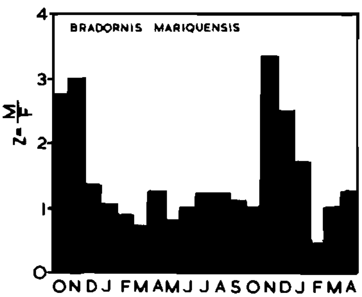


Fig. 21

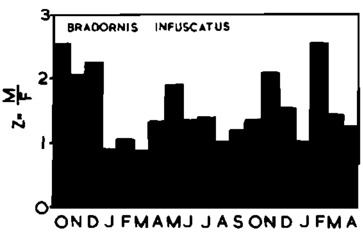


Fig. 22

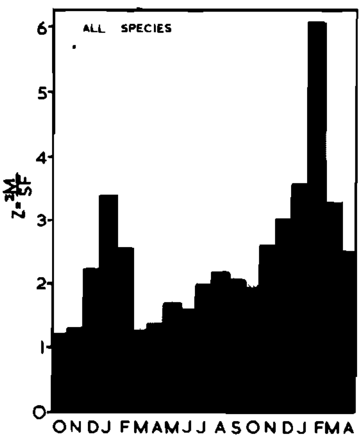


Fig. 23

FIGURES 18 TO 23

Monthly populations in the study area throughout the study period of: Fig. 18—*Serinus flaviventris*, an exclusively granivorous resident passerine, Fig. 19—*Dicrurus adsimilis*, an insectivorous resident passerine, Fig. 20—*Myrmecocichla formicivora*, an insectivorous resident passerine, Fig. 21—*Bradornis mariquensis*, an insectivorous resident passerine, Fig. 22—*Bradornis infuscatus*, an insectivorous resident passerine, Fig. 23—all bird species. (For an explanation of the formula $Z = \frac{\Sigma M}{SF}$, see text).

One more aspect emerges from a comparison of Figs. 9, 15 and 16 on the one hand with Figs. 17-22 on the other. Generally speaking, as the nomadic populations increase, so the resident populations decrease and *vice versa*. If this points to some sort of competition between the two categories of birds, then we have an interesting problem worth detailed investigation. When all the data for nomads are pooled (Fig. 11) and compared with the pooled data for residents (Fig. 7), the inverse ratio between the two categories emerges with even greater clarity. Indeed, if Fig. 7 is turned upside down and the wrong way round and superimposed on Fig. 11 (its approximate reciprocal) the trends are almost identical in the two histograms. The competition is most likely for food since many nomadic species feed their young on insects, as do most of the residents (Maclean in preparation).

Finally it may be mentioned that only two of the 11 nomadic species in the study area (*Cisticola juncidis* and *Creatophora cinerea*) are entirely insectivorous. The rest are all partly or predominantly granivorous. This reflects again the constancy of insect and other invertebrate food in the Kalahari sandveld as I have already suggested (Maclean 1967).

7. *Overall picture for all species in the study area*

Fig. 23 shows the population fluctuations of the entire avifauna of the study area. The overall result seems to indicate something like this: From a rather low population density in the early summer of 1964, an increase in bird numbers occurred, reaching a peak in January, 1965, mainly as a consequence of incoming migrants and nomads brought into the area by the December rains. As conditions worsened because of increasing drought toward the middle of March, bird numbers fell off again. After good rains from the middle of March to the middle of April, nomads moved into the area once more and most birds began to breed (Maclean in preparation), so that numbers climbed steadily through the winter. With the onset of warmer weather in October, 1965, and aided by the moisture still remaining in the soil because of the low evaporation rates in the cold months, the vegetation began to show some regeneration (especially the summer grasses). This was accompanied by a steady, but slow, influx of nomads again (Fig. 11) and also a few migrants on their way south.

Torrential rains fell on 17 and 18 January, 1966, followed by several smaller showers up to 4 February. The effect on the birdlife was dramatic. Populations of nomadic and occasional species (Figs. 8–11) reached particularly high peaks in February, 1966. However, the hot midsummer sun soon diminished the effects of the rain and by the end of April many nomads had disappeared, breeding was at an end and the young had largely dispersed.

