A STUDY OF THE ECOLOGY, BEHAVIOUR AND SYSTEMATICS OF *TOCKUS* HORNBILLS

by

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TOCKUS FLAVIROSTRIS male

Photo: W. Massyn.

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SECTION 1. INTRODUCTION.

During the last decade, ecology and behaviour have become of major importance in African ornithology. Not only have more individual species been studied in detail, but behaviour and ecology have been used in a more general sense in regional works (Benson et al 1971) and in zoogeographical treatises (Moreau 1966, Hall and Moreau 1970). As part of a world-wide trend, behaviour and ecology have also become important in systematics and taxonomy eg. Hall's 1963 study of francolin, and Benson et al's 1971 erection of the bush shrike family Malaconotidae. This dissertation fits into this trend, beginning with a detailed study of the ecology and behaviour of three species of hornbill of the genus Tockus, and extending the observations in less detail to five other members of the genus. Combined with the literature, these observations allow an analysis of the systematics and evolution of the genus Tockus to be undertaken, as well as supplying descriptive information on Tockus biology.

Bucerotidae, the family of hornbills, is one of the most discrete families of the order Coraciiformes, and is usually placed as most closely related to the hoopoes (Upupidae, Phoeniculidae). Hornbills have an Ethiopian and Oriental distribution, and in the latest revision fo the family (Sanft 1960) were divided into 45 species. 23 species in ten genera occur in the Oriental region, and 22 species in five genera in the Ethiopian region. The genus Tockus is the largest genus, with 14 species, and the only hornbill genus occurring in both zoogeographical areas, although the majority of species (12) are Ethiopian.

In all hornbills the plumage is coloured brown, grey or black, with areas of white, and in most species there is no sexual dimorphism of plumage colour. The bill, eyes and naked skin around the eyes and on the throat are usually brightly coloured, in black, red, blue, orange or yellow, and often these soft -part colours are sexually dimorphic.

In all species the bill formation is sexually dimorphic, males having the bill surmounted by a much larger casque than females, but the degree of dimorphism varies and is least in *Tockus* and *Bucorvus* species. In all species, females are mensurally about 5% smaller than males.

Eleven of the 14 genera of hornbills are frugivorous. The other three genera are mainly insectivorous, including the monotypic *Tropicranus* of the African lowland forests, the two species of *Bucorvus* of the African savannas, and the 12 African species of the genus *Tockus* which occur in forest, woodland and savanna. The two species of *Tockus* in the forests and woodlands of India and Ceylon are mainly frugivorous. The only hornbills that are not confined to forests are the two *Bucorvus* species and ten of the *Tockus* species. Most hornbills are large birds, and the genus *Tockus* is the main exception. The largest hornbills are the turkey-sized *Bucorvus* which weigh~~s~~ 3,5 - 4 Kg, and the smallest are in the genus *Tockus*, which range from the crow-sized *T. birostris* of about 375 g down to the dove-sized *T. camurus* of about 80 g.

Almost all literature on hornbills is either taxonomic, or is concerned with the unique nesting habits of the family which make hornbills the most highly evolved hole nesting-birds (Courtenay-Latimer 1942, Hoesch 1937, Kilham 1956, Moreau 1936, 1937 and 1938, Moreau and Moreau 1941, Ranger 1931). In all but the two *Bucorvus* species, the female seals herself into the nest hole, leaving a narrow vertical slit through which she is fed by the male. The female remains in the hole for all, or the greater part, of the incubation and nestling period. In most species the female is reported to undergo a complete rectrix and remex moult while enclosed. I have discussed some of the advantages and disadvantages of this sealed-in nesting method (Kemp 1971). Ranger (1949-52) is the only worker to have made detailed observations on the behaviour and ecology of a hornbill besides the breeding habits, working on *Tockus alboterminatus* in the eastern Cape Province, South Africa.

The members of the genus *Tockus* are confined to either forest, woodland or savanna. Often four species, and in some areas even five species, may be found living sympatrically, and so are suitable animals for comparative ecological studies. This study of the genus *Tockus* was started with a comparative ecological study of *T. nasutus*, *T. erythrorhynchus* and *T. flavirostris* in the Kruger National Park, South Africa, from November 1966 to April 1969. From February to May 1970 the breeding biology of *T. monteiri* was studied on Valencia Ranch, South West Africa. *T. bradfieldi* was observed during April and October 1971 in the Wankie National Park, Rhodesia, while studying the habitat preferences of the hornbills in that area. Incidental observations were made on three species during travels in Africa, observing *T. alboterminatus* in Rhodesia and South Africa, and *T. deckeni* and *T. hemprichii* in Kenya. For further information, especially on the six species that I have not observed alive, I have drawn on the literature and personal communications. The various study areas are described in detail in the pertinent sections of the thesis.

The order of this dissertation follows that in which the work developed. The non-breeding ecology of *T. nasutus*, *T. erythrorhynchus* and *T. flavirostris* is considered in two parts. In section 2 the habitat preferences of the species in the Kruger National Park are analysed, and compared to observations made in the Wankie National Park. In section 3 the feeding ecology of the species is described. The next three parts (sections 4 - 6) deal with three aspects of the breeding of *Tockus* hornbills and are papers that have already been published, or are in press. Section 4 is a consideration of the sealed-in nesting method of hornbills, section 5 is a study of the breeding biology of *T. monteiri*, and section 6 is an analysis of some of the factors that affect the timing of onset of breeding in four *Tockus* species. Section 7 describes the breeding ecology and biology of the three species studied in the Kruger National Park, and in section 8 the moult of these species is examined, with special emphasis on the moult of the breeding female. Finally, section 9 describes the known behaviour of the members of the genus Tockus, and how it is related to their external morphology. The behaviour, ecology and morphology are used in a discussion of the zoogeography, evolution and systematics of the hornbills of the genus Tockus.

Since each section of the thesis forms an entity, each section has its own introduction and discussion, although where necessary the findings of another section are referred to and the source noted. For convenience while reading the text, all line drawings and photographs (numbered as Figures), all Tables and all Appendices are bound in a separate volume, in the order in which they appear in the text. Tables, figures and references for the published work bound into the thesis (sections 4 and 5) are not included with the rest of the sections.

SECTION 2. HABITAT PREFERENCES OF THREE SPECIES OF HORNBILL IN THE KRUGER NATIONAL PARK, WITH SUPPLEMENTARY EVIDENCE FROM THE WANKIE NATIONAL PARK.

INTRODUCTION.

A preliminary visit to the Kruger National Park in July 1966 indicated that there were three species of hornbill, *Tockus nasutus*, *T. erythrorhynchus* and *T. flavirostris*, coexisting in the same area. They were often seen together especially T. *erythrorhynchus* and *T.flavirostris* which are so similar in plumage that they are only easily separated on bill colour. The comparative ecology of these three species was investigated from November 1966 to April 1969, in the central region of the Kruger National Park. The results found for the habitat preference of each species were then checked for another part of the range of the species, in the Wankie National Park during April and October 1971. These two study areas are marked on Figure 1. The habitat preference study is considered in two parts, with the detailed work from the Kruger National Park subsequently compared to the observations from the Wankie National Park.

A. KRUGER NATIONAL PARK.

STUDY AREA AND METHODS.

The study area and its position in the Kruger National Park are shown in Figure 2, indicating the areas where special projects were done. The study was based at the Satara rest camp ($23^{0}24$'S $31^{0}47$'E), in the flat lowlands (average elevation 300m a.s.l.) just out of the tropics.

The vegetation, geology and drainage systems of the Park have been described in detail (Pienaar 1963, 1966, 1968). The study area, tilted slightly eastwards, is divided by a north-south line of sandstone outcrops in the western third, and bounded on the eastern side by the low hills of the Lebombo range. The area is intricately furrowed by the drainage lines of many seasonal rivers and streams, a few draining to the Timbuvati River on the north and west corner of the study area, but mostly draining to the east to pass through the Lebombo hills at the Nwanedzi gorge. The only permanent water in the area is provided by a few natural waterholes, and by windmills and dams scattered throughout the area. A series of tourist roads and firebreaks provide a network that can be travelled by Land Rover, except in very wet weather.

The sandstone divide also divides the geology into Ecca sandstone on the west side and Stormberg sandstone of the Karroo series on the east side. The soils to the east, also of the Karroo series, are basaltic, dark and heavy. The granitic soils to the west are pale and sandy. On the extreme east, the basalt soils grade into the rhyolite of the Lebombo hills.

The vegetation is dependant on the soil types and four main vegetation associations are found in the study area. On the basalt soils to the east, *Acacia nigrescens* - *Sclerocarya birrea* parkland savanna (Fig. 3) predominates with scattered trees about 15 m high, a stratum of low scattered bushes, and a dense grass cover. *Acacia nigrescens* is the dominant over *Sclerocarya birrea* in the association, other tree species commonly found in the area being *Lannea kirkii*, *Acacia tortilis*, *Combretum imberbe*, *Lonchocarpus capassa*, *Diospyros mesptiliformes* and *Albizzia harveyi*. The main species in the bush stratum are various *Grewia* species, *Dahlbergia melanoxylon*, *Dicrostachys cinereus* and *Commiphora* species, with *Euclea divinorum*, *Acacia exuvialis* and *Terminalia prunnoides* predominating to the north and east of the study area. In these latter regions the parkland gives way to a denser bushy association, dominated by bushes and small trees of *Acacia nigrescens*. The dominant grass cover in this area is *Bothriochloa insculpata*. Along the extreme eastern edge of the area where the Lebombo rhyolite appears, *Combretum apiculatum*, *Acacia tortilis* and *Euphorbia* species become most evident.

To the west of the sandstone reef, the vegetation is mixed Combretum savanna. In the study area, large Acacia nigrescens trees still create a parkland conformation, but there is a predominance of Combretum species, especially Combretum apiculatum, and in some areas these form dense bush associations. Other trees that are most common in the western half of the area are Bolusanthus speciosus, Sclerocarya birrea, Terminalia sericea, Terminalia prunnoides, and Acacia gerradi. The grass cover, of several species, has a density inversely proportional to the density of the bush cover, but the main cover is still of Bothriochloa insculpata in the open areas.

A dense parkland association occurs along the sandstone divide and the banks of the watercourses for some distance further east. The dominant trees are Acacia delagoensis, Spirostachys africanus, Diospyros mesptiliformes and Combretum imberbe. The bush stratum is also dense, mainly Euclea divinorum and Dicrostachys cinereus, but grass cover is sparse.

A fourth vegetation type is found along the watercourses, where there is much underground water. The trees are more evergreen than their strictly decidous counterparts away from the watercourses, and many are over 25 m high. Acacia xanthophloea occurs on the most poorly drained soils, and the commonest trees are Acacia robusta, Diospyros mesptiliformes, Ficus sycomorus, Kigelia pinnata, Pseudocadia zambesiaca and Schotia brachypeltata. The bush stratum is often dense, mainly of Euclea, Grewia, Salix and Maytenus species. The mixed grass cover is high and often dense.

Two seasons characterise the climate of the area. The cool dry season, from May to August, warms up in September and October to the hot wet season with rainfall restricted from October to April. The rainfall and temperature figures for the study period are given in Table 1, where the considerable seasonal variation is notable.

To study the habitat preferences of the hornbill species, a transect road passing through the main habitats was chosen. The road, named Picnic Road, extended 10,6 miles (17,1 km) from the Nsemane windmill to the Timbuvati Picnic Spot (Fig. 2). The main features of the road are shown diagrammatically in Figure 4. The following counts and transects were done along the road:

i. Counts of hornbills.

Marker posts were erected at each tenth of a mile (161 m) along the road, numbered from zero at the south end of the road. The numbers of hornbills of each species seen anywhere within each tenth of a mile were recorded during regular counts. The counts were begun at the south end of the road at two hours (+- 15 minutes) after sunrise, driving north along the road at 10 - 15 miles (16 - 24 km) per hour. A second observer always accompanied the driver. From three to 15 counts were done per month (average 11,4) for 17 months, from November 1967 to March 1969.

ii. Grass cover transects.

Transects were done once every three months for a year; at the end of October 1967, January, April and July 1968. At each tenth of a mile marker post, 50 paces (approximately 50 m) were taken on each side of the road, perpendicular to the line of the road. Along this effectual 100 m transect, the predominant grass cover surrounding the point of the toe at each step was judged to be :

A - non-existent (bare ground),
B - present, but shorter than 10 cm (short grass),
C - present, 10 - 30 cm long (medium grass),
D - present, over 30 cm long (long grass).

iii. Tree and bush transect.

This transect was done from August to October 1968. At each tenth of a mile, a plot 50 m on each side of the road and 100 m long was marked off to the north side of each marker post. Within each plot, effectually one hectare, all plants above long grass level (over 60 cm) were identified, and classed by height as :

A - under 1,5 m (small bushes),
B - 1,5 to 3,5 m (large bushes),
C - 3,5 to 7,0 m (small trees) ,
D - over 7,0 m (large trees).

iv. Herbivorous mammal count.

During each hornbill count, for the 12 months from April 1968 to March 1969, all herbivorous mammals seen within each tenth of a mile were identified, and the numbers of each species counted.

To provide evidence for seasonal movements or changes in number, hornbills were ringed while nesting, and by trapping them at Satara rest camp and Mzanzene picnic spot. Many of the birds were individually marked with coloured leg rings. During the study 18 *T. nasutus*, 205 *T. erythrorhychus* and 203 *T. flavirostris* were ringed.

RESULTS.

The total numbers of hornbills of each species counted within each tenth of a mile during the 17 months of counts (194 counts) are shown in Figure 5. It is clear that *T. nasutus* is less common than either *T. erythrorhynchus* or *T. flavirostris*. Actual numbers recorded are 251 *T. nasutus*, 910 *T. erythrorhynchus* and 936 *T. flavirostris*, giving a ratio of relative abundance of 1: 3,6: 3,7 respectively. However, whereas *T. nasutus* and *T. flavirostris* occur all along the road in varying densities, *T, erythrorhynchus* is restricted to the first 5,0 miles of the road, with only very few scattered sightings elsewhere.

Figure 6 shows the percentage of grass cover of categories A and B recorded at each tenth of a mile transect along Picnic Road. These combined percentages of bare ground and short grass are hereafter referred to collectively as *sparse grass cover*. A high percentage of sparse grass cover is present between 0,5 and 5,0 miles, and on the last 0,2 miles of the road. Another peak of sparse grass cover is present at 7,6 to 9,0 miles in October 1967 and January 1968, but it is mainly composed of short grass cover and not bare ground. Figure 6 demonstrates that the amount of sparse grass cover is not the same throughout the year, the average percentages during the study period being :

October 1967 - end of dry season - 50,6%
January 1968 - mid-wet season - 58,4%
April 1968 - end of wet season - 40,3%
July 1968 - mid-dry season - 55,4%

It is clear that the amount of sparse grass cover is greatest during the dry season, and the October peak of sparse grass cover at 7,6 to 9,0 miles is due to the longer grass categories C and D being reduced to short grass category B. The reduction in grass cover during the dry season may be due to several factors such as grazing, dying back of the leaves, burning and trampling. January 1968 followed burning and poor rains, hence the high figure for the sparse grass cover.

The total numbers of all trees and bushes per hectare at each tenth of a mile are shown in Figure 7, with a graph of a moving point average superimposed. Tree density is above 150/ha in all but the 3,0 to 4,9 mile area, and above 200/ha in all but the 2,3 to 5,1 and 7,4 to 8,6 mile areas. In the 7,4 to 8,6 mile area, the low tree density recorded is due to a lack of trees on a grassy area along only one side of the road. The predominance of the two main vegetation associations in the study area is shown in Figure 8. Thorny species, especially *Acacia nigrescens*, are dominant in all but the 5,0 to 7,0 mile section of the transect road, where *Combretum* and *Terminalia* species dominate. However, the latter vegetation association is much commoner in the last section of the road after 7,0 miles. The dominant plant species along the road, from the absolute numbers recorded for all the transect plots, in descending order of abundance, are *Terminalia sericea*, *Grewia* species, *Combretum apiculatum*, *Acacia nigrescens*, *Dicrostachys* species and *Cassia* species.

Using average weights of each species of herbivorous mammal encountered along Picnic Road (Appendix 1), it was possible to calculate the biomass of mammals recorded per tenth of a mile. The average biomass recorded per tenth of a mile for 153 counts (Fig.9) could then be used as an index of the concentration of mammals important in grazing and trampling in the area. The average biomass per count only exceeds 125 Kg/0,1 miles in the first 5,0 miles of the road. What appears as marked peaks at 1,4 1,5 8,0 and 9,1 miles are due to isolated encounters with herds of such massive herbivores as elephants and buffalo. The main peak, where recorded biomass exceeds 200 Kg/0,1 miles, is from 2,1 to 4,9 miles, in the area surrounding the Ngirivane windmill and the rock waterhole at 4,7 miles (Fig. 4).

STATISTICAL CORRELATIONS.

Knowing the results of individual transects and counts, it is necessary to test whether significant correlations exist between apparently related features, such as predominant sparse grass cover, high herbivore concentrations and large numbers of *T. erythrorhynchus.* Seasonal fluctuations in hornbill numbers were indicated by the counts, and it is also necessary to test that these fluctuations are not merely sampling variation. The following tests were done :

i) A three factor analysis of variance, to test whether hornbill numbers along Picnic Road are affected by the species considered, by the amount of sparse grass cover, and by the seasons during which the counts were done.

ii) One factor analyses of variances were done for each hornbill species separately, to test for relationships between the numbers of the species counted and the amount of sparse grass cover, and between the numbers of the species counted and the seasons in which the counts were done.

iii) Calculation of a correlation coefficient between the amount of sparse grass cover and the recorded biomass of herbivorous mammals.

iv) A one factor analysis of variance to test the relationship between the numbers of T. nasutus (observed to be an arboreal species) and the tree and bush densities.

The hornbill numbers are too few to allow monthly comparison of the figures, or comparisons for individual tenths of a mile. The counts were grouped into three month seasons, for periods that correspond to the main seasons for the area:

Early wet season - November to January,
Late wet season - February to April,
Early dry season - May to July,
Late dry season - August to October.

Since the numbers of counts done per season are not the same, it is necessary to use the average numbers of hornbills recorded per count for each season.

Furthermore, the hornbill numbers compared in each sample were increased by dividing Picnic Road into five grass cover sections. The division of the sections was done using Figure 10, where the sparse grass cover at the end of the dry season (October) and the end of the wet season (April) are plotted. The following divisions of the road were then made (Fig. 4) :

1) 0,0 - 1,6 miles. Where the percentage sparse grass cover is, on average, all below 40% at the end of the wet season, although in parts it may rise up to 57% by the end of the dry season.

2) 1,7 - 5,3 miles. Where the percentage sparse grass cover is above 40% throughout the year.
3) 5,4 - 7,5 miles. Where the percentage sparse grass cover is below 40% throughout the year.
4) 7,6 - 9,0 miles. Where the percentage sparse grass cover is below 40% at the end of the wet season, but rises to above 40% at the end of the dry season.
5) 9,1 - 10,5 miles. Where the percentage sparse grass cover is, on average, below 40% throughout the year.

Since the five sections of the road are of different length, the final figures used are the *average numbers of hornbills per count per tenth of a mile*. The figures are given in Table 2.

Similar figures, for *T. nasutus* only, were calculated with the transect road divided into three sections derived from the tree and bush densities shown in Figure 7. The sections used are:

A) 0,0 - 2,9 miles. Tree and bush density above 150/hectare,
B) 3,0 - 4,9 miles. Tree and bush density below 150/hectare,
C) 5,0 - 10,5 miles. Tree and bush density above 150/hectare.

The figures are given in Table 3.

A three factor analysis of variance was first applied to the figures in Table 2, comparing hornbill species, grass cover sections and seasons. The results with a 95% level of significance are:

i) Effect of species $(F_{2,40} = 18,28;\ P = < 0,001)$
ii) Effect of seasons $(F_{5,40} = 3,17;\ P = 0,05)$
iii) Effect of grass cover sections $(F_{4,40} = 11,09; P = < 0,001)$
iv) Effect of species and grass cover sections $(F_{8,40} = 9,05;\ P = < 0,001)$

The null hypothesis is that none of the effects are significant, and so the four effects found to be significant may be interpreted as follows:

i) The recorded numbers of at least one of the hornbill species differ significantly from the numbers of at least one other species.

ii) The hornbill numbers recorded for at least one season differ significantly from those recorded for at least one other season.

iii) The hornbill numbers recorded for at least one grass cover section differ significantly from the numbers recorded in at least one other section.

iv) The hornbill numbers of at least one species, considered for at least one grass cover section, are significantly different from the numbers of other species and other grass cover sections.

To isolate these effects in more detail was in part possible by using the s-test for judging all contrasts (Scheffé 1959). In this test a probability of 90% is considered significant due to the stringency of the test. To compare the species, the overall means used were : *T. nasutus* 128,4, *T. erythrorhynchus* 313,5 and *T. flavirostris* 440,7. *T. nasutus* numbers were found to be significantly lower than numbers of *T. flavirostris*, but not than *T. erythrorhynchus*. However, if *T. erythrorhynchus* and *T. flavirostris* are considered as a pair, then they differ significantly from *T. nasutus*.

To test the effects of grass cover sections and seasons on the numbers of individual hornbill species, one way analyses of variance were done, using the overall means taken from Table 2. The means used, and the levels of significance obtained, are given in Table 4. The null hypothesis is that the numbers of an individual species counted in each grass cover section and each season do not differ significantly. The significant difference in numbers shown in Table 4 may be interpreted as follows.

T. nasutus and *T. erythrorhynchus* numbers differ significantly for different grass cover sections. The means indicate that *T. nasutus* is most abundant in grass cover sections 1 and 3, and *T. erythrorhynchus* in sections 1 and 2. Only *T. flavirostris* shows a significant seasonal difference in numbers, being most common in the early dry season and least common in the early wet season. Qualitative observations in the study area indicate a decrease in *T. nasutus* numbers during the dry season, as is indicated by the means in Table 4. However, the differences between the means are insignificant (P =0,10 - 0,05) and this may be due to the small numbers of *T. nasutus* encountered, compared to the other two species.

When the percentage sparse grass cover and the recorded biomass of herbivores are compared for each tenth of a mile, using a test of the coefficient of correlation (Hoel 1963), a highly significant correlation exists (r = 0,39; N= 110 ; P = 0,005). This shows that an increase in the biomass of herbivores on an area is correlated with an increase in sparse grass cover.

A one factor analysis of variance applied to the figures in Table 3 shows no significant correlation between *T. nasutus* numbers and the tree and bush sections with different plant densities ($F_{2,15}$ = 1,03 ; P => 0,10). This shows that, with the counts available, there is less than a 90% probability of *T. nasutus* being commoner in one of the three tree and bush sections.

Most ringing, apart from chicks in nests, was done on birds attracted to the rest camps for scraps during the dry season, making trapping of them easy. Colour ringing was discontinued after one dry season, as the impossible colour combinations seen the next year showed that the birds were able to break the rings off. Figure 11 shows the resightings or recoveries of ringed birds. Even with the paucity of results, interesting differences are found between the species. No *T. nasutus* were recovered.

T. erythrorhynchus were only resighted close to the site of ringing, and the greatest recorded distance travelled by a bird was only 7 km. Also many of the returns are specimens collected along the specimen-collection road to the east of Satara (Figure 2). *T. flavirostris* were mostly resighted close to the site of ringing, except for three records: two different specimens seen at the Timbuvati Picnic Spot 22 km away, and one record from Olifants rest camp. The last record, 48 km to the north of the ringing site was reported for *T. erythrorhynchus*, but the observer was doubtful and, knowing the species in that area, I would expect it rather to be *T. flavirostris*. It is also notable that no *T. flavirostris* were shot during the course of specimen collection.

DISCUSSION.

The habitat preferences of each hornbill species in the central region of the Kruger National Park are clear.

T. nasutus, the least common species, occurs throughout the area, in a variety of grass cover types and tree and bush densities. The significantly higher numbers found in grass cover sections 1 and 3 bear no relation to the ecology of the species for it is a tree-living bird. Rather, the high numbers are due to there being active nests of this species in these areas (Fig. 4), making sightings of this uncommon species more likely. This error would not be averaged out by year round counts as *T. nasutus* appears to be less common during the dry, non-breeding season.

T. erythrorhynchus is clearly restricted to areas with a high percentage of sparse grass cover. Sparse grass cover and the high biomass of herbivorous game mammals are highly correlated so that it is impossible at this stage to decide whether it is the many herbivores or the sparse grass cover that is controlling the numbers of *T. erythrorhynchus*; probably both. The species shows no significant seasonal fluctuations in numbers, and appears to have little local movement, as indicated by the ringing results.

T. flavirostris occurs throughout the area with no preference for any particular grass cover or density of trees and bushes. However, it is the one species to show very obvious seasonal fluctuations in number, and it is thought that this may be due to local movements of the species. T. flavirostris appears to have the most extensive local movements as suggested by ringing, and is most common at the beginning of the dry season and least common throughout the wet season. It may be that the species spreads out during the wet season to breed, and at the end of the wet season the population, swelled by the immatures now present, moves to wintering areas of smaller area than the breeding area. I have reports (Ringdahl pers. comm.) of this species coming to farms at the base of the escarpment to the east of the study area, only during the dry season.

B. WANKIE NATIONAL PARK.

STUDY AREAS AND METHODS.

It was decided to check the habitat preference results from the Kruger National Park in a different area where all three hornbill species are found together. This would determine how far the Kruger National Park results could be used to interpret the total African distribution of these hornbills.

Two months of counts were done in the Wankie National Park in April (end of the wet season) and October (end of the dry season) 1971. During these two extremes of the year, counts and transects, designed to be directly comparable to those from the Kruger National Park, were done as follows :

i) Counts of hornbill numbers and herbivorous mammal numbers were done along a transect road as for the Kruger National Park, except that 19,0 miles of road were covered, and the tenths of a mile were taken from a vehicle milometer, not marked with posts.

(ii) Grass cover transects were done as for the Kruger National Park, but only at each 0,5 miles. With these results as a guide, the sparse grass cover, to the nearest 10%, was estimated for each tenth of a mile.

No tree and bush transects were done, and comments on the vegetation types are qualitative.

It was necessary to do counts along two different roads in the Wankie National Park (Figure 12), because the area lies at the eastern edge of T. flavirostris distribution, and the western edge of T. erythrorhynchus distribution. The Tchabema Road passes through habitat of the former, and the Lukosi River Road through habitat of the latter. T. nasutus occurs in both areas. The main features of the two transect roads are shown diagramatically in Figures 13 and 14. The first half of each month was spent doing nine counts along the Lukosi River Road, and the last half of the month doing nine counts along the Tchabema Road.

The habitat along the two roads was markedly different because of different soil types. The Lukosi River Road passes through dark loamy soils, except for the rocky hills, and the dominant vegetation is mopane woodland (Colophospermum mopane). Often the road passes close to the riparian vegetation of the Lukosi River, where large trees such as Acacia albida predominate. Grass cover throughout most of the area is poor. Scattered annual grasses are the most important.

The Tchabema Road passes over sandy soils, until at 15,0 miles it passes on to the dark loams with mopane vegetation. On the sandy soils, teak woodland (Baikaea plurijuga) and bush associations predominate.

RESULTS.

The total numbers of hornbills of each species recorded during the 18 counts along each transect road are given in Table 5. The marked predominance of *T. erythrorhynchus* along the Lukosi River Road, and *T. flavirostris* along the Tchabema Road is clear, with *T. nasutus* uncommon along both roads.

For the two seasons, the results of hornbill numbers, recorded biomass, and percentage sparse grass cover are shown per tenth of a mile in Figures 15 and 16, for the Lukosi River and Tchabema Roads respectively. The biomass and sparse grass cover are plotted as graphs using a moving point average, due to the small number of counts available. The small number of counts also make detailed analysis impossible, but despite this certain features are apparent.

Along the Lukosi River Road (Fig. 15) *T. nasutus* is only regularly recorded along the area where the road passes close to the river from 5,2 to 15,0 miles, where large trees are present. *T. erythrorhynchus* occurs all along the road, but at the end of the dry season, numbers are especially concentrated from 0,0 to 2,0 miles and 9,0 to 10,0 miles, and this appears to be correlated to a high biomass of herbivores in these two areas. This high herbivore biomass is not, however, clearly, correlated to a high degree of sparse grass cover, and most of the road has well over the critical 40% sparse grass cover of the Kruger National Park. *T. flavirostris* was only found very uncommonly along the southern half of the road, with no clear preference for any grass cover or other factor.

Along the Tchabema Road (Fig. 16) *T. flavirostris* was recorded throughout, being most common, especially at the end of the dry season, from 11,0 to 15,0 miles. This concentration may be due to this area having many open patches of short grass, often surrounding temporary pans, but with very little bare ground. This is in the transition area from sandy soils to dark loams, and sparse grass cover was not caused by over-grazing primarily, as shown by the low biomass of herbivores recorded. T. erythrorhynchus was almost entirely restricted to the areas of dark loam soil with mopane vegetation (the same as occurred on the Lukosi River Road) and was not found on the sandy soils, despite the much higher biomass of herbivores recorded there. T. nasutus was recorded all along the road, but mainly in the areas of sandy soil, where large teak trees and dense bush occurred.

One marked feature of Wankie National Park at the end of the dry season was the very large flocks of T. erythrorhynchus in the Lukosi area. These account for the large numbers at 0,8 and 0,9 miles on the Lukosi River Road, and flocks up to 43 birds were seen elsewhere in the area. Such a phenomenon has not been seen in the Kruger National Park, but is also reported for Mana Pools on the Zambesi River in Rhodesia (Begg, Ellis pers. comm.).

GENERAL DISCUSSION.

The habitat preferences differ markedly for each hornbill species, as do the relative numbers of each species, within the area studied. Table 6 compares the overall densities of the hornbills recorded along the three transect roads, and it appears that the numbers in the Kruger National Park are lower than for the Wankie National Park. Moreover, in the Wankie National Park a fourth Tockus species T. bradfieldi coexists with the others, although in smaller numbers (Lukosi River Road 0,02/mile/count; Tchabema Road 0,11/mile/count). The very high densities of T. erythrorhynchus and T. flavirostris within their respective areas of Wankie National Park are most marked, and may account for the formation of the large flocks of the former species in the dry season.

T. nasutus and T. flavirostris have a wide range of habitate tolerance. The tree and bush density can vary considerably for the tree dwelling T. nasutus as shown in the Kruger National Park, and this is reflected in the overall distribution of the species (Fig. 17). The range corresponds with that of the drier types of savanna and woodlands in Africa, from the scattered bushes in semi-desert (southern Sahara and South West Africa), to the less dense forms of Brachystegia woodland (Zambia and Rhodesia). It appears that the lower threshold at which T. nasutus ceases to occur, is that at which there are few trees and bushes. At the upper threshold it is replaced by other Tockus species. It is replaced by T. pallidirostris, a very closely allied species, in the denser Brachystegia woodlands (Benson and Irwin 1966), and in riparian, coastal and montane forests by T. alboterminatus.

T. flavirostris has habitat preferences that were not clearly defined by this study, However, it has a distribution (Fig. 18) which indicates that it prefers dry savannas, especially thorn savanna. The absence of the species on the dark loam soils in Wankie National Park, while common on the adjoining sandy soils, is a mystery at present. It may be due to competition from the higher densities of T. erythrorhynchus on the sparsely grassed, loamy soils. The two species coexist in the Kruger National Park, but at much lower densities than are found in the Wankie National Park.

