

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

by

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Degree of Doctor of Philosophy

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Figure 1. The two hornbill study areas in Africa were the Kruger National Park and the Wankie National Park.

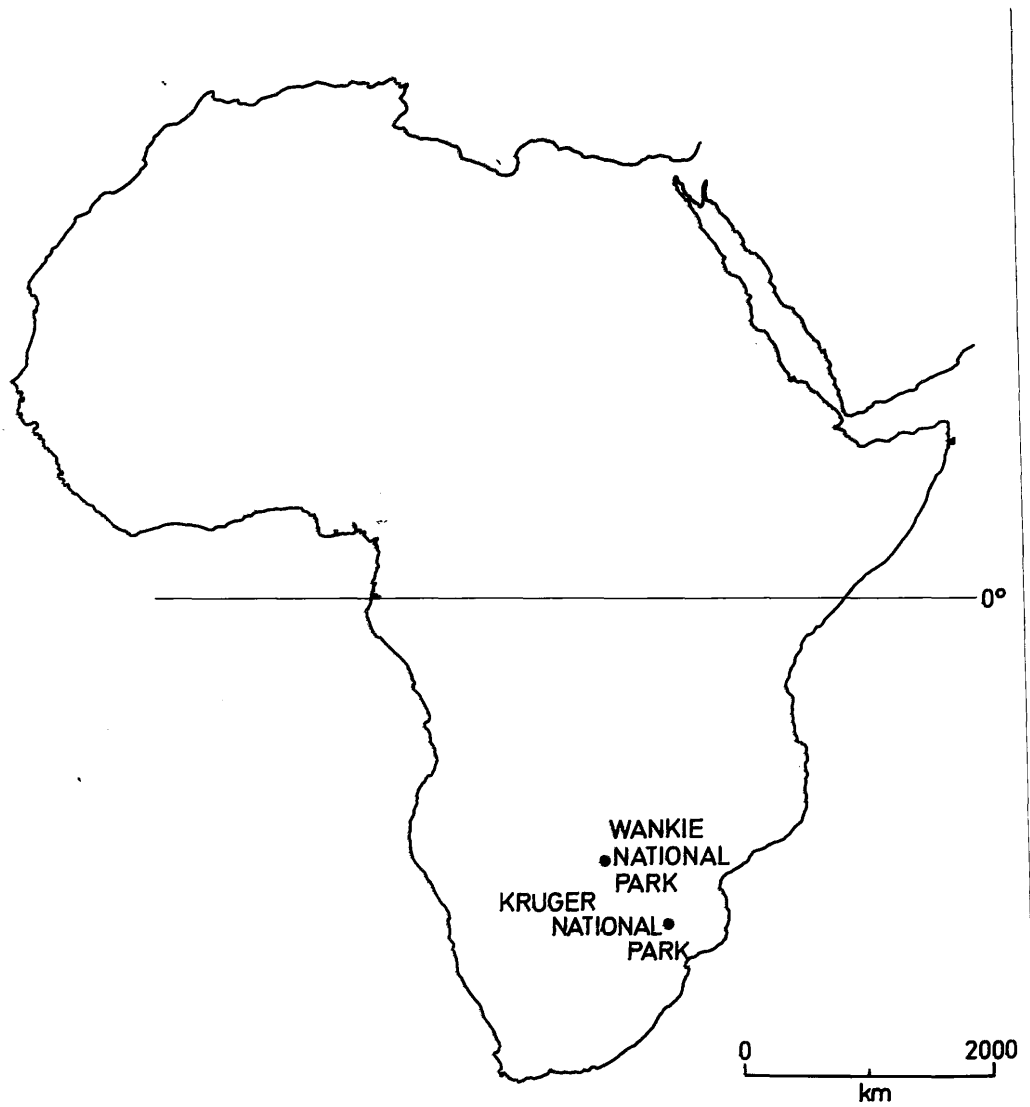


Figure 2. Map of the central Kruger National Park study area, showing the main features and marking the areas where intensive studies were conducted. Inset shows the position of the study area (black) within the Kruger National Park outline.

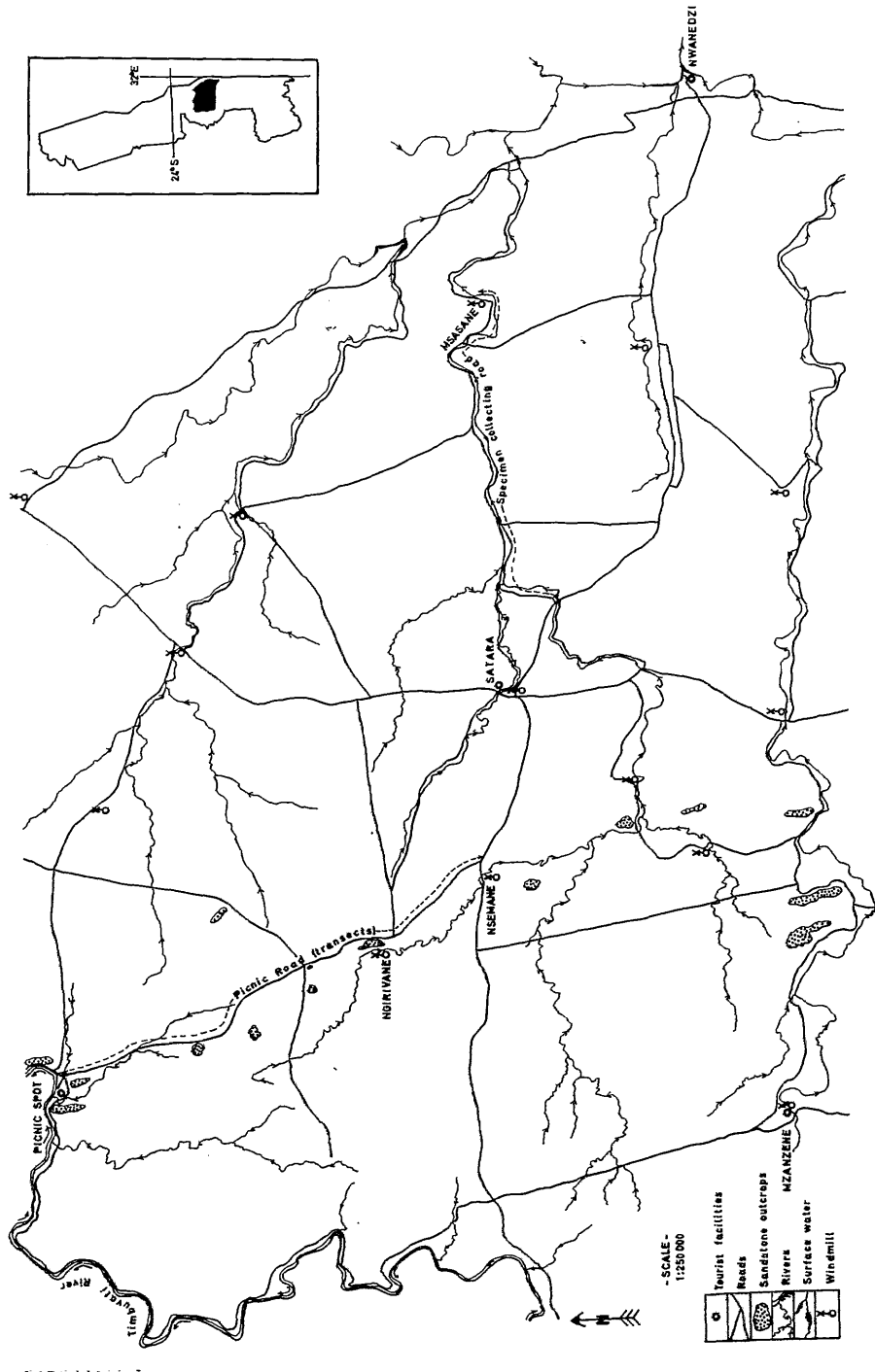


Table 1. The monthly rainfall, mean maximum and mean minimum temperatures recorded during the study period at Satara rest camp in the Kruger National Park.

Year and Measurement	Jan.	Feb.	March	April	May	June	Month July	August	September	Oct.	Nov.	Dec.
Rainfall, mm												
1966								10,4	6,5	59,2	29,0	164,2
1967	31,6	207,9	65,5	42,3	0,0	0,0	0,0	0,0	0,0	43,3	29,0	16,5
1968	26,5	118,4	77,8	72,1	9,6	25,8	0,0	3,0	0,0	13,2	69,5	168,4
1969	55,2	100,0	106,2	25,0	3,0	0,0	0,0	0,0	24,6	132,6		
Average :	37,7	142,1	83,1	46,4	4,2	8,6	0,0	3,4	7,8	62,1	57,7	116,3
Mean maximum temperature, °C												
1966											30,9	31,2
1967	31,7	-	29,6	28,8	31,9	26,6	23,9	26,1	29,0	30,2	33,9	32,8
1968	35,3	31,8	30,1	28,8	27,7	24,9	26,4	27,4	29,7	30,6	30,6	32,4
1969	34,1	34,7	32,6									
Average:	33,7	33,3	30,8	28,8	29,8	25,8	25,2	26,8	29,4	30,4	31,8	32,1
Mean minimum temperature, °C												
1966											18,6	20,1
1967	20,0	-	18,0	16,3	12,4	9,0	7,4	10,0	12,2	16,3	18,3	17,2
1968	20,1	20,0	18,2	14,8	15,1	4,7	8,8	11,7	12,9	15,3	16,6	19,2
1969	21,0	19,9	18,8									
Average:	20,4	20,0	18,3	15,6	13,8	6,9	9,1	10,9	12,6	15,8	17,8	18,8

Figure 4. Diagram of the Picnic Road transect route in the Kruger National Park, showing the main features along the road. The grass cover sections (see text) are numbered along the side. The road is marked off in miles, and hornbill nests found along the road are marked (n - *I. nasutus*, e - *I. erythrorhynchus* and f - *I. flavirostris*.)

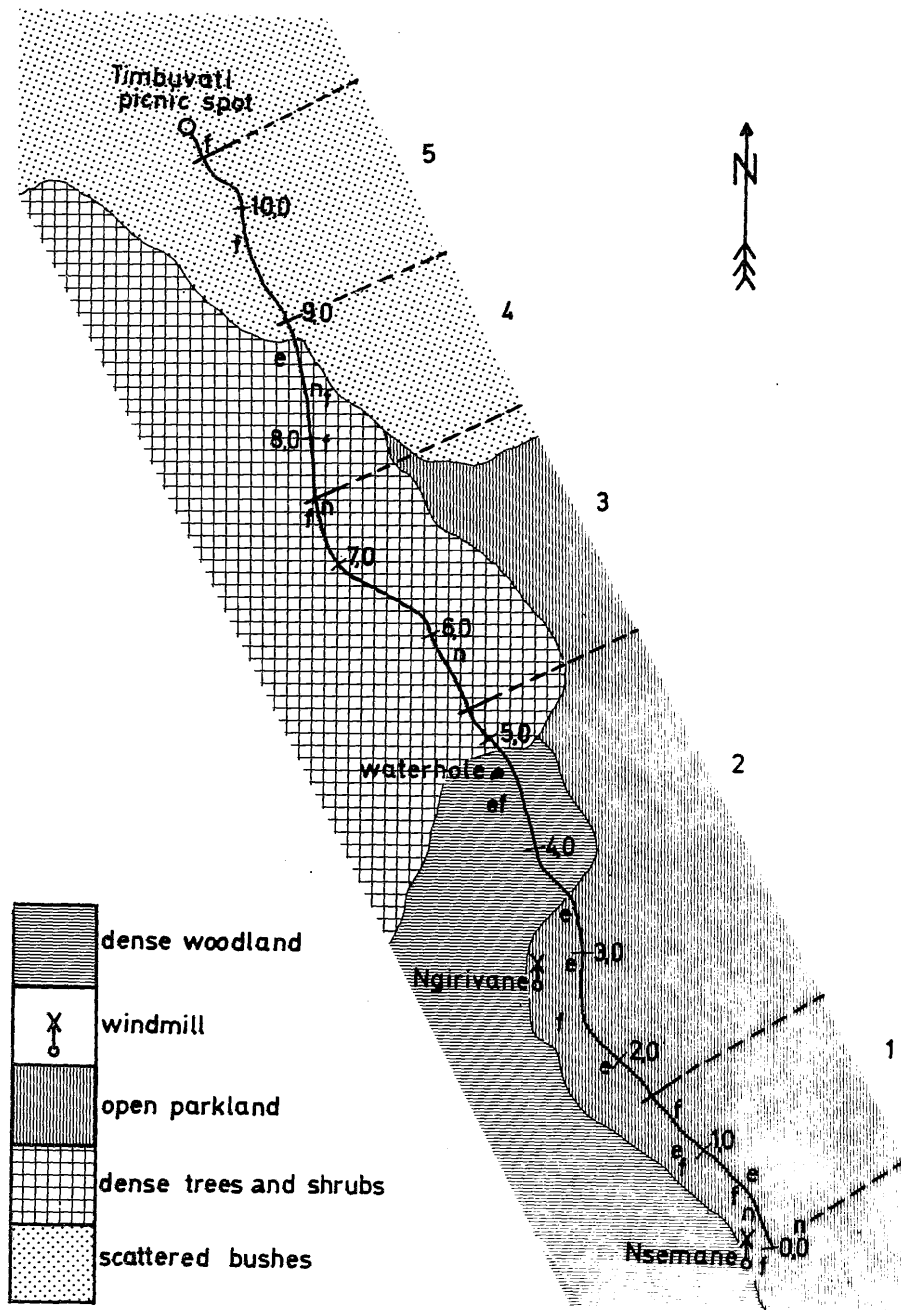
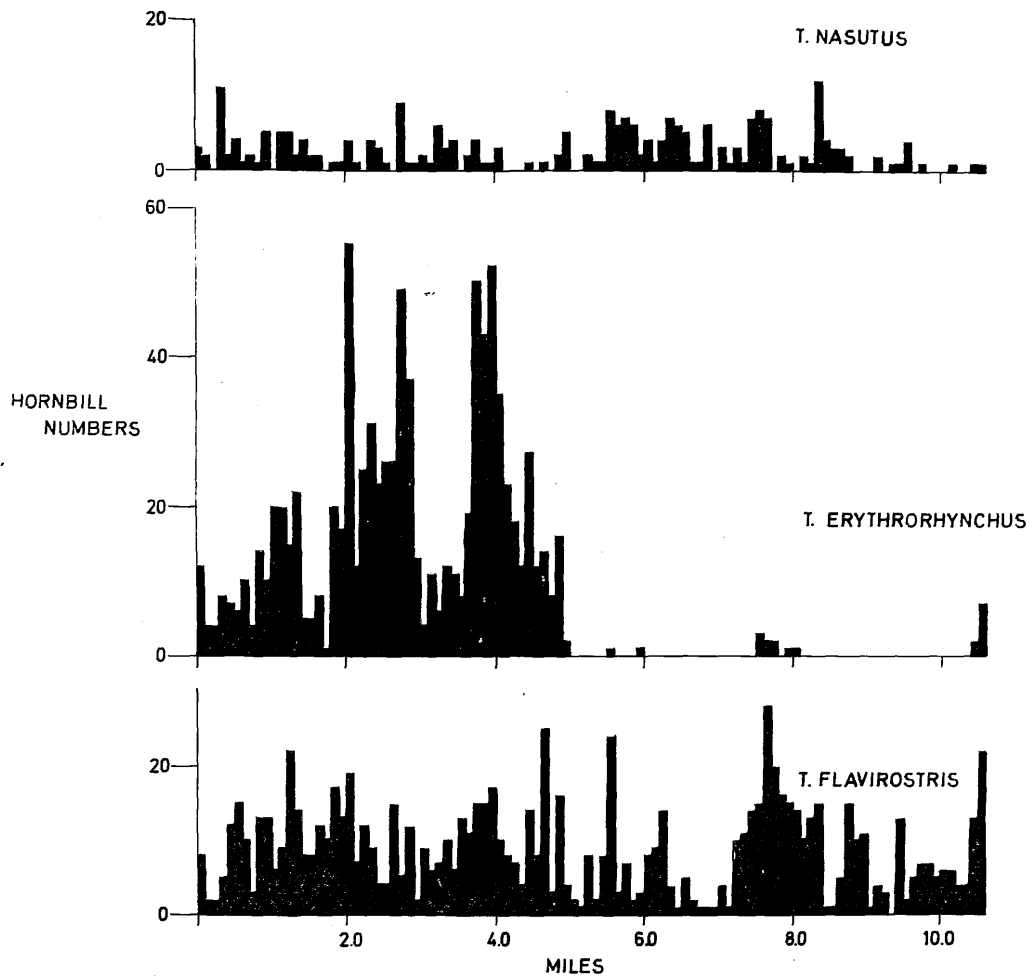


Figure 5. Histograms of the total numbers of three species of hornbills recorded in each tenth of a mile along Picnic Road, for 194 counts covering 17 months.



**Figure 6.** Histograms of the percentage sparse grass cover at each tenth of a mile along Picnic Road at three month intervals from the end of October 1967 to the end of July 1968. Solid areas are the percentages of bare ground (cover A) and open areas the percentages of short grass (cover B).