DISCUSSION

Since each section has been largely discussed already and the whole avifaunal picture succinctly outlined in section 7 above, it remains only to deal with the shortcomings from which a population analysis of this sort suffers. The sampling methods are necessarily in the form of transects, so that counts will be biased to some extent in favour of larger and more conspicuous bird species, especially when done from a moving motor vehicle. This is unavoidable, but, since it is only with the *trends* that this study is concerned, it is a small fault. At times of high population density even the most cryptic skulker becomes difficult to overlook.

A more positive error arises in the method of determining the value of Z using the number of field trips as a correction factor, because the nature of the field trips was variable. Nossob trips extended for 25 miles in a motor vehicle and lasted up to more than eight hours; they also included some *Acacia* savanna not found on the other trips. Dune counts by contrast extended over little more than four or five miles, were done on foot, and lasted for as little as two hours. It was possible, therefore, to count *Dicrurus adsimilis* on Nossob trips only and *Eremomela icteropygialis* on dune trips only, while a count in the Auob-Nossob dune triangle might include *Lophotis ruficrista*, which was seldom seen elsewhere. On the other hand, *Passer melanurus* was usually common on all field trips. Once again, however, the trends are not affected, although sparrows may appear excessively common and warblers excessively rare. As long as this is borne in mind, the figures derived from the field counts retain their usefulness in the assessment of population fluctuations and structure.

The principal drawback of this study is the severely limited knowledge of the ecology of the birds concerned. On analysis it is possible to see *what* is happening in the avifauna, but very difficult and, in most cases, impossible to say *why* it is happening. Rainfall clearly exercises a tremendous influence on the birds of the Kalahari, but how directly or indirectly it does so can only be guessed at. Do nomadic species enter an area immediately after rain because they have seen (or otherwise sensed) that rain has fallen there, or do they move about more or less randomly, happen upon these areas and remain in them as long as good conditions last? How does the presence of nomadic species affect the resident species? To what extent are the so-called "resident" species nomadic or even migratory? That the numbers of resident birds are at times augmented by birds other than the products of their own breeding activities seems beyond doubt. Where do these other birds come from?

There are indications in at least one nomadic lark (*Eremopterix verticalis*) that more than one subspecies may breed in the same area at different times (Maclean 1970). It is, therefore, possible that many of the nomads must move over vast areas. How regular are these movements and how are they determined?

These are only a few of the more immediate questions posed by this study, but because of the necessarily casual attention paid to most species and the comparatively short study period of 19 months, these questions must for the most part remain unanswered until further elucidation of the ecology of the Kalahari sandveld. It is most important that ecological conditions of areas adjacent to a study area also be known in order fully to understand why some species may be more abundant in a seemingly poor season than in a seemingly better one, as in the case of *Oenanthe pileata* for example.

This study also shows that the more field trips done per month the more reliable the information obtained. Seven was the minimal number of monthly counts that gave reasonable data, but 12 is a safer minimum. This would mean one count a week in each of the three sections of the study area (or three counts a week if only a single transect were involved). In an area of such erratic climatic conditions as the Kalahari it is also desirable to conduct an avifauna survey over a period of as many years as possible and not just a year and a half as in the present case.

SUMMARY

The avifauna of a study area in the southern Kalahari Gemsbok National Park was studied over a period of 19 months. The 148 species of birds in the area were divided into five categories of occurrence (resident, nomadic, breeding migrant, non-breeding migrant and occasional) and seven categories of abundance (abundant, very common, common, fairly common, uncommon, rare and very rare) each with a numerical value, the "abundance index". Populations of most species were affected directly or indirectly by rainfall; resident populations and nomadic populations showed an inverse ratio, indicating some competition.

Most nomadic species are granivorous as adults, but those that feed their young predominantly on insects increased in numbers sooner after rain than those feeding their young mainly on seeds. Insectivorous passerines are less affected by rainfall and include only two nomadic species, reflecting a relatively constant insect food supply.