Conversely, the absence of T. erythrorhynchus on the sandy soils of the Wankie National Park is a puzzle. This species does not appear to favour such dry savannas as T. flavirostris, at least in Southern Africa, as shown by its overall distribution (Fig. 19). In the Kruger National Park T. erythrorhynchus certainly prefers the areas of sparse grass cover and high herbivore concentration, and this appears to be equally true where the species occurs in the Wankie National Park. However, there are areas in the Wankie National Park on the sandy soils where the grass is heavily over-grazed by very large numbers of herbivores, and yet there are no T. erythrorhynchus. It was noted at at the end of the dry season (October) that these apparently ideal areas for *T. erythrorhynchus* were greatly favoured by large flocks of *T. bradfieldi*. The latter species favours teak woodlands (*Baikaea plurijuga*), which are confined to the sandy soils, and appears to forage mainly in the foliage during the summer. However, in the dry season, flocks forage a great deal on the ground in the sparsely grassed areas (pers. obs.; Rushworth pers. comm.). This may provide competition for *T. erythrorhynchus* in its favoured habitat at the end of the dry season ; the leanest time of the year.

The seasonal fluctuations in numbers of *T. nasutus* and especially *T. flavirostris*, in the Kruger National Park, are only partly understood. *T. nasutus*, with low numbers in the dry season, probably leaves the area because its arboreal habitat deteriorates when the deciduous trees lose their leaves at this time. Fluctuations in numbers of *T. flavirostris* may also be due to local movements associated with seasonal changes in food supply. Ringing indicates that this species may be nomadic, at least when compared with the sedentary *T. erythrorhynchus*.

Rowan (1969), with her work on the ecology of the Cape Robin *Cossypha caffra*, shows the caution necessary when extending conclusions from one area to explain the overall distribution of a species. These observations on the habitat preferences of the three hornbill species may be, at least in part, applicable throughout their African range. The three species are the most widespread of the genus *Tockus*, and are divided into northern and southern subspecies which have clear external morphological and/or behavioural differences (Section 9). *T. nasutus* has a continuous distribution (Fig. 17), and the subspecies meet approximately along the equator. *T. flavirostris* (Fig. 18) and *T. erythrorhynchus* (Fig. 19), have a discontinuous distribution, the division being effected by the moist woodland across central Africa. Extrapolation of the habitat preferences of the southern subspecies fails to explain why *T. flavirostris* does not spread all across the sub-Saharan savanna, or why *T. erythrorhynchus* does and so inhabits much drier areas than it does in the south. It is possible that the northern subspecies, with different morphology and behaviour, may also show a different ecology. It may be expecting too much for a widespread species to exhibit the same ecology and habitat preferences throughout its range, which includes a variety of vegetation associations, climates and interspecific relationships. This may be illustrated by the seasonal movements of *T. nasutus*, which is known to be nomadic along the southern edge of the Sahara (Sanft 1960), and probably also in the Kruger National Park, and yet appears to be resident in the moist woodlands of central Africa (Benson *et al* 1971). *T. erythrorhynchus* and *T. flavirostris* are the only ground-feeding *Tockus* species in the Kruger National Park, and *T. bradfieldi* may be added to the list in the Wankie National Park. *T. monteiri*, *T. erythrorhynchus* and *T. flavirostris* occur together around the Waterberg inselberg in South West Africa. In the Lake Baringo area of Kenya *T. flavirostris*, *T. deckeni* and *T. erythrorhynchus* occur together, and yet only *T. erythrorhynchus* extends across the extensive savannas of West Africa. The related species living sympatrically may also modify the habitat preferences of the other species in the area. A distillation of the main features of the habitat preferences of the three hornbill species studied in the Kruger National Park will only become possible when detailed studies have been done in other parts of their range, especially in East and West Africa.

SECTION 3. FEEDING ECOLOGY OF THREE SPECIES OF HORNBILL IN THE KRUGER NATIONAL PARK.

INTRODUCTION.

In Section 2, the habitat preferences of *Tockus nasutus*, *T. erythrorhynchus* and *T. flavirostris* were examined in the Kruger National Park. During the same period, regular collections of hornbills were made along a firebreak about 10 km east of Picnic Road (Fig. 2). The stomach contents of these specimens form the basis of this study of the feeding ecology of the three hornbill species. They allow a comparison of the diet of the three species, and a consideration of how the diet changes with the seasons. This is complemented by studying how the hornbills obtain their food, by watching live birds. Finally, it is possible to compare the diet and foraging behaviour of the hornbills with their known habitat preferences in the central Kruger National Park.

METHODS.

The diet of the hornbills was found from:

a) Food identified from the stomach contents,
b) Food seen to be brought to the occupants of nests,
c) Food remains found below nest holes,
d) Food identified while observing foraging behaviour.

Collection of specimens was standardised. It was confined to the 12 km of firebreak road, from the drift over the Nwanedzi River near Satara up to the Msasane windmill (Fig 2). Specimens were collected over a three-day period in the middle of each month, in June 1967 and from September 1967 to October 1968, a total of 15 months. Ten specimens of *T. erythrorhynchus* and *T. flavirostris* were collected each month, as near to equal numbers of each sex as possible, giving a sample for each species of 150 birds. *T. nasutus* was less common and more wary, and only 50 specimens were obtained, with an uneven monthly distribution (June 1967 three, September seven, October five, November four, December two, January 1968 five, February five, March three, April three, May two, June to August nil, September four and October 1968 seven).

Within three hours of being shot, the stomach of each specimen was removed and preserved in 10% formaldehyde solution. The weight of the specimen, and of the discrete fat body attached to the stomach, was recorded, to give an index of the condition of the specimen. The stomach contents were analysed by counting the maximum numbers of each food item represented by the fragments found in the stomach. A food item here refers to the most specific taxon that the food remains were identified to during the analysis e.g. lepidopterous larva, large black ant, or *Chiromantis xerampelina* tree frog. The most complete food remains were identified in as much detail as possible by specialists, but this could not be done in the overall analysis due to the fragmentary nature of the material. Animal food items were usually identified to family (sometimes even to genus or species).

Vegetable food items were numbered, as the majority could not be traced back to the plant from which they originated. The numbers recorded of each food item were tabulated for each specimen.

The three hornbill species are omnivorous, and therefore the numbers of different food items eaten has little meaning when comparing the contribution to the diet of different food items. For example, the contribution to the diet of 100 termites cannot be compared numerically with that of one locust. The weight of each food item was used as an estimation of the contribution that each food item makes to the diet, being the simplest method to employ in the field. To achieve this, fresh specimens of all the animal food items recorded during stomach content analysis were collected and weighed. The fresh specimens may not have been the same species as those eaten by the hornbills, but they were of similar size and were taken in the same area where hornbills were shot. The average weight of a single food item was calculated (Appendix 2), and used to work out the weight contribution of each animal food item to the diet.

Weight contribution could not be used for the vegetable food items, as only few could be identified. The seeds found in the stomach could not be weighed, as many were thought to have come from fleshy fruits and the amount already digested was unknown. The numbers of seeds of each vegetable food item has to be compared; a poor compromise as some of the seeds are thought to come from many-seeded fruits.

The foraging behaviour of each hornbill species was established by following the birds in a vehicle and noting details of their feeding. A qualitative assessment was made of where the food was taken from, judged as trees (above 3,5 m), bushes (1,5 - 3,5), long grass (above 30 cm), medium grass (10-30 cm), short grass (under 10 cm) and bare ground. The method of obtaining food was ascribed to one of seven feeding methods: picking up the food where found, digging up the food, levering over objects for the food, chasing food along the ground, hawking food on the wing, swooping down to food spotted from a perch, and plucking up food while on the wing. Details of these feeding methods are given in Section 9.

RESULTS.

DIET

The diet recorded for the three hornbill species in the central region of the Kruger National Park is listed in Appendix 3.

All three hornbill species are omnivorous, most of the food being insects, with relatively few vegetable foods recorded.

COMPARISON OF THE DIET OF EACH SPECIES.

For comparison with Section 2, the specimens were grouped according to the same four seasons. The sample size per season is given in Table 7.

The food items eaten each season, from the stomach contents of the sample collected during that season, are shown for each species in Appendix 4.

The degree of similarity between the dietary components of each hornbill species can be expressed by the coefficient of similarity, $C = \frac{2w}{a + b}$ where,

w is the sum of all food items in the diet which two species share in common,

a is the sum of all food items in the diet of one species, and b is the sum of all food items in the diet of the other species.

As used here, when $C = 0$ there is no similarity in the diet of two species, and when $C = 1$ the dietary components are exactly the same for each species. The coefficients of similarity, overall and for each season, are given in Table 8. The overall similarity in diet is greatest between *T. erythrorhynchus* and *T. flavirostris*, and least between *T. nasutus* and the other two species. *T. nasutus* differs most markedly from the other two species during the early dry season, but there is no clear seasonal trend in the dietary similarity of *T. erythrorhynchus* and *T. flavirostris*.

The diversity of the diet can be expressed by the index derived from information theory, $H = \sum P_i \log_e P_i$.

H is the index of diversity, and

P_i is the proportion that the numbers or weight of one food item form of the total numbers or weight of all food items. This means that for two specimens eating equal numbers of food items, the one which eats nearest to equal numbers of each food item will have the highest diversity index. For two specimens in which the proportion by weight contributed by each food item to the diet is the same, then the specimen with the highest number offood items in the diet will have the highest diversity index.

A diversity index was computed for each specimen, firstly for the numbers of each food item, and secondly for the weight of each food item. The diversity indices for each specimen were then grouped under seasons, and the means are given in Table 9a and b. A two-way analysis of variance was done on each of the two sets of indices, assuming that species and season are both fixed effects. For both the numbers of food items and the weight of food items, there is an overall significant difference at the 5% level between species, There is also a significant interaction between species and seasons for the numbers of food items, and an overall significant difference between the seasons for the weight of food items.

By applying the multiple comparison method of Scheffe (1959), significant differences between the species were determined. The Scheffe critical constant is taken to be $S = (2F_{2,331}(\alpha))^{\frac{1}{2}}$. The results are shown in Table 10. A significant difference in overall diversity indices for the numbers of food items is shown between *T. nasutus* and the other two species, *T. erythrorhynchus* and *T. flavirostris*. Examination of Table 9a shows that *T. nasutus* has higher diversity indices for the numbers of food items, indicating that this hornbill uses comparatively more food sources and exploits them more evenly. For the diversity indices of the weight of food items, *T. erythrorhynchus* differs significantly from *T. nasutus* and *T. flavirostris*, having a higher diversity index (Table 9b). This indicates that *T. erythrorhynchus* exploits its food items to obtain closer to the same proportion by weight to the diet from each item than do the other two species.

The multiple comparison method was also applied to test the contrast between each species within each season. The results for the numbers of food items are shown in Table 11. *T. nasutus* differs significantly from the other two species only in the late dry season, when the diversity indices for this species (Table 9a) are much higher than for the other two species.

Comparison of species and seasons for the weight of food items show no clear pattern of significance (Table 11). *T. erythrorhynchus* differs from *T. nasutus* in the first early and late dry seasons and the late wet season, in each case having a higher diversity index than the other species (Table 9b).

If the seasonal means of the diversity indices for the numbers of food items are examined (Table 9a), the trend for *T. nasutus* is opposite to the other two species. The diversity indices for the numbers of food items are lowest for *T. nasutus* in the wet season, and highest during the dry season. For *T. erythrorhynchus* and *T. flavirostris*, the indices are highest in the wet season and second early dry season, lowest in the other dry seasons.

The seasonal means for the diversity indices of the weight of food items (Table 9b) showed no clear trends.

SEASONAL VARIATIONS IN DIET.

For each season, the total weights and numbers of each food item eaten by the sample of specimens collected for that season, were calculated. The total weights were calculated by multiplying the numbers of a food item by the average weight of a single unit of that food item, using the average weights in Appendix 2. The percentage that the weight or numbers of a food item constitute of the total weight or numbers of all food items taken in one season, gives a relative figure for the contribution of that food item to the diet, either by weight or by frequency of occurrence.

Since the hornbills are omnivorous, they eat many food items that contribute very little to the diet, either by weight or number. These "incidental food items" cannot be of great significance to the biology of the hornbills, so that only those animal food items that contribute over 5% to the diet by weight are considered as "important animal food items". Table 12 shows the seasonal contributions that these "important animal food items" make to the diet, and the small proportion that the "incidental food items" form. "Important vegetable food items" are taken as those that contribute over 5% by frequency of occurrence to the diet. This is the best compromise because the weight contribution of vegetable food items could not be determined.

The seasonal contributions to the diet of "important animal food items" and "important vegetable food items" are given in Table 13. The contribution of the "important animal food items" is also shown diagramatically in Figure 20, shaded areas being of food items important to more than one hornbill species in the same season. The importance of these shared food items, and the seasons when this occurs for each hornbill species, is shown in Table 14. It is clear that _T. nasutus_ and _T. erythrorhynchus_ have little overlap of "important animal food items", and where there is overlap, the food items are of least importance to _T. nasutus_. There is much more overlap between _T. nasutus_ and _T. flavirostris_, but if rodents are disregarded, because they were very common during a population explosion in the 1967 dry season, then the overlap between these two hornbills occurs only during the wet season. _T. erythrorhynchus_ and *T. flavirostris* share the most food items, shared items forming 9% to 75% of the diet by weight. There is a tendency for the overlap between these two species to be greatest during the wet season. The wet season overlap in diet for all species is of less biological importance when it is noted that the food items involved are mainly seasonally abundant items, such as caterpillars, acridids, solifugids and harvester termites. Overlap of such perennial food supplies as tenebrionids and ants is probably of greater biological importance, but is relatively slight. This indication of the abundance of food items that can be successfully shared between species in the wet season, is further augmented by evidence from vegetable foods (Table 13). Almost all the shared "important vegetable food items" are taken during the wet season.

FORAGING BEHAVIOUR.

Observations on where and how each hornbill species obtained food items were made 76 times for *T. nasutus*, 776 times for *T. erythrorhynchus* and 632 times for *T. flavirostris*.

Distribution of where each species obtained its food in the vegetation is given in Table 15. If the foraging niches are shown as percentages in a histogram (Fig. 21), the arboreal foraging of *T. nasutus* is clearly opposed to the terrestrial foraging of *T. erythrorhynchus* and T. flavirostris. Slight seasonal trends are evident, in that *T. nasutus* appears to come down to the lower levels of vegetation slightly more during the wet season. In the dry season *T. erythrorhynchus* appears to use areas with some grass cover, especially if very short, and *T. flavirostris* also concentrates on the short grass and bare ground areas.

The methods used by the hornbills to obtain food are detailed in Table 16, and illustrated diagramatically in Figure 22. All species obtain much of their food by merely picking it up where it is found, and this is especially true of *T. flavirostris*. Other than this method, *T nasutus* mainly relies on methods involving flight, (such as hawking, swooping and plucking) and *T. erythrorhynchus* obtains much food by digging. *T. nasutus* frequently hawks during the wet season, possibly because so many insects have imagos on the wing at this time. *T. erythrorhynchus* oscillates between picking up most food in the wet season (with digging secondary) and digging up most food during the dry season (with picking secondary). Except for a slight increase in the role of digging during the dry season, *T. flavirostris* picks up most of its food throughout the year.

FAT DEPOSITS OF SPECIMENS

The fat bodies attached to the stomach appear to be good indicators of the amount of fat present in the rest of the body. The weights of the stomach fat body were converted to a percentage of the body weight for each specimen, and the monthly averages are shown in Figure 23. During the study period, fat condition was lowest at the end of the dry season (October), increasing slightly during the wet season, but falling off by the end of the wet season. Peak fat condition occurred during the middle of the dry season (June to August). This trend is clearest for *T. erythrorhynchus* and *T. flavirostris*, but is probably indistinct for *T. nasutus* due to the erratic sampling of the latter species.

DISCUSSION.

Before considering the results in detail, there are shortcomings in the study which must be mentioned. Results based on analysis of stomach contents have inherent errors. The rate at which different food items digest cannot be compensated for, so that numbers of hard items in the stomach are likely to be higher than numbers of soft items. Furthermore, the identification of the food items in the stomach tends to be superficial, especially in hornbills where the food is highly fragmented, because identification can rarely be done in a quantitative way below the family level. This tends to make different species appear closer in their diet to one another than they really are. For instance, all three hornbill species have acridids as an "important animal food item" during the wet season, and so would appear to overlap in diet. However, looking at the species eaten (Appendix 3), only T. nasutus eats arboreal grasshoppers such as Rhytidacris punctata, untouched by the other two hornbills because they do not forage in the trees. To some extent these errors are reduced by collecting hornbills over the same period, in the same area, and randomising the time of day at which they are taken.

Use of the weight of a food item to indicate its contribution to the diet is only an approximation. The degree of assimilation of a food, the energy expended in obtaining the food, and the different nutritional values of foods are not considered, and are taken as being constant. Slobodkin (1961) found that different insect tissues are very similar in terms of the calories per ash-free gram, and here weighing the food items was used, being the best method for field use.

Some problems are peculiar to this study. The vegetable food items, mainly fruits and seeds, could not be directly compared with the animal food items, except by frequency of occurrence, and the inaccuracies of this method have been pointed out. However, the effects of the inaccuracies are reduced, in terms of the ecology of the hornbills, in that the main period when vegetable food items are much used is the wet season when all food items appear to be at their most abundant. Vegetable food items do not augment the diet during the late dry season, when food is hardest to obtain. Furthermore, vegetable food items are rarely fed at the nest, despite breeding occurring during the wet season, when hornbills require large amounts of food.

The lower numbers and greater wariness of T. nasutus relative to the other two species, meant that sample sizes were smaller and quantitive results less reliable for this species. To offset this, T. nasutus is more different in diet and foraging from the other two species than they are from one another, so that the conclusions drawn are likely to be true.

Although the year was divided up into four seasons, variation in the timing and duration of the rains can influence the seasons, so that they resemble different seasons more than they do the same seasons in different years. The seasons used in the calculations represent the average duration of these seasons during a year. The monthly rainfall figures during this study are shown in Figure 24, including the rainfall immediately preceding the study. The first dry season (1967) was extremely dry, but was somewhat ameliorated by the heavy rains of the preceding late wet season. However, the second early dry season (1968) was much wetter than the first, with some rain extending into June. The two late dry seasons (1967, 1968) were very similar. Even though rain is shown for October of the first late dry season, the rain fell after the specimens were collected in the middle of the month. Only the 1967-1968 wet season was considered, and the bulk of the rain fell in the late part of the season. The effect that rain has on the arthropod populations is shown in Figure 25. Samples were taken in an area of medium and long grass near Satara camp, doing 100 sweeps through the grass with a 60 cm diameter net in two adjacent areas. Exactly the same area was only swept once in every four samples to allow the arthropods to restabilise themselves. Samples were taken every 3 days in the mid-afternoon, the weight of arthropods in each 100 sweep sample being taken, and the average for the two samples recorded. Figure 25 shows that the arthropod biomass is at a low level during the dry season, increasing slightly with the warmer weather of October, and then once the rains begin to fall, building up at a steady rate to 12 times greater than the dry season average. Related to the seasons during which hornbills were collected, the following suppositions can be made of what happened to the arthropod biomass. The very dry conditions throughout the first dry season (1967) kept the arthropods at a low level. The arthropods began to increase with the rains in late October 1967, but the increase was limited by 65 days of drought that were experienced in the early wet season. Peak arthropod biomass was attained in the late wet season when good rains fell, and was extended into the early dry season by the late rains. The second early dry season (1968),therefore, supported more arthropods than the first early dry season, and the lateness of the 1967-68 rains also tended to ameliorate the second late dry season.

The amount of overlap in "important food items" between the three hornbill species during the wet season indicates the wet season as a time of maximum food availability. This is borne out by sampling of the arthropod biomass, and because the wet season is when the hornbills breed and undergo their annual moult.

The analysis of the feeding results does not consider the sexes separately, because the results did not indicate sexual differences in food or foraging. Among others, Selander (1966) has pointed out the possibility of sexes having different feeding niches, due to sexual dimorphism in bill size or shape. Table 17 shows that there is a clear sexual dimorphism in bill length of the hornbills studied, and the bill is clearly longer (and larger) in males, even in the field. However, the feeding habits, as defined by the types of food items eaten, shows complete overlap between the sexes because the birds are omnivorous and take such a wide range of food items. In size, food items range from 30g mice down to single termite workers, and it is thought that sexual or specific differences in foods will be most obvious in the largest food items. *T. erythrorhynchus* has the smallest bill of the three species, and this could account for the lack of mice in its diet, despite mice being exceptionally abundant during a plague in the first dry season. *T. erythrorhynchus* also never ate a large purple species of Coprinae commonly taken by the other two species of hornbill, in spite of being the only hornbill to have Coprinae as an important food item. The reason for the large bill in the male hornbills may rather be linked to his having to feed the female and chicks throughout the prolonged nesting cycle, when a large bill would allow food to be rapidly subdued and crushed, so that minimum time is wasted in coming to the nest.

To co-ordinate the results for the feeding of the three hornbill species, it is easiest to consider the annual cycle of each species in turn, comparing with the other species where necessary. Where pertinent, reference will also be made to Section 2, to relate the feeding results to habitat preferences and seasonal movements of the hornbills.

T. nasutus is an arboreal-foraging species, and apart from picking, uses aerial methods, such as hawking and plucking, to obtain much of its food. This would be facilitated by the noticeably more boyuant and dextrous flight of this species, compared to the two ground-foraging species (Section 9). Because it is able to take passing insects, and food on the ground, these habits do not restrict *T. nasutus* to areas of dense vegetation, as shown by the wide distribution of the species in Africa. The strong indication in Section 2 that *T. nasutus* numbers decline in the dry season in the Kruger National Park is backed up by general observations in the area, and the difficulty of shooting specimens at this time. This is probably because the trees are mostly deciduous, the loss of leaves in the dry season effectively eliminating the preferred habitat of this hornbill. From observations in other regions of the Kruger National Park during the dry season, it appears that *T. nasutus* moves to mopane savanna (*Colophospermum mopane*) and riparian vegetation habitats which are not so markedly deciduous. The nomadic habits of *T. nasutus* during the dry season are well known in the northern range of the species in Africa (Bates 1934; Chapin 1939 ; Hutson and Bannerman 1931 ; Lynes 1925 ; Paludan 1936). In the southern part of its range I have noted nomadism in the Kruger National Park, and dry season influxes of the species onto the highveld of the Transvaal in very dry years (i.e. 1970-71). I believe that this is because *T. nasutus* spreads over a wide breeding range in the wet season, and then moves in the dry season to moister areas where there is most foliage and food. Notably, Benson *et al* (1971) find no seasonal movements of *T. nasutus* in the *Brachystegia* woodland of Zambia, a relatively moist area with only few markedly deciduous trees. In the Kruger National Park *T. nasutus* feeds mainly on *Chiromantis xeranpelina* tree frogs and m/ Buprestids, both animals of trees and bushes, and seldom eaten by other species of hornbill. In the first dry season rodents were an important part of the diet, but only because they were present in unusual abundance. They cannot be counted on year after year. Chameleons were important in the second late dry season, and although normally arboreal, I have seen *T. nasutus* swoop on a chameleon as it walked across a road. Other important arboreal food animals, reflecting the arboreal foraging of of *T. nasutus*, are coccids, Cetoniinae, Melolonthinae and cerambycids. The remaining important foods, such as acridids, harvester termites, Coprinae and solifugids are mainly taken by hawking or swooping, especially during the wet season when the arthropods are generally abundant and active. *T. nasutus* also has five important vegetable foods, mainly taken during the wet season, especially fruits of *Lannea stuhlmanii*, *Securinega virosa* and an unidentified fruit with a 4 mm long pitted yellow seed. Overall, the difficulty which *T. nasutus* has obtaining food during the dry season may be shown by the marked lowering of the coefficient of similarity between this species and the other two species during the early dry season, and the significantly higher diversity index that is found for the numbers of food items. These results indicate that *T. nasutus* is less able to make use of the foods available to the other two species in the early dry season, and evenly exploits what food is available to it in the late dry season, so raising the diversity index. The reason why *T. nasutus* was found to be one third as common as the other two species in the area may also be due to its arboreal foraging. The surface area of trees available would be less than the ground area available per unit area of habitat.

T. erythrorhynchus is exclusively a ground-foraging species, taking food especially in medium grass, short grass and on bare ground. This preference for sparse grass areas is clearly shown in Section 2, and the use of bare areas is shown by the extent to which this hornbill digs for food, especially in the dry season. Furthermore, the diet, and the regular habit of digging in game droppings, points to the necessity of high game concentrations with associated over-grazing, and not merely poor grass cover alone. *T. erythrorhynchus* is closest in diet to *T. flavirostris*, the other ground-foraging species, as shown by the high coefficient of similarity between the two species. The change in *T. erythrorhynchus* foraging from mainly picking in the wet season to mainly digging during the dry season, is shown by the food taken. Such foods as acridids, caterpillars and maggots are of chief importance during the wet season. Items that have to be obtained by digging, such as tenebrionids, ants and termites, are most important in the dry season. Only one vegetable food item is important to T. *erythrorhynchus*; a 5 mm long oval brown seed that is only taken in the dry season, and may help to augment the food supply at that time. For all the hornbills, the end of the dry season is the time when they are lowest in fat condition, and when food is most limited. At this time *T. nasutus* leaves the area, but *T. erythrorhynchus* concentrates on the over-grazed, dropping-rich areas around the watering points, and digs for most of its food. Digging decreases when the arthropod biomass increases in the wet season, when picking becomes the main foraging method. The difference in the diversity index of *T. erythrorhynchus* from the other two hornbills for the weight of food items eaten may be due to the indication that it cannot eat the larger types of food as easily as the other species, and so tends to exploit the smaller food items more evenly.

T. flavirostris is the least specialised of the three hornbills. It feeds mainly on the ground among the medium and short grass, but forages at all levels in the vegetation. It has no specialised foraging method, merely picking up most of its food. This would explain its wide distribution in the study area shown in Section 2, but the seasonal fluctuations in numbers, (commonest in the early dry season and least common in the early wet season) cannot be explained on the basis of food supply. The unspecialised feeding habits cause this species to overlap in diet with T. *nasutus* and even more with *T. erythrorhynchus*. During the dry season *T. flavirostris* eats mainly ants and workers of harvester termites found in the medium and long grass, a niche least used by the other two hornbill species. Rodents were taken in the first dry season, due to the plague in the area. The rest of the important food items, and those taken during the wet season, compromise active prey found mainly on the ground, such as solifugids, centipedes, scorpions, acridids and some beetle families. Vegetable foods are important only in the wet season, especially 4 mm long pitted pale yellow seeds, seeds of *Securinega virosa* and of a *Coccinium* species.

The diversity indices indicate that hornbills are quite diverse feeders. Orians (1966) reported an index of up to 0,39 for Yellow-headed Blackbirds *Xanthocephalus xanthocephalus* and Snelling (1968) recorded 3,17 and 2,62 for Red-winged Blackbirds *Agelaius phoeniceus* and Common Grackles *Quiscalus quiscula* respectively. These high figures of Snelling are probably due to the great detail in which he was able to identify his food items, when compared to the fragmented remains in the hornbill stomachs. The hornbill results might have been higher with more detailed identification.

SOME OBSERVATIONS ON THE SEALED-IN NESTING METHOD OF HORNBILLS (FAMILY: BUCEROTIDAE)

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INTRODUCTION

Hornbills may be considered the most highly specialised family of birds to have adopted the habit of nesting in holes. With the exception of the aberrant genus *Bucorvus*, the most obvious aspect of hornbill nesting is that the female seals herself into the nest hole, remains there during the incubation of the eggs and rearing of the chicks, and is fed throughout by the male. The details of the pattern differ for species and genera, but the data are very scanty, especially for the Oriental species. Of the Ethiopian species, Moreau's (1941) study of *Bycanistes brevis*, Ranger's (1949-52) study of *Tockus alboterminatus*, and Kilham's (1956) observations on *Bycanistes subcylindricus* are the only comprehensive studies done on hornbill breeding. Moreau summarised the available information on the nesting of Ethiopian species in 1937, with additions in 1940.

However these works only fill in the details of the nesting behaviour of each species, as well as describing the various adaptations that this family have evolved with respect to the sealed nest hole. During a 30-month study of hornbills in the Kruger National Park, South Africa, fromNovember 1966 to April 1969, data were obtained on the significance of the nesting method to the family, in terms of the advantages and disadvantages that the method conferred on the family. The work was concentrated on three species of the genus *Tockus: T. nasutus, T. erythrorhynchus* and *T. flavirostris;* but observations were also made on the breeding of *T. alboterminatus* and *Bucorvus leadbeateri*. After an account of the adaptations which the hornbills show to their peculiar nesting method, and the consequences of this method, suggestions will also be made on how the method may have evolved.

ADAPTATIONS BY HORNBILLS TO THE SEALED-IN NESTING METHOD

The adaptations considered below are not considered in great detail, but are given to illustrate the highly specialised nature of the nesting method, and the difficulties associated with it. The adaptations are as follows.

(a) *The sealing technique*. The sealing is done by a side-to-side rattling of the bill in the entrance hole to the nest cavity, the sealing material being held in the bill tip, and squeezing out of the sides during the sealing. The sealing material is thus applied in thin layers, leaving only a narrow, vertical slit leading into the nest (Figure 1). The material used and the sexes involved in the sealing appear to differ for each genus. Females of the genus *Tockus* use their own droppings once they are ensconced in the nest hole, but mud is used (at least by *T. erythrorhynchus* and *T. flavirostris*) before the female finally enters the hole. All sealing activity is carried out by the female. In the genus *Bycanistes* mud is used for sealing, which is done only by the female, but the material is brought to her by the male. The two species of the genus *Bucorvus* are the only hornbills that do not seal up the nest hole. Once dry, the sealing material becomes very hard, and also tends to camouflage well with the tree or rocks in which the nest is situated.