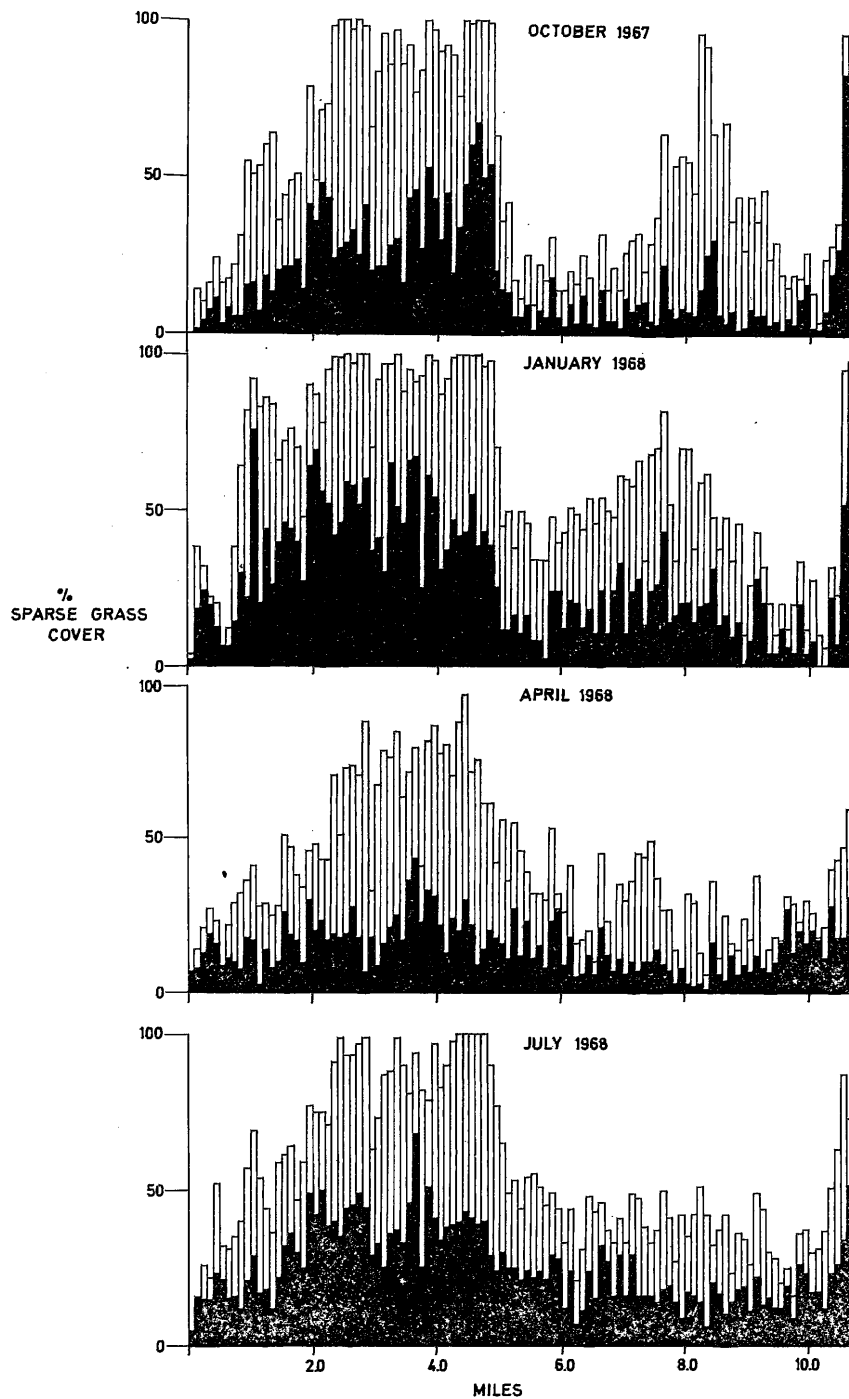


Figure 7. Total numbers of trees and shrubs recorded per hectare plot at each tenth of a mile along Picnic Road, with a graph of a moving point average (ten units per point) superimposed.

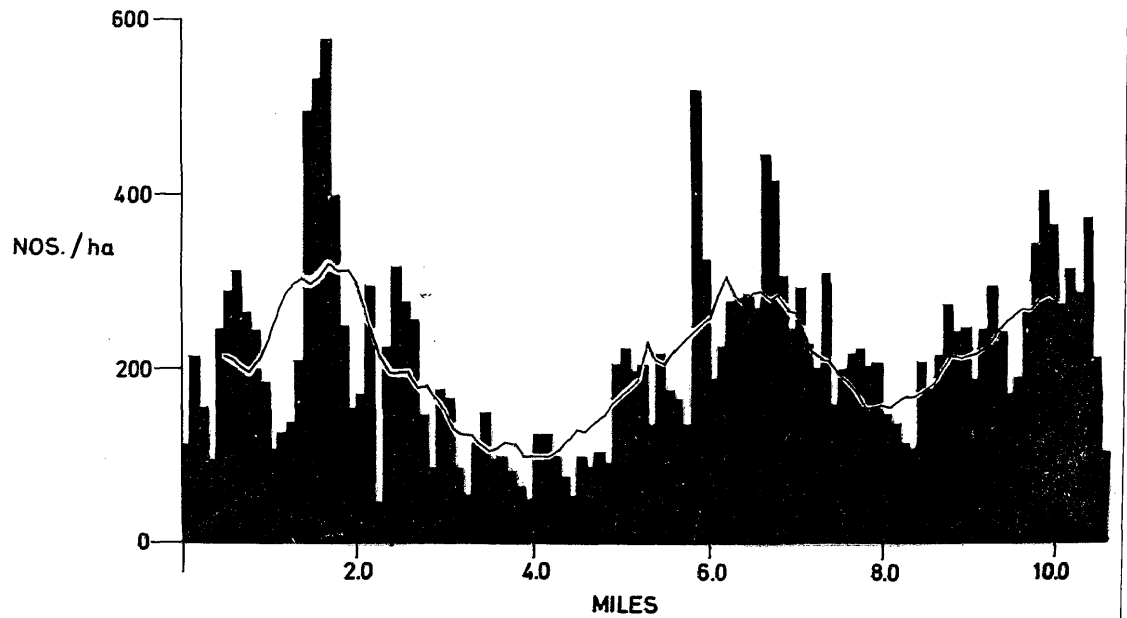
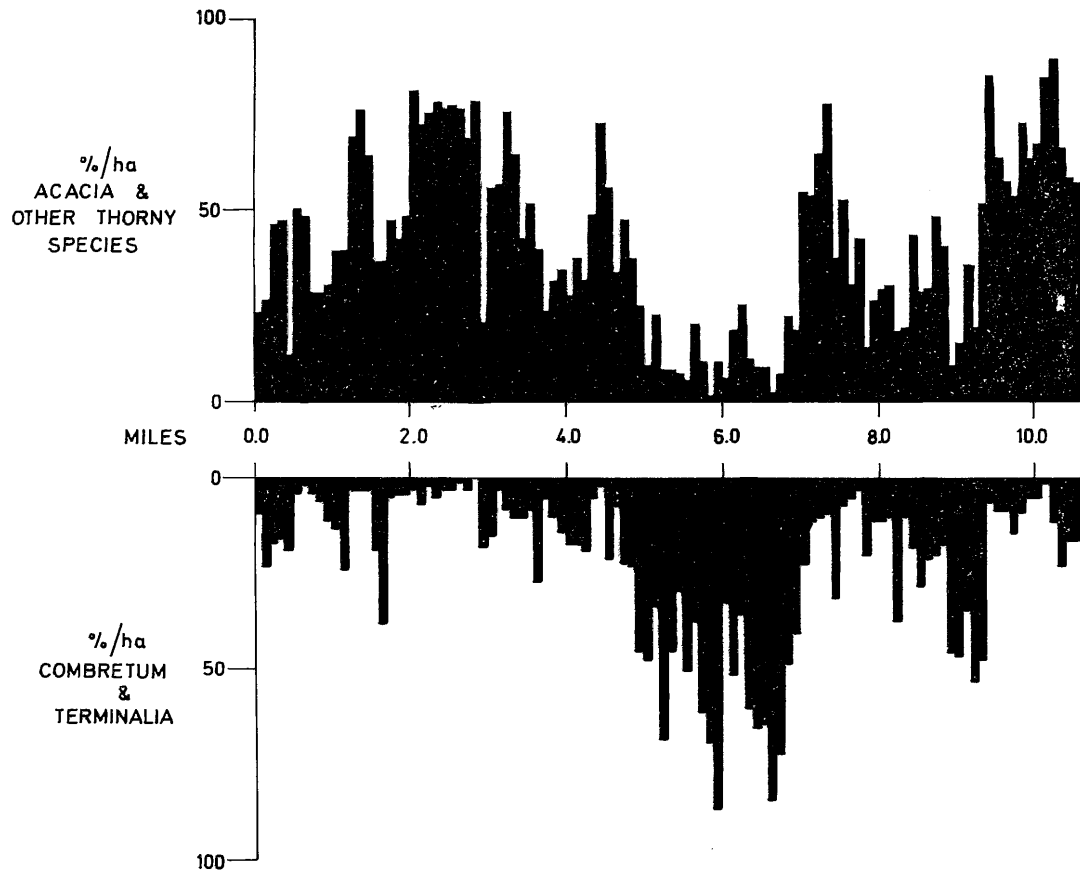


Figure 8. Histograms comparing the percentages of Acacia and thorny trees and bushes with percentages of Combretum and Terminalia trees and bushes, recorded per hectare at each tenth of a mile along Picnic Road.



Appendix 1. Estimations of average weight of herbivores used in calculating the biomass recorded during hornbill transects. Weights adapted from Smithers (1966).

Herbivore species	Average weight in kg used in calculations of biomass
African Elephant ( <u>Loxodonta africana</u> )	4995
Cape Buffalo ( <u>Syncerus caffer</u> )	545
Giraffe ( <u>Giraffa camelopardalus</u> )	908
Zebra ( <u>Equus burchelli</u> )	363
Warthog ( <u>Phacochoerus aethiopicus</u> )	64
Wildebeest ( <u>Connochaetes taurinus</u> )	227
Eland ( <u>Taurotragus oryx</u> )	454
Kudu ( <u>Tragelaphus strepsiceros</u> )	204
Roan antelope ( <u>Hippotragus equinus</u> )	227
Sable antelope ( <u>Hippotragus niger</u> )	182
Waterbuck ( <u>Kobus ellipsiprymnus</u> )	227
Impala ( <u>Aepyceros melampus</u> )	50
Duiker ( <u>Sylvicapra grimmea</u> )	18
Steenbok ( <u>Raphicerus campestris</u> )	11
Sharpe's Grysbok ( <u>Raphicerus sharpei</u> )	11

Figure 9. Histogram of the average biomass of herbivorous mammals recorded per count within each tenth of a mile of Picnic Road. The superimposed graph is of a moving point average (ten units per point).

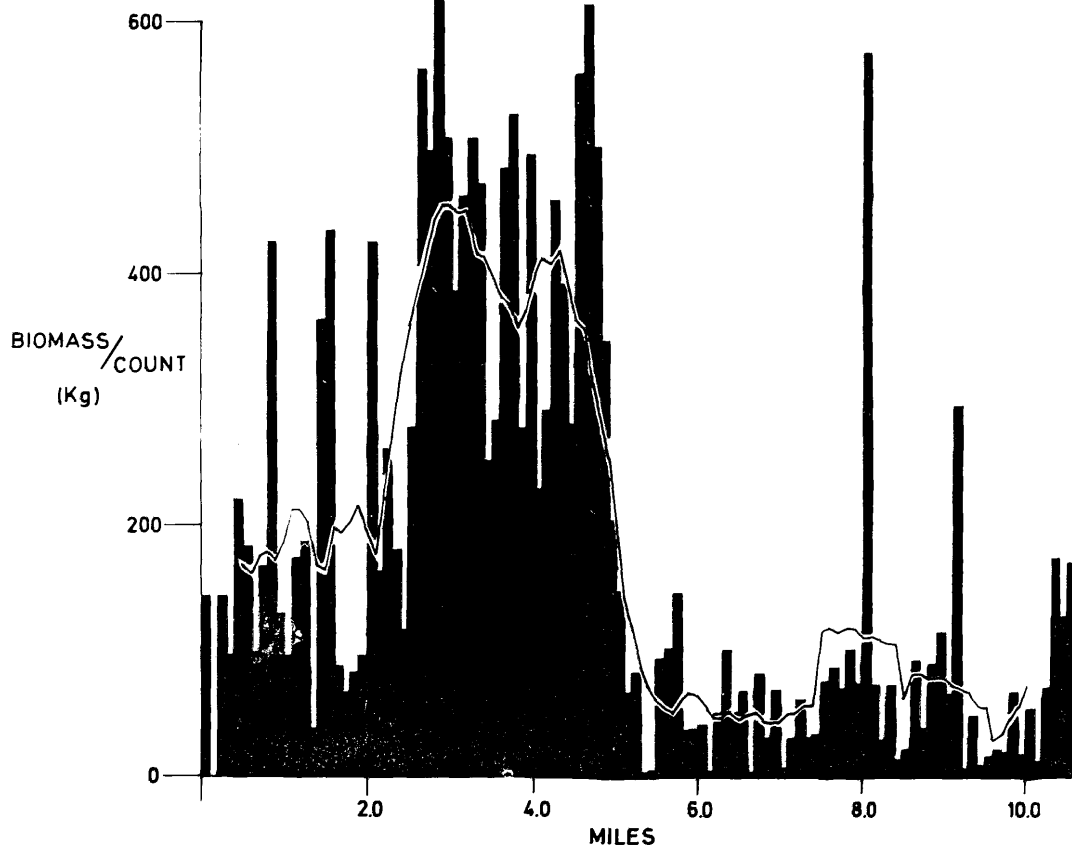


Figure 10. Two graphs of the moving point average for the percentage sparse grass cover for October 1967 (solid line) and April 1968 (broken line) along Picnic Road (adapted from Figure 6). The critical level of 40% is marked, and the five grass cover areas used in statistical analysis are shown.

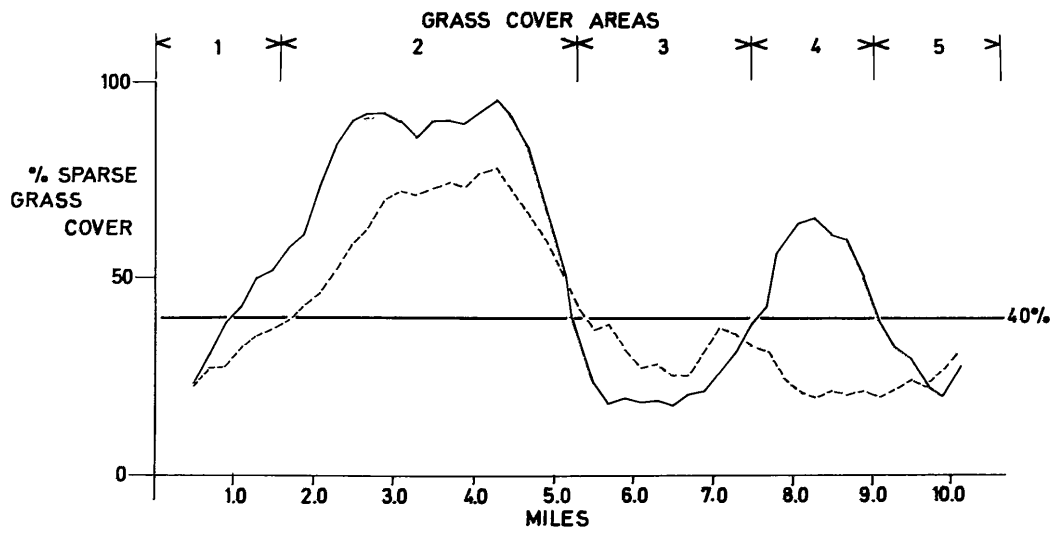


Table 2.

Hornbill numbers recorded per count per tenth of a mile along a transect road in the Kruger National Park in different seasons and different grass cover sections, from November 1967 to March 1969. The numbers were calculated to four decimal places, but were then multiplied by 10 000 to eliminate the decimal point for ease of calculation.

Season	Grass cover	Hornbill species		
		<u>T. nasutus</u>	<u>T. erythrorhynchus</u>	<u>T. flavirostris</u>
Early wet (1967-68)	1	133	436	322
	2	78	802	610
	3	205	30	235
	4	151	0	172
	5	43	0	344
Late wet (1968)	1	117	1059	635
	2	86	638	465
	3	163	0	91
	4	27	27	560
	5	27	27	267
Early dry (1968)	1	129	861	602
	2	59	1364	745
	3	210	33	1075
	4	130	81	1317
	5	0	33	455
Late dry (1968)	1	51	218	336
	2	62	1722	348
	3	169	0	195
	4	38	0	647
	5	0	76	419
Early wet (1968-69)	1	181	181	498
	2	173	548	284
	3	244	0	151
	4	205	0	359
	5	85	34	205
/ Late wet (1969)	1	409	588	614
	2	82	646	446
	3	277	0	158
	4	203	0	261
	5	115	0	406

/ Only the two months of February and March were counted in this season, but since the figures are averages, this season is included in the Table.

Table 3. Numbers of Tockus nasutus recorded per count per tenth of a mile along a transect road in the Kruger National Park in different seasons and different sections of tree and bush densities. Mean multiplied by 10 000 to eliminate decimal point.

Season	Tree and bush sections		
	A	B	C
Early wet (1967-68)	98	85	141
Late wet (1968)	120	84	77
Early dry (1968)	73	103	116
Late dry (1968)	48	60	85
Early wet (1968-69)	103	135	189
Late wet (1969)	319	29	191

**Table 4.** Means used in one way analyses of variance to test for significant differences in hornbill numbers recorded in different grass cover sections and in different seasons, with the results of the analyses.