ZUSAMMENFASSUNG

Nach 19-monatiger Untersuchung wurde das Vogelleben des südlichen Kalahari Gemsbok National Parkes analysiert. Die 148 Arten wurden in fünf Kategorien des Vorkommens (Stand-, Nomaden-, brütende Zug-, nichtbrütende Zugvögel und gelegentliche Vögel) und sieben Kategorien der Häufigkeit (reichlich, sehr häufig, häufig, ziemlich häufig, ungewöhnlich, selten und sehr selten) verteilt. Populationen wurden meist durch Regenfall beeinflußt. Populationen von Standvögeln und Nomadenvögeln zeigten ein umgekehrtes Verhältnis, zweifellos als Folge eines Wettbewerbes.

Die meisten Nomadenvögel sind Samenfresser. Diejenigen aber, die ihre Jungen hauptsächlich mit Insekten füttern, zeigten nach Regen eine frühere Populationszunahme als diejenigen, deren Jungen auch Samen fressen. Populationen insektenfressender Passeriformes wurden weniger vom Regen beeinflußt, und es sind unter ihnen nur zwei nomadische Arten, was auf einen relativ stetigen Insektenvorrat hinweist.

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See Tables on following pages

TABLE 1

NUMBER OF BIRD SPECIES WITHIN EACH CATEGORY OF OCCURRENCE IN THE STUDY AREA

Category	*Number of species*
Resident	63
Occasional	50
Breeding nomadic	11
Breeding migrant	5
Non-breeding migrant	19
Total	148

TABLE 2

CATEGORIES OF ABUNDANCE OF BIRDS IN THE STUDY AREA, WITH THEIR "ABUNDANCE INDICES" (= A)

Category of abundance	A
Abundant	$>100 \cdot 00$
Very common	$50 \cdot 00 - 100 \cdot 00$
Common	$10 \cdot 00 - 50 \cdot 00$
Fairly common	$4 \cdot 00 - 10 \cdot 00$
Uncommon	$2 \cdot 00 - 4 \cdot 00$
Rare	$1 \cdot 00 - 2 \cdot 00$
Very rare	$<1 \cdot 00$

TABLE 3

THE RESIDENT BIRDS OF THE STUDY AREA IN ORDER OF ABUNDANCE, WITH THEIR ABUNDANCE INDICES (= A) AND CATEGORIES OF ABUNDANCE

Species	*A*	*Category of abundance*
Passer melanurus	132·00	Abundant
Sporopipes squamifrons	69·19	Very common
Serinus flaviventris	60·31	„ „
Certhilauda albofasciata	51·38	„ „
Struthio camelus	44·31	Common
Vanellus coronatus	44·00	„
Dicrurus adsimilis	40·19	„
Lamprotornis nitens	37·88	„
Myrmecocichla formicivora	34·44	„
Rhinoptilus africanus	31·31	„
Bradornis infuscatus	25·19	„
Polihierax semitorquatus	22·63	„
Bradornis mariquensis	22·06	„
Mirafra africanoides	21·81	„
Meliërax musicus	18·06	„
Afrotis afra	16·38	„
Lanius collaris	15·56	„
Malcorus pectoralis	15·00	„
Passer diffusus	15·00	„
Cercomela familiaris	14·50	„
Ardeotis kori	12·81	„
Sagittarius serpentarius	12·81	„
Prinia flavicans	11·25	„
Gyps africanus	11·13	„
Erythropygia paena	10·31	„
Aquila rapax	7·94	Fairly common
Parisoma subcaeruleum	7·19	„ „
Merops hirundineus	7·06	„ „
Ploceus velatus	6·69	„ „
Mirafra sabota	5·56	„ „
Parus afer	4·63	„ „
Circaëtus pectoralis	4·56	„ „
Bubo lacteus	4·56	„ „
Falco rupicoloides	4·00	„ „

continued on next page

Table 3 continued

Species	*A*	*Category of abundance*
Batis pririt	3·81	Uncommon
Laniarius atrococcineus	3·75	,,
Torgos tracheliotus	3·75	,,
Nilaus afer	3·25	,,
Micronisus gabar	3·06	,,
Falco biarmicus	3·00	,,
Vidua regia	3·00	,,
Bubo africanus	2·94	,,
Mirafra apiata	2·88	,,
Coracias caudata	2·88	,,
Eremomela icteropygialis	2·69	,,
Lophotis ruficrista	2·50	,,
Streptopelia senegalensis	2·25	,,
Polemaëtus bellicosus	1·69	Rare
Terathopius ecaudatus	1·56	,,
Upupa africana	1·50	,,
Rhinopomastus cyanomelas	1·50	,,
Malaconotus zeylonus	1·44	,,
Anthoscopus minutus	1·06	,,
Tockus flavirostris	0·94	Very rare
Dendropicos fuscescens	0·75	,, ,,
Tyto alba	0·69	,, ,,
Burhinus capensis	0·44	,, ,,