(b) *Adaptations by the female to her long period of enclosure*. With the exception of *Bucorvus*, the females of all species remain in the nest hole during the whole incubation period, and for most of the development period of the chicks. The period of enclosure, as far as has been recorded, ranges from 42 days in *T. nasutus* up to 119 days in *Bycanistes subcylindricus* (Kilham 1956). During her enclosure the female moults, but the degree of moult appears to vary considerably between genera. So far as has

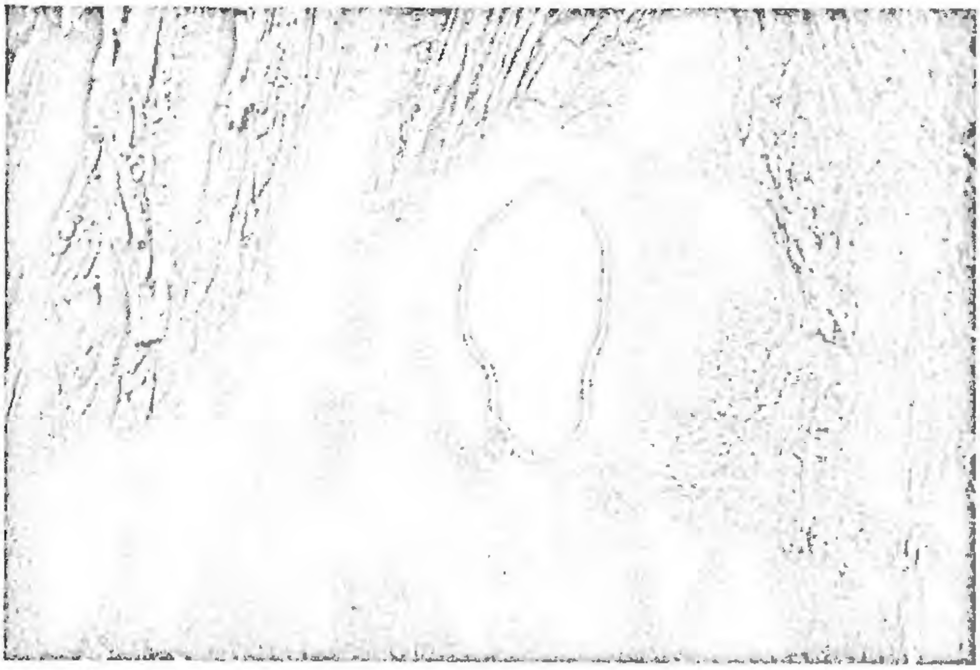

Figure 1. The sealed-in nest hole of *Tockus alboterminatus*. The white line shows the edge of the nest entrance before sealing.

been ascertained, most species undergo a gradual moult as in other birds, although this might be accelerated during the period of enclosure.

However, in *Tockus* species and possibly *Bycanistes bucinator*, the female drops all her rectrices and remiges early in the incubation period. Regrowth of the feathers commences immediately (Figure 2) so that by the time the female emerges from the nest hole she is again fully feathered. Moult of the body feathers is not simultaneous but proceeds in a rapid succession and is almost complete by the time the female emerges. This adaptation during the nesting period is unique among birds, and may have evolved because of the confined nature of the nest hole, or because it confers an advantage on the female to have her full feather complement when she emerges. The moult is made possible by the sealed nest being safe from predators, as will be shown later. Prozesky (1965) records a female *T. flavirostris* taken from a nest, which was lacking claws. This was suggested as an adaptation to avoid damaging the chicks in the nest hole, but since no corroboration has been obtained, the specimen was probably malformed.

(c) *Adaptations to an enclosed nest with limited space.* The development period of hole-nesting birds is generally longer than for species that nest in open nests (Lack 1966), and this trend is also obvious in the hornbills. Thus *T. erythrorhynchus* which only weighs about 140 g. has an incubation and nestling period totalling 70 days, and *Bycanistes subcylindricus* which weighs about 1,000 g. has been recorded taking 119 days for the same events (Kilham 1956). The chicks are then able to emerge in an advanced state of development. In the hornbills the plumage of the chicks is as developed as the adults on emergence and the chicks are immediately capable of sustained flight. The long tails, characteristic of the family, are a problem in the enclosed nest, but the female and chicks hold the tail up over their backs while they are in the nest. The precocity of the chicks in the nest is also remarkable. In the genus *Tockus* the female breaks out of the nest hole about half way through the development period of the

Figure 2. The feathers growing in on a female *Tockus nasutus* taken from the nest at the time of hatching of the first egg, show the sudden moult that this genus of hornbills undergo during nesting. The similar length of the rectrices and remiges show how rapidly the feathers are dropped, and the feathers of the abdomen indicate the degree of body moult.

chicks, and the chicks then reseal the entrance hole themselves. The sealing is not as well executed as by the adult birds, but the result is the same in terms of making the nest impregnable. The stage of development of the chicks when they undertake the sealing can be seen (Figure 3). At this stage the legs of the chicks are almost fully developed, whereas the wings have grown little since hatching, and this differential growth of the limbs may ensure that the chicks have sufficient mobility and stability to perform the sealing activity. The development of the legs may also be associated with the well developed nest sanitation that the hornbills practise. The coraciiform families have notoriously dirty nest holes due to the accumulation of food remains and faeces, but in the family Bucerotidae the female and the chicks (when they are old enough) clean the nest. Food remains and debris are thrown out of the nest with the bill, and the faeces are forcibly ejected through the nest slit. The small chicks defaecate on the nest floor, but the faeces are thrown out with other debris, and so the nest is kept clean.

(d) *The role of the male.* Throughout the nesting period the food for the female and chicks is supplied by the male. In *Bucorvus*, and possibly some Oriental species, the birds occur in social groups, and the whole group feed the female and chicks. The female assists with the feeding of the chicks in the species where she emerges before they leave the nest. Visual and tactile contact between the male and female is impossible for the nesting period. This lack of contact may account for the invariable, and often loud noises that the female (and later the chicks) make when they accept food. It is suggested that this noise stimulates the male, and maintains contact between him and his mate.

Figure 3. The stage of development of the chicks at the time when the female emerges from the nest and the chicks reseal the hole by themselves. The chick is of *Tockus nasutus*. Note the advanced development of the legs.

ADVANTAGES AND DISADVANTAGES OF THE SEALED-IN NESTING METHOD OF HORNBILLS

The comments made here are based on the results of the study of the *Tockus* hornbills in the Kruger National Park. The information is based on a sample of 149 nestings which were intensively studied: 22 of *T. nasutus*, 73 of *T. erythrorhynchus* and 54 of *T. flavirostris*. The nesting method makes detailed recording of the nest contents very difficult, and a successful nest is here taken as one rearing chicks, the success of individual eggs and chicks not being taken into account.

The most striking aspect of the study was the lack of predation occurring at the nest. Only *one* nest of *T. flavirostris* was robbed, and the circumstances of the predation only stress the safety of the sealed-in nest. The branch in which the nest was sited was bent down by an elephant, causing the nest cavity to split down the sides. The female hornbill, with small chicks, made a vain attempt to seal the splits, but a week later the nest was completely empty, although the pair of adults was seen near the nest. This nesting success can be compared with the success of similar-sized hole-nesters breeding in the same area, to illustrate that potential predators are present. Of six *Coracias caudata* nestings 33% were preyed on, of seven *Upupa epops* nestings 29% were preyed on, and of 12 *Lamprotornis australis* nestings 42% were preyed on.

Related to the subject of nest predation are the instances where the male bird was thought to have been killed. Hornbill remains have been recorded from the nests of *Terathopius ecaudatus*, *Aquila wahlbergi*, and especially of *Polemaëtus bellicosus* and *Aquila fasciata*. The consequences of death of the male hornbill are disastrous, since the chicks are nidicolous, and the female has temporarily lost the powers of flight. However, this was suspected to have occurred at only six nests (four *T. erythrorhynchus* and two *T. flavirostris*) representing 5.5% and 3.7% of the samples respectively. The female may not be affected in other genera of hornbills that do not undergo a complete moult, since Kilham (1956) reports no predation in 16 *Bycanistes subcylindricus* nests, but the male was killed at one nest. In this case the female was able to leave the nest.

The prolonged nesting period is a disadvantage insofar as whatever risks and vulnerabilities exist are prolonged. The death of the male parent is just such a risk. Another factor of interest, although of little consequence to the overall nesting success, is the risk of tree growth during nesting. The trees of the Kruger National Park are mainly deciduous, with the main growing period when the hornbills nest, during the rainy summer season. At three nests (two *T. nasutus* and one *T. erythrorhynchus* (9.1% and 1.4% of the respective samples)), the growth of the tree was such that by the time the chicks were ready to leave the nest, the entrance hole had grown together to such an extent that this was impossible. All three nests were in the marula tree *Sclerocarya caffra*, and the female, which leaves about 23 days before the chicks, was able to escape in each case. As the drive to feed the chicks diminishes, the consequences are fatal.

Dependence on the male for food is also a disadvantage, but only during dry summers when the food supply is low. Hornbills lay the eggs at intervals, but commence incubation with the first egg, so that the chicks are of different ages. The smallest chicks then perish from starvation during dry years, but this factor has never been known to eliminate a whole brood.

The effect of other factors is more difficult to assess. Two nests of *T. erythrorhynchus* and two nests of *T. flavirostris* (2.7% and 3.7% of the respective samples) were unsuccessful and were thought to have been flooded out. An advantage of the sealed-in nesting habit may also be that the chicks leave at an advanced stage of development which enhances their survival on leaving the nest, and the same may be true of the female emerging with her full feather complement. However, weighing up the evidence from the Kruger National Park study, the success of hornbill nesting (Table 1) may be considered as very good.

TABLE 1

AN ESTIMATION OF FACTORS AFFECTING THE NESTING SUCCESS OF *TOCKUS* HORNBILLS IN THE KRUGER NATIONAL PARK

Species	*T. nasutus*	*T. erythrorhynchus*	*T. flavirostris*
No. of nests regularly examined	22	73	54
% preyed on	0	0	0.9
% where male parent killed	0	5.5	3.7
% where tree growth closed the exit ...	9.1	1.4	0
% probably flooded	0	2.7	3.7
Total success	90.9%	90.4%	91.7%

HOW THE SEALED-IN NESTING METHOD MAY HAVE EVOLVED

It is important to the understanding of the nesting method to determine how it might first have evolved. The following are the factors that are thought to have evolved in order that the normal hole-nesting method, for example of the other members of the Coraciiformes, could have developed into the specialised hornbill nesting method:

(a) An increased and reinforced pair bond, and closely associated with this, the activities of the male to continue bringing food to the nest throughout the nesting period:

(b) The development and perfection of the sealing technique.

Firstly, within the hornbills it appears that the adult female has a rather special status compared with that of most other birds. The case of the social groups of *Bucorvus leadbeateri* has already been mentioned (Kemp 1969), where each group usually has only one adult female which is the centre of the social structure of the group, and is fed on the nest by all the members of the group. This character may also be exhibited by the Upupidae, the family most closely related to the hornbills among the Coraciiformes. Skead (1950) mentions two males of the normally monogamous *Upupa epops* feeding a female on the nest. It is also thought, from observations on three groups in the Kruger National Park, that the social groups of the wood-hoopoe *Phoeniculus purpureus* are centred around a single adult female. Here also the whole group feeds the incubating female and the chicks. *Bucorvus* is the only hornbill genus that does not seal the nest hole and their similarity in social structure to the related hoopoes indicates that this may be a primitive character. It is also possible that some of the hornbills which seal their nest holes are also social and may be centred on a single adult female. Hose (in Shelford 1899) records shooting a male of the Oriental hornbill species *Buceros rhinoceros* at the nest hole while it was feeding the female and reports that then "the young male birds fly to the nest and assiduously ply the bereaved widow with food". Sharpe (1890) also reports shooting five specimens of another hornbill *Anorrhinus galeritus* in a nest tree, two while they were in the act of feeding the female in the nest. Unfortunately the sex of the specimens is not recorded.

A further pointer to the importance of the adult females in the Bucerotidae is the fact that the juvenile birds either resemble the adult male, or are dissimilar to either adults in their secondary sex characters. Thus the bill colour of the juvenile *T. erythrorhynchus* is similar to that of the male; the bill of the *T. nasutus* juveniles approximates that of the male in colour; the bill of *T. flavirostris* juveniles has the same shape as the male; and Stonor (1937) describes the male characters of the immature female of *Rhyticeros plicatus*. Juveniles of the genus *Bycanistes* lack the large casque of the adults, which is only formed as they mature. The evidence of the importance of the adult female hornbill in the behaviour of the family is suggested as a vital factor in the development of the strong pair bond necessary to keep the male feeding the female throughout nesting.

With regard to the continuous feeding of the female by the male, this may be derived originally from courtship feeding. Feeding of the female by her mate is widespread in the coraciiform families, and has been recorded for the Meropidae, Coraciidae and Upupidae. In the Bucerotidae, courtship appears to consist almost entirely of the male feeding the female, but the feeding of the female on the nest is not restricted to this family alone. In all members of the Upupidae that have been observed, the male feeds the female while she is incubating, and the whole family for the first few days after hatching. Exactly the same has been observed for *Bucorvus leadbeateri*. In all these cases the female does leave the nest at times, but only for short periods. An extension of the feeding habits of *Bucorvus* or the Upupidae would then make possible the hornbill method of feeding the female and chicks throughout the nesting period. The loud call uttered by the female and chicks when taking food has been mentioned, and its role as a reinforcement to the activities of the male may be of importance in the evolution of this feeding method.

The sealing activities at the nest hole do not appear to require any special morphological adaptation by the hornbills. The technique is possible to any bird with a bill that displays sufficient lateral surface area, and the diversity of bill shape within the hornbills illustrates the range of "tools" that can be used. It is here suggested that the sealing behaviour derived from the commonest displacement activity of hornbills, that of bill cleaning. The cleaning actions (of stropping and wiping the bill on an object) are used in context after food has been handled, but they are also commonly done during conflict situations, as when captured birds are released or when low-intensity territorial disputes occur. It is possible that sealing evolved after nest sanitation: after handling nest debris the birds may have cleaned the bill on the nest entrance, the dirt on the bill adhering to the sides of the entrance. The members of the

SECTION 4. SOME OBSERVATIONS ON THE SEALED-IN NESTING METHOD OF HORNBILLS (FAMILY : BUCEROTIDAE).

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genus *Tockus* still produce effective sealing using dirt from the nest floor—food remains and their own faeces. The safety of the sealed-in nesting method has been shown, and so the ancestors to employ this method would probably have been favoured by selection.

SUMMARY

Adaptations which hornbills (Family Bucerotidae) show to their method of sealed-in nesting are considered. The method is highly specialised, and the advantages and disadvantages of the method are discussed. Most important is the freedom from nest predation that the sealed nest supplies, at least for the hornbills in the Kruger National Park.

Evolutionary trends for development of this nesting method are proposed. The special status of the adult female hornbill and the highly developed courtship feeding are thought to be very important. The sealing technique is suggested to have derived from a common hornbill displacement activity, bill cleaning.

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A STUDY OF THE BIOLOGY OF MONTEIRO'S HORNBILL

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(With one Plate and five Text-figures)

INTRODUCTION

A detailed ecological study of three species of hornbill of the genus *Tockus* [*T. nasutus* (Linnaeus), *T. erythrorhynchus* (Temminck) and *T. flavirostris* (Rüppell) (Kemp, in prep.)] in the bushveld of the Kruger National Park pointed to the need for a consideration of an arid region hornbill. After the first author made a reconnaissance of Valencia Ranch, South West Africa, for four days in July 1969, *Tockus monteiri* (Hartlaub) was chosen. Accordingly both authors returned on 9 February 1970 to spend three and a half months observing the hornbills.

Observations on the behaviour of *T. monteiri* are in preparation. The present paper deals with the biology, especially the breeding biology, of this hornbill.

STUDY AREA AND METHOD

Figure 1 shows the areas visited in South West Africa during the study, and their position in relation to the total distribution of *T. monteiri*. The bulk of the work was done on Valencia Ranch, 23°10'S, 16°25'E, with short visits of two days to the Jensen's study area on the farm Ameib in the Erongo Mountains near Usakos, to Daan Viljoen Game Reserve outside Windhoek, and to the Waterberg inselberg.

Valencia Ranch is situated just on the lip of the escarpment where the South West African highlands drop to the Namib Desert. At an altitude of about 1700 m above sea level, the terrain is of very rugged steep hills of mica schist, rocky and sharply contoured due to the low average rainfall of 100 mm per annum. The Hakos Mountains rise out of the escarpment along the western edge of the Ranch, and the bed of the seasonal Hakos River runs along their base.

The study area was centred on our camp Howaldt at the confluence of the Hakos and Tsowasis Rivers (fig. 2) and extended about 2,3 km south and 1,3 km north of the camp. The rivers and their tributaries cut deep into the terrain, and have large exposed vertical rock faces at places. The rock faces are important to the hornbills. Large trees (Acacia karroo, Zizyphus mucronata with fewer A. giraffae and scattered Tamarix species) grow along the beds of the Hakos and Tsowasis Rivers. Away from the rivers the only large trees are occasional Boscia albitrunca, and the vegetation is mainly Acacia detinens bushes on the hillsides and flats, Combretum apiculatum dominating on the steepest slopes, Dombeya rotundifolia on the floors of the gorges into the Hakos Mountains, and bushes of Bauhinia species and Grewia species scattered throughout. Grass was in scattered tufts throughout, but for a few small patches on the silt beside the river beds. Plate 23 shows the general aspects of the area.

The total rainfall for the 1970 season, up to the end of the study on 15 May 1970, was 91 mm. The rainfall régime was December: 7 mm, January: 56,5 mm, February: 22,5 mm, March: 3,5 mm and April: 1,5 mm. By 13 February, 86 mm (or 95%) of the season's rain had fallen, and this allowed us to compare conditions during the dry season of our July visit and during the wet season.

Our observations were confined to the study area, except for recording nests that we found elsewhere. Work was done on foot as roads are lacking in the area, which is near-natural with all wildlife conserved. Observations were made using 8x binoculars, but a 50x telescope was used for observations from hides.

RESULTS

All nests were numbered in the sequence found, and their positions are shown in figures 2 and 3. All nests used in the study area were found, but due to the extreme wariness of the birds we often had to climb to the crest of the Hakos Mountains and watch for the whitish specks below that were hornbills. While arduous, this method permitted us to keep large areas under surveillance at one time, and allowed us to plot out the territories of the pairs with some accuracy. Once nests had been located, hides near the nests permitted detailed observations.

NEST SITE. Eleven nests were located in the study area, and another four were found elsewhere on the Ranch. Table 1 gives the details for each nest site. Eleven of the nests were in rock holes, four in tree holes, and of the latter only one was in the study area.

The height of nests above the ground varied from 0,2 to 39 m, being highest on some of the rock faces. The majority of the nests had a westerly aspect (60%), because the mica schist was inclined in that direction and so cliffs were formed on the western side, but remaining nests faced in all directions. The nest cavities were large, averaging 32 cm at their widest, the floor being only 10 cm below the nest entrance on average. Only 13% of the nests had good "funkholes" in which the female or chicks could hide, because the rock holes were rather round in shape.

Most of the nests had very large entrance holes, especially those in rock holes. As the females of *T. monteiri* seal up the entrance to leave a small slit, these require much work to be sealed. The largest (nest 14) required some 600 cm^2 of sealing area. Nest 1 with an approximate area to be sealed of 294 cm^2 required at least 14 days for closure. However this work is only needed for the initial sealing, for often the same hole is used year after year (Port, pers. comm.), and when they break out of the nest they only make a hole about 4 x 5 cm, and this is all that has to be closed the following year.

As with other members of the genus, the female does all the sealing work, using mud collected after the rains for the initial work, and her own droppings and nest debris for closing the small hole through which she finally enters. However in this species the male will occasionally assist by bringing mud to the female, passing it to her as in courtship feeding. He will rarely feed her a millipede, which she does not eat but uses for sealing. The nest lining consists of dry leaves, Acacia pods, grass stems, bark flakes and snail shells, and is brought by the male. Food remains are also mixed into the lining. These lining items are brought most frequently during the early part of the female's enclosure, but occasionally throughout the nesting cycle.

NEST TERRITORY. Figure 3 shows the spacing of the nests in the study area, and the area around each nest that was defended and utilized by the pair. X was a pair of birds whose nest hole was not found, but which certainly never bred. The territories were marked by following the movements of the birds from the mountain crest, and also noting where territorial conflicts were seen. The average area of a territory is 0,15 km^2. A large proportion of the study area was not utilized by hornbills: the higher reaches of the Hakos Mountains and the open flats between the Hakos and Tsowasis Rivers. It appears that suitable nest cliffs sufficiently well spaced so that pairs are not in conflict, may be in short supply. Holes in the cliffs were abundant, and were therefore not a limiting factor. Thus the nesting territories were strung out along the rivers where the cliffs are, the mountains and flats without nest sites being vacant.

NESTING CYCLE AND SUCCESS. Details of the activity at each nest are given in Table 2.

No nests which were subsequently used for breeding were found before laying had started. Any interval between the female sealing herself into the nest and laying the first egg could therefore not be accurately determined, but indirect evidence was obtained that indicated an interval of at least four days. Subsequently nests were examined each afternoon, so that incubation and nesting periods were found to the nearest day. The average incubation period was found to be 25 days (24 days for three eggs, 25 days for two eggs and 27 days for one egg). The nestling period for five chicks varied; 43 days, 44 days, 45 days for two chicks, 46 days. Incubation starts with the first egg and so the chicks hatch at intervals (Table 3). The interval between laying of successive eggs in a clutch increases as the clutch proceeds, and is reflected in the intervals between the hatching of the chicks. From this it is useful to record the interval between the hatching of the first and last chicks, determined in four instances as 10 days (for a clutch of five), nine days (for a clutch of four), six days (for a clutch of four) and four days (for a clutch of three). The time of emergence of the female from the nest, recorded in four instances, and expressed here as the number of days after hatching of the first chick was 21 days for two nests, 22 days and 24 days. The chicks re-seal the nest themselves after the female has emerged.

Measurements of 13 eggs gave an average of 41,0 x 28,1 mm, with a range of 43,7 - 37,2 x 29,2 - 27,0 mm.

The average clutch, for eight nests, was 4,4 and ranged from three to five eggs. Two nests were robbed, probably by native shepherds, and in one nest an egg was broken while being measured: these unnatural factors are discounted in the following calculations. The resulting hatching success was 18 chicks from 23 eggs or 80%. The fledging success, expressed as chicks fledged from eggs laid was 30% (seven chicks from 23 eggs), or expressed as chicks fledged of eggs hatched was 39% (seven chicks from 18 hatched). The same observations were not possible on every nest, but for eight nests the average clutch was 4,4 eggs, for five nests an average of 3,8 chicks was hatched, and for ten nests an average of 1,5 chicks was fledged from the nest.

Taking the study area as a unit, there were 12 pairs present. Three pairs did not breed, one pair deserted before laying due to our disturbance, and the remaining eight pairs fledged a total of 15 chicks. This gives a replacement rate for this population during the 1970 season of 0,63 chicks per adult. Only one natural factor was responsible for this low reproductive rate and that was starvation of the chicks after hatching. In all the nests examined none of the chicks was naturally preyed on (excluding the two robbed probably by Natives) and the chicks died off in the opposite order to that in which they hatched. The smallest chicks became thin and weak and died, and as the dead chicks were too large to be thrown out of the nest they were always seen on the nest floor.

TIMING OF NESTING. The dates of commencement of nesting are estimated from the various periods found for the nesting cycle, and by accurate aging of the chicks by recording their development in detail. Figure 4 shows the rainfall régime for the area during the 1970 season, with the estimated number of nests started each day plotted above it. It is clear that breeding was started over a spread of 12 days, 23-35 days after the first heavy rains for the season fell on 30 January. By the time that nesting started all the vegetation had come out in new foliage, and new hatchings of many arthropods were apparent, so that by this time possibly the food supply was sufficient to trigger nesting.

FEEDING. Table 4 shows the items brought to nests during 28 hours of hide-observation; a sample of 95 items, with 4-hour observation periods spread over the whole nesting cycle. 19% of all the items were for nest lining or sealing, and of the food items, all of which were arthropods, 51 (70%) were the large "dikpens" crickets (*Acanthoplus* species). Feeding rates were recorded during the 4-hour observation periods, and ranged from one feed/hour up to 3,5 feeds/hour while only the male was feeding the nest inmates. When the female had broken out and was assisting the male in feeding the chicks, rates of 5,8 and 5,9 feeds/hour were recorded. In both observation periods the male fed more often than the female; 3,8 feeds/hour compared to 2,1 feeds/hour and 3,0 feeds/hour compared with 2,8 feeds/hour.

However, this is complicated by the fact that *T. monteiri* is the first African member of the genus found to carry more than one food item in the bill at the same time when coming to the nest. This is true of both sexes, and is done rather randomly, presumably being linked to the finding of several food items during one foraging trip. Twice it was seen how this is accomplished, the adult killing one insect in the bill by squeezing it, then dropping it to pick up and kill a second, then placing them on the ground and picking both up together. The maximum seen in the bill at one time was three items. At the nest the bill-full was presented and, when seized by the inmates, was released. If any of the food items were dropped they were picked up and re-presented, but at nest 9 the male would always place his load at the base of the nest cliff and then take them up to the nest one at a time. Possibly this was because this nest had no sill below the entrance, and so any food dropped fell to the base of the cliff and the male had accordingly learnt to modify his habits.

The birds did most of their foraging on the flatter areas above the rivers among the Acacia detinens bushes, with very little in the river beds or on the steep sides of the river beds. All food was seen to be taken on the ground, the birds picking up arthropods as they saw them. In July 1969, on the journey both to and from Windhoek, flocks of up to 47 hornbills were seen on the plateau. These birds were digging trenches up to 30 cm long and 5 cm deep into the pebbly substrate and were feeding on small bulbs that they found. At this time only four hornbills were seen on Valencia Ranch during four days. By the time we left Valencia Ranch on 15 May some flocks of up to six birds were seen for the first time in the area, only one to two weeks after the chicks had fledged.

DEVELOPMENT OF CHICKS. At the tree nest, nest 8, the side of the cavity was cut open so that the chicks could be measured and described at 4-day intervals. The nest had five eggs, hatched four chicks, but only one of these survived to fledging when 46 days old and this is the one here reported on. Figure 5 illustrates the growth pattern of the chick. It can be seen that the legs were fully grown by the 22nd day when the female left the nest, but wings, tail and bill continued to grow until it flew. The development of the chick can be described as follows:

Age (days)	*Description*
1	Naked, eyes closed, but abdominal feathers just visible through skin. Skin pink, and bill pinky-cream. Upper mandible about 2 mm shorter than lower.
4	Dark feathers showing through skin at base of bill, on elbows and upper tail coverts. Pale feathers showing on abdomen.

9	Fourth chick dead. Quills just emerging on head, legs, abdomen, upper tail coverts, upper wing coverts, auriculars. Claws darkening and legs just showing some grey colouring. Bill turning orange, especially near tip, but upper mandible still just shorter than lower. Eyes just beginning to open.
12	Feathers just breaking out of quills on breast, legs, wing coverts, head, tail coverts. Quills emerging on back, front of neck and eyelashes. Bill yellow-orange, legs grey, claws black. Eyes open, dark brown in colour. The mandibles are of equal length.
16	Third chick dies. Quills now out all over, even on the neck. Feathers breaking out of quills on back, eyelashes, front of neck, and about one-third out of quill on abdomen and legs, with the head, tail coverts and wing coverts a little more retarded.
20	Feathers almost covering the head and wing coverts, and covering the abdomen and legs completely. Remiges and rectrices now apparent as quills. Peri-orbital skin becoming yellowish.
25	Feathers covering all over, but for the upper back. Female left the nest when the chick was 22 days old.
28-46	Second chick dies when the oldest is 32 days old. Feathers are now covering all over, but the remiges and rectrices elongate until they are almost fully grown by the time that the chick emerges.

The newly fledged chick has the full adult plumage, except that the feathers, especially the wing coverts, are tipped with light brown. The eye is dark brown, and the bill orange compared to the bright red of the adults. The bill is also markedly shorter than that of the adult, rather thicker in appearance, and with the upper mandible sharply curving on the top edge without any sign of a casque. The feet and legs are black.

FEMALE MOULT. It was noted even before the females sealed themselves into the nest that some had tail moult in progress. Two females of nests 8 and 11 were examined for moult. They had dropped all their old remiges and rectrices simultaneously on entering the nest hole to breed, but had retained feathers that were new or growing prior to nesting. This gave them feathers of different lengths, a phenomenon not usually recorded for other species of *Tockus* females in the nest, in which moult starts only at nesting, so that all old feathers are shed simultaneously and new ones are growing in evenly. Body feather moult was in progress on both females examined.

DISCUSSION

T. monteiri has an extremely limited overall distribution, as shown in Figure 1. It is confined to the arid regions of the northern half of South West Africa and southern Angola, from the borders of the Namib Desert to varying distances further east up to about 200 km (Sanft, 1960). The area is predominantly rocky, and breeding appears to be confined to the hilly and mountainous regions. Hoesch (1937) mentions a tree-hole nest at the base of the Waterberg. We know also of a rock-hole nest in the Windhoek Museum from the hills above the city, six tree-hole nests found by the Jensens at Ameib in the Erongo Mountains and a rock-hole nest at the Daan Viljoen Game Reserve outside Windhoek (nest record card of C. Clinning). In our travels to Ameib and the Waterberg in February, and between Windhoek and Valencia Ranch during the study period we saw no *T. monteiri* away from the hilly areas. This was in marked contrast to the flocks seen on the plateau during the short July visit. We suggest that they breed in the hilly regions of their range and form into flocks that spread onto the flats during the dry season. It appears that digging for food is done mainly during the dry season. The birds thus adopt a special foraging method for the leanest time of the year. We have found this also in *T. erythrorhynchus* (Kemp, in prep.).

T. monteiri shows some interesting adaptations to its arid environment. With suitable nest holes in trees in short supply, holes in rocks are regularly used. This was also found to be true for other species of birds on the Valencia Ranch that are usually thought of as tree-hole nesters; the only three nests of *T. nasutus* found, and one of *Coracias naevia* Daudin, were in rock holes. It is difficult to determine whether the hornbills prefer rock holes or tree holes, but it appears that tree holes are used if available. The only tree found in the Valencia study area with a suitable hole was used (nest 8), although it was set among rock faces with many suitable holes. At Ameib six nests were in trees along the Kahn River, although rock holes were available in the nearby Erongo Mountains. However the mountain sites may have been occupied by other pairs.

Bringing more than one food item to the nest in the hill at one time was recorded for the first time for an African *Tockus* hornbill. This would be economical in reducing the number of visits that adults have to make to the nest, as well as allowing a food source at one spot to be quickly exploited. The role of the female in assisting the male with feeding the chicks once she has broken out of the nest is much greater in *T. monteiri* than for the other species we have studied (*T. nasutus, T. erythrorhynchus* and *T. flavirostris,* Kemp, in prep.). Both these patterns would be of use for a species in an arid region where starvation of the chicks during the nestling period can be a major factor limiting reproduction.

The irregular, limited rainfall of the region may also explain why the male sometimes assists the female by bringing mud for sealing as this is only temporarily available after rain. This assistance may also be linked with the large nest entrances that sometimes have to be sealed. Similarly the commencement of moult by the female before she starts to nest may be due to the uncertainty of when rain will fall to allow nesting to begin.

The large clutches laid, many of five eggs (R. Jensen has recorded a clutch of seven), indicate that this species may have a potentially higher reproductive rate than was recorded for our 1970 study. During our study period an average amount of rain fell for the season, but only 5 mm of the 91 mm fell after breeding had begun. As we observed, lack of rain after commencement of breeding means that the area becomes quite dry before the nesting cycle of 75 days is completed, with a corresponding decrease in the arthropod food supply. However, the hornbills could not estimate the rain that might fall subsequent to their starting to breed, and so the large clutches may be on the chance that good rainfall will follow. The clutch size may also be related to how good the conditions are prior to the start of breeding. The reproductive life of these birds is unknown, but with the replacement rate of 0,63 chicks per adult for the 1970 study, a pair would have to breed for four seasons merely to have replaced themselves in the population.

T. monteiri hops on the ground, in contrast to the other terrestrially foraging members of the genus which walk. This appears to be an adaptation to the rocky substrate on which it operates, where walking with its short legs would be difficult.