Means of grass cover sections	Hornbill species		
	<u>T. nasutus</u>	<u>T. erythrorhynchus</u>	<u>T. flavirostris</u>
1	1020	3343	3007
2	540	5720	2898
3	1268	63	1905
4	754	108	3316
5	271	170	2096
Results :	$F_{4,25} = 4,49$	$F_{4,25} = 15,5$	$F_{4,25} = 0,84$
	$P = 0,01-0,005^{++}$	$P < 0,005^{+++}$	$P = > 0,1$
Means for Seasons.			
Early wet	610	1268	1683
Late wet	420	1751	2018
Early dry	528	2372	4194
Late dry	320	2016	1945
Early wet	888	763	1497
Late wet	1087	1234	1885
Results :	$F_{5,24} = 2,66$	$F_{5,24} = 0,29$	$F_{5,24} = 4,3$
	$P = 0,10-0,05$	$P = > 0,1$	$P = 0,01-0,005^{++}$

\* The number of asterisks denotes the degree of significance

Figure 11. Diagrams showing the movements recorded of ringed hornbills from the place of ringing  
 A - Tockus erythrorhynchus and B - Tockus flavirostris.  
 Open circles - sightings of ringed birds, solid small circles - recoveries of ringed birds, solid large circles - areas of human habitation.

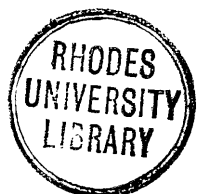
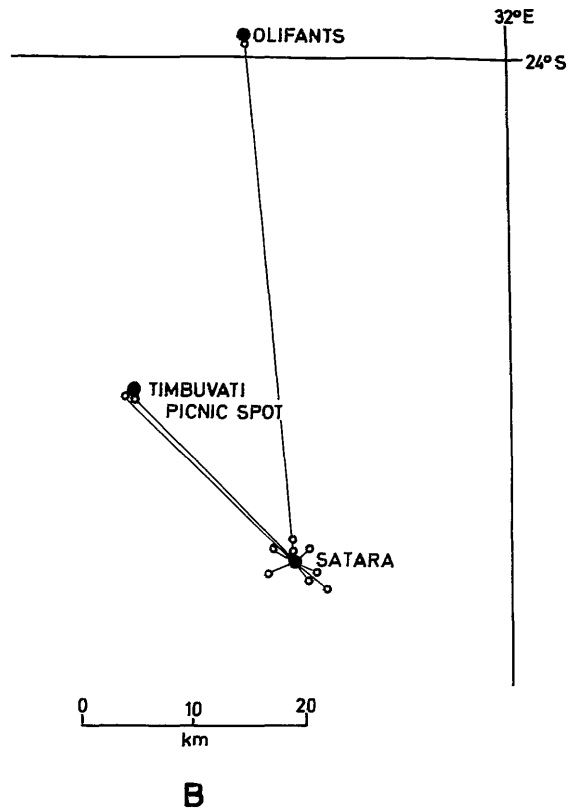
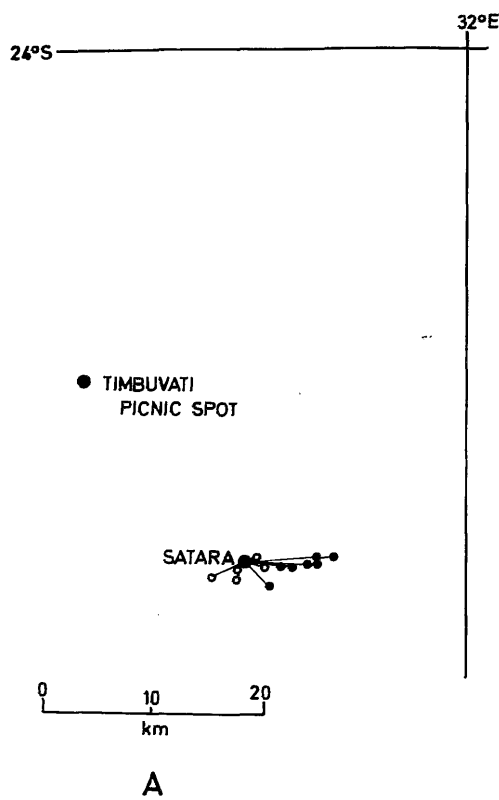


Figure 12. The position, within the Wankie National Park, of the two transect roads, studied - LRR - Lukosi River Road, TR - Tchabema Road.

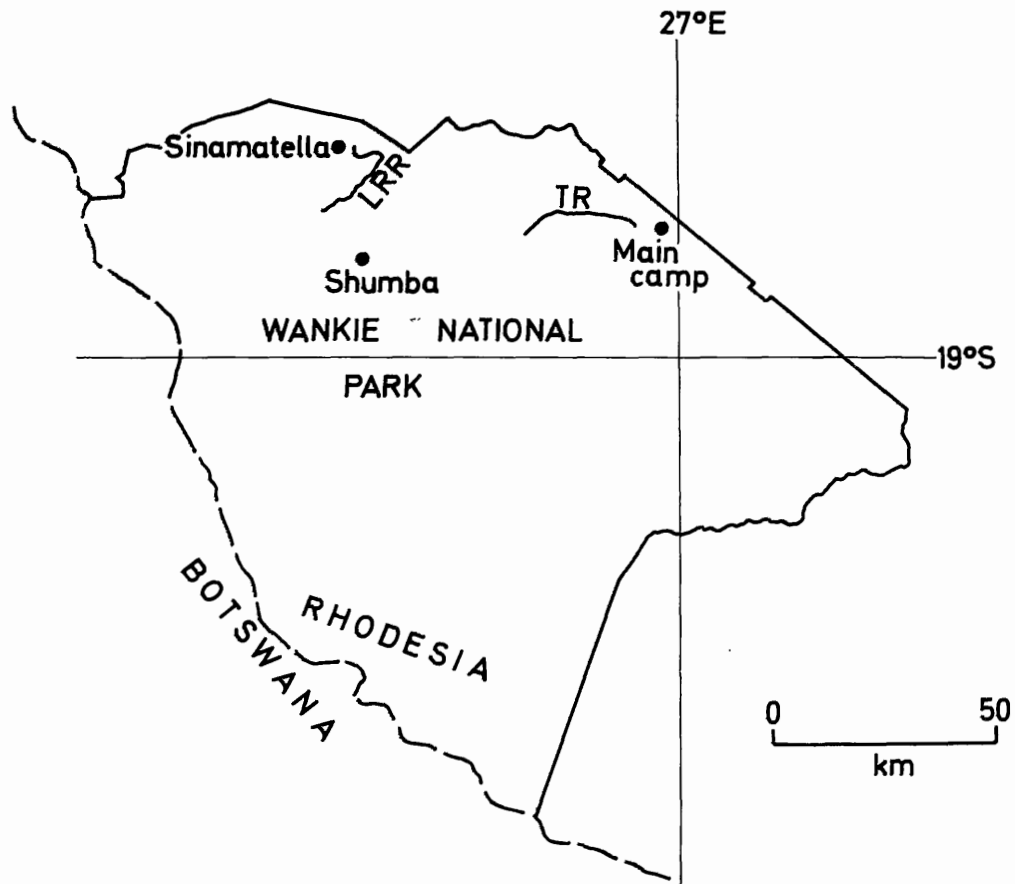


Figure 13. Diagram of Lukosi River Road transect route in the Wankie National Park, showing the main features of the road. The road is marked off in miles.

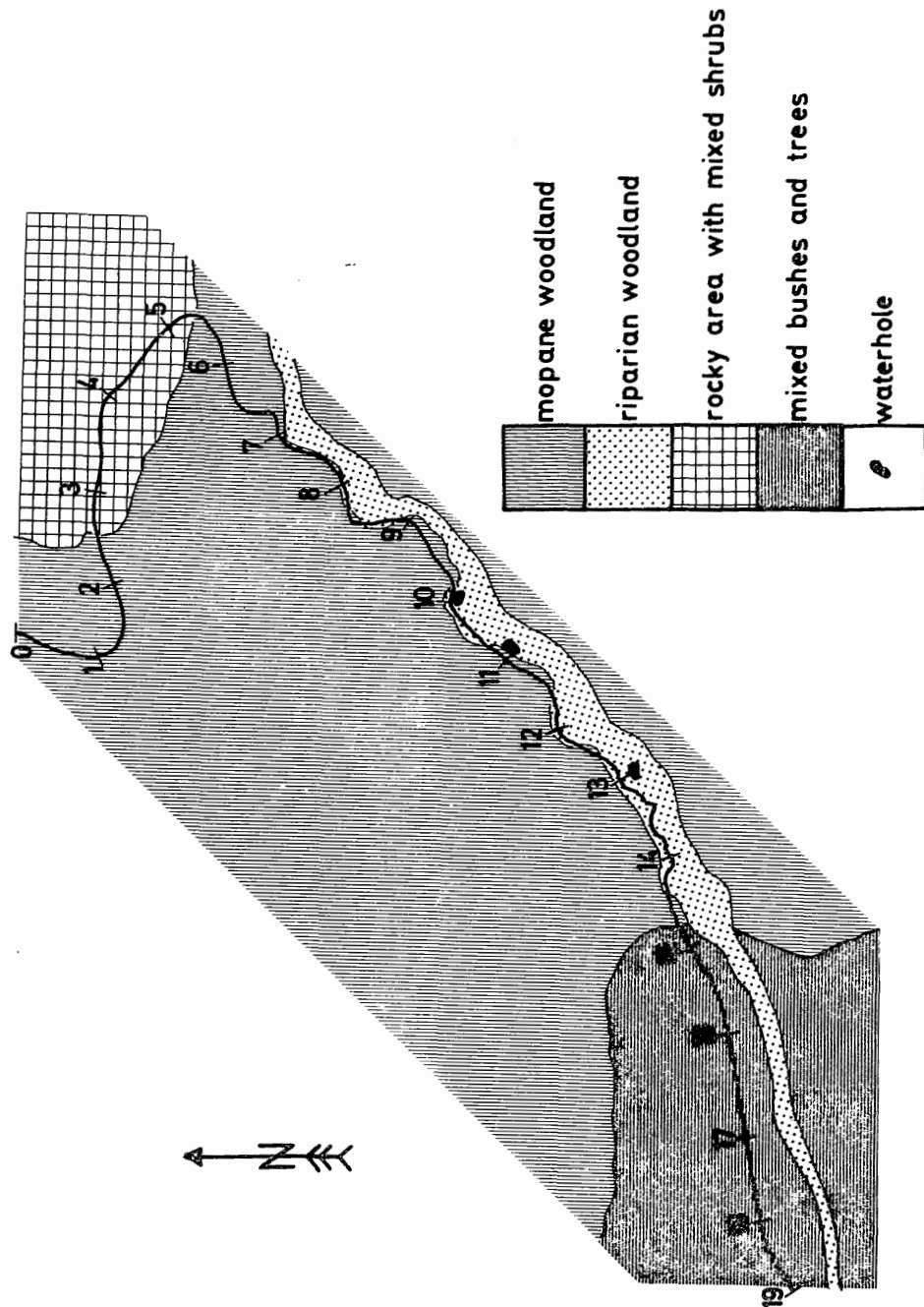


Figure 14. Diagram of Tchabema Road transect route in the Wankie National Park, showing the main features of the road. The road is marked off in miles.

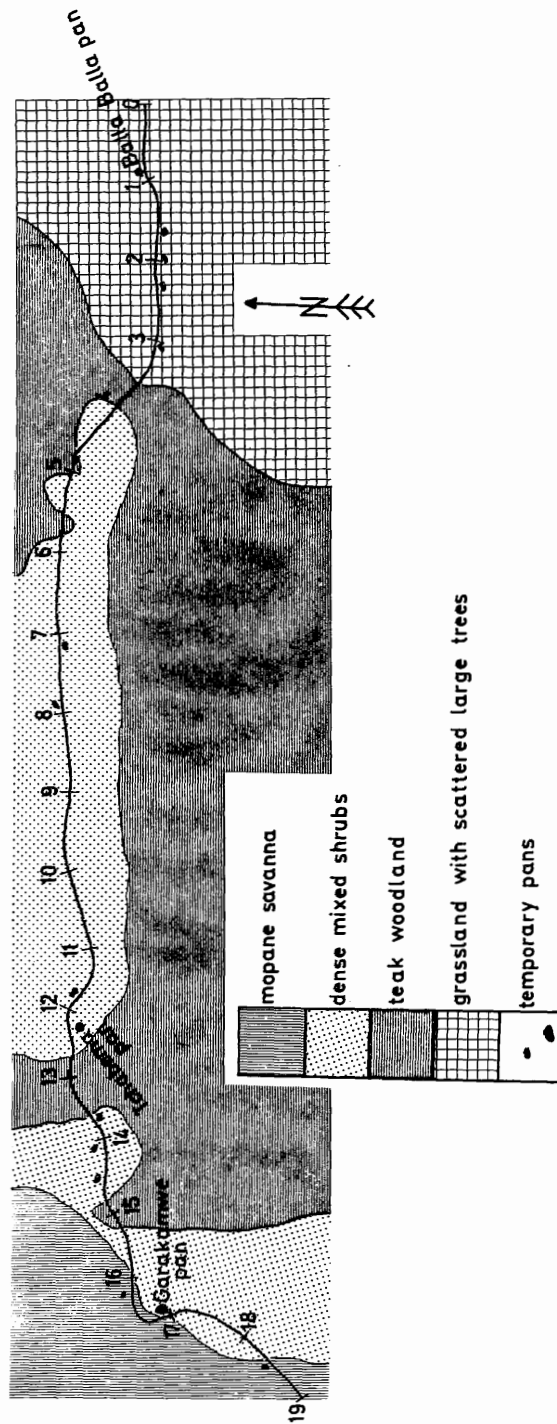


Table 5.

Numbers of three species of hornbill recorded along two transect roads in the Wankie National Park in two seasons, to show the relative abundance of the species. Nine counts were done on each road in each season

Hornbill species	Lukosi River Road			Tchabema Road		
	End of wet season (April)	End of dry season (October)	Total	End of wet season (April)	End of dry season (October)	Total
<u>T. nasutus</u>	20	18	38	49	77	126
<u>T. erythrorhynchus</u>	305	397	702	27	33	60
<u>T. flavirostris</u>	10	18	28	104	213	317

Figure 15. Results of transects done along the Lukosi River Road in the first halves of April and October 1971. Plotted, per tenth of a mile, are the average biomass of herbivorous mammals per count with a moving point average (ten units per point), the average percentage sparse grass cover with a moving point average (ten units per point), and the total numbers of each of three species of hornbill recorded.

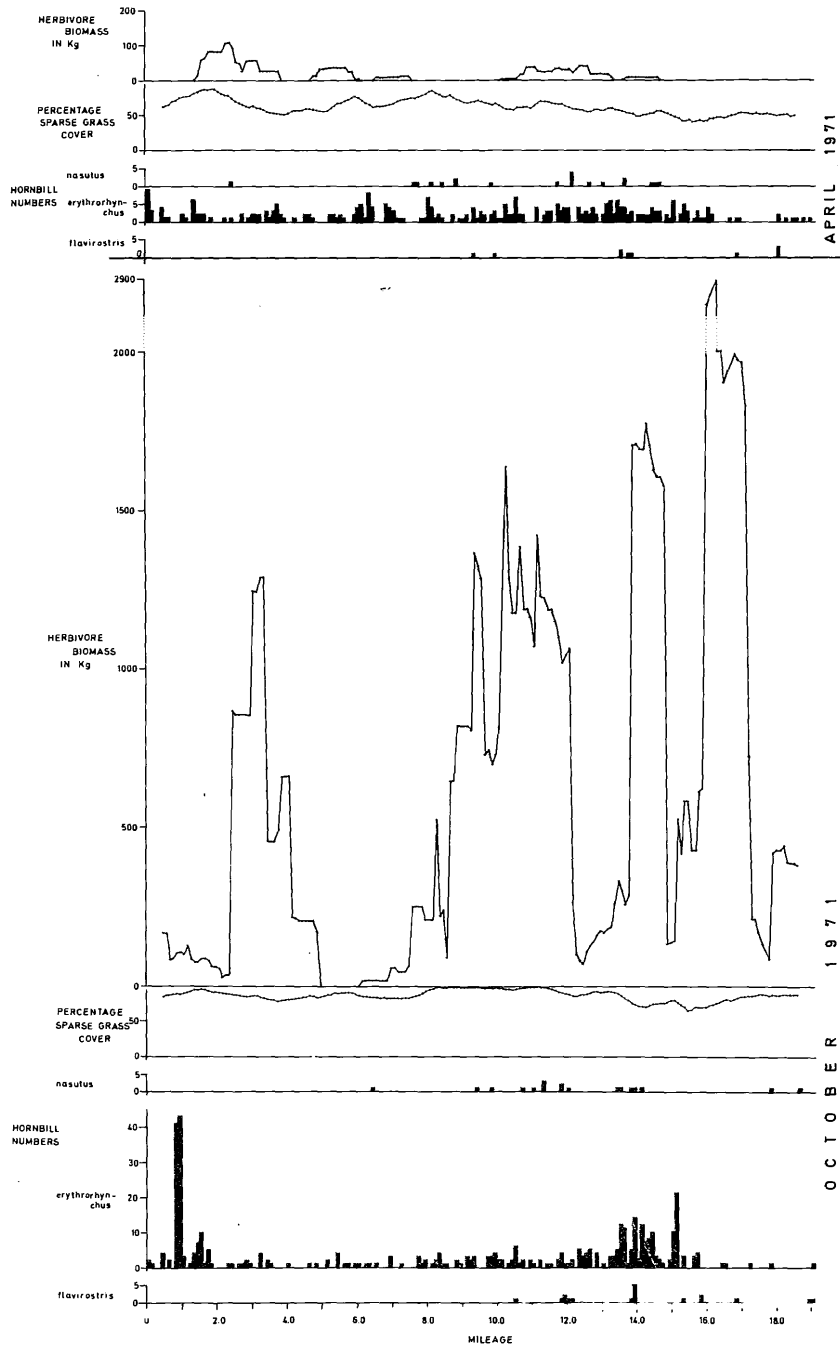


Figure 16. Results of transects done along the Tchabema Road in the second halves of April and October 1971. Plotted per tenth of a mile, are the average biomass of herbivorous mammals per count with a moving point average (ten units per point), the average percentage sparse grass cover with a moving point average (ten units per point) and the total numbers of each of three species of hornbill recorded.