TABLE 4

THE OCCASIONAL BIRDS OF THE STUDY AREA IN ORDER OF ABUNDANCE, WITH THEIR ABUNDANCE INDICES (= A) AND CATEGORIES OF ABUNDANCE

Species	*A*	*Category of abundance*
Apus barbatus	288·75	Abundant
Corcus capensis	7·56	Fairly Common
Falco tinnunculus	4·06	,, ,,
Euplectes orix	1·88	Rare
Anthus richardi	1·75	,,
Lybius leucomelas	1·50	,,
Neotis ludwigii	1·31	,,
**Alopochen aegyptiacus*	1·06	,,
Nectarinia fusca	0·75	Very rare
Serinus alario	0·69	,, ,,
Pycnonotus nigricans	0·69	,, ,,
Merops apiaster	0·56	,, ,,
Cecropis cucullata	0·50	,, ,,
Falco chiquera	0·50	,, ,,
Cercomela tractrac	0·44	,, ,,
**Vanellus armatus*	0·38	,, ,,
**Actophilornis africanus*	0·38	,, ,,
**Charadrius tricollaris*	0·31	,, ,,
**Ardeola ibis*	0·31	,, ,,
Sylvietta rufescens	0·31	,, ,,
Apus affinis	0·31	,, ,,
**Scopus umbretta*	0·25	,, ,,
**Ardeola ralloides*	0·25	,, ,,
**Ardea melanocephala*	0·19	,, ,,
Buteo rufofuscus	0·19	,, ,,
Circus maurus	0·19	,, ,,
Cursorius temminckii	0·19	,, ,,
Petrochelidon spilodera	0·19	,, ,,
Cisticola aridula	0·19	,, ,,
Calandrella cinerea	0·14	,, ,,
**Phalacrocorax africanus*	0·13	,, ,,
**Ardea cinerea*	0·13	,, ,,
**Ixobrychus minutus*	0·13	,, ,,
Milvus migrans parasitus	0·13	,, ,,

continued on next page

Table 4 continued

Species	*A*	*Category of Abundance*
Circaëtus cinereus	0·13	,, ,,
**Himantopus himantopus*	0·13	,, ,,
Apus caffer	0·13	,, ,,
Oenanthe monticola	0·13	,, ,,
Cercomela schlegelii	0·13	,, ,,
Acrocephalus baeticatus	0·13	,, ,,
**Podiceps ruficollis*	0·06	,, ,,
**Ciconia nigra*	0·06	,, ,,
**Anas erythrorhyncha*	0·06	,, ,,
Elanus caeruleus	0·06	,, ,,
**Porphyrio porphyrio*	0·06	,, ,,
Columba guinea	0·06	,, ,,
Hirundo albigularis	0·06	,, ,,
Hirundo dimidiata	0·06	,, ,,
**Motacilla capensis*	0·06	,, ,,
Quelea quelea	0·06	,, ,,

* = water birds.

TABLE 5

THE NOMADIC BREEDING BIRDS OF THE STUDY AREA IN ORDER OF ABUNDANCE, WITH THEIR ABUNDANCE INDICES (= A) AND CATEGORIES OF ABUNDANCE

Species	A	*Category of Abundance*
Eremopterix verticalis	504·56	Abundant
Oena capensis	373·31	,,
Eremopterix australis	111·50	,,
Creatophora cinerea	97·56	Very common
Spizocorys conirostris	62·06	,, ,,
Alauda starki	41·00	Common
Amadina erythrocephala	37·13	,,
Emberiza impetuani	33·38	,,
Cursorius rufus	4·06	Fairly common
Coturnix coturnix	2·69	Uncommon

TABLE 6

THE MIGRATORY BREEDING BIRDS OF THE STUDY AREA IN ORDER OF ABUNDANCE, WITH THEIR ABUNDANCE INDICES (= A) AND CATEGORIES OF ABUNDANCE