Two other members of the genus (*T. nasutus* and *T. flavirostris*) also lived and bred on Valencia Ranch during our study, but the ecological separation between the species was very clear. *T. monteiri* and *T. flavirostris* are terrestrial foragers, but while the former fed mainly on the slopes adjoining the rivers, the latter was confined to the river beds and the few flat, grassed areas away from them. *T. monteiri* bred frequently in rock holes, while the five nests of *T. flavirostris* found were all in trees on river banks, and none was in the study area. *T. nasutus* is an arboreal forager and most feeding was done in the riparian vegetation with short forays to the bushes above the rivers. Three nests of this species were found, all in rock holes in the study area, two of them on the same rock faces as used by pairs of *T. monteiri*, indicating that there is no direct competition between the species.

ACKNOWLEDGEMENTS

The work was made possible by a grant for running expenses from the South African Council for Scientific and Industrial Research. The success of the study was in large part due to the facilities and hospitality given by the owners of the Valencia Ranch, Mr and Mrs Attila Port, whom we thank most gratefully. Drs Rolf and Mary Jensen helped with comments, and by showing us hornbills in one of their study areas. Prof. J. M. Winterbottom allowed us to examine the nest record cards housed at the Percy FitzPatrick Institute of African Ornithology. Drs G. L. Maclean and C. K. Brain made many useful comments after reading the manuscript.

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TABLE 1—Details of *Tockus monteiri* nest sites on Valencia Ranch, South West Africa, in the 1970 season.

Nest no.	*Nest site*	*Cliff height (m)*	*Height of nest from ground (m)*	*Direction in which nest faces*	*Depth of cavity (cm)*	*Depth of floor from entrance (cm)*	*"Funkhole" present*	*Nest entrance width × height (cm)*	*Area of territory (km²)*
1	Rock face	30	15	west	27	8	—	21 × 14	0,11
2	Rock face	7	2	west	cavity not measured.				0,11
3	Rock face	10	7	north	40	10	—	23 × 22	0,10
4	Rock face	25	1,6	west	35	1	—	10 × 20	0,18
5	Rock face	7	5	west	30	12	—	27 × 22	0,21
6	Rock face	40	25	north	35	5	—	13 × 8	0,13
7	Rock face	40	39	west	nest in inaccessible position.				0,14
8	Trunk of Boscia albitrunca	—	2	east	20	8	—	7 × 9	0,15
9	Rock face	7	4	west	32	8	—	7 × 6	0,16
10	Rock face	3	2	north-west	40	12	—	25 × 12	0,12
*11	Dead stump of Acacia karroo	—	2,3	south	17	10	—	44 × 10	—
*12	Trunk of live Acacia karroo	—	3	south-west	17	10	—	38 × 3,5	—
13	Rock face	50	3	north	25	12	—	15 × 16	0,12
*14	Rock face	10	4	north	60	12	+	20 × 30	—
*15	Base of trunk of dead tree	—	0,2	north-west	34	18	+	13 × 5,5	—

X Pair with territory in study area whose nest was not found, but which never bred. 0,21

* Nests outside the study area.

TABLE 2—Individual details of nesting cycle of *Tockus monteiri* nests on Valencia Ranch, South West Africa, in the 1970 season.

Nest no.	*Breeding attempted*	*Estimated date of ♀ entering the nest hole*	*Clutch*	*Chicks hatched*	*Chicks fledged*
1	+	24 February	♀ deserted before laying due to our interference		
2	—	—	—	—	—
3	+	22 February	5	5	2
4	+	24 February	4	4	2
5	—	—	—	—	—
6	+	4 March	4	3	1
7	+	—	nest inaccessible		1 (seen with adults soon after leaving nest)
8	+	1 March	5	4	1
9	+	26 February	4	—	2
10	+	28 February	5	3 (one egg broken during measuring)	1
*11	+	6 March	5	nest robbed, probably by Natives	
*12	+	6 March	3	nest robbed, probably by Natives	
13	+	1 March	—	—	1
*14	+	24 February	—	—	1
*15	+	1 March	—	—	3
X	—	—	—	—	—

* - nests outside the study area.

TABLE 3.—Interval between laying of eggs and hatching of chicks in nests of *Tockus monteiri* on Valencia Ranch, South West Africa, during the 1970 season.

Interval, to the nearest day		*Nest 3*	*Nest 4*	*Nest 8*	*Nest 10*
Laying interval between:	1st and 2nd eggs	—	1	—	—
	2nd and 3rd eggs	—	1	—	—
	3rd and 4th eggs	—	3	—	—
Hatching interval between:	1st and 2nd chicks	1	1	1	2
	2nd and 3rd chicks	4	2	2	2
	3rd and 4th chicks	1	6	3	—
	4th and 5th chicks	5	—	—	—

TABLE 4.—List of items brought to nests by *Tockus monteiri* on Valencia Ranch, South West Africa, in the 1970 season.

Item brought	*Nos. brought*	
Seed pods, snail shells, bark, grass	15	(used for nest lining)
Millipedes	3	(used for sealing)
Centipedes	1	
Tettigoniidae	1	
"Dikpens" crickets (*Acanthoplus* species)	51	
Large white moths	3	
Catepillars	3	
Buprestidae	1	
Meloidae	1	
Unidentified arthropods	14	
TOTAL	95	

Other remains found below nests: Tenebrionidae, Acrididae, Cetoniidae, large lepidopterous pupa.

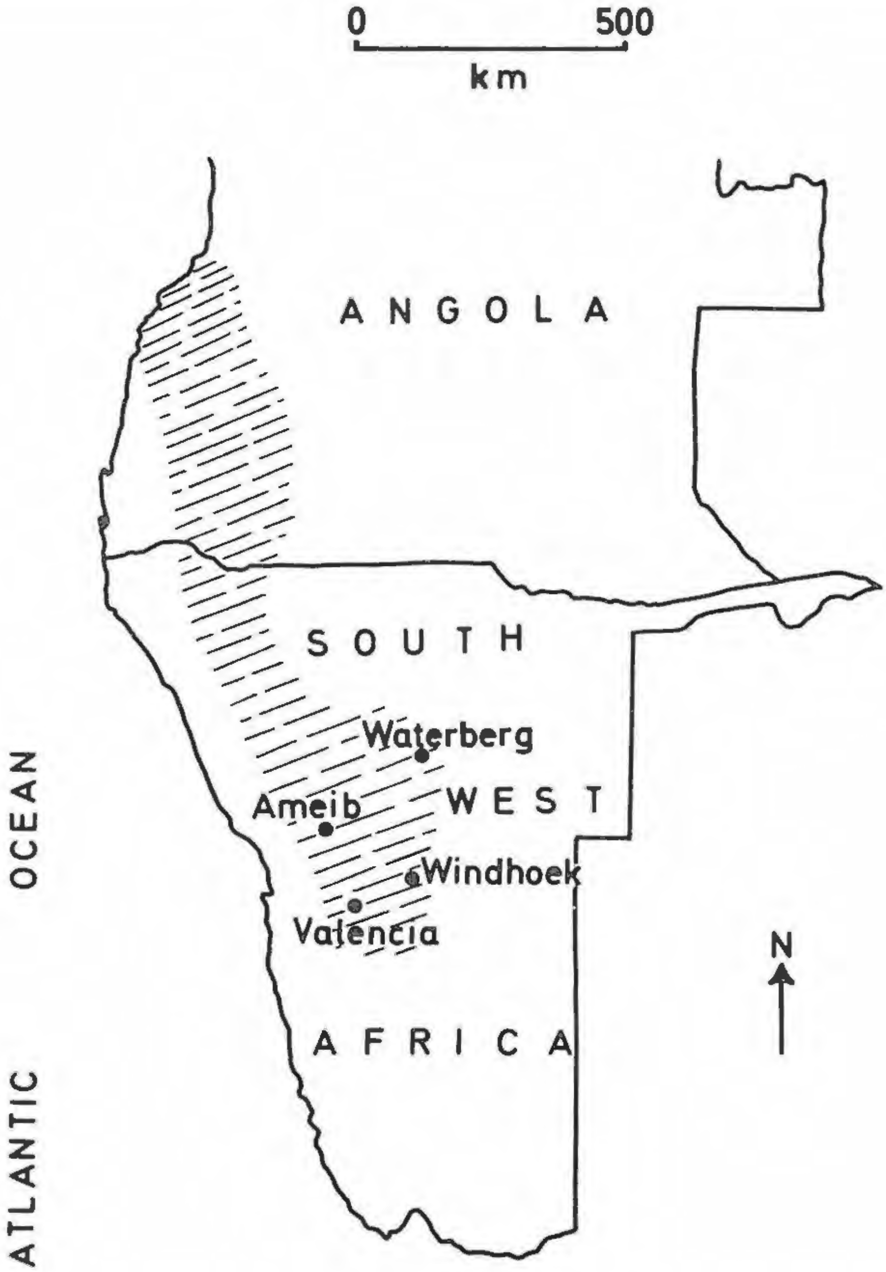


Fig. 1. Map of South West Africa, showing localities visited during a study of *Tockus monteiri*. Cross hatching - total distribution of *Tockus monteiri* (after Sanft 1960).

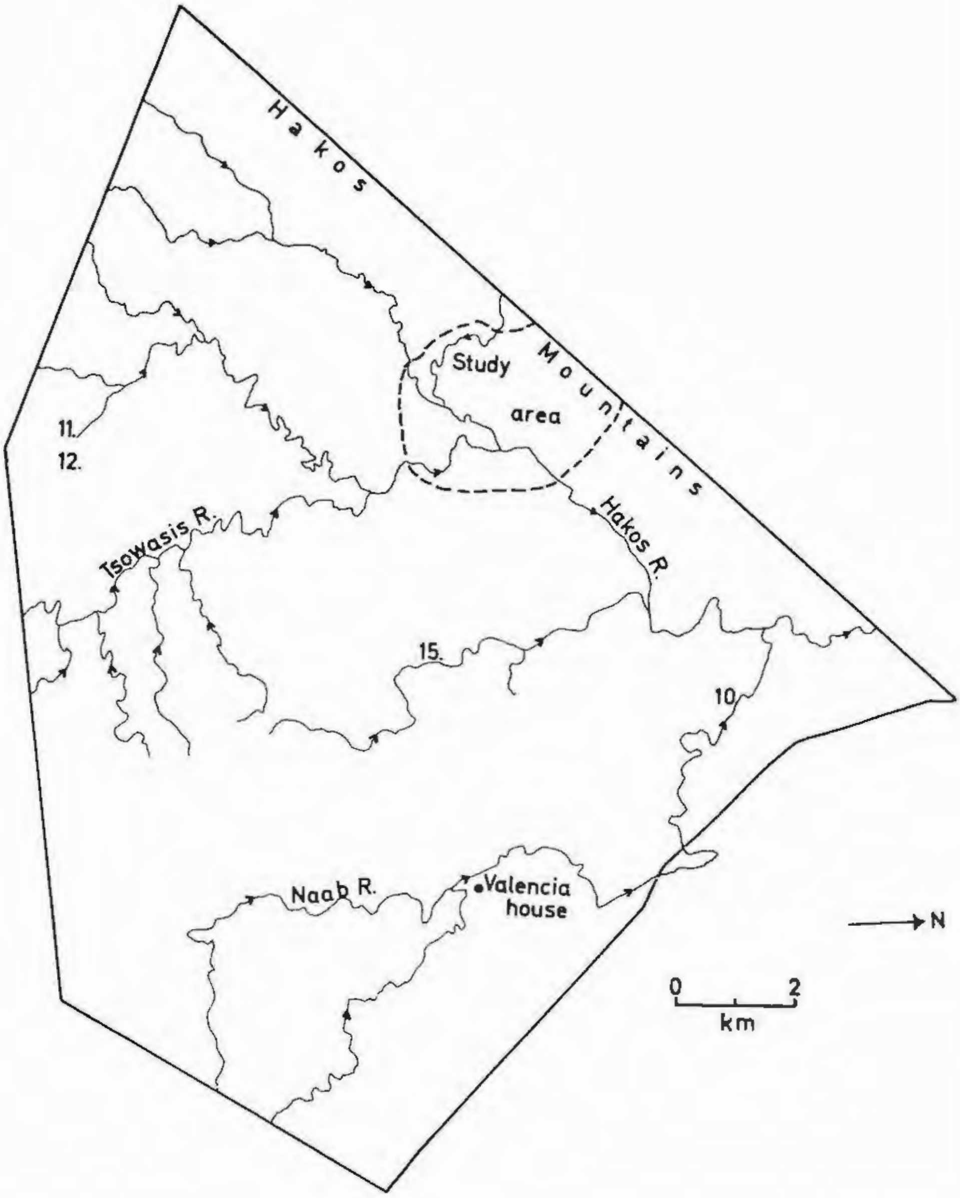


Fig. 2. Map of Valencia Ranch, South West Africa (combining farms Valencia and Portsmut), showing position of the study area. Numbers are of nests found outside the study area, to show their position on the Ranch.

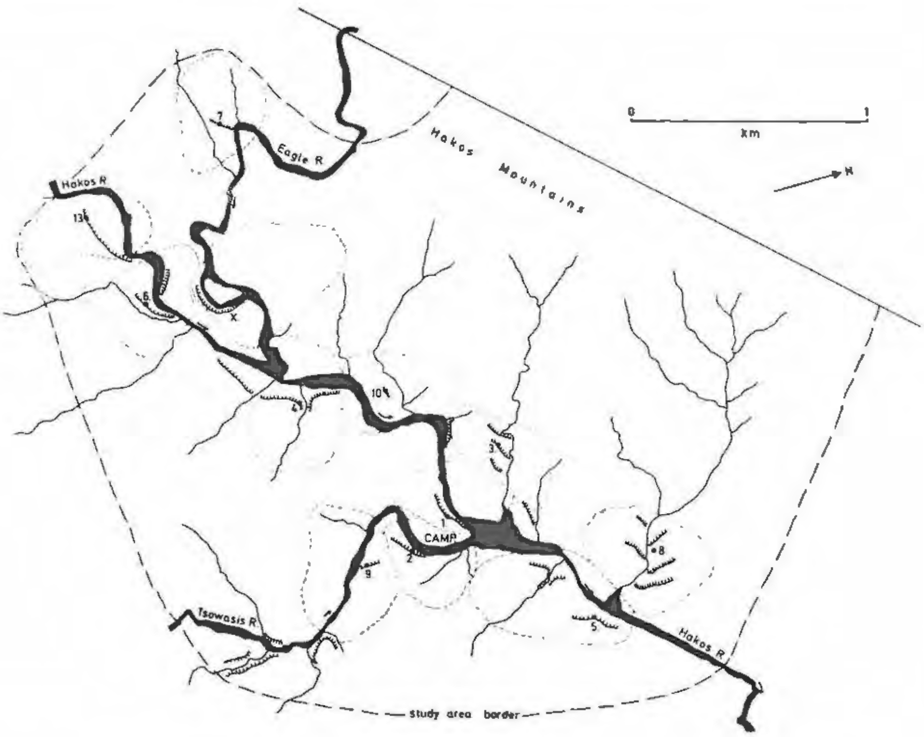


Fig. 3. A map of the Valencia Ranch study area, from an aerial photograph, showing the rivers (solid black) and cliff faces (- - - -) in the area. The positions of nests of *Tockus monteiri* are marked and numbered, and the boundaries of each territory (– – – –) marked.

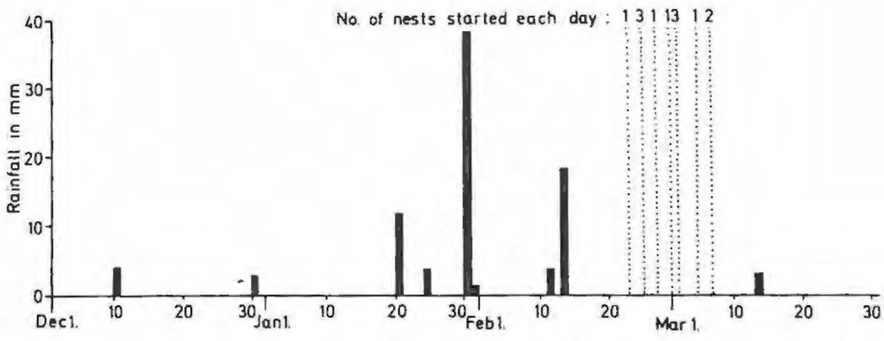


Fig. 4. Histogram showing the rainfall régime on Valencia Ranch during the 1970 season, with the number of nests started each day plotted above it.

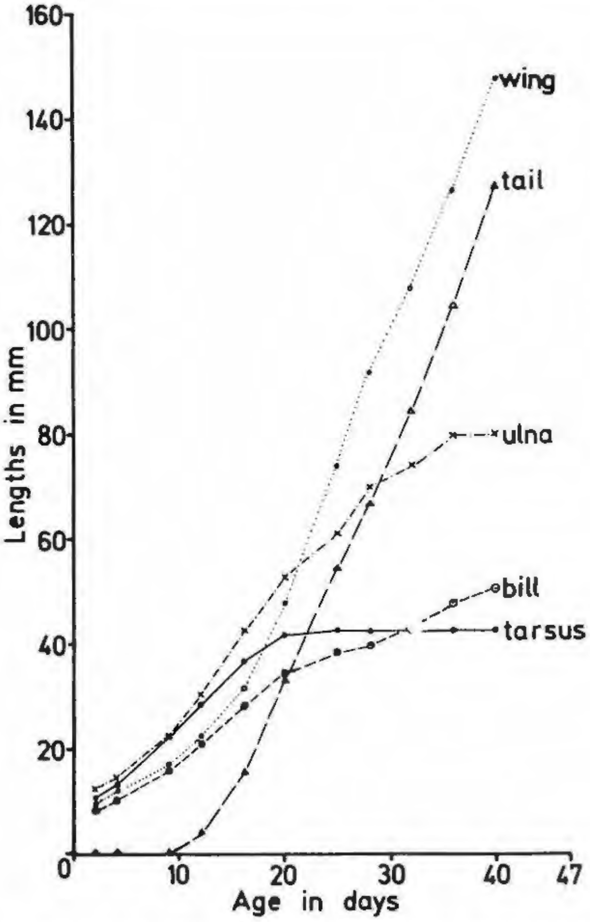


Fig. 5. Growth pattern of a *Tockus monteiri* chick, shown by graphs of regular measurements of the lengths of wing, tail, ulna, bill and tarsus.

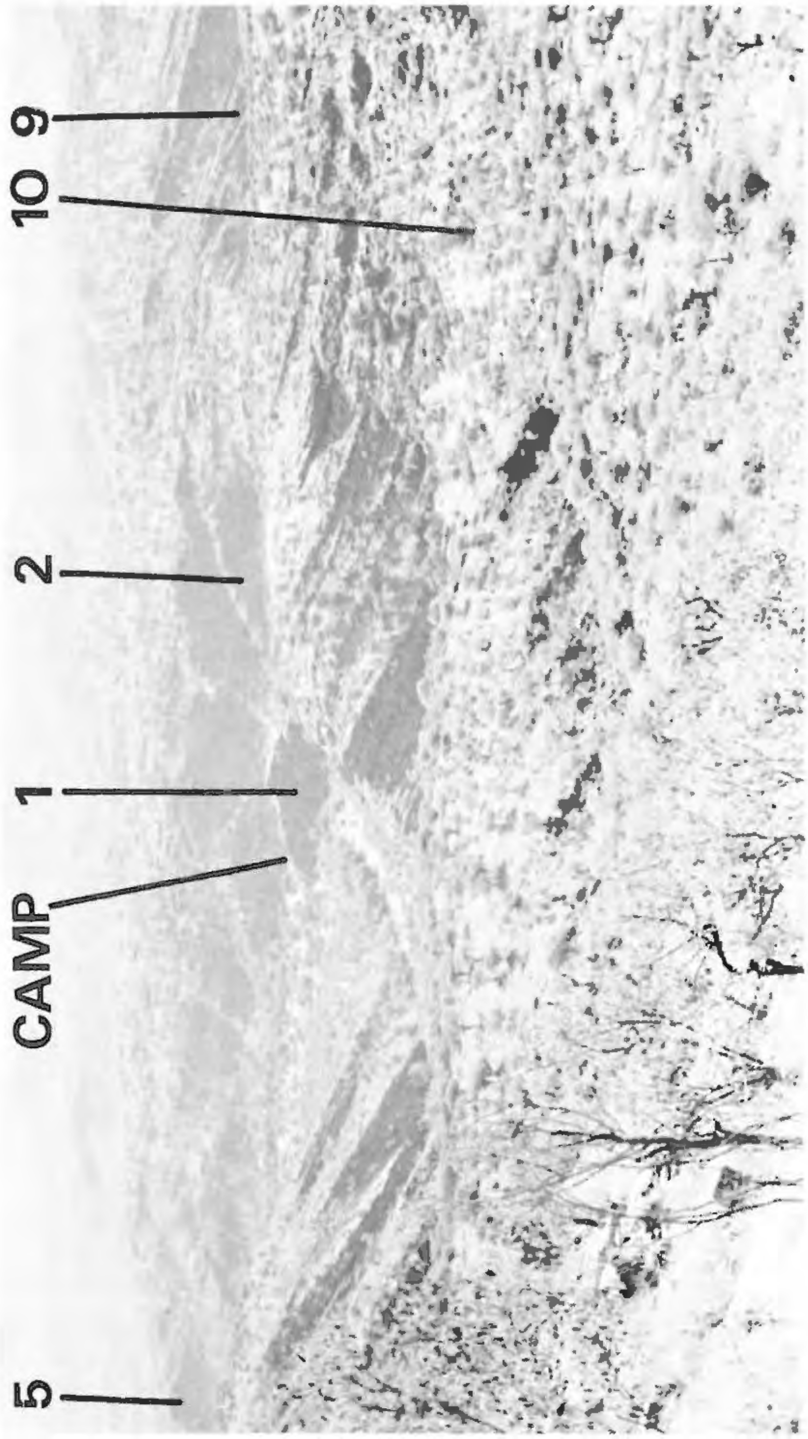
PLATE 23

A view over the Valencia Ranch study area from the crest of the Hakos Mountains. The camp at the confluence of the Hakos and Tsowasis Rivers is marked, and the numbers show the position of nests in the area.

SECTION 5. A STUDY OF THE BIOLOGY OF MONTEIRO'S HORNBILL.

Paper co-authored with my wife, published in Annals Transvaal Mus. 27(13):255-268.

Annals Transv. Mus. *Vol. 27, No. 13* *Plate 23*



SECTION 6. ENVIRONMENTAL FACTORS AFFECTING THE ONSET OF BREEDING IN SOME SOUTHERN AFRICAN HORNBILLS (BUCEROTIDAE).

INTRODUCTION.

This section is a modification of a paper presented at the Third International Symposium on Comparative Reproduction (Edinburgh, 1972) and is in press for the proceedings to be published in the *Journal of Reproduction and Fertility*.

The breeding of *Tockus nasutus*, *T. erythrorhynchus* and *T. flavirostris* was observed in the central Kruger National Park during the wet seasons of 1966-67, 1967-68, 1968-69 and for a brief period at the beginning of the 1969-70 season. From February 1970, a complete breeding season of *T. monteiri* was observed in South West Africa (Section 5), with supplementary observations on *T. nasutus* and *T. flavirostris* in that area.

It was possible, by knowing, or calculating, the dates of onset of nesting for all hornbill nests, to compare these dates to known variables such as temperature, day length, rainfall and arthropod abundance. The comparisons allow some deductions on the relative importance of these variables in determining the timing of onset of breeding, ? and the results concur well with the behaviour which precedesnesting.

METHODS.

Nest contents were examined when a nest was first found, and where possible at intervals thereafter. Knowing the duration of each phase of the nesting cycle, and especially the exact development pattern of the chicks (Section 7), it was possible to estimate the date, accurate to about three days, when the female entered the nest.

Daily rainfall and maximum and minimum temperatures were recorded at the centre of each study area, at Satara ($23^o24'S$, $31^o47'E$) in the Kruger National Park, and at Howaldt ($23^o10'S$, $16^o25'E$) on Valencia Ranch, South West Africa.

Within 1 km of Satara, Kruger National Park, arthropod biomass was sampled at three day intervals from June 1968 to April 1969. Two methods were used. Two funnel traps, of 15 cm diameter, were sunk in the ground, and arthropods falling in were weighed at each collection. This had to be discontinued in December 1968 when a baboon troop also found the traps productive! Secondly, as detailed in Section 3, 100 sweeps were made through long grass with a 60 cm diameter net, in two adjacent areas. Arthropods collected in the net were weighed at the end of each 100-sweep transect.

In June 1967, and from September 1967 to October 1968, hornbills shot near Satara (Section 3) for stomach content samples were also examined for breeding condition. The diameter of the largest follicle in the ovaries of females, and long and short diameters of both testes of males were measured. The volume of the testes was calculated, and averaged for each specimen, using the formula for the volume of an ellipsoid: $V = 4/3 \pi a^2b$, where a = ½ the shorter diameter, and b= ½ the longer diameter.

RESULTS.

The dates of the commencement of nesting, plotted against the maximum and minimum temperatures and rainfall, are shown in Figure 26, for *T. nasutus*, *T. erythrorhynchus* and *T. flavirostris* in the Kruger National Park. Similar results, for a single season on Valencia Ranch, are shown in Figure 27, for *T. monteiri*, *T. nasutus* and *T. flavirostris*.

In the Kruger National Park, the date of the earliest nesting varies between species and seasons. The range is for *T. nasutus* from 20 October to 8 November, for *T. erythrorhynchus* from 30 October to 27 November, and for *T. flavirostris* from 24 October to 18 November. The latest dates of onset of nesting recorded are 3 December for *T. nasutus*, 1 March for *T. erythrorhynchus*, and 19 December for *T. flavirostris*, except for one record of a second brood of the latter starting on 7 March. The spread of nesting onset varies for the species and is compact at 22-25 days for *T. nasutus*, and 26-37 days for *T. flavirostris*. *T. erythrorhynchus* may have the nesting onset spread from 29 days (1968-69 season) up to 95 days (1967-68 season). This excludes the instances of second broods (of *T. erythrorhynchus* and *T. flavirostris*) in the 1968-69 season, and all results of the 1969-70 season which was not covered completely.

The small sample from South West Africa (Figure 27) indicates similar results, with an especially compact nesting onset of *T. monteiri* of 12 nests over 12 days, from 22 February to 6 March. The dates of nesting onset of *T. nasutus* and *T. flavirostris*, beginning on 26 December and 3 February respectively, are about two months later than those in the Kruger National Park for the same summer.

There is no correlation between maximum and minimum temperatures and onset of nesting. Temperatures are higher during the summer wet season, but have considerable short-term fluctuations. This makes temperature, as such, an unlikely proximate factor in initiating nesting. This was emphasised in mid-November 1968, when unseasonal cold, together with almost continuous rain, invaded the eastern half of southern Africa. It was so severe that widespread mortalities of birds and mammals were reported throughout the sub-continent (Steyn and Brooke 1971). At this time, in the Kruger National Park, the first nests of all three hornbill species were being started, and courtship and nest preparation were continued.

In all four Tockus species nesting onset is coincident with rainfall, and no nests were recorded before the first rains of each season. The amount of rain falling before the onset of nesting appears to vary for each species, being least for T. nasutus, intermediate for T. flavirostris, and most for T. erythrorhynchus and T. monteiri in their respective areas. Figure 28 indicates the degree of "wetness" recorded before onset of nesting for each hornbill species. For all seasons studied, the "wetness" threshold is lowest for T. nasutus, intermediate for T. flavirostris and highest for T. erythrorhynchus. The same sequence was found in South West Africa, except that T. monteiri takes the place of T. erythrorhynchus, and the threshold appears to be low for all the species involved. Seasonal differences in threshold appear to be linked to the amount of early rainfall before nesting onset. The fewer the days with rain (i.e. the higher the ratio of total days of the wet season to the number of days with rain), the more rain that falls before the onset of nesting.

The pattern of rainfall during a season appears to be related to the spread of nesting onset, especially in T. erythrorhynchus. In the 1966-1967 season, although the start of the rains appears normal, subsequent rain fell in small amounts, although quite frequently. Nesting onset was very spread out in T. erythrorhynchus, with most nests starting during the heavier rains of December 1966. During this season the spread of nesting onset in T. flavirostris was also the widest recorded. The 1967-68 season also started normally, but was followed by a prolonged and severe drought in December and January. Some nests of T. erythrorhynchus were started after each major rainfall that followed the drought, and the latest dates of onset of nesting were recorded in that season. In both seasons, the first nests of *T. erythrorhynchus* started after the second good falls of the season. The 1968-69 season may be considered an ideal season, with regular heavy falls of rain throughout the season. All three *Tockus* species began to nest after the first good falls, although the majority of *T. erythrorhynchus* nests were again started on, or after, the second good falls. It is notable that the first records of second broods, of *T. erythrorhynchus* and *T. flavirostris*, were recorded in this season, with the continued plentiful rainfall. The 1969-70 season is notable for very early rains, and the early nesting recorded for *T. erythrorhynchus* and *T. flavirostris*. However, the relatively large amounts of rain and "wetness" preceding nesting in all three species (Figure 28) are notable.

The samples of arthropod biomass are shown in Figure 29, plotted against rainfall, temperature and dates of onset of nesting for the 1968-69 season. An increase in the biomass appears in mid-October, when the higher summer temperatures are first recorded. A steady increase begins once the first rains have fallen, and continues, under the ideal rainfall pattern of the 1968-69 season, to a peak in February. The wet season peak is 20 times greater than the average dry season biomass, and the wet season average is 12 times above the dry season average. This is for the grass sweeps, but a similar trend, for the beginning of the season, is shown by the funnel traps. The November 1968 cold snap does not appear to affect the arthropod build-up except possibly temporarily. The three hornbill species begin to nest as the wet season build-up of arthropods is commencing, and about 30 days after the first increases in mid-October. Second broods were started when arthropod biomass was at its highest.

Figure 30 shows the gonad measurements of specimens collected in the Kruger National Park, plotted below the amount of rain for the month since the last collection. Specimens with active gonads, activity indicated by their larger size, were only obtained just before, or during, the recorded period of onset of nesting in the 1967-68 season. Enlarged gonads were only found, therefore, in September to November in *T. nasutus*, October to March in *T. erythrorhynchus*, and September to January in *T. flavirostris*. Odd specimens do not conform exactly to these limits, females with slightly enlarged follicles being found over the most extended period. Most striking, is the presence of males and females with enlarged gonads in September and October, before any rain has fallen. *T. nasutus* is especially early, and *T. erythrorhynchus* rather late in this respect.

DISCUSSION.

The breeding season of all four *Tockus* hornbills falls within the summer wet season, when the arthropod food supply is maximal. As for most birds (Lofts and Murton 1968), the ultimate factor selecting for this breeding season is an abundant food supply. In this case the food is necessary to feed the female during her annual moult, as well as to feed the chicks. Food supply during the breeding season appears to be an especially important limiting factor in these hornbills (Sections 5 and 7). Apart from a 20% hatching failure, food supply is the only major factor limiting the reproductive success of these species. Food supply may also be important in determining the duration of the nesting cycle, especially the pre-laying, laying and nestling phases; variation from 72-95 days being possible for the overall cycle. However, to isolate the proximate factors controlling the onset of breeding is more difficult.