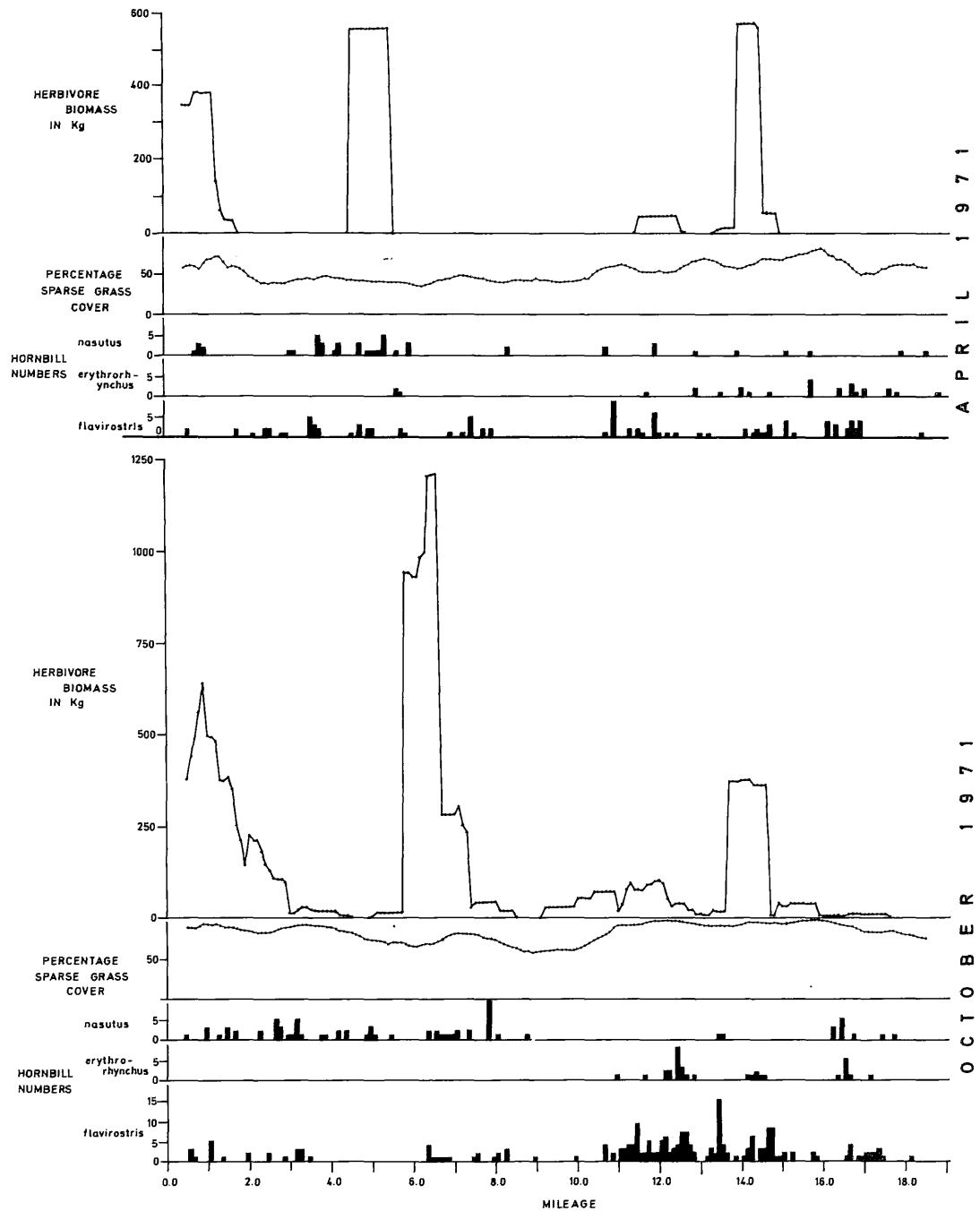
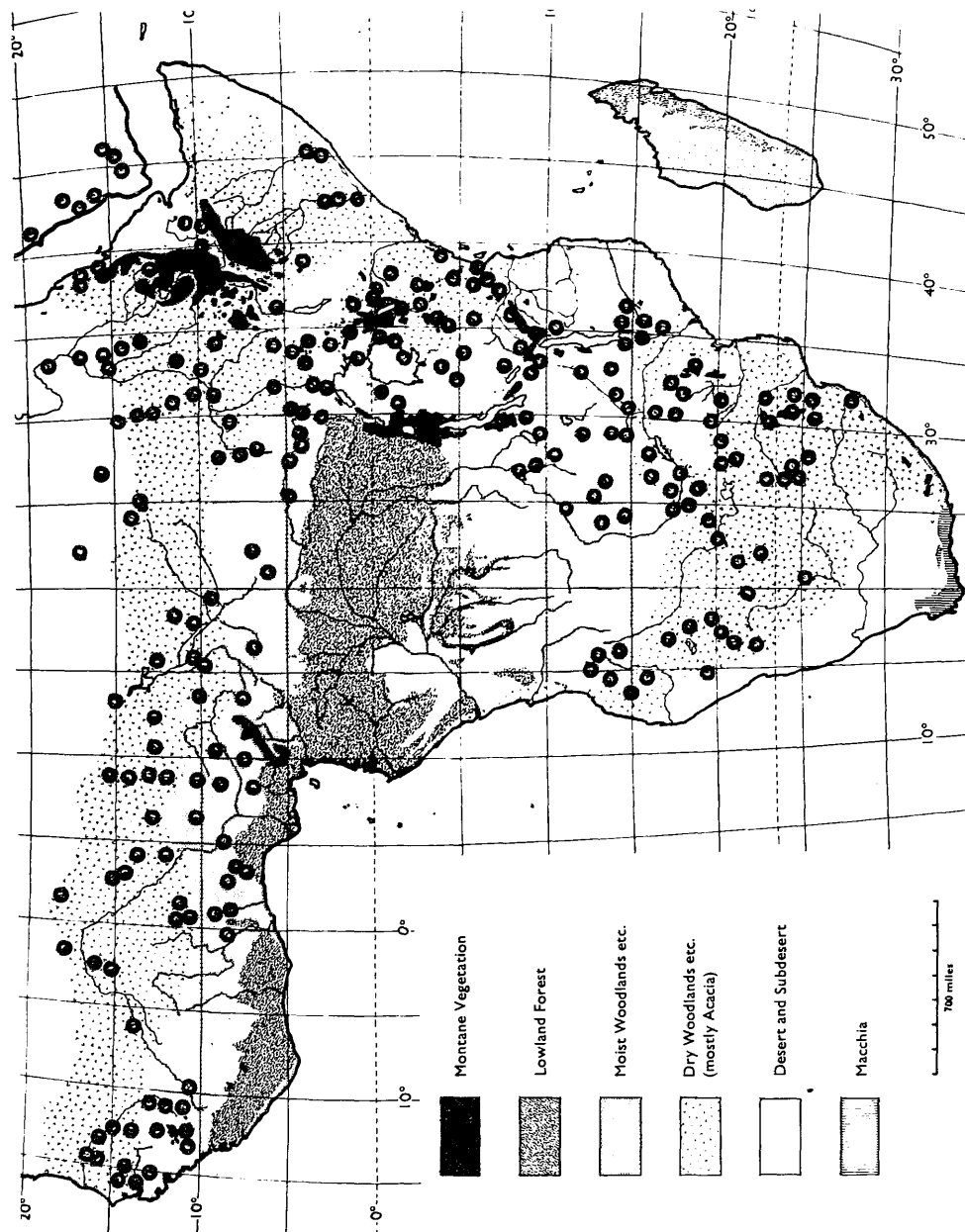


Figure 17. The total distribution of *Tockus nasutus* (after Sanft 1960), plotted over a simplified vegetation map of Africa (after Keay 1959).



**Figure 18.** The total distribution of *Tockus flavirostris* (after Sanft 1960), plotted over a simplified vegetation map of Africa (after Keay 1959).

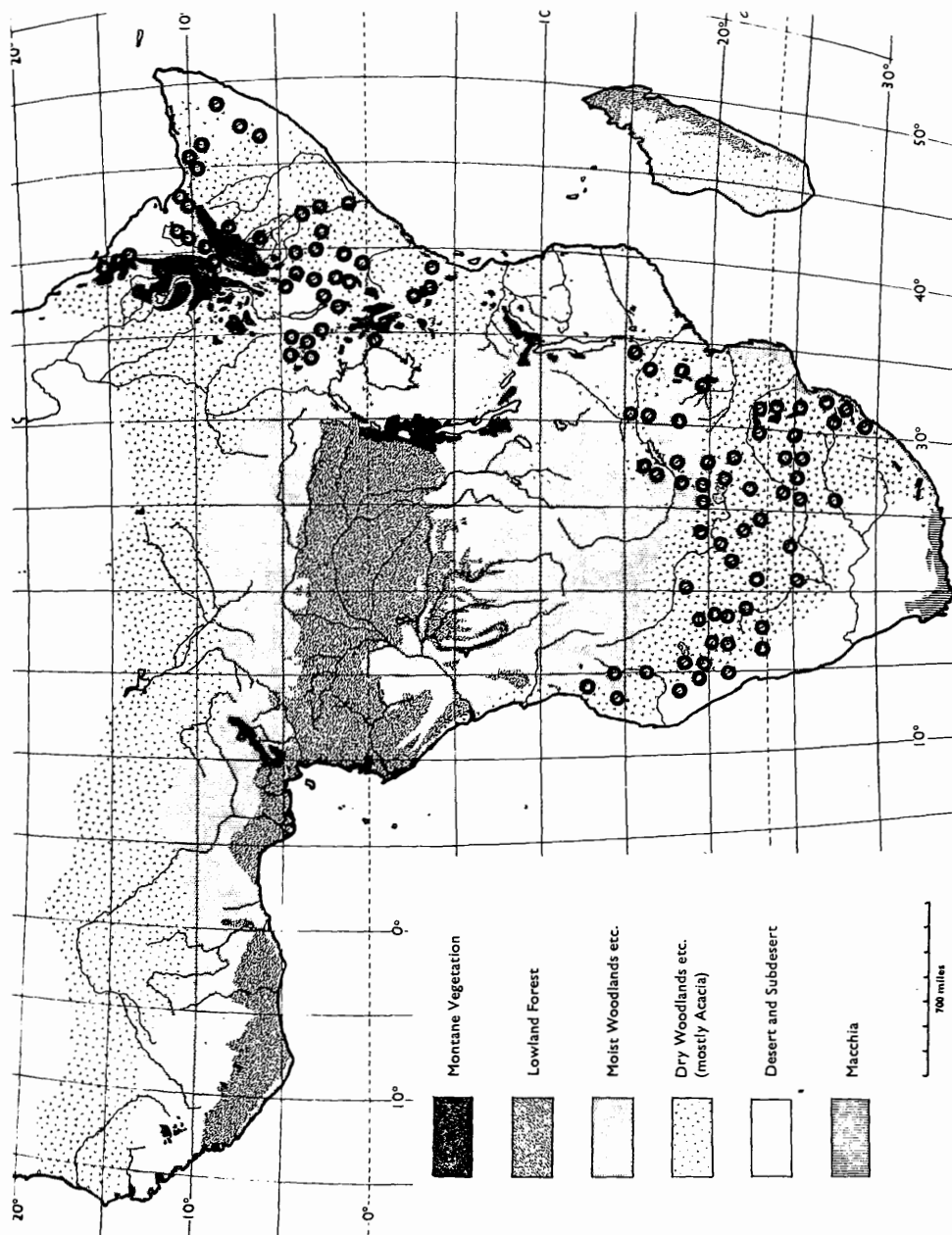
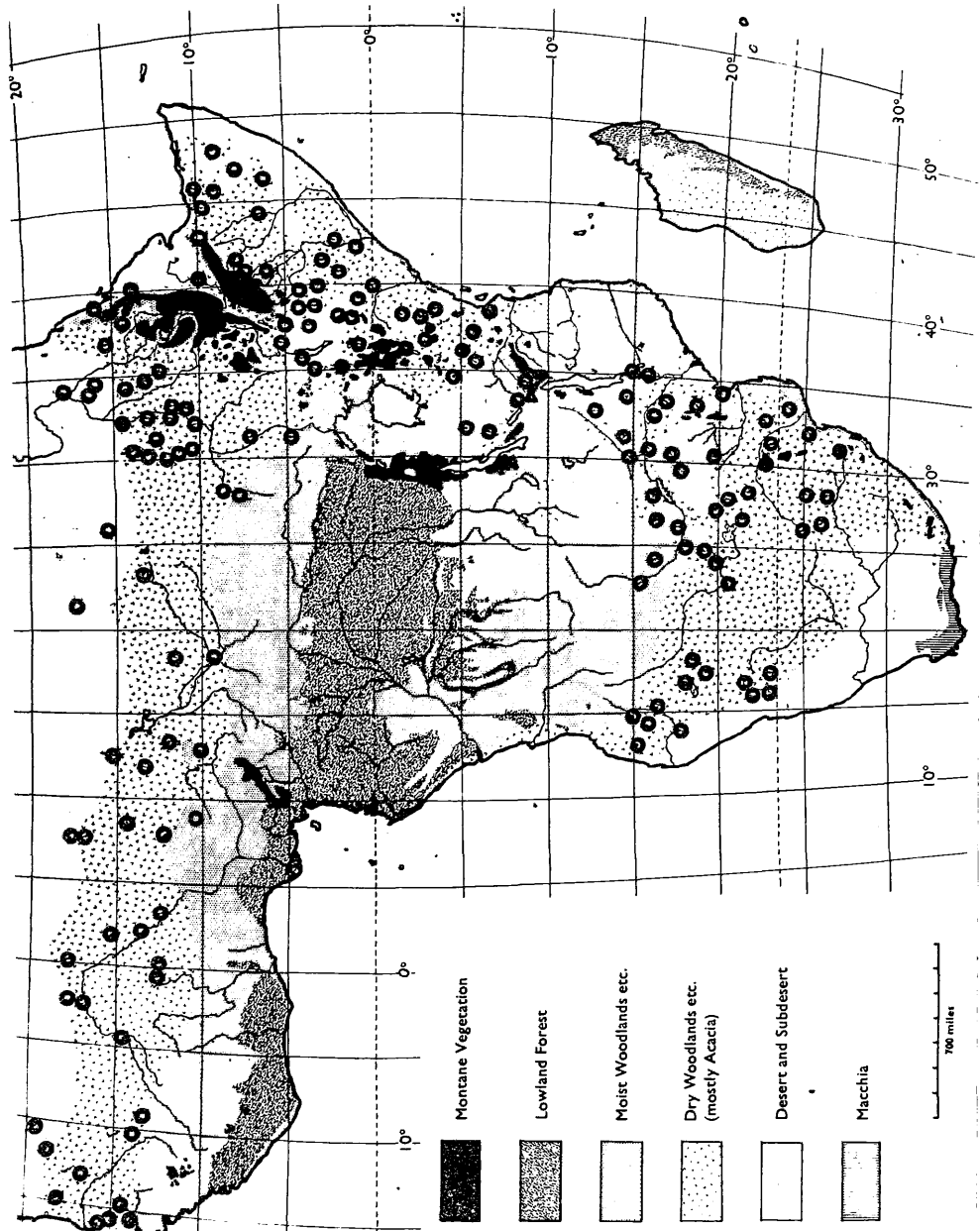


Figure 19. The total distribution of Toeckus erythrorhynchus (after Sanft 1960), plotted over a simplified vegetation map of Africa (after Keay 1959).



Appendix 2. Weights of animal food items identified during analysis of hornbill stomach contents. The size of the sample collected, the weight of the sample, and the average weight of each food item are given.

Food item	Numbers collected	Weight in g	Average weight in g
MAMMALIA			
<u>Mastomys</u> -size mice	51	1695,00	33,00
REPTILIA			
<u>Leptotyphlops</u> sp. about 5 cm long	1	0,60	0,60
<u>Chamaleo dilepsis</u> about 20 cm long	2	41,90	20,80
AMPHIBIA			
<u>Chiromantis xerampelina</u>	15	251,00	33,50
MOLLUSCA			
Basommatophora 2 cm long	2	1,00	0,50
ARTHROPODA			
Diplopoda millepedes	39	29,47	0,76
Chilopoda centipedes	14	23,99	1,71
Aranea, about 1 cm long	62	2,94	0,05
<u>Nephilia</u> sp.	50	43,61	0,87
Scorpionida	27	52,72	1,95
Solifugida	14	24,52	1,75
Acarina ticks	2	0,06	0,03
Insecta			
Tettigoniidae, up to 5 cm long	70	20,32	0,29
Saginae-sized	11	20,37	1,85
Gryllidae	35	27,30	0,78
Acrididoidea, over 7 cm long	44	117,13	2,66
3-7 cm long	114	148,48	1,30
under 3 cm long	247	25,52	0,17
Phasmida	24	2,56	0,11
Blattidae	67	7,93	0,12
Mantidae, adults	125	27,09	0,22
egg cases	1	0,43	0,43
Hodotermitidae	34	4,00	0,12
Termitidae	300	0,82	0,003
Cecropidae	6	0,18	0,03
Membracidae	taken as same as Cecropidae		

Appendix 2. (Cont.)