Species	*A*	*Category of abundance*
Oenanthe pileata	41·00	Common
Chrysococcyx caprius	1·14	Rare
Cuculus canoris gularis	0·25	Very rare
Clamator jacobinus	0·06	,, ,,
Caprimulgus rufigena	0·06	,, ,,

TABLE 7

THE NON-BREEDING MIGRATORY BIRDS OF THE STUDY AREA IN ORDER OF ABUNDANCE, WITH THEIR ABUNDANCE INDICES (= A) AND CATEGORIES OF ABUNDANCE

Species	*A*	*Category of abundance*
Hirundo rustica	10·06	Common
Milvus migrans migrans	6·56	Fairly common
Ciconia abdimii	2·13	Uncommon
Lanius collurio	1·31	Rare
**Philomachus pugnax*	1·19	,,
Oriolus oriolus	0·88	Very rare
**Calidris minuta*	0·81	,, ,,
**Tringa glareola*	0·44	,, ,,
Lanius minor	0·38	,, ,,
Circus pygargus	0·38	,, ,,
Muscicapa striata	0·31	,, ,,
Circus macrourus	0·31	,, ,,
**Tringa nebularia*	0·19	,, ,,
Phylloscopus trochilus	0·13	,, ,,
Hieraaëtus pennatus	0·13	,, ,,
**Chlidonias leucoptera*	0·13	,, ,,
**Tringa stagnatilis*	0·06	,, ,,
Ciconia ciconia	0·06	,, ,,
Oenanthe oenanthe	0·06	,, ,,

* = water birds.

TABLE 8

FIRST AND LAST DATES OF SIGHTINGS OF SOME NON-BREEDING MIGRATORY BIRDS IN THE STUDY AREA IN TWO SUCCESSIVE SUMMERS

Species	*Sightings*	*1st summer*	*2nd summer*
Milvus migrans migrans	1st date	3.11.64	18. 1.66
	Last date	16. 2.65	22. 1.66
Circus macrourus	1st date	28.12.64	11.11.65
	Last date	27. 2.65	—
Circus pygargus	1st date	29. 1.65	—
	Last date	11. 2.65	24. 2.66
Philomachus pugnax	1st date	28.11.64	25.10.65
	Last date	30.12.64	—
Calidris minuta	1st date	12.10.64	15.11.65
	Last date	15. 4.65	—
Tringa nebularia	1st date	8.12.64	24. 1.66
	Last date	—	—
Tringa glareola	1st date	—	1.10.65
	Last date	—	24. 1.66
Hirundo rustica	1st date	29.10.64	14.10.65
	Last date	4. 4.65	26. 3.66
Oriolus oriolus	1st date	1.11.64	11.11.65
	Last date	28.12.64	13.12.65

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Table 8 continued

Species	*Sightings*	*1st summer*	*2nd summer*
Muscicapa striata	1st date	—	—
	Last date	25. 3.65	29. 3.66
Phylloscopus trochilus	1st date	18.12.64	—
	Last date	1. 1.65	—
Lanius minor	1st date	29.12.64	—
	Last date	16. 4.65	1. 3.66
Lanius collurio	1st date	30.11.64	22.11.65
	Last date	12. 4.65	5. 2.66

TABLE 9

THE GRANIVOROUS PASSERINE BIRDS (EXCLUDING *Philetairus socius* AND *Passer domesticus*) OF THE STUDY AREA IN ORDER OF ABUNDANCE

Species	*A*	*Category of abundance*	*Category of occurrence*
Passer melanurus	132·00	Abundant	Resident
Sporopipes squamifrons	69·19	Very common	,,
Serinus flaviventris	60·31	,, ,,	,,
Amadina erythrocephala	37·13	Common	Nomadic
Emberiza impetuani	33·38	,,	,,
Passer diffusus	15·00	,,	Resident
Ploceus velatus	6·69	Fairly common	,,
Vidua regia	3·00	Uncommon	,,
Euplectes orix	1·89	Rare	Occasional
Serinus alario	0·69	Very rare	,,
Quelea quelea	0·06	,, ,,	,,