Temperature and photoperiod do not appear to be important proximate factors. Temperature is subject to too many short-term fluctuations and the November 1968 cold snap indicates temperature not to be a vital factor. The two month difference in onset of nesting in the 1969-70 season, in the study areas only differing by 14' of latitude, indicates photoperiod not to be a vital proximate factor. This is also shown, for T. erythrorhynchus, by the extended nesting onset in some seasons. Changing daylength is also unimportant as all species, except T. monteiri, have been recorded starting to nest on increasing and decreasing daylengths (before and after 21 December). However, the longer and warmer days of the summer may have an influence, especially in starting gonad activity before there is rain.

No measure of the effect of the general appearance of the environment on the onset of breeding was made. Appearance of green foliage, especially grass, will bring some birds into breeding condition (Disney and Marshall 1956; Brooke 1966), and may have some effect on the hornbills, especially T. nasutus. This species is an arboreal-forager and the trees come into new leaf well before the rains.

Onset of nesting appears linked to rainfall in all four species of hornbill. The only primary effect of rain, important to the hornbills, is to make mud available. The mud is used for preparatory sealing of the nest hole, closing off unwanted holes into the nest cavity, and beginning closure of the final entrance hole. The presence of mud, and its use in sealing, certainly has a stimulating effect on T. erythrorhynchus, T. flavirostris and T. monteiri, and there is a marked increase in their breeding activity (courtship, nest preparation) after the rain. I have no observations, or indications, of T. nasutus ever using mud. However, mud cannot be an essential proximate factor for the onset of nesting. Some nest holes do not require preparatory sealing. Pairs nesting close to a permanent supply of mud (near a waterhole or regularly watered garden) do not breed at a different time to the rest of the population. Furthermore, most nests do not require more mud than thatsupplied by one good fall of rain, except for some of the very large holes used by T. monteiri (Section 5) where up to 600 sq. cm of sealing may be needed.

Food supply appears to be the main proximate factor for the onset of nesting in these hornbills. As a secondary effect of rainfall, the build up in arthropod biomass during the wet season when the foliage is abundant, appears to be the main factor.This is supported by the known feeding ecology of each species, and pre-laying behaviour of these hornbills.

It is known, from Section 3 and 5, that T. nasutus is the only arboreal-foraging species of the four. Onset of breeding, both in gonad development and timing of nesting, is up to a month ahead of the other species. Most of the trees in the savanna inhabited by this hornbill are deciduous, coming into leaf about 4-6 weeks before the first rains. It is suggested that the new foliage, presumably with an increased arthropod community, makes sufficient food available to this hornbill to bring it into breeding condition ahead of the other species. Immelmann (1971) has stressed the effect of this pre-rain foliage in inducing breeding in some arboreal-foraging African birds, well before their Australian ecological counterparts which live in evergreen foliage. Rain itself may also be a proximate factor in T. nasutus, as little as 3,5 mm producing onset of nesting, and possibly acting as a "sign" of the start of the wet season. The apparent lack of use of mud during nest preparation by this species also indicates an independence of large amounts of rain, before onset of nesting. The early rains of the 1969-70 season did not cause breeding to commence any earlier than usual in this species. This indicates that the hornbills were not in correct physiological condition any earlier, possibly due to not having enough time to feed in the new foliage, which appeared at its normal time.

T. flavirostris is a terrestrial-foraging species, but an unspecialised feeder, merely picking up most of its food throughout the year. The increase in arthropods with the warmth (and probably increased humidity) of summer may bring the birds into breeding condition. However, nesting only starts after a good fall of rain, which apart from the stimulation of making mud available, also produces the beginning of the build-up in arthropod biomass, The arthropods then increase, as the grass and herbs come into new foliage, by which time most nests of *T. flavirostris* have been started. With unspecialised feeding habits, this species may be immediately able to utilise the new crop of arthropods to attain breeding condition.

T. *erythrorhynchus* and *T. monteiri* are the last to start nesting in their respective areas. Both are terrestrial-foraging species, digging for most of their food during the winter dry season, but changing to picking up any available food during the wet season. This makes these species less well adapted to utilise the wet season arthropods, until they are sufficiently abundant to allow the change to the wet season feeding habits. This may be linked to the delay in nesting onset of these species, and the delay in the gonads becoming active in *T. erythrorhynchus*. The wetter conditions and better food supply required, may also explain the delay in nesting onset in *T. erythrorhynchus* when the rainfall is limited (1966-67 season) or drought intervenes in the rainfall pattern (1967-68 season). Both these conditions would probably be enough to halt, or even reverse, the wet season build up in arthropod biomass.

Average annual rainfall is only 100 mm on Valencia Ranch, compared to 570 mm at Satara in the Kruger National Park. The more compact spread of nesting onset in *T. monteiri* (and *T. nasutus* and *T. flavirostris*) in South West Africa may be a response to more arid conditions. A rapid onset of nesting, once conditions are suitable, would be an advantage in an area of limited irregular rainfall. However, the quantitative response of arthropods to rain in arid regions is unknown, but may be stronger in these areas for a small amount of rainfall compared to higher rainfall areas.

The breeding behaviour also supports the view of food supply as the main proximate factor for nesting onset. The female becomes totally reliant on the male for food from a few days before she finally enters the nest hole. Therefore, the timing of onset of nesting may be determined not only by the food supply, but also how well the male exploits it. The food supplied by the male may further affect the phasing of the nesting cycle with the environment, by influencing the pre-laying period. The time between the females' entrance, and laying of the first egg, may vary from four to nine days (Section 7).

A further influencing factor, in a secondary way, is the pattern of the previous season. The rainfallof the previous year causes variation in the timing of leafing of the trees, the extent to which they flower, and also the species of arthropod that will be most abundant. The effect of these variations on the hornbills would be significant, but are not considered here.

Second broods are rare, only being recorded in the ideal conditions of the 1968-69 season. However, they indicate that T. erythrorhynchus and T. flavirostris are capable of re-cycling very rapidly. Only three weeks elapsed between the fledging of one brood and re-laying of the second clutch at a T. erythrorhynchus nest. The prolonged nesting cycle of at least 80 days makes the chances of survival of second broods very slight. Wet season conditions only prevail for about five months and chick starvation is known to be an important limiting factor even within a wet season, should drought occur (1967-68) or the rains be restricted to short period (Section 5).

None of the evidence is complete. The known timing of onset of nesting, the pre-nesting behaviour and the similar evidence for other species of birds (Lack 1966) all point to food supply being the main proximate factor in onset of nesting of Tockus hornbills. The evidence also indicates that food supply is the main ultimate factor in selecting the breeding season.

SECTION 7. BREEDING BIOLOGY OF THREE SPECIES OF HORNBILL IN THE KRUGER NATIONAL PARK.

INTRODUCTION.

The breeding biology of Tockus nasutus, I. erythrorhynchus and I. flavirostris was studied over the four summer breeding seasons of 1966-67, 1967-68, 1968-69 and the beginning of the 1969-70 season. Firstly, observations were directed to examine the breeding ecology of each species to compare with the non-breeding ecology described in Sections 2 and 3. Secondly, the details of the breeding biology, such as duration of the various phases, development and feeding of the young and nesting success, were recorded. Some of these results have been used to illustrate specific points in Sections 4, 5 and 6. Such results are only repeated where their omission would break the continuity of this section. The moult of breeding hornbills is described in Section 8, and the breeding behaviour is considered in Section 9.

STUDY AREAS AND METHODS.

All nests were examined, and numbered in the sequence found. Most nests were found in the central area of the Kruger National Park and are marked on Figure 31. This area is described in detail in Section 2. Most of the work was done in the 1967-68 and 1968-69 breeding seasons, but some preliminary observations were made in the 1966-67 season. I returned to the area for three days as the hornbills were beginning to lay in the 1969-70 season, and this enabled some long term observations to be extended.

When a nest was first found, notes were taken on the dimensions of the nest cavity and the lining of the nest and a qualitative assessment was made of the habitat surrounding the nest within a radius of approximately 50 m.

The nest entrance is sealed up to leave a narrow vertical slit about 0,5 cm wide (Figure 32), which makes examination of the nest contents difficult. Nest contents were usually examined using a dentist's mirror, while lighting the nest cavity with a torch bulb attached by a long piece of flex to a battery. At a few nests, a wedge was cut out of the tree, allowing access to the nest cavity without disturbing the sealed entrance. If necessary, the sealing was broken down, and was usually restored by the nest inmates within about six hours. However, this was avoided wherever possible, to limit unnatural interference with the nest. Nests were rarely examined more than once a day, so that phases of the nesting cycle are only known to the nearest day.

Accurate counting of the nest contents was difficult. At some nests very deep lining, an inaccessible position of the nest entrance on the tree, or an awkwardly shaped entrance hole, made counts impossible. Most awkward, is the way the female (and chicks once about 15 days old) run up the funkhole above most of the nests, so that the nest appears empty. Counts of chicks over 15 days old, and recording the presence of the female, could only be done at those nests lacking a funkhole. The female leaves the nest after about 50 days and the entrance is re-sealed by the chicks. By examining the sealing, it is possible to determine if the female has emerged, the chicks' sealing being more roughly applied. Desertion occurred if the nest was examined immediately after the female sealed herself in, before she had begun to lay. Thereafter, however, an advantage of the hornbill nesting habit is that desertion is almost impossible. The female is incapable of flight after moulting all rectrices and remiges, the chicks are nidicolous, and the male is unconcerned about brief examinations of the nest.

To check the dominant trees species in the dominant vegetation association of the study area, a count of the trees large enough to contain a hornbill nest was made on the Nwanedzi experimental plots (Fig.31). The area enclosed by the outer firebreak of the plots is about 125 ha.

An intensive study area (Fig. 31) of 293 ha was established adjoining the Satara rest camp. In the 1968-69 breeding season, the locations of all nests within the area were recorded, to examine the nesting density and territory size of the hornbills. The area was regularly travelled and all records of birds returning to nests with food, or of territorial conflicts, were recorded. Details of the vegetation and topography were obtained from aerial photographs.

At a few nests, the chicks were weighed, measured and described every evening during the nestling period. This was to obtain details of the growth and development of the chicks.

The feeding rates were recorded at all nests watched for long periods, in the Satara study area or elsewhere.

All instances of hornbill predation or other causes of natural death were recorded. I was fortunate that Mr. J.C. Snelling was studying large raptors in the same area over the same period as the hornbill study. He has kindly made available his records of hornbill remains found in raptor nests.

RESULTS.

166 Nest holes were found, and over four seasons were used for a total of 249 nestings by three hornbill species.

NEST HABITAT.

The habitat within an approximate radius of 50 m of each nest was divided into three sets of variables (Table 18). The sample is for 178 nests because some nest holes were used by different species and are included under each. Most of the nests are in parkland, the dominant vegetation form in the study area. _T._ _nasutus_ appears to show a slight preference for areas with long grass, and *I. erythrorhynchus* a marked preference for areas with sparse grass cover. *I. flavirostris* shows no preference in grass cover. The majority of nests were situated away from watercourses and riparian vegetation.

NEST SITE.

All 166 nest holes were in trees. The average dimensions of the nest holes used by each hornbill species are given in Table 19, with the range of size used. No significant differences are apparent between the requirements of each hornbill species, as shown by the range of sizes of nest holes used. The basic nest site for all species is a hole 3-4 m up in a tree. The nest cavity should have a diameter of 20 cm, with the nest floor about 10 cm below the lip of the entrance hole. A nest cavity with a funkhole or chimney leading up from the nest is preferred; this funkhole may extend up for as much as 2 m. The entrance hole to the nest cavity can have minimum dimensions of 2,5 cm wide and 3,5 cm high.

The types of trees in which nests were found are given in Table 20. To check whether the observed preferred tree species were merely a reflection of the dominance of those trees in the area, all trees large enough to contain a hornbill nest were counted within the 125 ha of the Nwanedzi experimental plots. The distribution of species within the 195 trees counted is given in Table 21 being a sample of the dominant vegetation in the study area; *Acacia nigrescens* - *Sclerocarya birrea* parkland. The three commonest tree species in the sample are the three species most used by the hornbills. The only exception is the extensive use of *Acacia delagoensis* trees by *I. erythrorhynchus*.

NEST OCCUPATION.

The sequence of use of nest holes, used in more than one season or for more than one brood, is given in Appendix 5.

Nest holes may be used every year, either by the same or different species of hornbill. We observed 58 holes for two seasons, 20 for three seasons and two for four seasons, giving a total of 184 nesthole-seasons (nhs). In 121 nhs (66%) holes were re-used by the same hornbill species, and in 15 nhs (8%) by another hornbill species. In 4 nhs (2%) holes were used by other hole-nesting birds, and in 44 nhs (24%) holes were not utilised.

A wide range of nest successions are evident, and of factors affecting nest succession. Nest holes were made unsuitable mainly due to tree breakage by elephants (four instances), or bees taking over the hole (two instances) - except those which I broke open to examine and take chicks (six instances). Abandonment of a nest hole may be due to natural interference such as a monitor lizard or python living in the hole (two instances), flooding of the nest in the previous season (once), or the chicks or female dying in the nest (three instances). Causing birds to desert will also result in abandonment of the hole, although in all cases the hole was subsequently used by another hornbill species. Abandonment twice appeared to be merely for another hole nearby, and no reasons were apparent in a further 16 instances.

Nest holes may be used by other types of birds. Two nests were used by Pearl-spotted owls Glaucidium perlatum in the previous season. Old sealing showed one nest to have been a hornbills' hole even before the owls took over, and between its use by the owls and re-use by hornbills it was used by Purple Rollers Coracias naevia. Another hole with old sealing was used by Lilac-breasted Rollers Coracias caudata, and one abandoned hornbill hole was taken over by a pair of Greater Starlings Lamprotornis australis.

Interchange of holes between different hornbill species had been recorded for all three species :

same nest hole used by _I. nasutus_ and _I. erythrorhynchus_ - 3 times

I. nasutus and _I. flavirostris_ - 4 times

I. erythrorhynchus and _I. flavirostris_- 4 times

The interchange may occur in successive seasons (seven instances), when one species starts to breed after the other is finished in the same season (three instances), or with one species starting a second brood after the other has finished its first (once). The records of late starting are all for _I. erythrorhynchus_ in the 1967-68 season. The case of a second brood is for _I. flavirostris_ taking over from _I. erythrorhynchus_. The first nest of _I. flavirostris_ was not found although they were seen carrying food in the vicinity, and the late date of commencement suggested a second brood (or second nesting attempt).

NEST TERRITORIES.

The main features of the Satara study area are shown in Figure 33. Positions and occupant species of known nests for the 1968-69 season are marked, as are the main vegetations divisions. The position of nests, and the estimated territory of each pair known for the study area are shown in Figure 34. One pair with a nest and one suspected pair of _I. nasutus_ inhabited the area, with another pair with a nest close to the boundary of the study area. Nine pairs of _I. erythrorhynchus_ lived in the area, seven with nests, and seven pairs lived along the borders, five with nests just outside the study area. Eight pairs of _I. flavirostris_ lived in the area, seven with nests, and three pairs along the borders all with nests just outside the study area.

The areas of individual territories, estimated by connecting the furthest points from which birds were seen bringing food to nests, are given in Table 22. *T. nasutus* has a markedly larger average territory of 63 ha, compared to the 10 ha of *T. erythrorhynchus* and 17 ha of *T. flavirostris*. The territories are maintained only intraspecifically, so that different species of hornbill may be nesting close together. This was found generally in the overall study area, those nests in closest proximity being shown in Table 23. Spacing between nests of the same species in the overall study area indicated that territory sizes were no smaller than in the Satara study area.

Large parts of the 293 ha Satara study area are not utilised by the hornbills, especially the large bare area in the centre of the study area, with a dense clump of *Acacia tortilis* trees. From the number of pairs present in the area, and the average territory of each, the amount of the study area not utilised is about 46% for *T. nasutus*, 59% for *T. erythrorhynchus* and 48% for *T. flavirostris*.

PRE-LAYING PERIOD.

The dates at which the females entered the nest to seal themselves in finally, are given in Section 6. The average time between final entrance and laying of the first egg is six days (Table 24).

Observations indicate that this is the time when the male brings most of the lining for the nest, although some is brought in small quantities both before and after this time.

NEST LINING.

All three species line their nests with a variety of materials, most commonly dry grass, dry or green leaves and bark flakes. Fragments of the shell of the large

Achatina snail are brought regularly to the nest throughout the nesting cycle and may be for lining, or for something for the nest occupants to break up and so clean their bills. This latter function may also be the reason for the bark and leaves brought during nesting, although the same materials brought in large quantities during the pre-laying period are primarily for lining. Visits to the nest with lining may exceed the number of visits with food made by the male during the pre-laying period.

A specific difference exists in the predominant lining material used, in the Kruger National Park. *T. nasutus* uses bark flakes almost exclusively. *T. erythrorhynchus* uses mainly green leaves in large quantities. *T. flavirostris* has a preference for any dry material such as dry grass, leaves or bark. The lining is often the only way to identify a nest if the adults or chicks cannot be seen.

LAYING AND HATCHING PERIODS.

The eggs are incubated from the laying of the first egg. Therefore, the hatching interval between chicks should be the same as the laying interval between the eggs. This was tested by marking the four eggs laid by *T. erythrorhynchus* in nest 100, as they were laid, and then noting the hatching interval. The intervals, to the nearest day, correspond exactly.

Observations are given in Table 25. Despite the limited data, especially for the laying intervals, the interval between laying of eggs increases as the clutch proceeds, and this is shown in the hatching interval between the chicks. Clutches of two to five eggs are recorded, and the overall duration of laying (and hatching) appears to range from two, to at least nine days.

EGG AND CLUTCH SIZES.

The eggs of all species are white, ovoid in shape, and with a pitted surface. They become much discoloured during incubation. Average sizes of eggs measured in the central Kruger National Park (range in brackets) are:

Nine eggs of _T_. _nasutus_ : 37,0 x 26,2(40,0-34,2x27,3-25,0)mm
12 eggs of _T_. _erythrorhynchus_: 33,6 x24,1(35,2-31,8 x 24,7 -23,0)mm
22 eggs of _T_. _flavirostris_: 36,6 x 25,5(41,0-31,5 x 27, 2-21,3)mm

On average, _T_. _erythrorhynchus_ appears to lay a slightly smaller egg than the other two species. However, comparing the ratio of the egg sizes to the average female body weight (Table 26), _T_. _erythrorhynchus_ appears to lay a proportionately larger egg than the other two species. _T_. _flavirostris_ lays a proportionately smaller egg than the other two species.

Clutch sizes recorded during three consecutive breeding seasons are shown in Table 27. Clutches range from two to five eggs, although three is the smallest clutch recorded for _T_. _nasutus_. On average, _T_. _nasutus_ lays the largest clutches and _T_. _flavirostris_ the smallest clutches. Only the 1967-68 and 1968-69 seasons can be compared, indicating that for all species the average clutch size was smaller during the 1967-68 season, especially for _T_. _erythrorhynchus_.

INCUBATION PERIOD.

Incubation periods could not be taken from the last egg laid to the last egg hatched due to the lack of data, except in _T_. _erythrorhynchus_ nest 100 where the eggs were marked as laid. This showed that the eggs hatch in the order laid, and the records in Table 28 are all for individual eggs. The incubation period of 24 days may vary slightly.

HATCHING SUCCESS.

Appendix 6 gives details of nest contents where these could be checked by regular visits and accurately counted. The number of nests with a known number of hatched chicks exceeds the number for which the clutch size is known. Often it was easier to count the chicks than the eggs, and some nests were found only with newly hatched chicks. Hatching success is given in Table 29. It is calculated firstly from the number of chicks hatched from a known number of eggs, and secondly from comparing the average clutch size to the average brood size with newly hatched chicks. By both methods, the hatching success is about 80% for all three hornbill species.

EMERGENCE OF FEMALE.

When the chicks are about half-grown, the female breaks the sealing and leaves the nest. The chicks re-seal the entrance hole unassisted, and the female helps the male to feed the chicks. The average emergence time (Table 30) of 21 days is taken as the number of days after hatching of the first chick. The youngest chick of a brood left in a nest by the female was 13 days old.

NESTLING PERIOD.

Table 31 gives the nestling period for chicks from 13 different nests. The age at which the chick leaves the nest varies within the species, and between the siblings of one brood. The trend is for the younger chicks to take longer to leave the nest compared with their elder siblings. The overall average nestling period is 45 days, but, even comparing the eldest chicks of different broods, there may be up to six days difference in age at leaving the nest.

DEVELOPMENT OF CHICKS.

The development pattern for the chicks of all three hornbill species is basically the same, except for specific colour differences, especially in the bill. The development, with specific differences where they exist, and illustrated with stage by stage photographs, is given in Appendix 7.

The growth of the chicks is also basically the same for each species (Figure 35), only one example of an eldest chick of each species being illustrated. Tarsus growth is very rapid, and complete within 20 days of hatching. The overall body growth, as indicated by growth of the ulna, is complete about 26-33 days after hatching, and in each case coincides with the attainment of peak weight during the nestling period. Thereafter the weight declines somewhat erratically by about 15% to the level at which the chick leaves the nest. Feather growth, of the rectrices and remiges, is not complete by the time the chick leaves the nest, and observations on tame birds indicate that completion requires approximately two more weeks.

Weight increase occurs at a similar rate for all species, with rapid increments from the second day after hatching, The rate of weight increment begins to decrease at about the time the female leaves the nest and when the tarsus growth is complete. Increases in weight cease once the birds are full grown in the body, when about 26-33 days old.

The widely differing nestling period appears to be due to different growth rates, as shown by the weight gains of individual chicks in broods of each species. (Figure 36). Results for two broods of _T. erythrorhynchus_ are shown separately in Figure 37. No more than 1,5 km separated any of the nests where the chicks were weighed, those used in Figure 37 being weighed during the 1967-68 season, and those in Figure 36 during the 1968-69 season. The rainfall and maximum temperature figures plotted are, therefore, directly applicable to all the nests, which were all close to the Satara weather station.

The weight gains of smaller chicks of a brood are only slightly less than for the older chicks. However, the smaller chicks show a greater weight loss, and for a longer period, during adverse conditions. Weight drops of all chicks can be correlated with temperature drop especially if it is associated with prolonged rainfall. This is especially clear in Figure 37, where temperature drop and rainfall from 13 - 18 April 1968 resulted in the death of chick 3 in nest 16, a halt in the weight gain of chick 2, but only a slight drop in weight gain of chick 1. The marked effect of weather in this season may be related to food supplies being limited, as evidenced by the rapid deaths of chick 4 in nest 16 and chicks 3 and 4 in nest 42.

At one nest in the study area, found with one emaciated T. flavirostris chick sitting in the rotting remains of its siblings, the chick was taken for rearing. So retarded was its development that it only broke out of its artificial nest an estimated six weeks later than it would have normally done so. This indicates the degree to which the growth rate can be affected, and the chick was healthy once out. It was killed in the wild, by a car, five months after flying.

FEEDING RATES.

Feeding rates at nests by males, or males and females, are recorded in Table 32, from 138,5 hours observations. Considerable variation exists, from 0,7 to 16,7 feeds/ hour. The feeding rates are on average higher once the chicks have hatched (7,8 feeds/hour) than when the female is incubating (3,2 feeds/ hour), and especially once the female has broken out and is assisting the male (8,9 feeds/hour). The feeding rate is also high immediately after the female has entered the nest and before laying (5,2 feeds/hour). During this period the male is very active as he is also bringing the nest lining; sometimes more often than food. A drop in feeding rate may be indicated just before the chicks leave the nest, but the data on feeding rates are too few to be conclusive.

The role of the female in assisting the male varies from very slight assistance to supplying more food than the male. These may merely be individual variations, but even if the assistance from the female is slight, she is no longer taking food supplied by the male.

NESTING SUCCESS.

I have previously (Section 4) commented on the nesting success of these three hornbill species, taking as successful any nests which fledged chicks. These results, illustrating the value of the sealed-in nesting habit, are summarised in Table 33.

These results do not take into account any losses of eggs or chicks within the nest. Hatching success has been shown to be about 30% (Table 29). The limited data on how many chicks leave the nest appear in Appendix 6. The difficulty of accurately counting live chicks, coupled with the ease of counting chicks dead on the nest floor in nests which were total failures, bias the results in Table 34 toward a very low nestling success. The estimated nesting success, overall, and excluding the total losses of nest contents, are given in Table 35, the latter results probably being closer to the true facts. Comparing all these figures, it appears that about 55-60% of eggs laid produce chicks that leave the nest for _I_. _erythrorhynchus_ and _I_. _flavirostris_, and up to 80% for _I_. _nasutus_. The percentage of chicks leaving of eggs hatched is nearer 70% for _I_. _erythrorhynchus_ and _I_. _flavirostris_, and almost 100% for _I_. _nasutus_. These figures apply to the 90% of the nests shown in Table 33 to have reared at least some chicks.

The main factors that appear to limit the production of a nest are mainly internal. Failure to hatch accounts for about 20% of the eggs of each species, and all such eggs examined were either infertile or had small dead embryos in them. The only other limiting factor is starvation of chicks, accounting for up to half of the brood in some nests, although other unrecorded factors may also be operating.

PREDATION.

All records of hornbill predation from the Kruger National Park during the period of study are given in Table 36. Only one record of *T. nasutus* predation exists, compared to the other two hornbill species that fall prey to all of the major large raptors in the study area. The plumages of *T. erythrorhynchus* and *T. flavirostris* are very similar and the species could often not be separated in the prey remains, although both species are clearly separable from *T. nasutus*. The most important predators of *T. erythrorhynchus* and *T. flavirostris* appear to be the African Hawk Eagle *Aquila fasciata* during the day and the Giant Eagle Owl *Bubo lacteus* at night. The Bateleur *Terathopius ecaudatus* appears to be an important predator, but this may be due to its scavenging habits and hornbills being frequent road kills in the park, although it would also be able to catch hornbills. The Martial Eagle *Polemaetus bellicosus* is suspected to be a more important predator than shown, but ~~they are~~ it is relatively less common in the study area than the other species. The results are biased towards the role of raptor predation, as many of the data come from Snelling's (*in litt.*) records while studying the raptors. Even so, avian predation is thought to be the most important on hornbills.

Snelling's results also show that there is a seasonal variation in the main birds preying on hornbills (Table 37). He recorded the predators of 48 hornbills in 1967, 34 in 1968 and 41 in 1969. In 1967 *B. lacteus* and then *A. fasciata* were the most important of the six predators, in 1968 *T. ecaudatus* and then *A. fasciatia*, and in 1969 *A. fasciata* and then *T. ecaudatus*.

Another natural cause of death is when hornbills become entangled in thorny branches. I caught a bird that was so caught and very weak, and Snelling (in litt.) found a dead bird thought to have died in this way; both were *T. erythrorhynchus*.

POPULATION DYNAMICS.

The estimated numbers of chicks leaving the nest in Table 35 (when applied to the 90% of the nests rearing some chicks (Table 33) and adding the nests suffering total losses) allows the replacement rate of the population to be calculated. 2 *T. nasutus* nestings would rear 68 chicks (1,55 chicks per adult), 73 *T. erythrorhynchus* nestings would rear 158 chicks (1,10 chicks per adult) and 54 *T. flavirostris* would rear 90 chicks (0,83 chicks per adult).

During the monthly collection of specimens for stomach contents along the same 12 km of road over 15 months (Section 3), it was notable that birds were only very rarely encountered during the last month. They appear to have been eradicated, as the difficulty of obtaining specimens increased steadily during the last months. 120 specimens each of *T. erythrorhynchus* and *T. flavirostris* were shot from November 1967, the beginning of the breeding season, to October 1968, just prior to the beginning of the following breeding season. Estimating three pairs per kilometre, from the known territory sizes (Table 22), there would be 72 birds of each species along the road, By the end of the breeding season, using the replacement rates above, there would be 151 *T. erythrorhynchus* and 132 *T. flavirostris* present. With 120 birds of each species being removed, the paucity of birds can be explained. Influx from local movements would tend to increase the numbers, but specimens shot while nesting would decrease the numbers available by eliminating a female and potentially some chicks from the population. Without details of the nesting density of the raptors available the impact of the natural predators cannot be estimated.

DISCUSSION.

The lack of ecological separation between the three hornbill species studied in the Kruger National Park during the breeding season is marked. No special part of the habitat is chosen for the nests, except that *T. erythrorhynchus* continues to display its preference (Section 2) for sparsely grassed areas. Otherwise, most of the nests are merely sited in the parkland that forms the main part of the study area.

No specific differences are evident, even in the type of nest hole. All three species require a nest hole of similar dimensions, and preferably with a funkhole above the nest. The presence of a funkhole appears to be a feature of the nest holes of a number of hornbill species, certainly of the genus *Tockus*. This is evident from the frequent mention of a funkhole in the literature for several species - *T. erythrorhynchus* (North 1942; Root and Root 1969); *Tropicranus albocristatus* (Chapin 1926) and *T. monteiri* (Section 5). Together with the sealed-in entrance, the funkhole adds to the safety of the nest by providing a secure hiding place. It is unlikely that a predator large enough to break the sealing, and withstand the attack of the inmates, would be able to fit in the entrance hole and reach up the funkhole. It is worth noting the dual response to predators shown by females and chicks (Section 9), where they attack a small object at the nest entrance, but run up the funkhole if presented with a very large one.

No preference is shown in the type of tree in which the nest is sited, the commonest tree species being the most commonly used. The only exception is the frequent use of *Acacia delagoensis* by *T. erythrorhynchus*. However, *Acacia delagoensis* is the commonest tree in the transition woodland down the centre of the study area. Being associated with a sparse grass cover, it therefore dominates in the preferred habitat of *T. erythrorhynchus*.

The lack of separation in the breeding ecology of the three hornbill species is further emphasised by the frequent interchange of nest holes. A complete overlap in territories also occurs between the species, even to having two species nesting in the same tree at the same time (Figure 38, Table 23).

The interchange of nest holes could indicate a shortage of suitable holes, but this does not appear to be so. Firstly, many holes lie vacant for a season or more and are then re-used later. Secondly, a few cases indicate that there are many suitable nest holes available within the territory of a pair. Nest holes 16 and 91 are 40 m apart. The former was used in the 1966-67 season by *T. erythrorhynchus*, the male of the pair being recognisable by an extremely long bill. The pair was preparing a new hole, in a tree 5 m away, at the beginning of the 1967-68 season because a wedge cut into hole 16 fell out during the dry season. When the wedge was replaced the pair moved back to use nest 16 in the 1967-68 season. In the 1968-69 season building operations were proceeding near nest 16 and the pair moved 40 m away to use nest 91. Hole 91 was an old hornbill nest, as shown by the old sealing around the entrance, and was known to have been used in the 18 months prior to the hornbills' re-occupation for breeding by *Glaucidium perlatum* and then *Coracias naevia*. Nest 25, also of *T. erythrorhynchus*, was used in the 1966-67 season; in the 1968-69 season the same species was nesting at hole 137 in the neighbouring tree only 20 m away. Nest 40 was used by *T. erythrorhynchus* in the 1967-68 season, and a stump at the base of the tree, only 5 m away, was used by the same species the following year. The close proximity of some of the nests of different species (Table 23) also supports the view that nest holes are abundant. The three most commonly used trees in the area, *Acacia nigrescens*, *Sclerocarya birrea* and especially *Combretum imberbe*, frequently form cavities, either by rotting of broken branches, or in dead wood.