Food item	Numbers collected	Weight in g	Average Weight in g
Coccidae	5	0,89	0,18
Reduviidae	20	0,81	0,04
Lygaeidae	307	7,73	0,03
Phyrracoridae	taken as same as Lygaeidae		
Coreidae	2	1,18	0,59
Pentatomidae	11	5,20	0,47
Mantispidae	taken as same as Phasmida		
Myrmeliontoidea larvae	11	0,25	0,02
Lepidoptera moths, under 2 cm long	65	5,58	0,09
Lepidoptera larvae	50	27,49	0,55
Lepidoptera <i>Acrea</i> sp.	taken as same as moths		
Asilidae	2	0,12	0,06
Sarcophagidae	63	14,72	0,23
Muscidae larvae	taken as same as Coleoptera larvae		
Ichneumonoidea	8	1,12	0,02
Chalcidoidea	1	0,06	0,06
Chrysididae	7	0,58	0,08
Mutillidae	34	2,41	0,07
Gasteruptiidae	2	0,25	0,13
Formicidae, large black ants	42	0,85	0,02
large red ants	taken as same as large black ants		
small red ants	600	5,17	0,0009
small black ants	700	0,35	0,0005
'sugar' ants	116	1,70	0,01
ant larvae and pupae	55	0,46	0,008
Pomilidae	2	0,68	0,34
Vespidae	12	1,03	0,09
Sphecidae	4	0,13	0,03
Apoidea	7	0,33	0,05
Carabidae	taken as same as small Tenebrionidae		
Staphylinidae	taken as same as small Curculionidae		

Appendix 2. (Cont.)

Food item	Numbers collected	Weight in g.	Average weight in g.
Scarabidae			
Cetoniinae	70	68,14	0,97
Melolonthinae	89	12,58	0,14
Coprinae, under 1 cm long (Scarabinae)	1214	26,76	0,02
1-3 cm long	301	55,02	0,18
over 3 cm long	63	148,16	2,35
Buprestidae	18	18,99	1,06
Elateridae	4	0,38	0,10
Coccinelidae	44	0,18	0,004
Tenebrionidae, under			
1 cm long	129	1,811	0,06
1-3 cm long	73	70,44	0,14
- over 3 cm long	4	4,73	1,18
Meloidae	25	21,15	0,74
Cermabycidae	158	30,15	0,19
Chrysomelidae other than Cassidinae	91	10,74	0,12
Cassidinae	12	0,50	0,04
Anthribidae	8	0,12	0,02
Curculionidae, under 2 cm long	135	1,67	0,01
Curculionidae over 2 cm long	17	4,68	0,28
Coleoptera (mainly Tenebrionidae) larvae	7	3,58	0,51

Appendix 3. A systematic list of all food items recorded as diet of three species of hornbill in the Kruger National Park, N - T. nasutus, E - T. erythrorhynchus and F - T. flavirostris.

Food item	Hornbill species		
	N	E	F
<b>ANIMAL FOODS</b>			
<b>MAMMALIA</b>			
Rodentia	x		x
<u>Rhodomys pumilio</u>	x		
<b>REPTILIA</b>			
<u>Leptotyphlops</u> sp.		x	x
<u>Chamaeleo dilepsis</u>	x		x
<b>AMPHIBIA</b>			
<u>Breviceps</u> sp.			x
<u>Chiromantis xerampelina</u>	x		
<b>MOLLUSCA</b>			
Basommatophora			x
<b>ARTHROPODA</b>			
Chilopoda	x	x	x
<u>Scolopendra morsitans</u>	x	x	x
Diplopoda	x	x	x
Aranea	x	x	x
Argyopidae			
<u>Nephilia senecalensis</u>	x		
<u>Araneus</u> sp.	x		x
<u>Caerostris</u> sp.			x
Palpimanidae			
<u>Palpimanus transvaalicus</u>		x	
Lycosidae			
<u>Lycosa</u> sp.		x	
<u>Evippa</u> sp.			x
Zodariidae			
<u>Caphaeris</u> sp.			x
<u>Caesetius</u> sp.		x	
Scorpionida	x	x	x
Scorpionidae			
<u>Cheloctonus jonesi</u>		x	x
<u>Opisthophthalmus glabrifrons</u>			x

Appendix 3. (Cont.)

Food items	Hornbill species		
	N	E	F
Buthidae			
<u>Uroplectes olivaceus</u>			x
Solifugida	x	x	x
<u>Solpuga conservatorum</u>		x	x
Acarina		x	x
<u>Rhipicephalus appendiculatus</u>		x	
<u>R. evertsi</u>		x	x
<u>Hyaloma truncatum</u>		x	
<u>Ambylomma hebraeum</u>		x	x
<u>A. marmoreum</u>			x
Insecta			
Orthoptera			
Tettigoniidae	x	x	x
Saginae	x	x	x
Gryllidae		x	x
Gryllacrididae			x
Eumastacidae	x	x	x
<u>Thericles sp.</u>	x	x	x
Pyrgomorphidae			x
<u>Ochrophlebia sp.</u>			x
Acrididae	x	x	x
<u>Acrida turita</u>		x	
<u>A. sulphuripennis</u>			x
<u>Rhytidacris punctata</u>	x		
<u>Oedaleus citrina</u>		x	
<u>Ambylphymus rubripes</u>		x	x
<u>Pseudoarcyptera sp.</u>		x	
<u>Cyrtacanthacris tartarica</u>		x	
<u>C. aeruginosa</u>			x
<u>Gastrimargus sp.</u>		x	
<u>Cataloipus oberuthi</u>		x	
<u>Cataloipus sp.</u>			x
<u>Acrotylus sp.</u>		x	
<u>Orthochotha dasyncnemis</u>		x	
<u>Duopherula sp.</u>		x	
<u>Platypternodes brevipes</u>		x	
<u>Catantopus melanostictus</u>		x	x

## Appendix 3. (Cont.)

Food item	Hornbill species		
	N	E	F
<u>Phaecatantopus decoratus</u>			X
<u>Aelopus</u> sp.			X
<u>Cyrtacanthris aeruginosa</u>			X
<u>Paradontemelas brachypterus</u>			X
Phasmida			X
Dictyoptera			
Blattidae		X	X
Mantidae	X	X	X
Isoptera			
Hodotermitidae	X	X	X
<u>Hodotermes mossambicus</u>		X	X
Termitidae	X	X	X
Macrotermitidae			
<u>Macrotermes natalensis</u>		X	X
<u>H. ukusii</u>		X	
<u>Odontermes</u> sp.	X		
<u>O. badius</u>	X	X	X
<u>O. latericius</u>			X
<u>Ancistrotermes latinotus</u>		X	
Amitermitinae			
<u>Microcerotermes</u> sp.		X	
Hemiptera			
Cecropidae		X	X
Membracidae	X		X
Scutellaridae		X	
Cossidae	X		X
<u>Aspidoproctus ? mirabilis</u>	X		
Reduviidae	X	X	X
Lygaeidae	X	X	X
Coreidae		X	
Pentatomidae	X	X	X
Neuroptera			
Mantispidae	X		
Ascalaphidae, adult			X
larvae			X
Myrmeleontidae			
<u>Myrmeleon</u> sp larvae		X	X
Lepidoptera			
Heterocera			X
Rhopalocera			
<u>Acrea</u> sp			X



Appendix 3. (Cont.)

Food items	Hornbill species		
	N	E	F
Apoidea	x	x	x
Coleoptera			
Carabidae		x	x
<u>Grophopterus incanus</u>			x
<u>Harpalus</u> sp.		x	x
<u>Amblyetomus vittipennis</u>		x	x
Histeridae		x	x
Staphylinidae		x	
Scarabiidae (species below)	x	x	x
Cetoniinae	x	x	x
Melolonthidae	x	x	x
Coprinae	x	x	x
Scarabiinae	x	x	x
<u>Rhabdotia aulica</u>		x	
<u>Tephraea furfurosa</u>			x
<u>Scarabeus</u> sp.			x
<u>Onticellus pictus</u>			x
<u>O. triangulatus</u>		x	
<u>Onthophagus gazella</u>		x	
<u>Onthophagus</u> sp.		x	
<u>Rischista cincta</u>			x
<u>Pachynoda sinuata</u>			x
<u>Drepanocerus</u> sp.		x	
<u>Phalops amaragdinus</u>		x	
<u>Sisyphus</u> sp.		x	
Euprestidae	x	x	x
<u>Damarsila</u> sp.		x	x
<u>Acmaeodera faudrasi</u>			x
Elateridae	x	x	x
<u>Olophoeus protensus</u>		x	
<u>Olopuoeus</u> sp.			x
Cantharidae			x
Coccinellidae		x	x
<u>Isora anceps</u>		x	
Tenebrionidae	x	x	x
<u>Drosochrus</u> sp.		x	
<u>Zophosis</u> sp.		x	x
<u>Ossiparis fragilis</u>		x	
<u>Eurychora</u> sp.		x	

Appendix 3. (Cont.)

Food item	Hornbill species		
	N	E	F
Lagriidae		x	
Meloidae	x	x	x
Cerambycidae	x	x	x
<u>Litopus</u> sp.	x		
<u>Zoodes liturifer</u>		x	
Chrysomelidae	x	x	x
Megascelinae		x	x
<u>Chrysomela</u> sp.		x	
Cassidinae		x	x
Eumolpinae		x	
<u>Cassida tigrina</u>			x
Anthribidae		x	
Curculionidae	x	x	x
<u>Polycleis equestris</u>			x
Coleoptera larvae (mainly Scarabiidae and Tenebrionidae)		x	x

PLANT FOODS

<u>Grewia bicolor</u> fruit		x	x
<u>Euclea divinorum</u> fruit	x	x	x
<u>Lannea stuhlmanii</u> fruit	x	x	x
<u>Cassia abbreviata</u> flowers			x
<u>Corallocarpus</u> sp. fruit	x		x
<u>Coccinium rehmannii</u> fruit	x		x
<u>Solanum</u> sp. fruit		x	x
<u>Diospyros mesptiliformes</u> fruit	x	x	x
<u>Securinega virosa</u> fruit	x	x	x
<u>Crotalaria australis</u> fruit		x	x
<u>Ficus sycomorus</u> fruit	x		
<u>Trichlia emmetica</u> fruit	x		
<u>Enneapogon</u> sp. seed			x
<u>Abutilon quineense</u> fruit			x
<u>Hibiscus micranthus</u> fruit			x
<u>Commiphora africana</u> fruit			x
<u>Heliotropium nelsoni</u> fruit			x
<u>Tragus berteronianus</u> fruit		x	x

Appendix 3. (Cont.)

Food item	Hornbill species		
	N	E	F
<u>Ozoroa insignis</u> fruit	x		
<u>Cissus longicerifolius</u> fruit	x		x
Fruits of a <u>Coccoloba</u> sp. creeper			x
Buds of a small herb			x
Flowers of a shrub			x
Yellow flowers of a thick, thorny creeper			x
Red flowers and sticky fruit of an epiphyte		x	x
Small bulbs		x	
<u>Tribolium</u> -like seeds		x	x
Buds from terminal shoots of shrub	x		x
Purple and white coloured cotyledons			x
2 mm brown seed with style	x		
2 mm brown oval seed	x		
1 mm brown round seed	x		
4 mm pitted, pale yellow seed	x	x	x
6 mm very flat black seed	x	x	x
1 mm spherical- white seed	x		
2 mm yellow seed, hairy at one end		x	x
2 mm round cream seed		x	x
7 mm oval green and brown seed		x	x
5 mm cylindrical brown seed		x	
12 mm pointed-oval olive seed			x
5 mm pointed- oval elongate seed		x	
4 mm olive heart-shaped seed		x	
8 mm seed like orange pip			x
4 mm spiral corrugated seed			x
3 mm oval mahogany seed			x
6 mm spherical furry brown seed			x
10 mm almond-shaped olive seed			x
15 mm almond shaped seed pale pink			x
8 mm round mottled-brown seed			x
4 mm spherical seed			x
20 mm thin pale-green seed			x
2 mm fawn seed with style protruding		x	
3 mm oval tan seed with two stripes down it		x	
2 mm brown irregular-shaped seed		x	
3 mm spherical pale-yellow seed			x

Table 7. The seasons during which hornbills were collected in the Kruger National Park, with the numbers collected per season.

SEASON	SAMPLE SIZE								
	<u>T. nasutus</u>			<u>T. erythro-</u> <u>rhynchus</u>			<u>T. flaviros-</u> <u>tris</u>		
	♂	♀	Total	♂	♀	Total	♂	♀	Total
Early dry, 1967. (May, June, July)	2	1	3	5	5	10	5	5	10
Late dry, 1967. (August, September, October)	5	7	12	10	10	20	10	10	20
Early wet, 1967 (November, December, January).	6	5	11	15	15	30	15	15	30
Late wet, 1968. (February, March, April)	8	3	11	16	14	30	15	15	30
Early dry, 1968. (May, June, July)	2		2	13	17	30	11	19	30
Late dry, 1968 (August, September, October)	4	7	11	16	14	30	18	12	30
OVERALL	27	23	50	75	75	150	71	79	150

Appendix 4. The results of stomach content analysis of samples of three species of hornbill collected over six seasons in the Kruger National Park. Identity of food items and the numbers eaten by the sample each season are given.

A. TOCKUS NASUTUS.

Food items	1967		1967-1968		1968		Total
	Early dry	Late dry	Early wet	Late wet	Early dry	Late dry	
Rodents	3	3					6
<u>Chameleo</u>						1	1
<u>Chiromantis</u>		4	1	2	1		8
Centipede	1			2			3
Spiders			2		6	2	10
Scorpions			1	1			2
Solifugids				2		3	5
Tettigonidae		5		3	2	2	12
Acrididae		2	9	5	8	4	28
Mantidae	1	2	1			6	10
Hodotermitidae					190		190
Termitidae		5				6	11
Membracidae		8					8
Coccidae	1	40	3	5		32	81
Reduviidae		1					1
Lygaeidae		1	4			22	27
Coreidae		43	2			44	89
Pentatomidae		3	6	13	2	1	25
Mantispidae		1					1
Lepidoptera (larvae)	1	24		3	3	2	33
Chrysididae	1						1
Formicidae	2	161	63	63		43	332
Vespidae	2	1				24	27
Sphecidae						1	1
Apoidea		1				2	3
Cetoniinae			5			4	9
Melolonthinae			49	50			99
Coprinae			1		3	3	7
Buprestidae	7	7	15	25	132	26	212

Appendix 4.  
cont.

A.

Food items	1967		1967-1968		Early dry	1968 Late dry	Total
	Early dry	Late dry	Early wet	Late wet			
Elateridae	2	3	2	10	2		19
Tenebrionidae		14	5	12		6	37
Meloidae						4	4
Cerambycidae		5	29	46	6	14	100
Chrysomelidae	1	8	1	4		4	18
Curculionidae		2	49			13	64
Anthribidae				1		3	4
<u>Ficus sycomorus</u> fruit		13+	2			8	23
<u>Lannea stuhlmanii</u> fruit			95	7			102
<u>Euclea divinorum</u> fruit				20			20
<u>Corallocarpus</u> sp. fruit			1				1
<u>Coccinium rehmanii</u> fruit				7			7
2 mm brown seed with style	1						1
2 mm brown oval seed	1						1
<u>Diospyros mespitiliformes</u> fruit		17				26	43
1 mm brown round seed		7					7
4 mm pitted, pale yellow seed			130				130
6 mm very flat, black seed				12		3	15
<u>Trichlia emmetica</u> fruit				9			9
1 mm spherical white seed					7	6	13
<u>Securinega virosa</u> fruit				147			147
White tendrils				1			1
Buds from termi- nal shoots of shrub						1	1

Appendix 4. The results of stomach content analysis of samples of three species of hornbill collected over six seasons in the Kruger National Park. Identity of food items and the numbers eaten by the sample each season are given.

B. TOCKUS ERYTHORHYNCHUS

Food items	Seasons.						Total
	1967 Early dry	Late dry	1967 - Early wet	Late wet	Early dry	1968 Late dry	
Leptotyphlops					1		1
Millepede						1	1
Centipede		2	2		3	6	13
Spiders	1	6	6	6	15	16	50
Scorpions	1	3	3	5	1	8	21
Solifugids		5	4	2	2	26	39
Ticks	1	2	3		1	25	32
Tettigonidae				14	28		42
Gryllidae			3		1	2	6
Acrididae	12	11	77	105	162	23	390
Blattidae						1	1
Mantidae			4	2	4	2	12
Hodotermitidae	66	39	53	144	28	10	340
Termitidae	1029	7266	1397	2506	4028	4920	21146
Cecropidae					1		1
Reduviidae						1	1
Lygaeidae	4	4		27	2		37
Coreidae	8	36	2	33	205	201	485
Pentatomidae	1	1		2	8		12
Myrmeliontidae(larvae)		31			1	12	44
Lepidoptera(larvae)	2	2	2	148	58	2	214
Asilidae				1			1
Diptera(larvae)		4	116		4	11	135
Chalcidoidea		1					1
Mutillidae						1	1
Gasterupidae						1	1
Formicidae	879	3276	631	111	1812	748	7457

Appendix 4.  
cont.

B. Food items.	1967		Seasons. 1967 - 1968		1968		Total
	Early dry	Late dry	Early wet	Late wet	Early dry	Late dry	
Vespidae		2	1				3
Sphecidae	2	1			1	3	7
Apoidea	2			1			3
Carabidae	2	3	51	10	11		77
Staphylinidae		4				3	7
Cetoniinae			3				3
Melolonthinae		1	38			1	40
Coprinae	25	126	419	557	154	945	2226
Buprestidae		1	1	6	1		9
Elateridae			1				1
Coccinellidae	6	12	1	2	2	8	31
Tenebrionidae	52	262	221	416	1484	1561	3996
Meloidae						1	1
Cerambycidae			3	13	2		18
Chrysomelidae	15	4	6	14	5	5	49
Curculionidae	11	91	113	55	105	143	518
Coleoptera (larvae)	6	2	1	2	67	52	130
<u>Euclea divinatorum</u> fruit				31	18		49
<u>Grewia bicolor</u> fruit					10		10
<u>Lansea stuhlmanii</u> fruit			35	92			127
<u>Tragus berteronianus</u> fruit	3	45		3	3	4	58
<u>Tribolium</u> -like seeds		1	2			1	4
<u>Diospyros mespiliformes</u> fruit				11			11
<u>Solanum</u> sp. fruit	3	3					6
4 mm pitted, pale yellow seed			138	1	6		145
6 mm very flat, black seed					15		15
2 mm yellow seed, hairy at one end	4	16		33	271	139	463

Appendix 4.  
cont.

B. Food items	1967		Seasons. 1967- 1968		1968		Total
	Early dry	Late dry	Early wet	Late wet	Early dry	Late dry	
2 mm round cream seed					11		11
7 mm oval green and brown seed		4	2	2	43	6	57
5 mm cylindrical brown seed		49	1		1931	2266	4247
<u>Securinega virosa</u> fruit					20		20
<u>Crotolaria australis</u> fruit					15	28	43
5 mm pointed-oval elon- gate seed				1			1
4 mm olive heart-shaped seed					6		6
3 mm oval tan seed with two stripes down it						134	134
2 mm fawn seed with style protruding						2	2
Small bulbs			2				2

Appendix 4. The results of stomach content analysis of samples of three species of hornbill collected over six seasons in the Kruger National Park. Identity of food items and the numbers eaten by the sample each season are given.

C. TOCKUS FLAVIROSTRIS

Food items	1967		Seasons. 1967 - 1968		1968		Total
	Early dry	Late dry	Early wet	Late wet	Early dry	Late dry	
Rodents	1	2				1	4
<u>Leptotyphlops</u>				2			2
<u>Chameleo</u>						1	1
Basimatophora		1					1
Millipede					1		1
Centipede		3	1	8		1	13
Spiders	1	4	8	65	14	4	96
Scorpions	3	3	5	13	1	5	30
Solifugids		7	3	2	1	4	17
Ticks			1		1	3	5
Tettigonidae	1		1	67	11		80
Gryllidae	1		1			1	3
Acrididae	4	16	21	64	79	24	208
Phasmida		1	3			4	8
Blattidae		1		1		1	3
Mantidae		1	7		2	1	11
Hodotermitidae	83		13	1064	1221	500	2881
Termitidae	7	1524	542	321	1071	6979	10444
Cecropidae				1	1		2
Membracidae		5					5
Coccidae		3				8	11
Reduviidae		3					3
Lygaeidae		4		1		1	6
Coreidae	7	24		10	43	29	113
Pentatomidae		2	5	16	6		29
Myrmeliontidae(larvae)					1	2	3
Lepidoptera (moths)		2		1		7	10

Appendix 4.  
cont.

C.

Food items.	1967		Seasons. 1967 - 1968		1968		Total
	Early dry	Late dry	Early wet	Late wet	Early dry	Late dry	
Lepidoptera(larvae)	3		2	80	147	16	248
Lepidoptera (Acree)						1	1
Ortalidae					1		1
Ichneumonoidea	1			1	2		4
Chalcidoidea	10					3	13
Chrysididae			1				1
Mutillidae	1	3			1	6	11
Formicidae	4575	3052	1028	204	5347	3004	17210
Pompilidae		4			1	1	6
Vespidae		1			1	66	69
Apoidea			2			37	39
Carabidae	1		1	4	24	168	198
Cetoniinae		2	21	3		2	28
Melolonthinae		2	20			1	23
Coprinae	4	1	11	9	1	8	34
Buprestidae	4	1	26	30	48	8	117
Elateridae		2	24				26
Coccinellidae		5	1	9	3		18
Tenebrionidae	40	39	53	544	187	382	1245
Meloidae			1			18	19
Cerambycidae	1		5	23	8	5	42
Chrysomelidae	2	24	14	4	9	41	94
Curculionidae	23	88	190	19	5	229	554
Coleoptera(larvae)	7	10		1			18
<u>Grewia bicolor</u> fruit	48	11		3	106	25	193
<u>Tribolium</u> -like seeds	1		1				2
Red flowers and sticky fruit of an epiphyte	2						2
<u>Tragus berteroniamus</u> fruit				4		5	9

Appendix 4.  
cont.

C.

Food items	Seasons.						Total
	1967 Early dry	Late dry	1967 - Early wet	1968 Late wet	1968 Early dry	1968 Late dry	
<u>Euclea divinorum</u> fruit				101	46		147
Purple and white cotyledons				2		13	15
<u>Lannea stuhlmanii</u> fruit			95	12			107
<u>Cassia abbreviata</u> flowers		114	14			77	205
<u>Corallocarpus</u> sp. fruit	15	52	4	182	6	3	262
<u>Coccinium rehmani</u> fruit			43	379	18		440
<u>Solanum</u> sp. fruit				9	69	29	107
<u>Diospyros mespiti-</u> <u>lifomes</u> fruit		7			8	18	33
4 mm pitted, pale yellow seed			1243	58	3		1304
6 mm very flat, black seed			7	6	22		35
2 mm yellow seed, hairy at one end						3	3
2 mm round cream seed			3	21	15		39
7 mm oval green and brown seed		96			100	11	207
<u>Securinega virosa</u> fruit				336			336
<u>Crotalaria australis</u> fruit	3				14	7	24
8 mm seed-like orange pip	8			1	3		12
<u>Enneapogon</u> sp. seed		1	1				2
4 mm spiral corrugated seed		13	2				15
3 mm oval mahogany seed		4					4
10 mm almond-shaped olive seed			10				10
8 mm round mottled- brown seed				1			1

Appendix 4.

cont.

C.

Food items	Seasons.						Total
	1967		1967 - 1968		1968		
	Early dry	Late dry	Early wet	Late wet	Early dry	Late dry	
4 mm spherical seed				4			4
20 mm thin pale green seed					14		14
2 mm brown irregular shaped seed						80	80
6 mm spherical furry brown seed			106				106
15 mm almond- shaped seed, pale pink			9				9
Buds from terminal shoots of shrub				4		24	28

Table 8. The coefficient of similarity between three species of Tockus hornbill for the food items eaten over six seasons in the Kruger National Park.

SEASON	SPECIES COMPARED		
	<u>T. nasutus-T.erythrorhynchus</u>	<u>T.nasutus-T.flavirostris</u>	<u>T.erythrorhynchus-T.flavirostris</u>
Early dry	0,17	0,24	0,55
Late dry	0,40	0,55	0,54
Early wet	0,61	0,55	0,63
Late wet	0,49	0,49	0,58
Early dry	0,30	0,30	0,71
Late dry	0,52	0,56	0,59
Overall	0,57	0,59	0,73

Table 9. Means of diversity index per specimen, taken for the sample for each season, in three species of hornbill.

(a) Mean Diversity indices of the numbers of food items.

Species.	Seasons.					
	Early dry	Late dry	Early wet	Late wet	Early dry	Late dry
<u>I. nasutus</u>	1,60	1,57	0,93	1,21	1,75	1,90
<u>I. erythrorhynchus</u>	1,20	0,81	1,23	1,37	1,37	1,01
<u>I. flavirostris</u>	0,89	0,91	1,29	1,24	1,24	1,07

(b) Mean Diversity indices of the weights of food items.

Species.	Seasons.					
	Early dry	Late dry	Early wet	Late wet	Early dry	Late dry
<u>I. nasutus</u>	0,39	0,94	0,95	0,77	1,29	1,27
<u>I. erythrorhynchus</u>	1,20	1,42	1,31	1,24	1,51	1,33
<u>I. flavirostris</u>	0,96	1,18	1,09	1,05	1,09	1,35

Table 10. Significant differences between the overall diversity indices of three hornbill species, using the method of multiple comparison.  
 \* indicates significance at the 5% level.

Species compared	Numbers of food items	Weight of food items
<u>T. nasutus / T. erythrorhynchus</u>	*	*
<u>T. nasutus / T. flavirostris</u>	*	
<u>T. erythrorhynchus / T. flavirostris</u>		*

Table 11.

Significant differences between the diversity indices of three hornbill species during six seasons, using the method of multiple comparison. \* indicates significance at the 5% level.

Season	Species compared	Numbers of food items	Weight of food item
Early dry	<u>T. nasutus / T. erythrorhynchus</u>		*
	<u>T. nasutus / T. flavirostris</u>		
	<u>T. erythrorhynchus / T. flavirostris</u>		
Late dry	<u>T. nasutus / T. erythrorhynchus</u>	*	*
	<u>T. nasutus / T. flavirostris</u>	*	
	<u>T. erythrorhynchus / T. flavirostris</u>		
Early wet	<u>T. nasutus / T. erythrorhynchus</u>		
	<u>T. nasutus / T. flavirostris</u>		
	<u>T. erythrorhynchus / T. flavirostris</u>		
Late wet	<u>T. nasutus / T. erythrorhynchus</u>		*
	<u>T. nasutus / T. flavirostris</u>		
	<u>T. erythrorhynchus / T. flavirostris</u>		
Early dry	<u>T. nasutus / T. erythrorhynchus</u>		
	<u>T. nasutus / T. flavirostris</u>		
	<u>T. erythrorhynchus / T. flavirostris</u>		*
Late dry	<u>T. nasutus / T. erythrorhynchus</u>	*	
	<u>T. nasutus / T. flavirostris</u>	*	
	<u>T. erythrorhynchus / T. flavirostris</u>		

Table 12.

The percentage contribution by weight that "important animal food items" make to the diet of three species of hornbill in different seasons, compared to that made up by "incidental food items". An "important animal food item" is one that contributes over 5% to the diet by weight in any one season.

Season	Numbers of food items, and percentage contribution by weight.											
	<u>T. nasutus</u>				<u>T. erythrorhynchus</u>				<u>T. flavirostris</u>			
	Important Nos.	%	Incidental Nos.	%	Important Nos.	%	Incidental Nos.	%	Important Nos.	%	Incidental Nos.	%
Early dry (1967)	2	97	9	3	7	88	14	12	5	89	18	11
Late dry (1967)	2	85	21	15	5	77	23	23	4	79	28	21
Early wet (1967-68)	6	89	13	11	4	72	23	28	8	83	22	17
Late wet (1968)	4	79	14	21	5	85	19	15	6	89	22	11
Early dry (1968)	3	85	7	15	5	79	25	21	5	93	24	7
Late dry (1968)	5	74	20	26	6	82	25	18	6	68	31	32



## -KEY-







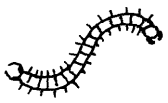














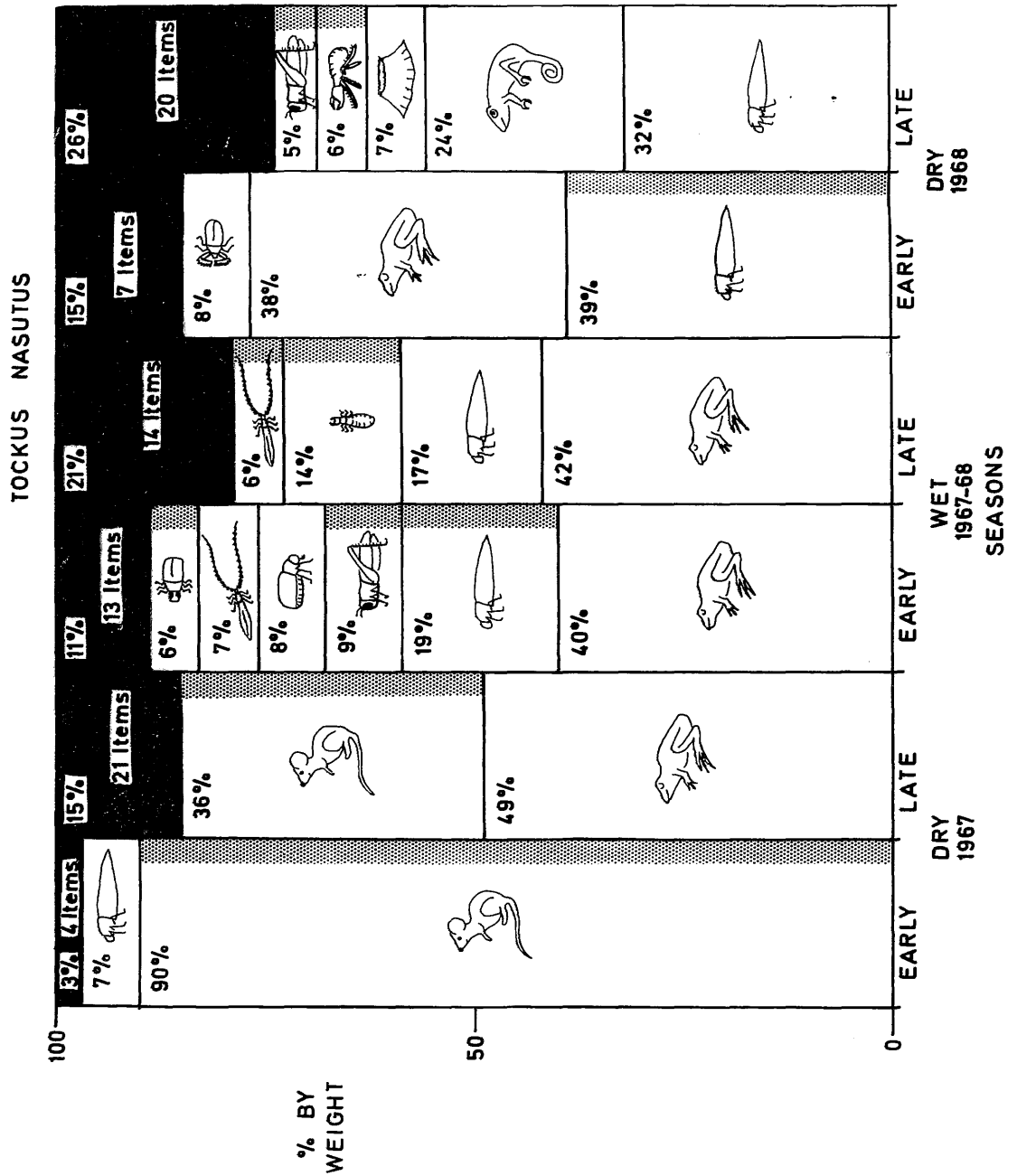






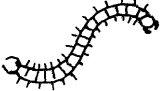














RODENTS			ANTS
CHAMAELEON			FLY LARVAE
TREE FROG			CATERPILLAR
CENTIPEDE			BUPRESTID
SCORPION			CERAMBYCID
SOLIFUGID			MELOLONTHINAE
ACRIDID			CETONIINAE
COCCID			COPRINAE
HODOTERMES			TENEBRIONID
TERMITES			CURCULIONID
			BEETLE LARVAE

Figure 20. Diagrams of the percentage by weight which "important animal food items" contribute to the diet of three species of hornbill in different seasons in the Kruger National Park. Black areas - remainder of the diet formed by the numbers of "incidental food items", stippled areas - "important animal food items" shared with another hornbill species in the same season.