Approximate territory sizes are available for five *Tockus* species, calculating those for *T. alboterminatus* from the map given by Ranger (1949). The ground-foraging species appear to have relatively small territories: *T. erythrorhynchus* 10 ha, *T. flavirostris* 17 ha and *T. monteiri* 15 ha (Section 5). The arboreal-foraging species have much larger territories: 63 ha for *T. nasutus*, and 142 ha for *T. alboterminatus* (Ranger 1949). This would explain the lower numbers of tree-foraging species encountered, especially the relative numbers of *T. nasutus* to the other two species in the Kruger National Park, shown in Section 2. The reason for large territories in tree-foraging species may be that trees form a smaller area per unit of ground surface area, and so present a smaller feeding area. *T. alboterminatus*, living in areas of forest or woodland that are largely evergreen, has a very large territory compared to the other species, which inhabit areas of deciduous vegetation. However, *T. alboterminatus* holds the territory throughout the year, and shares it with chicks of the previous breeding season until just prior to the next breeding season (Ranger 1949). Since up to three chicks were recorded as fledging (Ranger 1949), the area per individual is not much different than for a pair of *T. nasutus*. The variations in territory size, depending on the permanence of the territory and whether the food is obtained on the ground or in the trees, indicate that individuals require a similar amount of vegetation in which to obtain their food.

Arboreal species occupy a greater area than terrestrial species, and resident species occupy a greater area than species which only hold territories during the breeding season. It would be interesting to determine the territory size for *T. bradfieldi*, a species closely related to *T. alboterminatus* (Section 9), which forages in the trees in the wet season and on the ground in the dry season, and which only holds a territory during the breeding season. It is also remarkable in all studies that there is a large unused portion of the study area, up to 50%,due to lack of certain requirements. For *T. monteiri* it appears to be lack of nest sites (Section 5), and for the Kruger National Park hornbills it is the total lack of grass cover and paucity of trees in some areas.

Specific differences in the type of nest lining used were evident for the species in the Kruger National Park. However, these differences may not hold for the entire range of the species. *T. erythrorhynchus* lines the nest mainly with green leaves in South Africa and Rhodesia, but in Kenya Granvik (1934) records *Acacia* pods, dry grass, pieces of paper, leaves and cow dung, and North (1942) reports bark shavings and seed pods. A basic difference appears to be that the tree foraging species use almost entirely bark flakes as lining, as I have found for *T. nasutus*, Ranger (1952) and as I found for *T. alboterminatus*, and Hoesch (1937) for *T. bradfieldi*. The ground-foraging species use a variety of materials, usually dry, such as seed pods and dry grass (*T. monteiri* and *T. flavirostris*), but *T. erythrorhynchus* sometimes uses green leaves. Chapin (1926) and Moreau (1937) suggest that the nests are not lined, but this is incorrect, certainly for many *Tockus* species.

Most of the lining is brought during the pre-laying period, but some is brought at regular intervals throughout the nesting cycle. I have suggested that much of the latter may serve for bill cleaning, and also to replenish soiled lining thrown out during nest sanitation. The regular bringing of bark to nests has been noted in *Bycanistes brevis* (Moreau and Moreau 1941) and *B. subcylindricus* (Kilham 1956), and may serve a similar function.

The problems of examining the contents of these sealed-in nests, especially when the female and chicks disappear up the funkhole, have been described. This has permitted only small samples to be available for measuring the breeding stages and successes, but the nesting habit is very efficient in protecting the nest contents. Cases of desertion due to observer-interference are few.

The whole nesting cycle takes a long time, considering the size of the birds, and the maximum and minimum times for each phase of the cycle are shown in Table 38. These figures are approximately the same as recorded for *T. monteiri* (Section 5), and appear to be the same for all species of *Tockus* for which there is any information (Moreau 1937), including *T. deckeni* and also *T. alboterminatus* (Ranger in Kilham 1956). However, considerable variation is possible due to variation in duration of three main phases of the cycle, the pre-laying period, the laying period and the nestling period.

The duration of the pre-laying period might depend on the food supply received by the female. Sufficient food is needed by the female to form eggs, and prepare for an extensive and simultaneous growth of all the flight feathers, following their sudden moult. The higher feeding rates recorded during this period, compared to those during the incubation period, may reflect the importance of the food supply at this time, although the number of observations is small (Table 32). However, the female must attain a certain degree of physiological readiness to copulate with the male before she enters, and to seal herself into the nest.

The clutch size may also be determined to some extent by the amount of food supplied during the pre-laying period. The average clutch size was smaller for all species during the 1967-68 season compared to the 1968-69 season, especially for T. erythrorhynchus (3,3 eggs cf. 4,4 eggs). The onset of nesting of T. erythrorhynchus was very spread out during the 1967-68 season (Section 6), indicating insufficient suitable factors to initiate breeding. In the 1968-69 season all nests of this species were started within a short space of time. I suggest that food supply, linked to rainfall, must be sufficient to trigger breeding (Section 6) and so the indication of a lesser food supply during the 1967-68 season may also explain the smaller clutches in that season.

Food supply may also be the main factor influencing the duration of the laying period, which may last as long as 10 days in T. nasutus, T. erythrorhynchus and T. flavirostris in the Kruger National Park, and in T. monteiri in South West Africa (Section 5). However, this period may be much longer; Moreau (1938) reported five eggs laid by T. erythrorhynchus in Kenya at intervals of five to seven days, giving a total laying period of about 24 days. The increased interval between the laying of eggs as the clutch proceeds may indicate that as reserves are used up, it takes longer to obtain sufficient protein to form the next egg. Therefore, the more the female is fed during this and the preceding period, the faster she will be able to form and lay the eggs. Possibly insufficient food is also the reason why females break out without laying eggs reported several times for the fruit-eating Bycanistes hornbills (Kilham 1956; Moreau and Moreau 1941; Stonor 1937). The importance of the food supply in determining the timing of laying, the clutch size and the duration of laying of the clutch, would be in accordance with the similar results shown for several other bird species by Lack (1968).

Variation in duration of the nestling period, is also linked to the food supply. The shortest nestling periods are recorded in the 1968-69 season, when good rains fell at regular intervals throughout the season, and indications are that there was a good food supply (Section 6). From 39 days at this time, the nestling period may extend for as long as 50 days for the younger chicks of a brood during a less suitable year. In all cases there is an age difference between the members of a brood due to their hatching at intervals, and this also produces a size gradation (Figure 39). It is apparent from watching nests and hand-rearing broods, that the largest, strongest and most active chick will take food first, and only when it is sated will the next chick be able to obtain food. There is no way in which the parents can selectively feed the chicks, or respond to stronger begging calls from the hungry ones, since all food is merely presented at the nest slit. This means that, in a brood of four chicks, three must be sated before the fourth will receive any food at all. Sometimes this may never happen, as indicated by the weight curves in Figure 37. It is interesting that three other _T. erythrorhynchus_ nests, started at the same time as those in Figure 37, all had remains of dead chicks in them, indicating that the food supply was generally poor. All five nests were started at the beginning of March in the 1967-68 breeding season, the latest that any nests were ever found to start (Section 6). By this time the weather is beginning to cool towards the dry winter season, and rainfall is tailing off for the end of the wet season, both of which would cause a decrease in the arthropod food supply.

The increased duration of the nestling period for the younger chicks appears to be due to their greater response to times of food shortage, and slower recovery from such times (Figures 36 and 37). This is especially evident at times of temperature drop, especially if associated with wet conditions, which would reduce the food available, arthropods being the main food during breeding.

The most striking effect is that of cold and rain on the third chick of nest 42 (Figure 37), which never recovered from a cessation of weight gain. The role of the asynchronous hatching of a brood in tailoring the brood by starvation, to fit the available food supply is well documented (Lack 1968). These hornbills, which breed in areas of irregular rainfall and have a very prolonged nesting cycle, may place special emphasis on this role of asynchronous hatching. It is unlikely that they would be able to evolve a clutch size that would give the best average replacement rate of chicks to the population. Rather, they may produce as many eggs as possible on the food supply available at the beginning of nesting, and rely on the starvation of the youngest chicks to tailor the brood size to the food supply later in the season. This is suggested by the lack of correlation of the clutch size to the subsequent fledging success, especially for T. monteiri (Section 5), and the frequency of starvation of younger chicks. The variation in the threshold at which nesting starts, especially for T. erythrorhynchus and T. monteiri, resulting in delayed or extended onset of breeding, may also be a factor ensuring that these species make the best of the fluctuating conditions which exist within one season.

With food supply of such apparent importance to the breeding cycle of hornbills, the males' habit of bringing food to the nest in single items appears curious. Feeding rates of up to 16 visits/hour are recorded. It is notable that T. monteiri, restricted to a very arid habitat, often carries two and sometimes three food items in the bill at once. Therefore, the maximum feeding rates of 5,9 vists/hour recorded for this species (Section 5) give about the same supply of food items per hour as recorded for those Tockus species that bring the food items one at a time. Given a 13-hour day, the feeding rates of the Tockus hornbills would indicate a maximum of about 210 food items brought to the nest in one day. The fruit-eating species, such as Bycanistes and the two Indian species of Tockus, bring food in loads, regurgitating each fruit to feed the nest inmates (Abdulali 1942; Kilham 1956; Lowther 1942; Moreau 1936). Moreau and Moreau (1941) record 21 visits per day as the peak feeding rate for *Bycanistes brevis*, with an average of 25 fruits per load, giving about 525 food items brought in one day. However, the poor protein value of a frugivorous diet may also have some bearing on the higher feeding rates reported for the frugivorous species. Possibly the bringing of food in loads evolved among frugivorous species, and regurgitation of food items was no longer possible once an omnivorous diet was adopted. It is notable that *Bucorvus* hornbills which are omnivorous and mainly carnivorous, *Tropicanus albocristatus* which is mainly insectivorous (Chapin 1939), and the African species of *Tockus* which are mainly insectivorous, all bring food to the nest in single items. The Indian species of *Tockus* that are mainly frugivorous regurgitate food items at the nest (Abdulali 1942; Lowther 1942).

A marked drop in the feeding rate appears to occur at the end of the nestling period (Table 32). Moreau and Moreau (1941) note a similar feature at the end of the breeding cycle of *Bycanistes brevis*. At this time the chicks have attained peak weight, and then there is a drop in weight of about 15% to when they leave the nest. In part at least, this weight drop may be due to a reduction in the food supplied by the parents. Peak feeding rates, soon after the female has left the nest, are correlated with the attainment of maximum weight by the chicks. This may be only partly due to the assistance of the female, for in some instances her help is neglible, and the feeding rate of the male increases. However, the female may supply as much food as the male in some cases, and rarely even more (Table 32; Section 5; Hoesch 1933). Whatever the contribution of the female, she no longer taxes the male for food once she has broken out of the nest.

I have discussed previously some of the external factors limiting nesting success (Section 4). About 10% of the nests of all three species studied in the Kruger National Park are completely unsuccessful due to such factors as tree growth closing the nest entrance, flooding of the nest, or death of the male food provider. Only one instance of nest predation was ever recorded, in a tree broken by elephants and so making the nest unsealed (Figure 40).

It appears that internal factors may be the main limiting factors to the reproductive success of the hornbills studied, T. nasutus, T. erythrorhynchus, T. flavirostris, T. monteiri (Section 5), Bycanistes subcylindricus (Kilham 1956) and B. brevis (Moreau and Moreau 1941). For the latter species no details of the production rate of nests is available for a large sample, but in no instance did external factors affect the nests that did not produce any chicks. The two main factors limiting the breeding success of the Tockus species are a low hatching rate, and starvation of the younger chicks of a brood. Hatching success of about 80% has been found for all four Tockus species, and apart from infertility the reason for eggs not hatching is unknown. Possibly, the female only being able to copulate with the male before sealing herself into the nest, is the reason for the high infertility rate. The physiology and competence of sperm storage in hornbills has not been studied, but must be efficient as the last egg may be laid up to 24 days after entering the nest (Moreau 1938).

T. nasutus reared almost 100% of the chicks that hatched, and was the most successful species in this respect. T. erythrorhynchus and T. flavirostris rear about 70% of the chicks hatched, but this figure was as low as 39% for T. monteiri during the single season when this species was studied (Section 5). In all cases when the cause of chick loss was known, it was due to starvation of the younger members of a brood. However, the loss of the younger and smaller chicks appears to be a system evolved to adjust the number of chicks to the food supply available. Therefore, while the hornbills are safe in their sealed-in nest and highly adapted to their nesting habit (Section 4), internal factors limit their reproductive success. Annual replacement rates of from 1,55 chick/adult for *T. nasutus* and 1,10 chicks/adult for *T. erythrorhynchus* down to 0,83 chicks/adult for *T. flavirostris* and even as low as 0,63 chicks/adult for *T. monteiri* have been recorded. Mortality rates were not known, but there are good reasons for supposing that replacement rates and mortality rates are equal (Lack 1968). Accepting this assumption, the annual mortality rates would be *T.nasutus* 61%, *T. erythrorhynchus* 52%, *T. flavirostris* 45% and *T. monteiri* 38%. These figures fit well within the range for European passerines and the Wood Pigeon *Columba palumbus*, but may be low for essentially tropical species (Lack 1954 and 1966).

The unnatural predation, by shooting of specimens in a restricted area, indicates that predation may have a marked effect on hornbill numbers, at least of *T. erythrorhynchus* and *T. flavirostris*. The results of the predation by the commonest large raptors in the area, especially *Aquila fasciata*, *Bubo lacteus* and *Terathopius ecuadatus*, show that hornbills are common prey. The impact of natural predation cannot be estimated until the densities of the raptors are known. If natural predation is an important limiting factor to hornbill numbers, it would be contrary to most other predator-prey relationships of higher vertebrates (Errington 1967, Lack 1966, Pienaar 1969), although Blair (1948) thought predation to be a major controlling factor of rodents.

SECTION 8. SOME OBSERVATIONS ON MOULT OF THREE SPECIES OF HORNBILL IN THE KRUGER NATIONAL PARK.

INTRODUCTION.

Moult was examined on 50 specimens of *Tockus nasutus*, 150 specimens of *T. erythrorhynchus* and 150 specimens of *T. flavirostris*. These specimens were collected monthly in the same area along the Nwandezi firebreak in the central Kruger National Park, in June 1967 and from September 1967 to October 1968 (Section 3). It was possible to examine the timing of moult, to compare the sequence of moult with the results of Stresemann and Stresemann (1966), and to detail the moult of the breeding female. The moult of the breeding female is of special interest because of the rapid simultaneous moult of the flight feathers while in the nest.

RESULTS.

Males and non-breeding females.

Both these groups were found to moult in the same way, gradually over several months, and with the same sequence of feather replacement.

Moult of the rectrices, numbering pairs from the centre outwards, occurs in the order 1 -5 - 2 or 4 - 3. Moult of the primaries, numbering from the proximal primary outwards occurs in the order 10 - 4 - 5 - 3 - 6 or 2 - 1 and 9 - 7 - 8. No sequence could be found for the 12 secondaries. The same sequence was found for all three hornbill species studied. Rectrix and remex moult was usually highly assymetrical, frequently masking the basic pattern which was in progress on each side of the body.

Moult of the body areas does not follow a clear sequence because more than one area is in moult at once. The basic sequence is abdomen - upper back - breast - lower back and head - neck. This is the same for all three species, and is basically the same order in which the feather areas grow out on the young chicks (Appendix 7).

Table 39 shows the percentage of specimens showing any form of moult during the months of collection. Moult is largely restricted to the wet season from October to May, in all three hornbill species. Tail moult occurs mainly from December to March (Table 40), whereas wing moult occurs over a more extended period from November to May (Table 41). This is evident on individual birds, where wing moult has started before the tail, but the latter is complete before the wing moult is finished. Body moult occurs throughout the whole moult period, from December to May (Table 42).

The timing of moult may vary each year, as indicated by the active moult in June 1967, whereas all moult was completed by May 1968. This may be related to the start of the wet season, which was earlier in the 1967-1968 season (6 October 1967) than in the 1966-67 season (21 October 1966).

Breeding females.

After a female has sealed herself into the nest hole, an average period of six days elapses before egg-laying commences. By the time the clutch is complete, the female has moulted all rectrices and remiges, but these are regrown by the time she breaks out of the nest about 46 days after laying the first egg. All observations on moult of breeding females of the three hornbill species examined in the Kruger National Park are described below. A general pattern emerges, but there is much individual variation, and observations are fragmentary because often the female runs up the funkhole above the nest (Section 7), making consecutive observations difficult.

T. nasutus

Nest 3. Found at hatching of first egg; rectrices and remiges all growing in and of equal length indicating simultaneous moulting. Growth of feathers proceeded as follows :

20 November 1967 (estimated 31 days after first entering):
first egg hatching, wing 100 mm, tail 65 mm.

27 November (38 days after entering): wing 140 mm, tail 100 mm.

4 December (52 days after entering): female broken out of nest, apparently only recently because chicks still actively re-sealing the nest entrance.

Nest 5. Female enters on 22 November 1968. First egg laid after seven days. Three days later, three eggs laid, but no moult started. 12 days after entering, with four eggs laid, both wing and tail moult begun, and by 17 days after entering (ten days after laying the first egg) all rectrices and most remiges dropped.

Nest 10. Female enters on 13 November 1968. First egg laid five days later, and three eggs within nine days of entering, but no moult started. 13 days after entering (eight days after laying the first egg), all rectrices moulted, but not remiges. 19 days after entering remiges also moulted completely.

Nest 11. Female enters on 17 November 1968. First egg laid nine days later, the second the next day, but no moult started. The next day, 11 days after entering and 23 hours after previous observation, all rectrices moulted. 15 days after entering, the remiges also all moulted.

Nest 60 Found with one egg on 27 November 1968, the female with all rectrices already moulted, but no remiges dropped. Five days later, with four eggs, the remiges are also moulted. Four eggs was the complete clutch in this nest.

T. erythrorhynchus

Nest 9. Female found in hole with no eggs or moult started on 27 November 1968, and the same five days later. 14 days after first found, full clutch of five eggs laid, and female with all rectrices and remiges moulted.

Nest 17. Female with one egg on 17 January 1967, all rectrices moulted but no remiges.

Nest 33. Female with four eggs on 8 December 1968, all rectrices but no remiges moulted.

Nest 35. Female sealed in by 26 November 1968. First egg found six days later, and one rectrix in the nest. Still one egg after a further two days, but seven days after the first egg found there were three eggs and the female has dropped all rectrices and remiges. The complete clutch consisted of four eggs.

Nest 38. Female recently entered as sealing incomplete and still wet, with no eggs or any signs of moult started on 2 December 1968.

Nest 82. 4 December 1968, female sealed in but with no eggs or sign of moult. Five days later three eggs in nest and only the rectrices moulted.

Nest 85. 9 December 1968, female sealed in with no eggs or sign of moult. Seven days later one egg in nest, but no sign of moult.

Nest 89. Female only just entered nest, and sealing incomplete on 11 December 1968. Observed daily until first egg laid six days later, and no sign of moult.

Nest 97. Female sealed in by 16 December 1968, but with no eggs or moult started. 15 days later still no eggs, but female moulted all rectrices, but no remiges.

Nest 100 Female in nest with one egg on 20 December 1968, and with all rectrices moulted. Examined daily, second egg laid on 21 December, third on 23 December and fourth, completing the clutch, on 26 December. Remex moult was still not started by the last date, but commenced the following day and was complete within three days.

T. flavirostris.

Nest 3. 27 November 1968, the female in the nest with one egg and all rectrices moulted (Fig. 41). Five days later, with three eggs, the females' moult the same. A further nine days later, with the complete clutch of four eggs, the new remiges already measured 5 mm, giving a wing length of 49 mm, the tail measuring 29 mm. 24 December, and 13 days since the previous measurement, two of the eggs are hatched with the eldest chick estimated at three days old. Female has the wing 112 mm and tail 91 mm long.

Nest 42. Female enters on 25 November 1968. Three days later no eggs, but outer pair rectrices moulted. Five days after entering, one egg, rectrix moult is complete, and there is still only one egg two days later. 10 days after entering there are three eggs, and the same the next day, but remex moult has not started. However, 14 days after entering the fourth egg is present in the nest, completing the clutch, and all remiges moulted.

Nest 47. Female recently entered the nest, judging from the sealing, on 22 November 1968. Observed daily, and first egg present four days later at the same time as the first signs of rectrix moult appear. Rectrix moult complete the next day, and only one egg in nest six days after the female first entered. 10 days after the female first found, there are three eggs, and the remiges are all moulted, but two days later the fourth egg laid to complete the clutch.

Nest 58. Female in nest with two eggs on 1 December 1967. Her rectrices are all moulted, and remiges are beginning to moult. The remiges of the left wing are complete, as are the primaries of the right wing, but there are only three central secondaries remaining on the right wing. Two days later, still with two eggs in the nest, the right wing is the same, but now the left wing has moulted one primary and three secondaries. After a further two days, the right wing contains one secondary and the left wing two secondaries, and the clutch of three eggs is complete. The wing, with no feathers, measures 40 mm. Nine days after first found the wing measures 47 mm and the tail 25 mm (Fig. 42). 15 days after first found the wing measures 77 mm and the tail 50 mm (Fig. 43), and 24 days after found, with two chicks just hatched, the wing measures 120 mm and the tail 92 mm. By 43 days after first found, the female has left the nest, but only recently judging from the fresh sealing applied by the chicks.

Nest 65. One egg in nest and no sign of moult on female on 27 November 1968. Five days later, with one egg short of the complete clutch of four eggs, rectrix and remex moult complete.

Nest 69. One egg on 11 December 1968, and no moult started on female.

Nest 67. No eggs, or moult when found on 27 November 1968. Five days later, with three eggs laid out of the final clutch of five, the female has moulted all rectrices and remiges.

Nest 68. 27 November nest contains one egg, and female has dropped all rectrices. Five days later, with the full clutch of four eggs laid, remex moult is also complete.

Nest 74. Female appears to have just sealed herself into the hole on 25 November 1968. Three days later a single outer rectrix moulted, and two days later the first egg found and the rectrices moulted. Two eggs present seven days after entering, and four eggs present 10 days after entering. The next day, still with four eggs, remex moult is also noted as complete. The final clutch was of five eggs.

Nest 75. Female inside and hole completely sealed on 25 November 1968. First egg found five days later, and no moult started. 10 days after first found, there are three eggs and the tail moult is complete. After a further four days, with the fourth egg laid to complete the clutch, the remiges also moulted.

Nest 76. Female in nest with one egg and rectrices all moulted on 26 November 1968.

In all instances, no moult began before the female entered the nest hole, but thereafter there is considerable variation, especially in the stage at which moulting occurs. In all cases the rectrices are moulted first, and very rapidly, taking as little as 23 hours and at most two days for all feathers to drop out. A few days later the remiges begin to drop; it may take as long as four days for the remex moult to be completed. Regrowth of the new feathers begins almost immediately after the old ones have dropped, and proceeds rapidly until the female departs about 50 days after entering. However, judging by the measurements of the female from *I. nasutus* nest 3, compared with average wing size for unmoulted females, the feathers are not completely grown when she emerges.

There may be individual variation and specific variation as to when each stage of the moult occurs. In *I. nasutus* the rectrices are apparently moulted only after laying has commenced, and usually when the clutch is rather advanced. However there is one record of complete rectrix moult when there was only one egg. Remex moult follows immediately and is complete about four days after the rectrix moult, at or just after the completion of the clutch. In *I. erythrorhynchus* the rectrix moult usually occurs with the laying of the first egg to within a day, but rarely before laying. Nest 97 had an exceptionally long pre-laying period of at least 15 days and so may have precipitated an early moult. There is an interval of a few days before the remex moult begins. It may even be delayed until the clutch is completed. Remex moult takes about three days to be completed. *I. flavirostris* is the same as *I. erythrorhynchus*, but up to 10 days have been recorded between the rectrix and remex moults. However, the interval may also be very short, with only five days to complete both moults, as in nest 68. Rectrix moult may also begin before egg laying, although this is uncommon. The details for nest 58 indicate that there is no specific order in which the remiges are moulted, except that possibly they start with the secondaries. Tail moult similarly has no order, although the outer rectrices are often the first dropped. The moult is so rapid that it would be difficult to establish a pattern.

Body moult was only observed incidentally, beginning ventrally and proceeding dorsally and forward to end with the head and neck. Body moult only commences after the rectrix and remex moults are complete, and a few days after the laying of the last egg. Body moult appears to proceed faster than in non-breeding specimens, and is almost complete by the time the female leaves the nest.

The sequence of moult is basically the same as recorded in the detailed work of Stresemann and Stresemann (1966). The rectrix moult sequence is typical, starting with the middle and outer pairs and working inwards. I found no specimens with the regular order of remex moult described, starting at primary 3 (from the proximal side) and proceeding in either direction from there. Rather, the specimens most resembled the irregular order described, usually starting at the tip (primary 10) and primary 4, and working either way from the latter focus. On the distal moult progression primary 9 moults after primary 6, but then the distal progression continues.

Moult of the breeding female is variable, but follows a basic pattern, all rectrices and remiges being dropped by about the time that laying of the clutch is completed. It is interesting that the time the female is in the nest after moult has begun is about 45 days - the same time as taken for the chicks to complete their nestling period. However, the rectrices and remiges of the chicks start to grow only when the chick is about 12 days old, and so feather growth must be faster in the chicks. Both female and chicks appear to leave the nest with the remex growth not quite complete. Body moult is also completed by the time of the females' emergence, except for some feathers on the head and neck. At no stage does the female approach nakedness, as seen on Figures 41 - 43.

The few reports of moult of females of other _Tockus_ species taken from the nest indicate a similar pattern. Apart from the three species described here, the same moult is indicated for _T. bradfieldi_ (Hoesch 1937), _T. alboterminatus_ (Cowles 1926), _T. fasciatus_ (Chapin 1939) and _T. pallidirostris_ (Roberts 1912). Sometimes the female will begin to moult before she enters the nest, as found for T. monteiri (Section 5), and this may be shown by her retaining those feathers growing in or new when the remainder are suddenly dropped. Unmoulted feathers have been found for females in the nest of T. fasciatus (Chapin 1939) and T. griseus (Abdulali 1951), and may explain the comment of Stark and Sclater (1903) for T. alboterminatus that the female "before entering the nest begins to moult". I suggest that this may be due to a delay in suitable conditions for breeding, with the female beginning the moult of a non-breeding female until suitable conditions for nesting occur. The reported lack of moult in a breeding female of T. erythrorhynchus under captive conditions (Wieschke 1928) must have been due to the unnatural conditions.

The timing of moult to occur during the wet season indicates further that this is a time of optimum food supply. The male moults gradually, while having to feed himself, the female, who is undergoing an extensive moult and producing eggs, and later a brood of chicks as well. The cause of the simultaneous moult in the breeding female is unknown, but may be linked to the food supply. During the pre-laying phase the female is being frequently fed, while totally inactive (Section 7), and so could build up reserves, both for egg production and the start of the extensive new feather growth. This may explain why moult and egg production start simultaneously. However, the start of moult and egg production may be co-ordinated by a suitable hormone balance at that time.

That the female will be flightless while in moult in the nest is obvious, due to her lack of remiges, but I could find no indication that there is any psychological inhibition of flight. The female will flutter away as soon as there is enough surface area of wing to obtain lift. Any reference to the female being thin or weak during her enclosure (Moreau 1937) would also appear to be exceptional, as indicated by the condition of the birds examined (and shown in Figures 41 - 42).

SECTION 9. RADIATION IN THE BEHAVIOUR AND MORPHOLOGY OF THE MEMBERS OF THE GENUS TOCKUS, AND ITS BEARING ON THE SYSTEMATICS OF THE GENUS.

INTRODUCTION.

In this final section of the thesis, a general comparative approach is adopted for all species of the genus Tockus. The first section records what is known of the behaviour of Tockus hornbills, and the second part is a comparison of the morphology of all the species. This provides an understanding of the relationships between the species, and a framework wherein observations on the lesser known species can be fitted. Finally, the inter-relationships of the species of the genus Tockus is discussed, with comments on how the radiation may have evolved.

The behaviour of Tockus nasutus, T. erythrorhynchus and T. flavirostris was observed in South Africa, South West Africa, Rhodesia and Kenya, and includes observations on hand-reared specimens of each species. T. monteiri was observed in South West Africa, and T. bradfieldi was observed in Rhodesia, Botswana and South West Africa. Incidental observations on T. alboterminatus were made in Rhodesia and South Africa, and corroborate the detailed observations of Ranger (1949-52) for wild and hand-reared specimens in South Africa. Brief observations were also made on T. hemprichii and T. deckeni in Kenya. Therefore, the behaviour of the six southern African species of Tockus is well documented. For the remaining eight species, I have relied mainly on the literature and many personal communications.

I have not yet examined the taxonomy of the genus Tockus in detail, and have followed the subspecific classification of Sanft (1960) where necessary. I have treated T. jacksoni as a conspecific with T. deckeni. The "species" are only separable by the bill colour of the male and the presence or absence of white spots on the wing coverts. They occur together in several areas throughout their range in east and north-east Africa (Friedmann and Loveridge 1937), and have a similar total range. Sanft (1960) and von Erlanger (1905) consider *T. jacksoni* to be the sub-adults of *T. deckeni*. Others (Grant 1915; Rothschild 1924; van Someren 1922) consider them good species, although some are dubious of their specific status (Friedmann and Loveridge 1937; Jackson 1938). I observed both "species" in Kenya and am considering them conspecific until further evidence is available. Both forms were observed in pairs, feeding and heard calling, and I do not consider one the juvenile of the other. No differences were noted other than the external morphology mentioned that could be used to separate the species behaviourally or ecologically, as are so clear for the other species of the genus.

BEHAVIOUR OF *TOCKUS* HORNBILLS

Behaviour patterns that are not referred to specific species are patterns that occur in all six southern African species, and will, I suspect, be found to occur in all members of the genus. However, these patterns should be confirmed when other species are observed.

MAINTENANCE ACTIVITIES.

Progression.

Progression on the ground is either by hopping or by walking and running. Hopping has been recorded for *T. alboterminatus* (Ranger 1949), *T. bradfieldi*, *T. hemprichii* (Brown, *in litt.*), *T. nasutus* and *T. monteiri*. However, *T. monteiri* bounds rather than hops, and this may be due to the uneven terrain which it inhabits (Section 5). Walking and running have been observed for *T. erythrorhynchus*, *T. deckeni* and

T. flavirostris. All the above species hop when in trees.

Three different flight actions can be distinguished. A very direct flight of a few flaps followed by a glide is used by *T. erythrorhynchus*, *T. monteiri*, *T. flavirostris* and *T. deckeni*. A more buoyant flight, with deep wing strokes and following an undulating path, flapping a few times up the gradient and then swooping down with wings partly or completely closed, is used by *T. alboterminatus*, *T. bradfieldi*, *T. hemprichii*, and also *T. fasciatus* (Rand 1951; Elgood 1960). A similar flight, but with faster and shallower wingbeats and even more buoyant and dextrous, is used by *T. nasutus*, and probably also by *T. pallidirostris* (Mackworth-Praed & Grant 1952), *T. birostris* and *T. griseus* (Ali and Ripley 1970). These flight types are especially evident when the birds are flying some distance, usually above tree level. The birds of the first group are rather awkward on the wing, even on short flights among trees, compared to the latter two groups. The species with buoyant flight appear rather to float on the wing, but can display much aerial dexterity, as when pursuing flying insects.