**-KEY-**

RODENTS			ANTS
CHAMAELEON			FLY LARVAE
TREE FROG			CATERPILLAR
CENTIPEDE			BUPRESTID
SCORPION			CERAMBYCID
SOLIFUGID			MELOLONTHINAE
ACRIDID			CETONIINAE
COCCID			COPRINAE
HODOTERMES			TENEBRIONID
TERMITES			CURCULIONID
			BEE TLE LARVAE

TOCKUS ERYTHORHYNCHUS

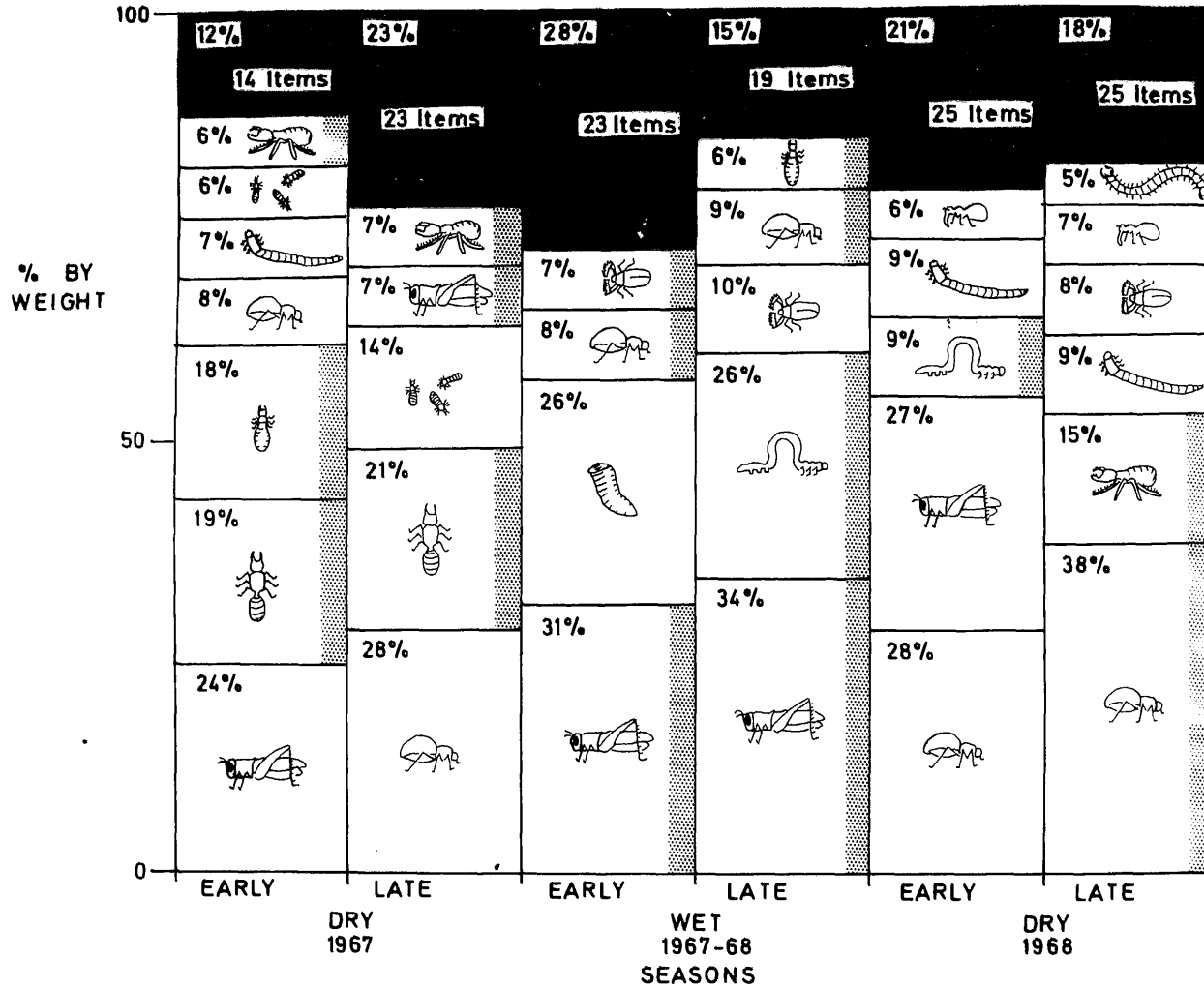






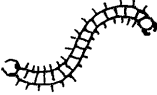
















Figure 20. (Cont.)

-KEY-

RODENTS			ANTS
CHAMAELEON			FLY LARVAE
TREE FROG			CATERPILLAR
CENTIPEDE			BUPRESTID
SCORPION			CERAMBYCID
SOLIFUGID			MELOLONTHINAE
ACRIDID			CETONIINAE
COCCID			COPRINAE
HODOTERMES			TENEBRIONID
TERMITES			CURCULIONID
			BEETLE LARVAE

TOCKUS FLAVIROSTRIS

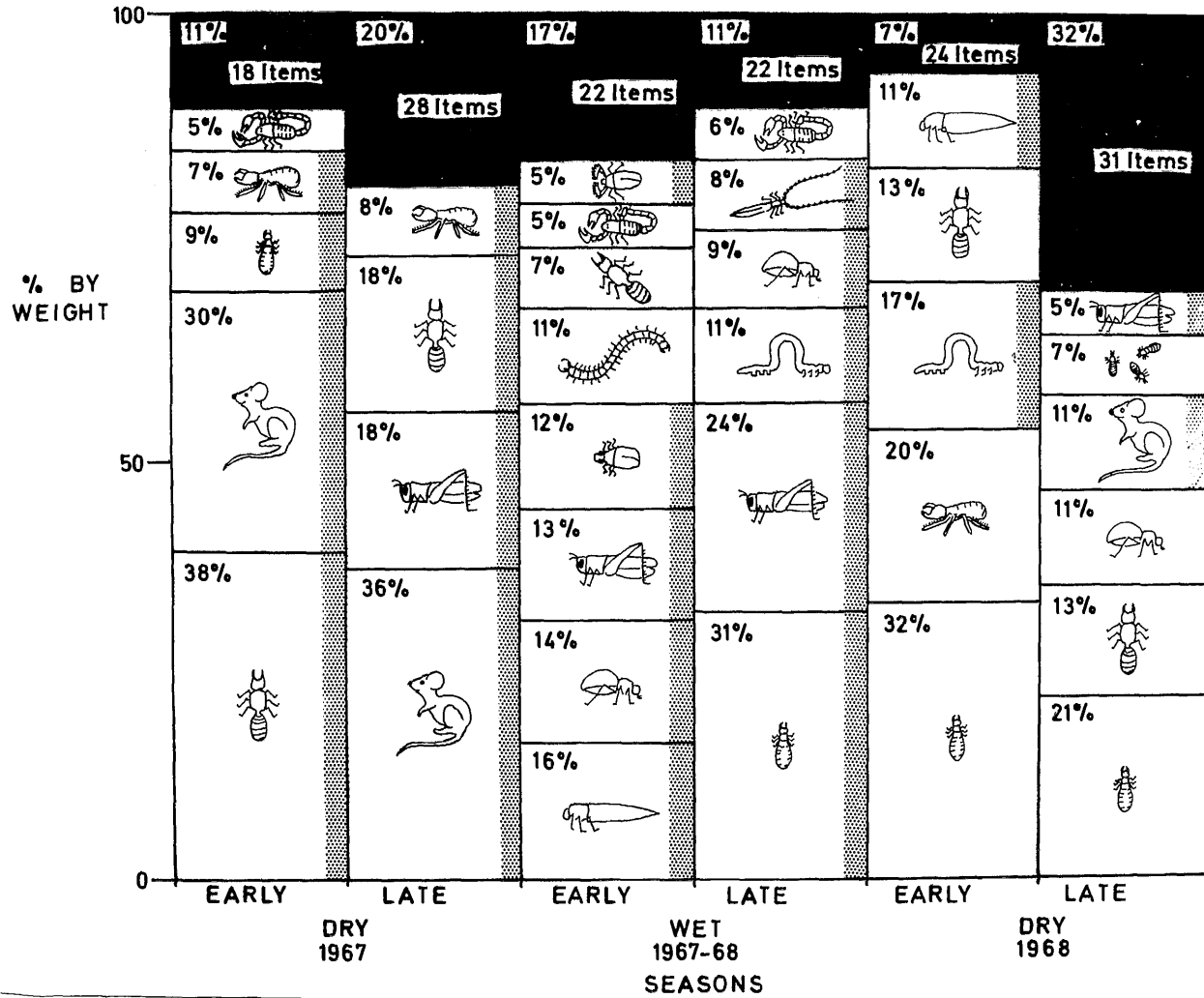


Figure 20. (Cont.)

Table 14. A table comparing the percentages by weight contributed by "important animal food items" that are important to more than one hornbill species during any one season.

Season			Species of hornbill compared							
	<u>I. nasutus</u>	<u>I. erythrorhynchus</u>	<u>I. nasutus</u>	<u>I. flavirostris</u>	<u>I. erythrorhynchus</u>	<u>I. flavirostris</u>				
Early dry (1967)			90%	Rodents	30%		6%	Solifugids	7%	
							18%	Hodotermites	9%	
							19%	Ants	38%	
Total % shared			90%		30%	43%			54%	
Late dry (1967)			36%	Rodents	36%		7%	Solifugids	8%	
							21%	Ants	18%	
							7%	Acridids	18%	
Total % shared			36%		36%	35%			44%	
Early wet (1967- 68)	9%	Acridids	31%		9%	Acridids	13%	Acridids	13%	
					6%	Cetoniinae	12%			
					19%	Buprestids	16%			
							7%	Coprinae	5%	
						8%	Tenebrionids	14%		
Total % shared	9%		31%	34%		41%	46%		32%	
Late wet (1968)	14%	Hodotermites	6%		14%	Hodotermites	31%	6%	Hodotermites	31%
					6%	Cerambycids	8%			
							9%	Tenebrionids	9%	
							26%	Caterpillars	11%	
						34%	Acridids	24%		
Total % shared	14%		6%	20%		39%	75%		75%	
Early dry (1968)					39%	Buprestids	11%			
							9%		17%	
Total % shared					39%		11%	9%	17%	
Late dry (1968)	6%		15%		5%	Acridids	5%			
							38%		11%	
Total % shared	6%		15%	5%	5%	38%			11%	

Table 15.

Food gathering niches of three species of Tockus hornbill. The seasons are taken as November to April (wet season) and May to October (dry season).

Hornbill species      Where food was obtained      Numbers recorded and percent they form, per season, and overall

	Wet season		Dry season		Overall	
	Nos.	%	Nos.	%	Nos.	%
<u>T. nasutus</u>						
Trees	28	50,0	14	70,0	42	55,3
Bushes	10	17,9	3	15,0	13	17,1
Long Grass	5	8,9	2	10,0	7	9,2
Medium Grass	2	3,6	-	-	2	2,6
Short Grass	7	12,5	-	-	7	9,2
Bare Ground	4	7,1	1	5,0	5	6,6
Total :	56	100,0	20	100,0	76	100,0
<u>T. erythrorhynchus</u>						
Trees	-	-	-	-	-	-
Bushes	1	0,9	-	-	1	0,1
Long Grass	-	-	-	-	-	-
Medium Grass	7	6,2	113	17,0	120	15,5
Short Grass	52	46,0	368	55,5	420	54,1
Bare Ground	53	46,9	182	27,5	235	30,3
Total:	113	100,0	663	100,0	776	100,0
<u>T. flavirostris</u>						
Trees	8	5,0	2	0,4	10	1,6
Bushes	5	3,1	8	1,7	13	2,1
Long Grass	3	1,9	2	0,4	5	0,8
Short Grass	59	36,6	32	6,8	91	14,4
Bare Ground	69	42,8	150	31,9	219	34,6
Total :	161	100,0	471	100,0	632	100,0

Figure 21. Histograms of the foraging niches used by three species of hornbill in the Kruger National Park, expressed as the percentage of the times that they are used during the wet season (November - April) and dry season (May - October).

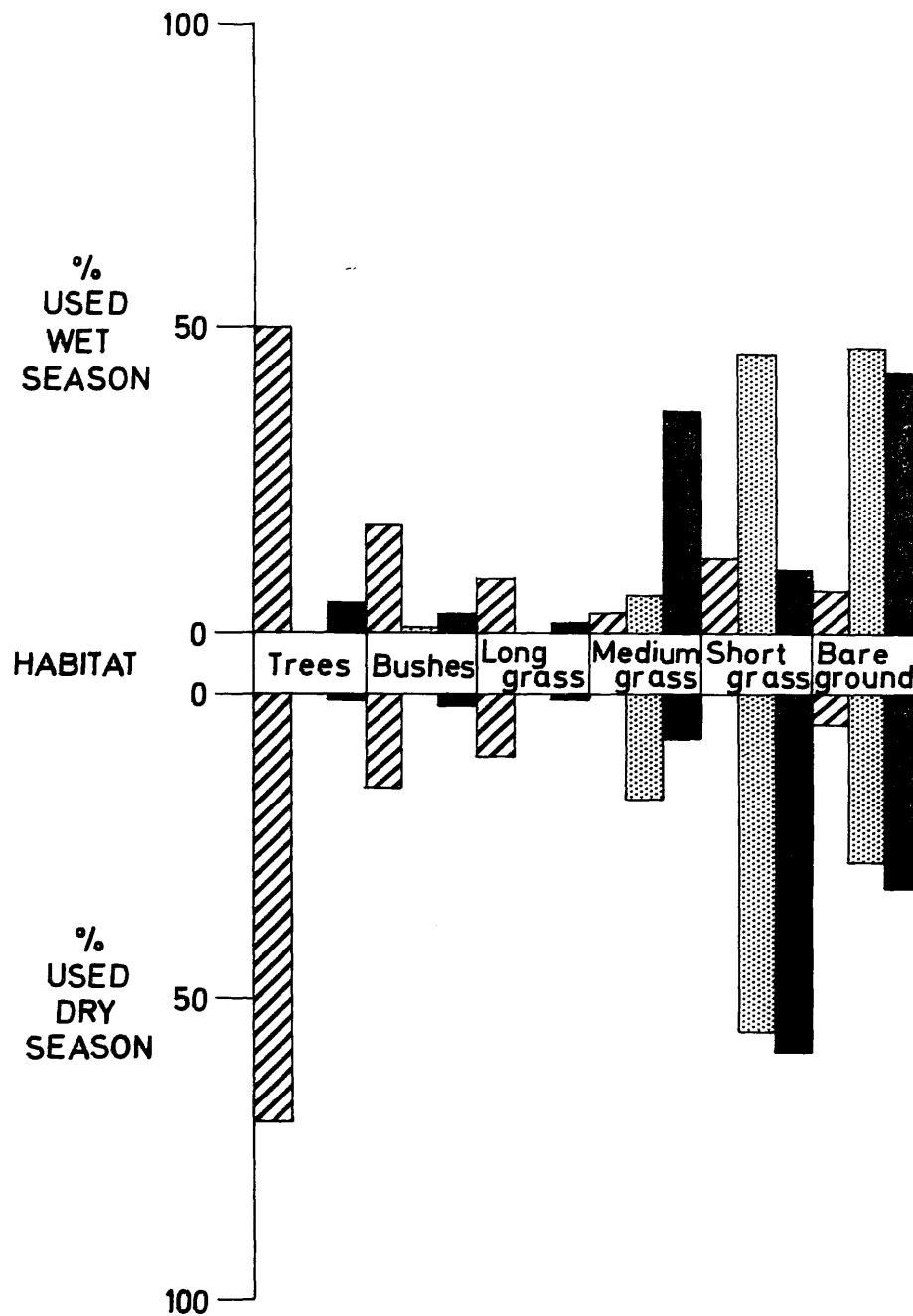


Table 16.

How three species of Tockus hornbill obtain their food. The seasonal division is November to April (wet season) and May to October (dry season).

Hornbill species	How food was obtained	Numbers recorded and percent they form, per season, and overall					
		Wet season		Dry season		Overall	
		Nos.	%	Nos.	%	Nos.	%
<u>T. nasutus.</u>	Picking	25	44,6	7	35,0	32	42,1
	Digging	-	-	-	-	-	-
	Levering	-	-	-	-	-	-
	Chasing	2	3,6	-	-	2	2,6
	Hawking	21	37,6	4	20,0	25	32,9
	Swooping	4	7,1	1	5,0	5	6,6
	Plucking	4	7,1	8	40,0	12	15,8
	Total:	56	100,0	20	100,0	76	100,0
<u>T. erythrorhynchus</u>	Picking	66	58,4	199	30,0	265	34,2
	Digging	36	31,9	453	68,3	489	63,0
	Levering	-	-	6	0,9	6	0,8
	Chasing	1	0,9	5	0,8	6	0,8
	Hawking	10	9,8	-	-	10	1,2
	Swooping	-	-	-	-	-	-
	Plucking	-	-	-	-	-	-
	Total:	113	100,0	663	100,0	776	100,0
<u>T. flavirostris</u>	Picking	140	87,0	385	81,7	525	83,2
	Digging	6	3,7	61	13,0	66	10,5
	Levering	-	-	18	3,8	18	2,8
	Chasing	3	1,9	4	0,8	7	1,1
	Hawking	12	7,4	-	-	12	1,9
	Swooping	-	-	3	0,7	3	0,5
	Plucking	-	-	-	-	-	-
	Total:	161	100,0	471	100,0	632	100,0

Figure 22. Histograms of the foraging methods used by three species of hornbill in the Kruger National Park, expressed as the percentage of the times they are used during the wet season (November - April) and dry season (May - October).