Feeding.

I have distinguished the following feeding methods that are used by *Tockus* hornbills:

i) Picking - The food item is picked up where it is found in the vegetation or on the ground, while the bird is motionless.

ii) Digging - Standing on the ground, the bird pushes the closed bill into the substrate and then flicks the dirt to one side, partly opening the bill at the same time. Food items are thus exposed.

iii) Levering - On the ground, the head is lowered to one side and the closed bill slid under an object. Raising the head causes the bill to work as a lever to turn over the object. This is used when the object is too large to be moved by the digging action, and exposes the food items underneath.

iv) Chasing - Pursuing an active food item on the ground.

v) Swooping - Flying down from a perch to obtain a food item that has been noticed on the ground below.

vi) Plucking - Picking up a food item from the ground or vegetation without landing.

vii) Hawking - Catching a flying food item while on the wing.

All members of the genus are omnivorous. Some species are more carnivorous and others more frugivrous, but each species will make use of several foraging methods to obtain food. However, the species form into two groups, one foraging mainly on the ground and the other mainly in the trees and bushes. The terrestrial-foraging species use picking, digging levering and chasing to obtain most of their food, and include *T. erythrorhynchus*, *T. monteiri*, *T. flavirostris*, *T. deckeni*, and probably also *T. camurus* to some extent (Mackworth-Praed & Grant 1952; Bates 1930). The arboreal-foraging species obtain food by picking, and the aerial manoevres of swooping, plucking and hawking and include the species *T. alboterminatus*, *T. fasciatus* (Elgood 1960), *T. bradfieldi*, *T. nasutus*, probably *T. pallidirostris* (Mackworth-Praed & Grant 1952), *T. hartlaubi* (Chapin 1939), and *T. hemprichii* (Brown, *in litt.*). From reports of the Indian species, it appears that *T. birostris* (Lowther 1942; Ali and Ripley 1970) and *T. griseus* (Abdulali 1942; Butler 1896; Henry 1971; Ali and Ripley 1970) are arboreal-foraging species, and largely frugivorous.

Details of the foraging behaviour of each species are not available, but some general differences do exist. *T. erythrorhynchus* and *T. monteiri* obtain much of their food by digging, especially during the dry season, and most of the remainder of their food is obtained by picking.

T. flavirostris is an unspecialised forager, obtaining much of its food by picking throughout the year, but making use of a wide range of foraging activities. *T. alboterminatus* (Ranger 1950), *T. hemprichii* (Brown, *in litt.*) and *T. nasutus* only rarely descend to the ground to obtain food. In contrast *T. bradfieldi* frequently feeds on the ground, especially during the dry season, but less so than the true terrestrial-foraging species.

Manipulation of food prior to swallowing is done in a characteristic fashion. Arthropods are swallowed at once if very small, but usually they are nipped to kill them, and larger ones are softened by being run back and forth through the bill and squeezed at each step. Hard items and large items naturally take longer to soften; a *T. flavirostris* male was seen to take 39 minutes to soften a mouse before swallowing it. Softening is also prolonged for distasteful items, such as caterpillars and smelly grasshoppers, probably to remove as much distasteful material as possible. Hairy caterpillars are frequently wiped against the perch, probably to remove urticating hairs from them, but this is done for all hairy objects, such as mice. Fruits are removed from the plant with a twist of the bill. Fruits with a thick skin may be skinned before removal, nipping off the skin with the bill tip, dropping the skin, and then twisting off the fruit. Fruit is rarely taken from where it has fallen to the ground, even by the terrestrial-foraging species.

Drinking has never been recorded for any hornbill species in the wild.

Comfort activities.

Where possible, terminology follows that employed by McKinney (1965) for the Anatidae.

Wing-and-leg stretch - The wing and leg on the same side are extended backwards. Only recorded for T. bradfieldi and T. flavirostris.

Double-wing stretch with wrists folded - Only recorded for T. flavirostris.

Jaw-stretch and regurgitation - Wide opening of the mandibles is sometimes done as an independent action, but more often it precedes regurgitation, which is common. Regurgitation, which is done with short forward jerking movements of the head and an arching of the neck, is the method by which indigestible food remains are disposed of (Fig. 44). Small items (fruit fibres, fragments of exoskeleton) are formed into a loosely compacted pellet, but large items (seeds, large pieces of exoskeleton) are regurgitated singly. Before being allowed to drop, some items are felt in the bill tip and may be reswallowed. Possibly the bird can detect if digestible material still remains.

Scratching - Scratching of the head is indirect (Fig.45). The body is held horizontal and the supporting leg is bent so that the body almost touches the substrate. The head is bent back to one side, the wing on that side is dropped slightly, and the foot on that side is brought up behind the wing to scratch the head.

Bill cleaning - The various forms of this behaviour are very commonly done, both in context after the bill has been dirtied during feeding, and as a displacement activity. Conflict situations in which I have seen bill cleaning include territorial conflict, when aggression is shown by another bird, or when released after being handled. In its most common form, the bill is stropped, first on one side and then the other, on the perch or a nearby breanch. In displacement situations the actions may be very vigorous, sometimes not directed at the side of the branch but actually hitting it. Only one side of the bill may be cleaned by rubbing that side back and forth on the perch, and the attention is often then transferred to the other side. The action of biting off pieces of leaf and twig and crunching them up in the bill may also be a form of cleaning for the inner surfaces of the bill.

What appears to be displacement digging when a conflict situation arises while the bird is on the ground, may be displacement bill cleaning and the bird appears to peck the ground.

Oiling preening - This form of preening is not very often done, and takes two forms. During nibbling preening, the bird may pause in the region of the preen gland and nibble at the gland tuft. This is usually followed by a stripping action down the remiges. Less often, the sides of the head are rubbed over the preen gland area. This is followed by rubbing the sides of the head over the scapulars and upper wing coverts (Fig. 46).

Nibbling preening - All regions of the body are preened but for the head and upper neck. The long bill of these birds causes some characteristic postures during preening. When preening the tail, the rectrices are held to one side and slightly fanned. The lower neck and upper breast are preened with the head held high and the neck arched. The remiges are preened in a typical fashion, (Fig. 47)., with the wing held out partly open and at right angles to the body, so that the remiges are preened from the ventral surface of the wing.

Bathing - Bathing in water has never been recorded. However, Ranger (1950) describes baths by T. alboterminatus, taken in wet foliage or dew-soaked grass, whereby the bird became quite wet. I have observed a tame T. flavirostris bathing in wet foliage.

Dust bathing is, however, common. I have seen it in *T. nasutus*, *T. erythrorhynchus*, *T. flavirostris*, *T. monteiri* and *T. bradfieldi*. Ranger (1950) has recorded it for *T. alboterminatus*, and Vernon (*in litt.*) for *T. pallidirostris*. The bird lies on its breast, shuffling into the dust with side to side movements of the body, laying the neck along the ground and scooping the wings back and forth to dust the back (Fig. 48). The feathers are all raised and the sequence is often repeated. During intervals between bathing, the birds often peck at small particles of earth and sand, and sometimes swallow these fragments.

Sunning - *T. erythrorhynchus* will droop both wings, fluff out the feathers and erect the rump feathers to expose the preen gland, with the back towards the sun (Fig. 49). A more abandoned form of sun-bathing has been seen for *T. flavirostris* and *T. alboterminatus* (Ranger 1950), where the birds lie prostrate on the ground or a branch, wings partly open, feathers fluffed, head lolling to one side, and the preeen gland exposed. I have also seen young immature *T. flavirostris* hold both wings completely open with the body feathers raised when suddenly introduced into early morning sunlight. A tame *T. nasutus* regularly adopted a typical posture for sun-bathing, lying on the ground with wings outstretched, body feathers fluffed and the preen gland exposed, but this was not seen in the wild (Fig. 49).

The bird sunbathes only when completely at ease, and so is rarely seen in the field. The indication that there may be species-specific sunning postures would make further observations valuable.

A warming response is shown when the sun shines from behind, both wings being dropped to expose the back. If the sun is from the side, then only the wing on that side is dropped, and the bird will change wings as it moves from side to side. Unlike true sunning, the feathers are not fluffed and the preen gland not exposed. Warming movements cease when the bird is too hot.

Drying behaviour - After light rain, a _T. flavirostris_ was seen sitting on a road with the feathers all fluffed out and the wings drooped to the ground, in an attempt to dry itself.

Heat loss behaviour - The commonest activity when a bird is too hot is panting with the bill open. This may be accompanied by holding the wings well away from the body and sleeking down the body (Fig. 50). Gular fluttering has never been seen in adults, but _T. monteiri_ chicks in a rock-hole nest that faced the afternoon sun did so at a rate of 120 flutters/minute.

Sleeping - When at rest or sleeping, the head is pulled well down between the shoulders, with the bill pointing forwards. The body is lowered so that the abdominal feathers cover the feet. This position is also adopted when it is cold, and would be a good position for heat conservation, although the large bill is still exposed.

DISPLAYS.

Territorial display.

This display, typical for each species, is the one most frequently recorded for _Tockus_ hornbills, and is very conspicuous due to the movements and calls involved. I have found descriptions of, or observed, the displays of ten members of the genus. No information is available for the two small lowland forest species of Africa, _T. camurus_ and _T. hartlaubi_. It appears that the two Indian members of the genus, _T. birostris_ and _T. griseus_, do not have displays, but merely territorial calls. Henry (pers. comm.), who was familiar with _T. griseus_ in Ceylon, describes calls for the species very close to those of *T. flavirostris*, but with no accompanying display. Ali and Ripley (1970) report calls for *T. birostris* that could be like *T. alboterminatus*, but no obvious display other than that during calling"tail depressed or doubled under perch and swung slowly back and forth". It is unlikely that the displays, so obvious in the African *Tockus*, would have been over~~f~~looked in the two Indian species.

The calls which accompany the displays are described under the section on calls. The displays fall into two groups, one pointing the bill up, and one pointing the bill down, as shown in Fig. 51.

The simplest form of head-up display is done by *T. fasciatus*, *T. alboterminatus* and *T. bradfieldi* (Fig.51A). The displays of *T. alboterminatus* and *T. bradfieldi* are indistinguishable in the field, and appear to be identical to the display described for *T. fasciatus* (Elgood 1960). The bill is pointed vertically up, and with each note of the call the body is jerked backwards and then forwards. At highest intensities the tail is fanned slightly in time with the backward motion.

The displays of *T. nasutus* and *T. pallidirostris* (Vernon *in litt.*) (Fig. 51B) are very similar, and are like the above group, except that when the body is rocked back the wings are flipped half open and then closed when the body comes forward. Tail fanning is slight, and again restricted to higher intensities.

The most elaborate of the head-up displays is that described for T. *hemprichii* (Fig. 51C) by Brown (in Urban *et al*. 1970). "Display consists of uttering a long series of piping calls, with the bill pointing vertically skywards, the body bobbing up and down and the wings partly spread. Towards the end of the series of calls, a break in the series is followed by shriller calls at an accelerated tempo, during which the tail is raised vertically over the back and partly spread to expose the white outer tail feathers". Apart from the finale of fanning the tail over the back, the display is typical of the head-up group.

The simplest head-down display is done by *T. erythrorhynchus* and *T. monteiri* (Fig. 51D), and the movements are the same for each species. The body is pulled upright, the bill points downwards, and the neck is well arched. With each note of the call the body is bobbed up and down. At highest intensities the wrists are held slightly away from the body and the tail is slightly fanned. It is noticeable that the northern subspecies of *T. erythrorhynchus* (*T. e. erythrorhynchus*) holds the wings pulled back and half open during territorial display, the display described being for the southern subspecies (*T. e. rufirostris* and *T. e. damarensis*). This would appear to be an intermediate display to that of the following two species.

The head-down display of *T. flavirostris*, and that described for *T. deckeni* (Moreau & Moreau 1937; Root *in litt.*), appear to be the same (Fig. 51E). The body is held horizontal with the bill pointing downwards and the head at the level of the feet. The wings are opened fully over the back with the wrists almost touching, and while in this position the bird bows slowly to left and right. The tail is always somewhat fanned, more so at high intensities.

As stated, all these displays are accompanied by calling, which starts off with a pre-display call and then breaks into a display call, the latter being in combination with the movements described for each species. The duration of the calling depends on the degree of stimulation. Sometimes the pre-display calling does not culminate in display, and at other times the whole display sequence is repeated several times over. The display is done by both sexes. A mated pair will often display together, usually but not invariably, with the calling initiated by the male. All members of family groups will also display together. The displays are not in any sort of unison, and to term this "duetting" (Payne 1971, for *T. flavirostris*) is possibly stressing the co-ordination between the birds too greatly. At the beginning of the breeding season males display more obviously; the display may have a role of female stimulation, or else the male is merely the first to come into physiological breeding condition. In the Kruger National Park, before the rains enable the birds to disperse into their breeding territories, as many as 12 birds concentrated at feeding grounds will display together. During the breeding season displays are most frequent in the mornings and evenings to advertise the territory, but at any time of the day in defence of the territory. If an intruder is only heard, the birds will fly to a commanding position, such as a tree top, before displaying. Displays may even be directed at objects other than members of the same species, such as a raptor, a man near the nest, or even a vehicle in the territory.

Within a fortnight of leaving the nest, the young also assist in territorial defence. They will even do a rudimentary form of territorial display and calling from about ten days before they leave the nest. The calls and movements are very basic, with movements hampered by the confined space of the nest, but are clearly territorial display.

Agonistic display.

Threat, in all species observed, consists of depressing the feathers, especially around the head and neck, and facing the antagonist with the bill raised above the horizontal. This exposes the coloured patches of bare skin on the throat. The slow and stiff movements of the aggressor are also characteristic, and if threat is shown while on the ground the bird appears to be almost on tip-toe, so stretched is the posture.

Threat may be used intra- or interspecifically. It is very evident during territorial conflicts, being interspersed with bouts of territorial display. It is also shown to any other bird that comes too close, as when at a food source, or if another bird lands too close.

In extreme cases threat may lead to fighting, when the combatants lower the whole bill and body into a horizontal plane, keeping exactly in unison, and grapple with the tips of their bills. Typically, they lock bill tips and flutter up into the air as high as 5 m.

The chicks have a posture, with threat elements (Fig. 52), which has not been recorded in the adults. The head and neck are extended and the feathers on top of the head are raised. This position is adopted when the chicks are taken from the nest, or when something is thrust into the nest and they attack it. There may be an element of fear in the display as the fright call is often given under continued stress, but the chick will still remain aggressive.

CALLS.

Calls are usually difficult to transcribe, but the calls of *Tockus* hornbills fall into two groups - whistles and clucks. All the species that perform head-up territorial displays whistle, and those with head-down displays cluck. The meaning and phrasing of the calls is so similar for the Southern African species that they will probably apply throughout the genus. Species known to whistle are *T. alboterminatus*, *T. hemprichii*, *T. fasciatus* and *T. bradfieldi*. The quality of their calls is the same, except that Brown (*in litt*.) believes that *T. fasciatus* is slightly squeakier than *T. alboterminatus*. The whistles of *T. nasutus* are more musical than the above four species, and very similar to calls of *T. pallidirostris* (Vernon, *in litt*.), except that the latter are slightly more raucous. *T. birostris* and *T. hartlaubi* whistle, but the comparative quality of their calls is unknown. *T. monteiri* and the northern subspecies of *T. flavirostris* (*T. f. flavirostris*) have the gruffest calls of the clucking species. *T. deckeni* and the southern *T. f. leucomelas* have similar calls and are less gruff, and *T. erythrorhynchus* has the highest clucks of all. The calls of *T. griseus* and *T. camurus* are described as clucks (Henry 1971; Ali and Ripley 1970; Chapin 1939), but the quality of their calls is unknown.

The main calls consist of clucks or whistles ofvarying volume and duration of phrases; those I have distinguished are:

Alarm call - A strong single note, either a clucking 'tok' or a whistling 'pi' depending on the species.

This call is uttered when a predator is suddenly seen, or if a bird is surprised. The call acts both intra- and interspecifically, alerting other hornbills and other birds such as *Lamprotornis* starlings or *Bubalornis* weavers. The response of all birds is to fly to the nearest cover. Although this call cannot be distinguished by human ear, as different to other single clucks and whistles, the reaction proves that it sounds different to the birds.

Fright call - A harsh grating squeal.

Uttered by all species if frightened, and may be prolonged if a bird is handled or if chicks are disturbed during nest examination. It is uttered by the loser in a fight when aggression becomes too intense, and may replace the alarm call as a single 'squark' if the bird is given a very sudden fright.

Anxiety call - A series of clucks ' tok tok tok ... ' or whistles ' pi pi pi ...', uttered faster the higher the intensity, and of duration depending on how long the stimulus lasts.

This call is given when some uneasiness is felt, as when a distant predator is seen or some birds fly up suddenly, and the calling rate increases as the danger becomes nearer.

The most intense form of anxiety call is uttered as the birds take off to fly away from the threat, when the notes become fused into a single sound; 'toktoktoktok' for the clucking species, and 'pipipipipi' for the whistling species. This sound is not a true flight call, as the birds will take off silently if there is no threat.

Territorial call - Consists of two phases of no set duration, the pre-display phase of calling only, and the display phase when calling is accompanied by the movements already described. In the clucking species the pre-display call is a series of clucks 'tok tok tok ...' which in the display phase either breaks into double time 'toktok toktok toktok ...' (T. erythrorhynchus and T. monteiri), or merges into a prolonged sobbing cry 'tokuarkuarkuark ....' (T. deckeni and T. flavirostris). The display movements are done in time with each phase of the display call. In the whistling species the pre-display call is a series of notes 'pi pi pi pi...', which breaks into double time in the display phase ' pipieu pipieu pipieu ...' the display movements occurring during each phase.

Contact call - This call is lacking in the clucking species that have been studied. In the whistling species it consists of a single drawn out 'pieu', which if repeated, is done so at intervals of about two seconds.

The call is uttered by members of a foraging party as they move through the trees, especially by one that has been left behind. The call often elicits an answer. During flight, the call often brings a deviating member of the party back onto the flight line of the rest of the group. Ranger (1949) gives special attention to the role of this call in T. alboterminatus, and called it the "family-circle call".

Displeasure call - A low gruff growl.

It may be uttered at roosting time when one bird edges too close to another (Ranger 1949), and is rarely given when a bird is doing the threat display. A female T. monteiri uttered this call when arriving at the nest with sealing material, she found the male with his head in the hole. Basically the call is only used in the very mildest agonistic context.

Acceptance call - A harsh screech.

It is uttered by the female and chicks when they take food from the male (or from either parent in the case of the chicks). This very loud call is invariably uttered as the food is taken, and I have remarked (Section 4) on the possible function of this call in maintaining contact between the inhabitants of a sealed-in nest and their food providers.

Begging Call - A loud high-pitched 'kek kek kek ...' varying in volume and frequency.

Uttered by the chicks when they are hungry, and when they see or suspect the presence of an adult with food. Young chicks utter only a low peeping. This call may be interspersed with the acceptance call at the moment that the food is taken from the parent.

NON - BREEDING BEHAVIOUR.

Daily routines.

The following generalisations probably apply to all *Tockus* species. At first light the birds leave the roost and move into the sunshine, where they preen and warm themselves. They then begin to feed actively, and during the dry season, may have to fly up to 3 km to suitable feeding areas. Feeding slackens off as the day advances, the hotter the earlier, and the middle of the day is spent resting in the shade and preening. Feeding is resumed in the late afternoon and may continue after sunset. The birds return to the roosting site in the last minutes of daylight. If the afternoon feeding ceases earlier, the birds move to the roosting areas earlier, but take up their roosting sites only at the very last light.

Roosting site.

T. nasutus and *T. alboterminatus* (Ranger 1949) roost on thin terminal branches, where they have open space below and above them. *T. nasutus* roosts on the tips of branches of large trees and *T. alboterminatus* chooses openings in the canopy of riparian vegetation. *T. alboterminatus* has been found by Ranger (1949) always to use favourite sites, but should the open space surrounding them be eliminated then the sites are immediately deserted.

In contrast, *T. erythrorhynchus*, *T. monteiri* and *T. flavirostris* all roost in well concealed positions. A roost deep within a thorny bush is favoured, but they will also roost against or under the large branches of a tree.

Juvenile behaviour.

Even when independent of the parents, immature birds show certain behaviour that is not seen in the adults.

From the time they leave the nest young birds frequently feel surfaces with their bills, pick up objects only to drop them again, or break off pieces where they can, always using the bill as the main exploratory tool. Young birds also peck and pull at the feet and tails of siblings or parents. These activities may constitute play.

Young birds sometimes fly very fast around bushes and trees, swerving through gaps, diving down, only to land and then take off to repeat the whole course again. This flying, probably to develop their flying ability, has been seen in *T. nasutus*, *T. erythrorhynchus* and *T. flavirostris*, and reported for *T. alboterminatus* (Ranger 1950).

The young birds have the same calls and displays as the adults, but at first their voices are less distinct and higher pitched than the adults.

Sometimes a young bird will run up to an adult with feathers raised, especially around the head, which is slightly withdrawn. No calls are audible, and on reaching the adult the display is terminated. It is not common, but has been seen in *T. erythrorhynchus* and *T. flavirostris*. It may be a greeting display. Hand-reared birds will also do it to the feet of their human foster parent.

Inquisitive behaviour.

When perched, and observing an object of which it is unsure, a hornbill will adopt a typical pose (Fig. 53). The body is held horizontal, close to the perch, while the head is dropped below the level of the feet on an extended neck, and the tail is slightly lowered.

Interspecific behaviour.

Interaction is very slight with hornbills of other species. Up to five species of *Tockus* may co-exist in one area, and as each is separated ecologically (Section 3 and 5), competition is negligible. During the breeding season each species is spaced into territories, independent of the territories of other species, so that different species may have their nests very close together; the most extreme case was *T. erythrorhynchus* and *T. flavirostris* with active nests in the same tree (Section 7).

The only time that conflict occurs between species is at a common food source. The threat display, common to all species, is recognised by other species, so that the intruder is usually the more successful in usurping another type of bird. *T. flavirostris* appears to be an aggressive species, regularly chasing other birds of many species away, even flying over to investigate where a bird has just landed in case food is available.

Relations between hornbills and other species of birds are varied. The *Tockus* hornbills will respond to the alarm calls of many other species, especially *Lamprotornis* starlings and *Vanellus* plovers. Hornbills will join other birds in mobbing; I have seen *Tockus erythrorhynchus* help to mob an immature Gabar Goshawk *Micronisus gabar*, and *Tockus nasutus* help mob a Barn Owl *Tyto alba*. One bird that is very intensely mobbed by *Tockus* hornbills is the Banded Harrier Hawk *Polyboroides radiatus*, a predator that specialises in raiding nests of hole-nesting species. The hornbills hover over this hawk as it flies, bombing it, and perching close to where it lands. Fright calls and very high intensity anxiety calls are uttered throughout. Reactions to potential predators of adult hornbills include flying into the air to watch the predator while uttering anxiety calls, and falling silent and diving for cover. The latter reaction occurs in response to the most dangerous avian predators such as Black Sparrowhawk *Accipiter melanoleucos* (Ranger 1950), African Hawk Eagle *Aquila fasciata* or Martial Eagle *Polemaetus bellicosus*.

Other birds will mob hornbills on occasion. As hornbills are often reported as robbing nests of small birds (Pitman 1928, Lowther 1942), this reaction is easily explicable. The most aggressive species to the hornbills, is the Fork-tailed Drongo Dicrurus adsimilis. Normally the mobbing does not appear to bother the hornbill, but once a T. erythrorhynchus flew over the small chicks of a Crowned Plover Vanellus coronatus. When bombed by the adult plovers, the hornbill evaded by an exaggerated dipping flight, rising to about 3 m and then diving down almost to ground level.

BREEDING BEHAVIOUR.

I have described the basic nesting sequence for Tockus hornbills and some of the adaptations shown (Sections 4 and 7). Here I shall deal with behaviour associated with each stage of the breeding cycle.

Courtship.

It is not known for how long Tockus hornbills remain paired, but Ranger (1949) found that pairs of T. alboterminatus remain constant until something happens to one of the pair. I have known a pair of T. flavirostris to remain paired for three successive breeding seasons. Possibly the pairs are formed for life, as pairs of birds sometimes feed and roost together throughout the non-breeding season, but some birds have had a new mate each season for at least three seasons (T. erythrorhynchus and T. flavirostris).

How the early stages of pair formation occur is unknown, but they may be linked with territory establishment which the male often initiates. The mutual stimulation of the pair defending the territory may then serve to increase the pair bond. For some time before the female enters the nest to lay, the male will present food to her in courtship. The male flies or walks to the female, presents the food to her holding it in the tip of his bill and stands rather erect; she takes the food, uttering the acceptance call as she does so. In the early stages of this courtship feeding she may not accept food, but later takes it regularly, and in the last few days before she enters the nest all her food is taken from the male and she does no foraging for herself. Courtship feeding in _T. flavirostris_ may last for as long as two months if suitable breeding conditions are delayed, and either culminates in breeding, or the female merely begins to do more of her own foraging.

In the latter stages of courtship feeding, regular attention is also given to the nest hole by the pair, especially the female. At this stage the attraction of the nest hole to the male may also be strong, as he will often present food at the nest hole while the female is perched close by, and only after several unsuccessful attempts will he transfer the attention to the female.

Nest hole selection and preparation.

The female is more active in this task than the male, although he usually accompanies her, in a more passive role. The female pokes her head into the holes in trees within the territory of the pair, and after the hole is selected (usually rather quickly) attention is only given to that hole. Often the same hole is used in successive years.

Once the hole is selected, the pair usually visit it in the mornings after feeding, and less often in the afternoons (Fig.54). The female begins by picking debris out of the hole, and later starts to seal up the cavity (Fig. 55). Often the female will climb into the nest hole for short periods, squeezing in on her side if the hole is small, scrabbling with the feet and with the wings trailing behind. Any holes leading into the nest cavity are sealed. Only the final entrance hole is not sealed up completely. The sealing of excess holes into the nest cavity is rather random, and any cavities on the outside of the tree, formed by peeling bark or knotholes are also sealed. Sealing, of what will be the entrance hole, progresses to a point where the female can just squeeze in and out. If conditions are suitable, the female will then enter and complete the sealing until only a narrow vertical slit remains, using her own droppings. If conditions are unsuitable, the female will merely do token sealing at the hole each day, but not effectively closing it any further. The final closure of the hole by the female, once she has decided to enter, is rapid, rarely taking up to 12 hours, and often as little as four. The male never assists the female in obtaining sealing material, except occasionally in _T. monteiri_ (Section 5). However, the male sometimes brings millipedes to the female which are used for sealing, and only rarely for food.

The male brings all the lining for the nest. The lining is brought and presented to the female as for food, and is often interspersed with food items. The bulk of the lining is brought in the first few days after the female has finally entered the nest, but some lining is brought throughout the nesting cycle. The material used for lining appears to differ for each species (Section 7).

Copulation.

Copulation has only rarely been observed. I have seen it twice for _T. flavirostris_ and once for _T. monteiri_. In each case it occurred within an hour of sunrise, the male hopping through the branches of a tree after the female, until he could hop on to her back, hold the feathers of the head with his bill, and copulate. The copulation of _T. monteiri_ took place near the nest, and the male had just fed the female. The copulations of _T. flavirostris_ were not near a nest, but North (1942) records this species copulating near the nest. Ranger (1951) reoords copulation for _T. alboterminatus_, the only record in his years of watching, near the nest, with both birds becoming very excited and uttering a screaming call. It occurred at the stage in breeding when the male had just begun to courtship-feed the female, and is the only instance where a call has been noted during copulation.

Sealing.

The sealing of the nest entrance is done by the female holding the material in her bill, and then patting the bill rapidly against the site to be sealed. When a hole is to be sealed, the bill is rattled from side to side within the hole. The material is thus applied in thin layers, and by varying the angle of the bill to the surface, the surface is smoothed off. North (1942) reports a male T. flavirostris sealing a hole, but this requires verification, being the first record of a male sealing.

Material used for sealing varies, but mud, if available, is used for the preparatory sealing and closure of the nest chamber (Fig. 55). However, I have never found mud to be used by T. nasutus. Millipedes, and food items that are of a sticky nature, are regularly used. Once the female has finally entered the nest hole, she uses her own droppings for sealing material. Sometimes she will pick up debris from the nest floor and attempts to use this, probably as a displacement activity, but often debris adheres to her droppings on the nest floor, and so becomes incorporated in the sealing. It is interesting that once the sealing is complete, the female expels her droppings with force from the nest (see nest sanitation), but she can control this at any time if sealing material is needed.

All chicks, of both sexes, seal up the nest at some time. The eldest chicks seal the nest when the female emerges, and when the chicks leave the nest at intervals, the remaining chicks will reseal the nest until they are ready to depart. The first sealing is undertaken by the chicks when they are 20-25 days old, and no assistance is given by the parents. Attempts at sealing begin when the chicks are strong enough, with their eyes open, at about 16-18 days old. As with the female, the chicks will seal up any hole made into the nest cavity, except for the one slit. The novice attempts of the chicks can be easily recognised, as the sealing is applied in layers and not properly smoothed off. However, the sealing by the chicks is as hard as that of the female.

Nest sanitation.

Droppings, unless used for sealing, are expelled with great force from the nest through the narrow slit. The bird turns about, cocks the tail over the back, positions itself against the slit, and squirts. Before the chicks are old enough to do this, they merely excrete on to the nest lining, and often the soiled lining is thrown out during general nest cleaning. Cleaning of the nest is rather haphazard. Objects are picked off the nest floor, some are thrown out using the bill, and others are dropped again. However, the general effect is to keep the nest very clean. Large items, such as dead chicks, cannot be passed out through the slit, and merely rot on the nest floor.

Feeding.

Feeding of the nest inmates is done by the male, assisted by the female after she has broken out of the nest.

In the African species, the food is carried to the nest in the bill tip. Only once have I seen a male *T. flavirostris* regurgitate two scarab beetles, which were then fed to the nest inmates. The food is carried in single items, except by *T. monteiri* which often carries up to three items in the bill at once (Section 5). In contrast, the two Indian species carry much of the food to the nest in the stomach and regurgutate it, piece by piece, to pass in to the nest inmates, as reported for *T. birostris* (Lowther 1942). Although *T. griseus* usually does the same, food items are sometimes carried to the nest in the bill tip (Abdulali 1942; Butler 1896).

Up to 24 food items have been brought up at one visit (Lowther 1942).

The bird carrying the food perches by, or hangs below the nest slit (as in Fig. 54). The food is presented, and is never released until the nest inmate has grasped it, uttering the acceptance call. Sometimes the food has to be manoeuvred to fit into the slit. If dropped, the food is always retrieved and presented again. Dropping of the food is especially evident in _T. monteiri_, as the several food items held in the bill are released at once, and rarely are all items held by the inmates. One male _T. monteiri_ would drop all his food items at the base of the nest cliff, and carry them up to the nest one at a time (Section 5).

The chicks take the food at the nest slit as soon as they are old enough to see and are sufficiently mobile (about 14 days old), but prior to this the female takes the food from the male and passes it to the chicks.

Activities of the chicks in the nest.

The chicks are very dependent on the female until about 14 days old. As the chicks hatch at intervals, up to 14 days can separate the ages of the eldest and youngest chick. The eldest chicks can therefore, always be the first to obtain food, for they are more mobile, beg louder, and are stronger. Only when the elder chicks are sated will the younger chicks get any food.

When about one day old, an air sac develops over the shoulder region of the chick, and extends over the whole back and onto the upper breast by the sixth day. This air sac is present until the quills on the back are well-developed (about 13 days old), when it soon disappears. The air sac is inflated if the chicks are handled or prodded, and it may serve as a cushion to protect the naked young chicks from being trampled by their siblings and mother in the confined nest as suggested by Prozesky (1965). The air sac may also be to prevent predators from pulling chicks out through the narrow slit of the sealed-up nest entrance.

Much time is spent by the chicks resting or sleeping, usually squatting on the tarsometatarsus, and with the tail up to save space (Fig. 56). As the chicks grow older, they sleep less. By the time the female leaves the nest, when the chicks are about 20-25 days old with the legs fully grown, they wait at the nest slit for food, peering out of the slit with one eye. The chicks can see well from within the nest, begging when the parents approach, and responding to predators outside. An interesting dual response is shown to predators. If something small is presented at the nest slit the chicks will attack it, but if it is something big they usually run up the funkhole above the nest. Funkholes are a very regular feature of _Tockus_ nests. Possibly chicks attack a small object that could break down the sealing. These responses are not absolutely constant. The chicks will fall silent if the adults utter the alarm call near the nest, but otherwise do nothing to conceal their presence; begging and squirting out droppings when hawks or baboons are close to or under the nest.

The chicks preen in the nest, but no attempt at wing exercises has been noted. During the last ten days of the nestling period the chicks begin to perform rudimentary territorial displays.

Breaking out.

The female and chicks break out of the nest by persistently chipping at the very hard sealing. Once this took a female _T. erythrorhynchus_ four hours. She would peck a while, try to squeeze out, and then continue pecking until at last the hole was big enough. Both chicks and the female can fly well on emergence.

Fledging period.

For the first few days after emerging from the nest, the chicks remain hidden in foliage near the nest, being fed by the parents and still uttering the acceptance call. After this time they accompany the parents and begin to assist in territorial defence. The chicks appear to be able to feed themselves within about 18 days of leaving the nest, but family parties are probably maintained almost until the following breeding season, at least in T. alboterminatus (Ranger 1949). However, many species have to leave their territories during the dry season, unlike T. alboterminatus, and this confuses the picture, but groups are usually composed of male, female and immatures.

EXTERNAL MORPHOLOGY OF TOCKUS HORNBILLS.

Tockus hornbills can be grouped into species with similar behaviour patterns, and here the external morphology is compared to the grouping by behaviour.

Table 43 lists the main features of the external morphology of each Tockus species. I have examined skins of all Tockus species, and have combined these observations, with the very thorough descriptions of species given by Sanft (1960), and some points from other authors, to produce the table.

The uncertain affinities of T. birostris, T. griseus, T. hartlaubi and T. camurus as to their behaviour, is equally true of their external morphology, and these species are considered individually.

The first behavioural division of the hornbills is into tree-foraging and ground-foraging species. The authenticated ground-foraging species (T. erythrorhynchus, T. monteiri, T. flavirostris and T. deckeni), show the following common characteristics of external morphology (Fig. 57). The two central pairs of retrices are black, and the remaining three pairs have large areas of white or are completely white. A black bar, or remnant thereof, is present through the white of the outer three pairs of rectrices. The upper wing coverts are white, edged with either brown or black. In the adult T. deckeni the upper wing coverts are all black, or are white edged with black in the form originally described as T. jacksoni. The primaries are black, with a small white spot about halfway down their length except on the first primary. The secondaries are black, but for the inner three (not the tertials) which are wholly or partially white.

T. camurus (Fig. 57), appears to be at least partly a ground-forager , but does not have all the external morphological characteristics of the main group. The upper wing coverts are brown, tipped with white. However, the primaries have a small white spot in their centre, and although the secondaries are all white tipped, the innermost three are almost completely white.

In the tree-foraging species (T. nasutus, T. pallidrostris, T. hemprichii, T. alboterminatus, T. fasciatus and T. bradfieldi) the central pair or two pairs of rectrices are dark (Fig. 57). The remaining rectrices are white-tipped or completely white. The outer pair of rectrices never has more than the tip white. The upper wing coverts are dark, edged with a paler shade. The remiges are all dark coloured, although in some species the secondaries are edged with a paler shade.

T. hartlaubi (Fig. 57), is a tree-foraging species, but its external morphology does not comply entirely with the main group. The central pair of rectrices are dark, and the remainder are white tipped The upper wing coverts are all black. The primaries have a small white spot halfway along their length, and the secondaries are all white tipped.

The two Oriental species *T. birostris* and *T. griseus* are also tree-foraging species, but differ in several aspects of their external morphology from all other *Tockus* species (Fig. 57). In *T. birostris* the rectrices are all white tipped with a narrow dark band immediately proximal to the white tip, and the central pair of rectrices protrudes about 30 mm past the rest of the tail. In *T. griseus* the rectrices are all white tipped, but the white is much reduced on the central pair. The upper wing coverts are a uniform grey, but in *T. griseus* the very tip of the feathers is darker. The primaries of *T. griseus* are white tipped, and all but the first have white spots halfway along their length. The secondaries are uniform dark grey. In *T. birostris* the first five primaries and all secondaries are white tipped, and the first five primaries have small white spots midway along them.

All *Tockus* species have the abdomen off-white or white, and the upper parts predominantly a dark colour. In *T. griseus* the upper wing coverts have a silvery sheen, and in *T. hartlaubi* the black areas have a green gloss. The back of all species is a dark colour. *T. nasutus*, *T. erythrorhynchus* and *T. flavirostris* have a narrow white stripe down the centre of the back.

The ground-foraging species, with their direct flap-and-glide flight and habit of running on the ground (or bounding in *T. monteiri*), appear to have proportionally shorter wings and longer tarsi than the tree-foraging species. The latter have undulating, dextrous flight, and hop while on the ground. The average wing/tarsus ratios for all species are arranged in descending order of magnitude (Table 44) and a clear separation between the tree-foraging and ground-foraging species is evident. The tree-foraging species have a wing/tarsus ratio exceeding 6,0, while ground-foraging species have a ratio of less than 4,8. The poorly known African forest species appear to fit in with what is known of their foraging behaviour, *T. hartlaubi* falling within the tree-foraging group with a wing/tarsus ratio of 6,27, and *T. camurus* coming very close to the ground-foraging with a ratio of 4,90. The Oriental species are intermediate between these two groups with values of 4,98 for *T. birostris* and 5,29 for *T. griseus* which place them nearest to the ground-foraging group although they are known to be mainly tree-foraging species.

The finer species groupings shown by behaviour, especially the territorial display, are not clearly reflected in the external morphology. In all *Tockus* hornbills the male is markedly larger than the female. This is also true of the bill sizes of the sexes; adults can be sexed by bill size alone. There is sexual dimorphism of the bill colour in *T. nasutus*, *T. erythrorhynchus* and most markedly in *T. deckeni*. In all species there is sexual dimorphism in the bill shape due to the greater development of the casque on top of the bills of males. This is especially clear in those species where the casque forms a distinct body on top of the bill in males, as in *T. birostris* and the southern subspecies of *T. nasutus* (*epirhinus* and *dorsalis*). The casque is also prominent in the males of *T. alboterminatus*, but somewhat less so in males of *T. fasciatus*, *T. hartlaubi* and *T. pallidirostris*. In the remaining species the casque exists only as a raised ridge along the top of the bill. In each species the casque of the female is similarly developed to the male, but extends only halfway along the bill, giving a notched appearance to the top edge.

Eye colour is constant for each species, colours in the genus ranging from brown to red-brown to yellow. All very young birds have the eye colour very pale blue-grey.

DISCUSSION.

The ecology, behaviour and external morphology of *Tockus* hornbills reveals a clear dichotomy within the genus. In Table 45, the main characters of the two groups are listed. Some of the more obscure behavioural characters, such as presence or absence of a contact call, roosting site and nest lining, are included as they apply to the species for which these details are known. However, they may become irrelevant when more data becomes available.

So little is known about the two diminutive African members of the genus, *T. hartlaubi* and *T. camurus*, that it is difficult even to hypothesise about their position within the genus. *T. hartlaubi* is restricted to lowland forest in Africa (Figure 58), and is rarely seen as it inhabits the upper parts of the trees (Chapin 1939). This indicates that it would be a tree-foraging species, which is borne out by its high wing/tarsus ratio, the whistling type of calls, and external morphology that is closest to that of the tree-foraging group. *T. camurus* also inhabits lowland forest in Africa (Figure 58). It is a species that is often encountered low down in the forest, often in dense secondary growth and where there are gaps in the forest canopy (Chapin 1939). It has been recorded feeding on the ground, and is reported to follow army ants for the insects that they disturb (Chapin 1939). The relatively low wing/tarsus ratio and the clucking type of calls point to its placing with the ground-foraging group, although the external morphology has several characters of the tree-foraging group. Both species are remarkable within the genus for their very loud, far-carrying calls (possibly an adaptation to living in dense forest), and for being the most markedly insectivorous of the species. It is probable that these two species have become so specialised for their forest, insectivorous niches that they do not fall into any exact species grouping.

Our present knowledge of the Oriental members of the genus, *T. birostris* and *T. griseus*, indicates that they differ in several respects from the other members of the genus. *T. birostris* is found in deciduous woodland in India (Fig. 59), and is replaced in the denser and non-deciduous woodlands and forest of India by *T. griseus* (Ali and Ripley 1970), which also occurs in Ceylon (Fig. 59). Morphologically, these species have characters that are alike, but which set them apart from the rest of the genus ; such characters as white tips to all the rectrices and some of the remiges, and being the largest members of the genus. Both species appear to lack territorial displays (the swaying of *T. birostris* while calling may be a rudimentary display), in marked contrast to the African members of the genus. Most strikingly, they regurgitate food to pass to the nest inmates - usually fruit, but also insects, lizards and birds eggs (Abdulali 1942; Lowther 1942). This is unique within the genus *Tockus* but is done by all other hornbill genera except for the two omnivorous *Bucorvus* species and the monotypic *Tropicranus*. All species which do not regurgitate food at the nest, but bring it in single items, are omnivorous. Regurgitation may not be possible with an omnivorous diet; although the two Oriental *Tockus* species indicate the feasibility of regurgitation of insects and small vertebrates, they are still primarily frugivorous. Loss of the ability to regurgitate may only be possible after certain specialisations. The two aberrant *Bucorvus* species (adapted for a terrestrial existence) live in small parties, have a predominance of males in the group, and all members of the group feed the incubating female or the single chick (Kemp 1969). This co-operative approach may allow for food to be brought to the nest in single items. The genus *Tockus* is unique among hornbills for the very fast moult of the breeding female, so that she is able to break out of the nest and assist the male in feeding the chicks for the latter half of the nestling period. The same may be found to occur for *Tropicranus*, but the breeding cycle of this species is unknown. In the other hornbill genera with sealed nests, the female leaves with the chicks. The early emergence of the female occurs with the two Oriental *Tockus* species, but is an adaptation which may have permitted the African species to radiate into savanna. If bringing single food items allowed a more proteinaceous diet than fruit to be adopted, radiation into savanna (where fruit is limited) and the adoption of an insectivorous diet could have occurred with the African species. It is notable that T. *monteiri*, the only arid species studied (Kemp and Kemp 1972; Section 5), often brings up to three food items to the nest at once. This indicates that the balance between bringing single food items to the nest, and maintaining a sufficient supply of food, is delicate. For these reasons, I suggest that regurgitation of food at the nest is a primitive character in hornbills, non-regurgitation having been evolved by two independant groups. The Mallophaga from *Tockus* hornbills indicate that the Oriental species have been isolated from the African species for a long time (Elbel 1964). Three species-groups of the louse genus *Chapinia* are found, the *actovulvatum* and *hirtum* species-groups in the Oriental and Australasian regions, and the *lophocerus* species-group in the Ethiopian region. *Chapinia clayae* (of the *actovulvatum* species-group) occurs on the two Oriental *Tockus* species. It resembles *C. actovulvata* from the Oriental hornbills of the genus *Anthracoceros* more closely than any members of the *lophocerus* species-group found on the African *Tockus* hornbills. This indicates more recent contact between the Oriental species of *Tockus* and *Athracoceros*, than between the Oriental and African species of *Tockus* (Elbel 1964).

The African species of *Tockus*, excluding *T. hartlaubi* and *T. camurus*, form into four species-groups, two of tree foraging species and two of ground-foraging species. The four groups which I propose are described below, although the reasons for the naming, and for not terming the groups superspecies, will be given later.

1. *bradfieldi* species-group.

This includes the species *T. bradfieldi*, *T. alboterminatus*, *T. fasciatus* and *T. hemprichii*. All species have whistling calls that are indistinguishable in the field and sexual dimorphism in the colour of the gular skin; black to dark blue in males and orange to blue-green in females. All species have the simplest form of head-up territorial display, except for *T. hemprichii* which fans the tail above the back at the end of the display. All species are large members of the genus although not as large as the two Oriental species. All species have a characteristic bouyant flight with deep wing beats.

All species appear to be allopatric (Fig.60). Sympatry appears to occur along the edges of their range, but the species will probably be found to be ecologically isolated, as indicated by the different habitats which the species occupy over the centre of their range. *T. fasciatus* inhabits the lowland forest of the Congo basin and West Africa. *T. alboterminatus* inhabits montane forest, riparian associations and coastal forest, the latter especially in the southern areas of its range. *T. hemprichii* is a montane species of the Abyssinian highlands up to 4300 m, where it frequents wooded gorges and valleys (Brown *in litt.*). A relic population also exists on cliffs and hills to the south of the Lake Rudolf depression, especially in the Lake Baringo area. This population which I have observed briefly, may have no contact with the bulk of the population in Ethiopia. *T. bradfieldi* also has a limited and apparently relic distribution. The bulk of the population is in the teak woodland (*Baikaea plurijuga*) and climax mopane woodland (*Colophospermum mopane*) of north-eastern Botswana, north-western Rhodesia, the Caprivi Strip and south-western Zambia. The population is bounded approximately, on the north and east by miombo woodland (*Brachystegia* sp.), and on the south and west by open thornveld. An isolated population occurs on the Waterberg "inselberg" in northern South West Africa, separated by 600 km of thornveld and the Okavango Swamps from the main population. I have observed both populations, those in the Waterberg being confined to the wooded gorges, which have large trees that remain with foliage, due to the springs that run off the top of the inselberg.

There are usually only one pair per gorge, and they only rarely forage out into thornveld surrounding the mountain.

2. *nasutus* species-group.

This includes the species *T. nasutus* and *T. pallidirostris*. Both species have very similar whistling calls, although different in tone to the *bradfieldi* species-group. The flight is also different to that group, being buoyant, but with a much shallower wing action. Both species have a head-up territorial display accompanied by wing flicking. They are medium-sized members of the genus, and the gular skin is dull grey in males and blue-green in females, so far as is known. *T. nasutus* inhabits woodland, savanna and arid steppe throughout Africa (Fig.61). It is replaced by *T. pallidirostris* in the moister and denser miombo woodland (*Brachystegia* sp.) across central Africa (Benson and Irwin 1966; Benson *et al* 1971).

3. *monteiri* species-group.

This includes the species *T. monteiri* and *T. erythrorhynchus*. Both species have clucking calls, although those of *T. monteiri* are much deeper than *T. erythrorhynchus*. The flight is a direct flap-and-glide, the same as for the following species-group. Gular skin is pink for both sexes of *T. erythrorhynchus*, but is sexually dimorphic in *T. monteiri* being black in males and grey-green in females. They have head-down territorial displays, bobbing up and down with the wings closed, except for *T. e. erythrorhynchus* which holds the wings half open above the back during display. Both species forage on the ground and dig for much of their food. *T. monteiri* is a large member of the genus, of similar size to members of the *bradfieldi* species-group, but *T. erythrorhynchus* is medium-sized. *T. monteiri* is confined to the arid, hilly areas of southern Angola and northern South West Africa (Fig. 62), and is sympatric with *T. e. damarensis* in some of these areas. However, the difference in size probably prevents competition between the species and would also help as a species isolating mechanism. *T. erythrorhynchus* inhabits savanna and steppe throughout Africa, being absent from the more wooded areas, and from the more arid areas in the south.

4. *flavirostris* species-group.

This includes the species *T. flavirostris* and *T. deckeni*. Both species have clucking calls, of similar tone, but that *T. f. flavirostris*, which occurs sympatrically with *T. deckeni* (Fig. 63), has much deeper calls. Both species have head-down territorial displays, with the wings fanned above the back and the head held at the level of the feet. The gular skin is pink in both species, but for the female *T. f. flavirostris* where it is black. The eye skin is black in *T. deckeni* and *T. f. flavirostris*, but is pink in *T. f. leucomelas*. Both are medium-sized members of the genus. *T. deckeni* inhabits thornveld in Ethiopia, Sudan and Kenya, and the adjacent peripheries of Uganda, Somaliland and Tanganyika (Fig. 63). *T. flavirostris* has a discontinuous distribution in thornveld and steppe, one group in southern Africa and the other in north-east Africa. The latter group, of the subspecies *T. f. flavirostris*, and *T. deckeni*, are sympatric over much of their ranges. *T. deckeni* is an unusual member of the genus, having very marked sexual dimorphism of bill colour (males orange, females black) and a two-tone plumage of areas of solid black and white. It also appears to be unique among hornbills, having the immature colours the same as the female and not the male. *T. flavirostris* is intermediate in this respect, males, females and immatures having the same bill colours and only being distinguishable by the size and shape of the bill. Very young birds have the bill blackish, but the adult colour is assumed within about a month of leaving the nest. Female *T. f. flavirostris* can, of course, be sexed by the black gular skin, compared to the pink of males, but unfortunately the colour of the gular skin of immatures of this subspecies is not recorded.

Before considering the possible evolution and systematics of the genus *Tockus*, it is necessary to comment on the monotypic *Tropicranus albocristatus*. This hornbill inhabits lowland forest in Africa, having a similar distribution to *Tockus hartlaubi* and *T. camurus* (Fig. 58). *Tropicranus* is largely insectivorous, foraging below the forest canopy, and is reported to follow bands of monkeys for the insects they disturb (Chapin 1939). Ecologically it is like a very large (slightly larger than *Tockus birostris*), arboreal-foraging *Tockus* hornbill, but that the tail is elongate and graduated and there is a loose crest formed by elongated nape feathers. The bill is *Tockus*-like in shape, without the huge casque present in the other genera of African forest hornbills, *Bycanistes* and *Ceratogymna*. All rectrices are tipped with white, the crest and face are white, and in the most wide-spread subspecies *T. a. cassini* the remiges and greater wing coverts are white-tipped. Furthermore, the chicks of *Tropicranus* have pink skin (Chapin 1939) like the known *Tockus* species, but *Bucorvus* chicks within a few days of hatching develop a dark blackish skin, as do chicks of *Ceratogymna* (Chapin 1926) and *Bycanistes* (Moreau and Moreau 1940; Kilham 1956). A most important similarity is that *Tropicranus* takes food to the nest in single items (Chapin 1926), as do all African *Tockus* hornbills. Reports also indicate that *Tropicranus* is a territorial species, only being encountered in pairs or family parties (Bannerman 1933, Chapin 1939). This is like *Tockus* species, but unlike another forest genus, *Bycanistes* (Kilham 1956; Moreau and Moreau 1941). Therefore, it appears that *Tropicranus* may be an aberrant form of Tockus, and should be included in a consideration of the latter genus. I am not suggesting that it is congeneric with *Tockus*, but the markings of the plumage are similar to the Oriental *Tockus* species, and with a wing length/tarsus ratio of 6,2 it has the proportions of a typical arboreal-foraging *Tockus*, and possibly a common ancestry.

Two questions are basic to a consideration of the systematics of the genus Tockus. To which other hornbill genera is it most closely related, and because it appears to be a specialised genus, from which genera might it have evolved? This is difficult to answer because of the paucity of information about other genera. Tropicranus appears very closely related to Tockus, but has so many similarities which are unique to these two genera, that a common origin is suggested. The Oriental genera Ptilolaemus and Penelopides have appearance and proportions that are similar to Tockus hornbills, which is not true for any other Ethiopian genera, but this is as far as one can proceed at this stage.

Secondly, did the genus Tockus originate in the Oriental or Ethiopian region? This is important as it is the only hornbill genus common to both regions, and also because it may shed light on the ancestral region for the family Bucerotidae, which is confined to these regions. The Oriental region has double the number of genera of the Ethiopian region (ten against five, including Tockus for each region). This indicates that radiation has been proceeding for considerably longer in the Oriental region. If we accept that frugivorous species (with regurgitation at the nest), are primitive, the radiation in the Oriental region is even more impressive, with nine frugivorous genera in the forest habitat, against two in the Ethiopian region. This indicates an Oriental origin for the hornbill family as a whole. The only indicator of an Oriental origin also for the genus Tockus is the lack of any suitable ancestral genus in Africa. The Oriental species of Tockus show many characters which I consider primitive for the genus, such as lack of territorial display, and regurgitation of food at the nest. They appear to have been isolated from the Ethiopian Tockus species for a considerable time, as indicated by their unique behaviour, plumage (which is most like that of

Tropicranus) and the divergence of the lice from the two groups (Elbel 1964). This indicates that the Oriental *Tockus* species are closest to the ancestral stock of the genus, but not of course that they are the ancestors of the genus.

Hall (1963) studied the genus *Francolinus*, which also has an Oriental (Indian) and Ethiopian distribution, and a predominance of species in the Ethiopian region (36 against five). She suggested that this was because of the paucity of suitable isolating mechanisms in the Indian region. The topography of the Indian region is generally monotonous, as is the climate. In contrast, Africa has a very variable topography and a wide range of climates. Climatic fluctuations would therefore cause considerable changes in the extent and distribution of habitat types, as is so well documented for the Pleistocene of Africa (Moreau 1963, 1966; Cooke 1964; Clarke 1967). This would provide more chances for isolation, and so for speciation to occur, in Africa than in India, and this would appear also to be applicable to the *Tockus* hornbills. Hall (1963) also thought that the lack of radiation of francolins in the Indian region may be due to the many other related genera of Phasianidae which occur in that area. This does not appear to be applicable to the hornbills, as no species in the Oriental region have radiated into the omnivorous niche, in contrast to the African species of *Tockus*, *Tropicranus* and *Bucorvus*. This may be because of competition from such omnivorous, mainly insectivorous families as Trogonidae, Dicruridae, Campephagidae, Timaliidae and Eurylaemidae which have radiated so widely in the Oriental forests.

The phylogeny which I suggest for the genus *Tockus* is shown in Figure 64. Because of this suggested phylogeny I have not termed the African species-groups as superspecies. The evidence (below) suggests that the species of similar behaviour and morphology did not radiate from a common ancestor, but rather gave rise to one another. This is supported by the distinct habitat preferences of the species within a group, indicating not that they have evolved during recent isolation, but that they are long established in that habitat. This is in direct contrast to Hall's (1963) studies of francolin and Passerines (Hall and Moreau 1970) where many species appear to only have been isolated recently and have diverged little from an obvious "parent" species. Furthermore, one could expect extinction of several francolin species with a change of climate (and redistribution of habitat types) in Africa. This would be very unlikely with hornbills which are confined to only the basic habitat types of forest, woodland or steppe. These habitats have probably always been present in Africa (Moreau 1966), although their relative extents have varied considerably. The radiation of the francolin species-groups, much of which probably occurred since the end of the last glaciation about 18 000 years ago (Hall 1963), appears comparable to the divergence of several of the *Tockus* subspecies. This is especially true of the species separated into northern and southern subspecies by the miombo woodland across central Africa (*T. nasutus* with the casque absent on the bill in the north; *T. erythrorhynchus* with the different eye colour and territorial display between the two areas; *T. flavirostris* with difference in call tone and colour of the female gular skin.). The lowland forest species have also developed subspecies, one in the Congo forests, and one or two in the forest blocks of West Africa (*T. hartlaubi*, *T. camurus*, *T. fasciatus*, and also *Tropicranus albocristatus*). This divergence into very distinct subspecies, compared to full species in the francolin, also indicates a slower rate of evolution for the genus *Tockus*.

The reasons for the phylogenetic order shown in Figure 64 are varied and scattered, but are in many cases suggestive. The following stages are postulated.

Stage 1: proto-*Tockus* evolves from a forest species to inhabit woodland in the Indian region.

Possibly this occurred in Ceylon, one of the few means of isolation in the Indian region, by the onset of a dry period. This would separate Ceylon widely from any other forest areas, and would later impose conditions of woodland during the isolation.

Stage 2: proto-*Tockus* emmigrates to Africa via Arabia.

This further suggests that proto-*Tockus* was a woodland bird, since the Arabian area has probably always been arid according to its geology (Clark 1954), and so may never have supported anything better than dry woodland. I suggest that proto-*Tockus* was similar to the present-day *T. birostris*. The assumptions about proto-*Tockus* would still apply if *Tockus* originated in the Ethiopian region and colonised India. It was probably at this time that the last contact existed between the two regions, since subsequent dry savanna across Arabia would allow several species, such as *T. nasutus*, to cross over. Therefore, the subsequent radiation of the lines within the two areas is not affected by whether the origin of the genus *Tockus* was Ethiopian or Oriental.

Stage 3: Preliminary radiation in the two zoogeographical regions.

a) proto-*Tockus* evolves to *T. birostris* in Indian woodland, and possibly the resident population in Ceylon, under moister conditions, evolves to *T. griseus* of moist evergreen woodland.

b) proto-Tockus in Africa radiates along one line to T. nasutus. The similarity of T. nasutus, but for the diminutive size, to T. birostris in colouration and the conformation of the casque on the bill of males is striking For some time the two species were placed together in their own genus (Elliot 1882). It is notable that T. pallidirostris, of moister woodlands than T. nasutus in Africa, looks very like T. griseus, with a cream bill, no casque, and grey plumage.

c) proto-Tockus in Africa radiates along another line to T. bradfieldi and/or T. alboterminatus. I have chosen T. bradfieldi as the oldest member of this species-group because it inhabits dry woodland; the habitat closest to that postulated for proto-Tockus. I consider both species as most primitive in the group because of the single pair of dark tail feathers, with the rest white tipped. This is closest to the plumage of the Oriental species of Tockus, and may also indicate that T. camurus developed at this stage. T. camurus, T. bradfieldi and T. alboterminatus also have bills of similar orange-red colour.

Tropicranus albocristatus possibly also evolved from proto-Tockus at this stage, retaining the elongated central rectrices like T. birostris.

Stage 4: Radiation of the bradfieldi species-group.

The evolution of a different tail pattern (Fig.57), with two central pairs of rectrices and the outer pair dark, and the intermediate two pairs white, may have followed. Possibly T. hartlaubi indicates an intermediate stage, with two pairs of central rectrices dark, but the rest white-tipped. T. fasciatus and T. hemprichii indicate the final stage. The unique territorial display of T. hemprichii indicates long isolation in the Abyssinian highlands. The individuality and isolation of the Abyssinian avifauna is well documented (Moreau 1958; Hall and Moreau 1962), but is inexplicable at present (Moreau 1966).

Stage 5: Establishment of the terrestrial-foraging line of *Tockus* hornbills.

The key species to the establishment of the ground-foraging line appears to be *T. monteiri*. The similarities in plumage and bill colour of *T. monteiri* and *T. hemprichii* are very striking, and both occupy hilly areas and frequently use rock holes for nesting (Section 5; Urban *et al* 1970). However, their behaviour, calls and plumage patterns are different, and characteristic of their particular foraging species-group. *T. monteiri* retains three characters of the tree-foraging group; the colour and sexual dimorphism of the gular skin, hopping when on the ground, and large size. The hopping appears adaptive to the rocky habitat (Section 5), but is associated with a much longer tarsus than the tree-foraging species. The tail pattern consists of two dark pairs of rectrices and the rest white, which means only the outer pair have become white from the condition in the advanced species of the *bradfieldi* species-group. However, characters of the ground-foraging species are also evident; three white inner secondaries, reversal of the wing coverts colours from a dark centre with pale edge to a pale centre with dark edge, and white spots in the primaries. Apart from hopping, all the behaviour of *T. monteiri* is typical of the ground-foraging group.

The establishment of this line in the arid region of south-western Africa is of interest. This area appears to have never been better than semi-arid (Clark 1960), in contrast to the fluctuations over much of the rest of Africa, at least during the Pleistocene (Bakker 1960; Moreau 1963, 1966). This stability may have made this area an important centre of speciation in Africa, as is indicated by the number of endemics for the area. Many of the endemics are primarily birds of the hilly areas (*Namibornis*, *Poliocephalus ruppelli*, *Francolinus hartlaubi*, *Achaetops*, *Agapornis roseicollis*), and some are more terrestrial than their relatives

(Lanioturdus, Achaetops). An illustration of how these species evolved may be the isolation of the small T. bradfieldi population on the Waterberg "inselberg" in South West Africa. Furthermore, there is faunal evidence for connection between the south-west African and Abyssinian highlands, from discontinuous distributions of such species of birds as Ploceus rubiginosus (Moreau 1966) and Poliohierax semitorquatus (Maclean 1970). This relates well to the similarities of T. hemprichii and T. monteiri, and the divergent evolution of the latter species.

Stage 6: Radiation of the terrestrial-foraging species of Tockus.

T. erythrorhynchus is a diminutive form of T. monteiri, with very similar behaviour and basic ecology. However, it is interesting that the southern subspecies (T.e. rufirostris and damarensis) have yellow eyes, unlike T. monteiri, while the northern subspecies (T. e. erythrorhynchus) has the same brown eyes as T. monteiri. The latter subspecies has a territorial display intermediate between that of the two main head-down types, indicating a stage in the evolution to T. flavirostris. Finally, T. deckeni, of the flavirostris species-group, appears to be the most recently evolved species. The stark pied colouring, striking sexual dimorphism of bill colour, and colouring of the immatures like the female, indicate that it is a specialised species. It may be the most highly evolved hornbill species, but may also be "unstable", as indicated by the two colour forms which exist, and which are often considered separate species.

This evolutionary sequence is not accurate, nor can the stages be even approximately dated. However, it invokes no changes in habitat distribution during African prehistory for which there is not already some evidence. The aridity of south-western Africa for the evolution of T. monteiri from a common ancestor with

T. hemprichii of the Abyssinian highlands - Disruption of the distribution of the savanna species, and subsequent reconnection, through the miombo woodland of central Africa, for the evolution of *T. bradfieldi*, *T. nasutus*, *T. pallidirostris*, *T. erythrorhynchus*, *T. flavirostris* and *T. deckeni* - Fragmentation of the lowland and montane forest patches for the evolution of *T. alboterminatus*, *T. fasciatus*, *T. hartlaubi*, *T. camurus* and *Tropicranus*. All these changes have satisfactory evidence for having occurred during the Pleistocene (Moreau 1963, 1966; Bakker 1969).

It is hoped that this dissertation, while showing many gaps in our knowledge, may further the study of the zoogeography and evolution of the African avifauna.

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