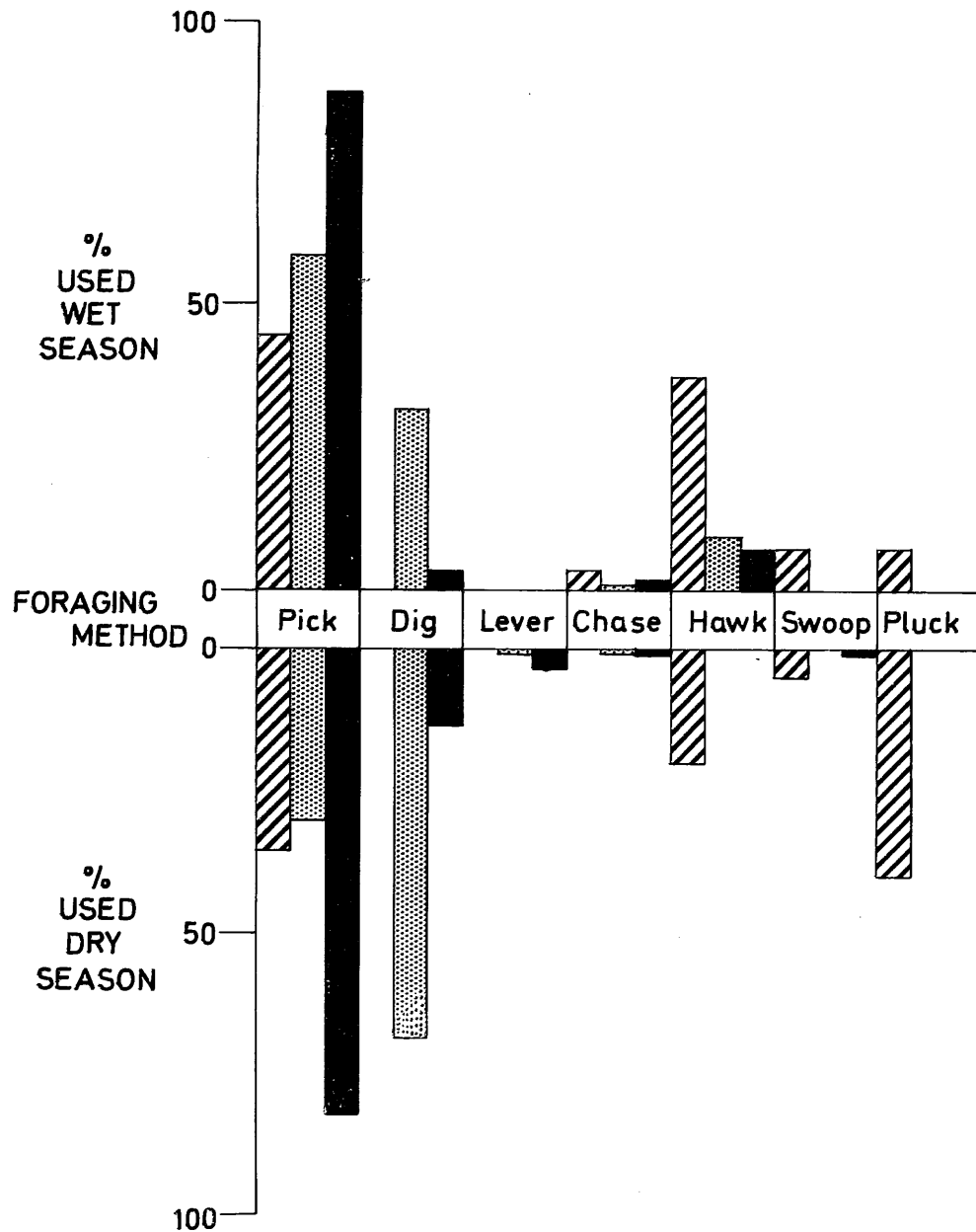


Figure 23. The average weight of the stomach fat body (expressed as a percentage of the body weight) for monthly samples of specimens of three species of hornbill collected in the Kruger National Park, to give an index of the condition of the specimens.

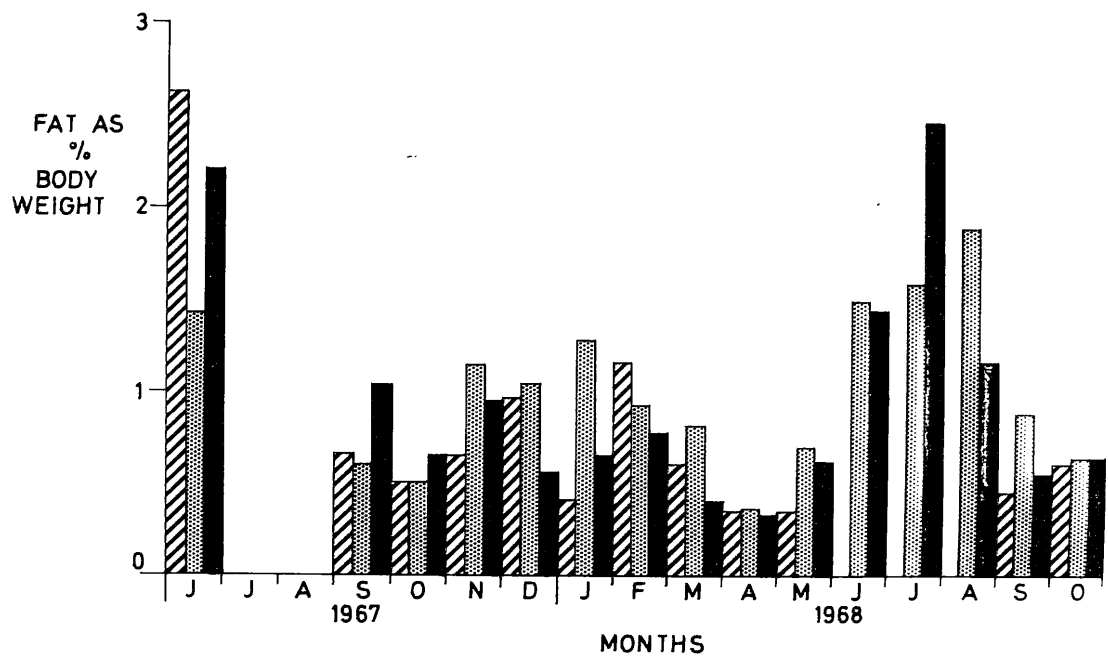


Figure 24. Monthly rainfall for the six three-month seasons during which hornbills were collected in the Kruger National Park for stomach content analysis, and for the preceding season.

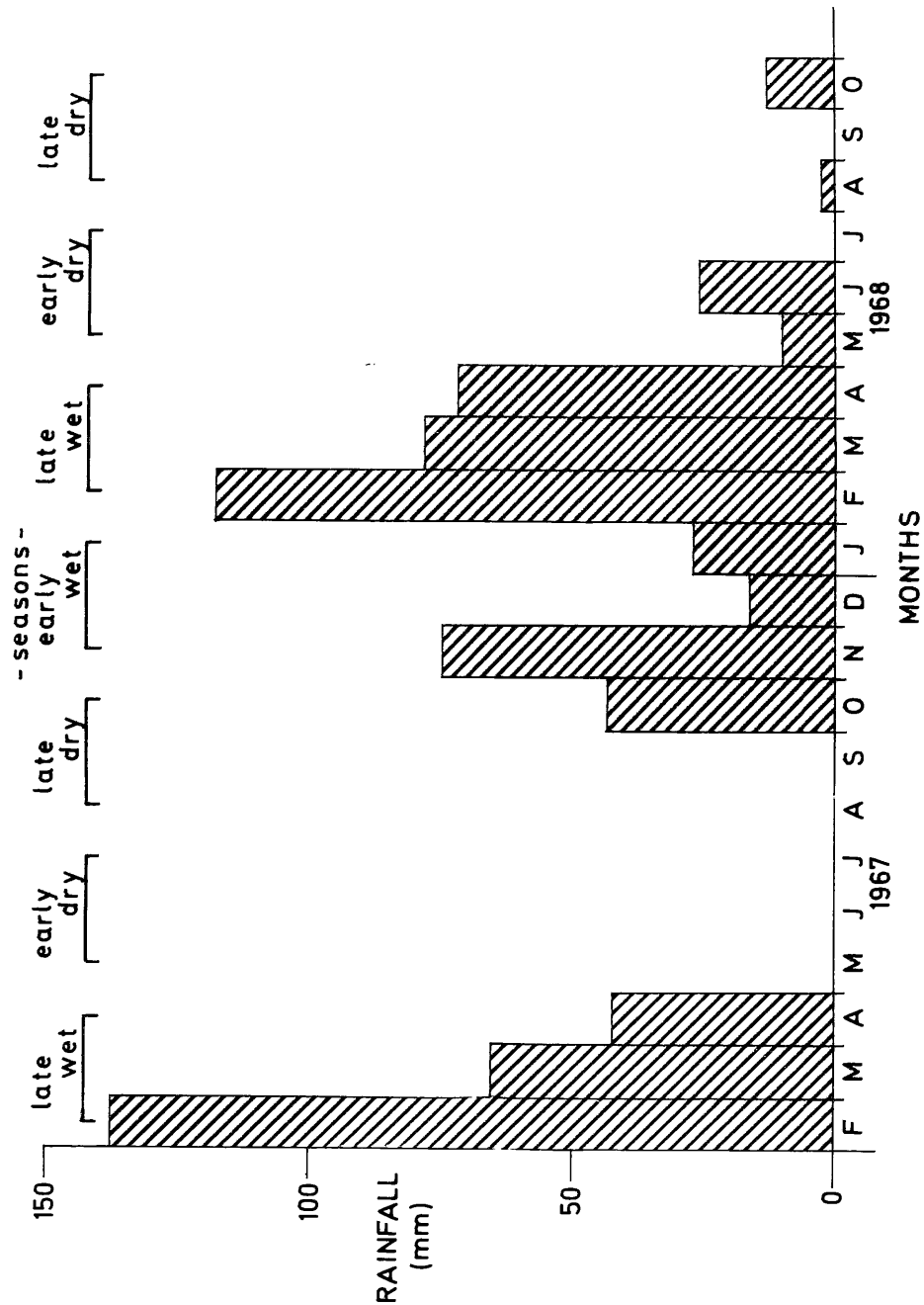


Figure 25. Histogram of the arthropod biomass sampled at three-day intervals in the Kruger National Park by sweeping, plotted below the rainfall figures for the three days intervening between samples.

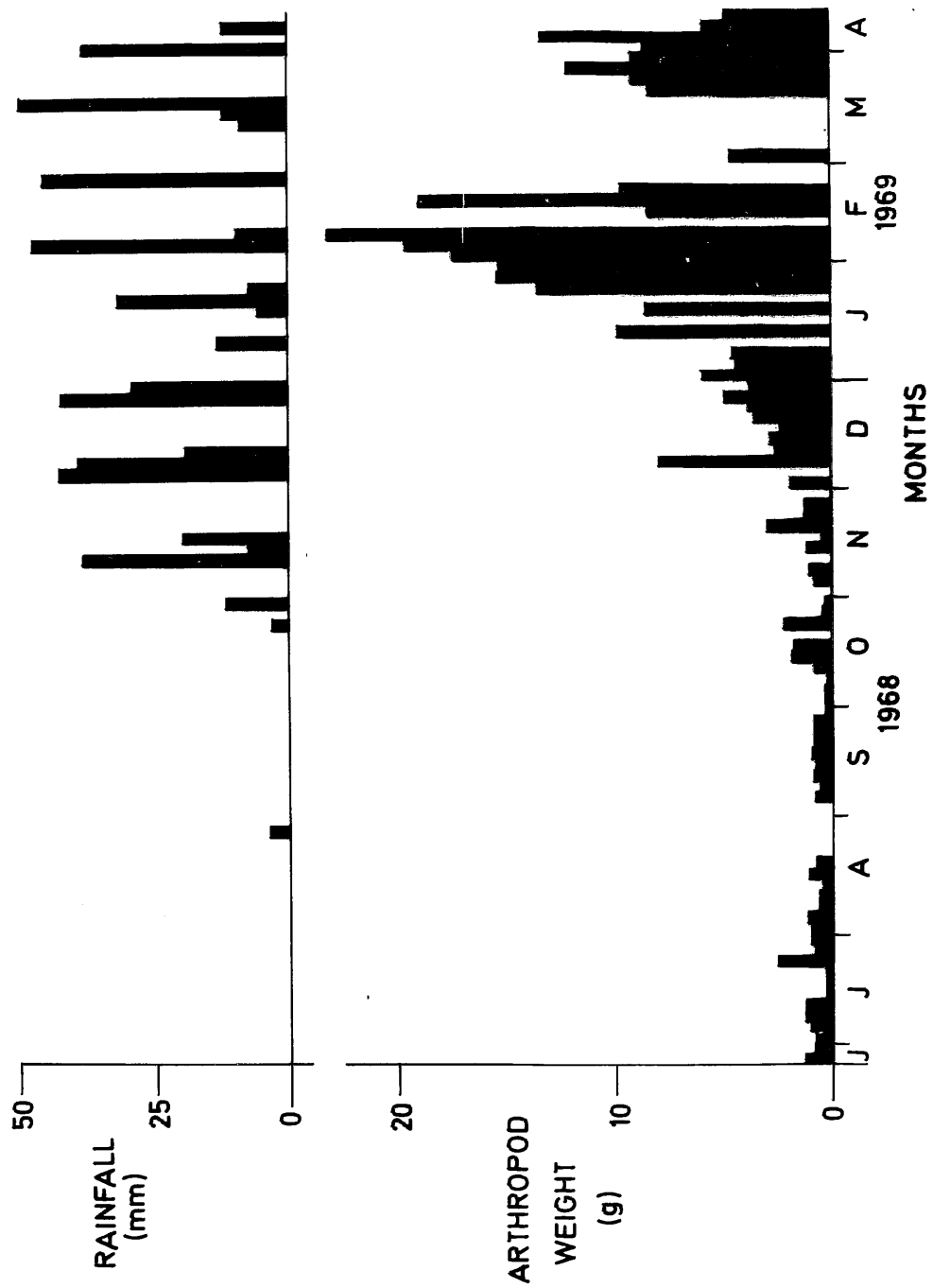


Table 17.

Average bill sizes for the sexes of three species of hornbill, from the samples collected for stomach content.

Hornbill species		Average bill length, mm	Range of length, mm	Sample size
<u>T. nasutus</u>	♂	64,1	47 - 72	27
	♀	50,7	50 - 62	22
<u>T. erythrorhynchus</u>	♂	63,5	51 - 71	76
	♀	51,2	44 - 59	73
<u>T. flavirostris</u>	♂	68,7	58 - 75	71
	♀	58,3	50 - 64	77

Figure 26. Number of nests started each day of *I. nasutus*, *I. erythrorhynchus* and *I. flavirostris* during four consecutive seasons (1966-67 to 1969-70) in the central Kruger National Park, plotted against the daily rainfall and maximum and minimum temperatures.

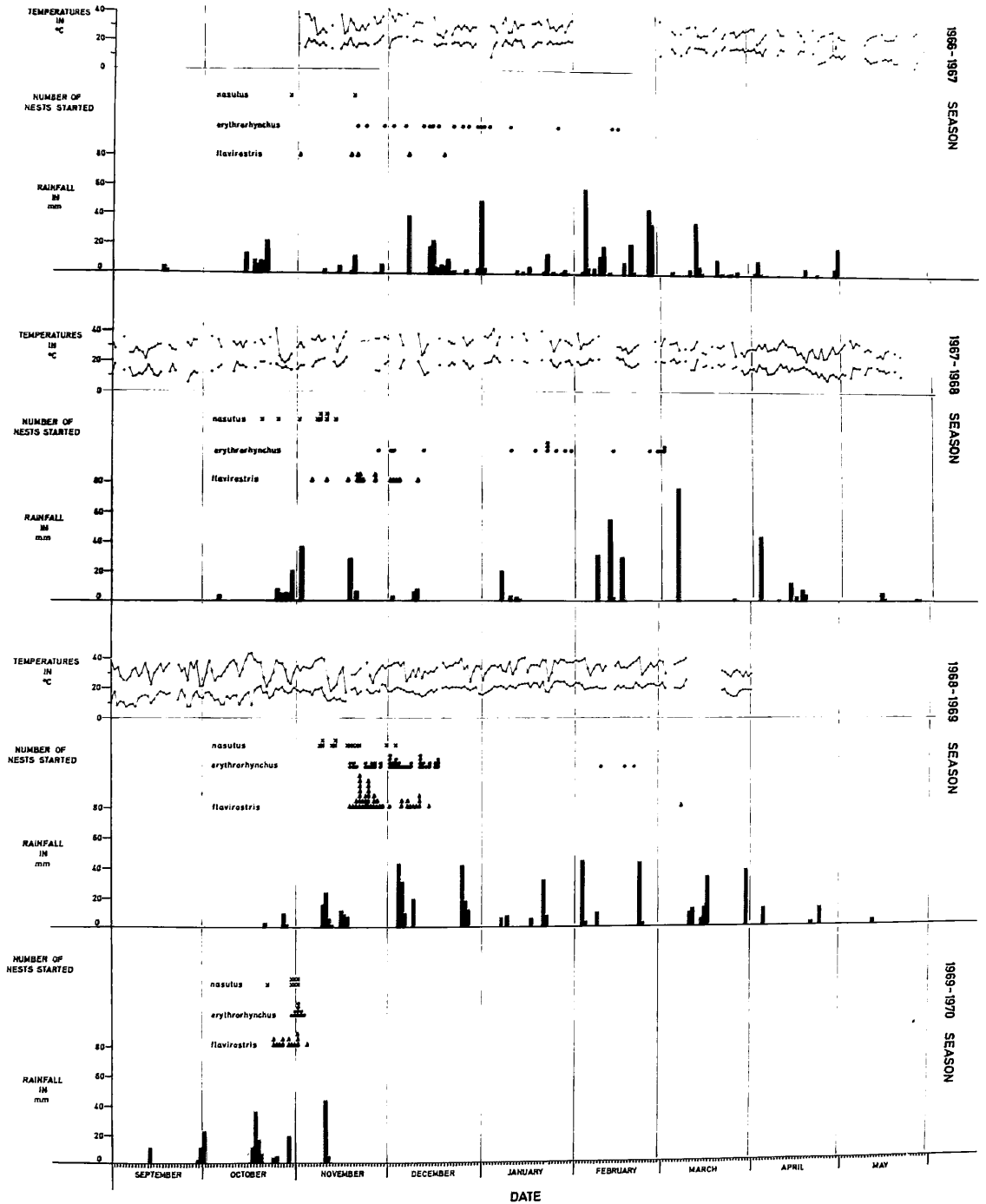


Figure 27, Number of nests started each day of *T. nasutus*, *T. monteiri* and *T. flavirostris* during the 1970 breeding season on Valencia Ranch, plotted against the daily rainfall and maximum and minimum temperatures.

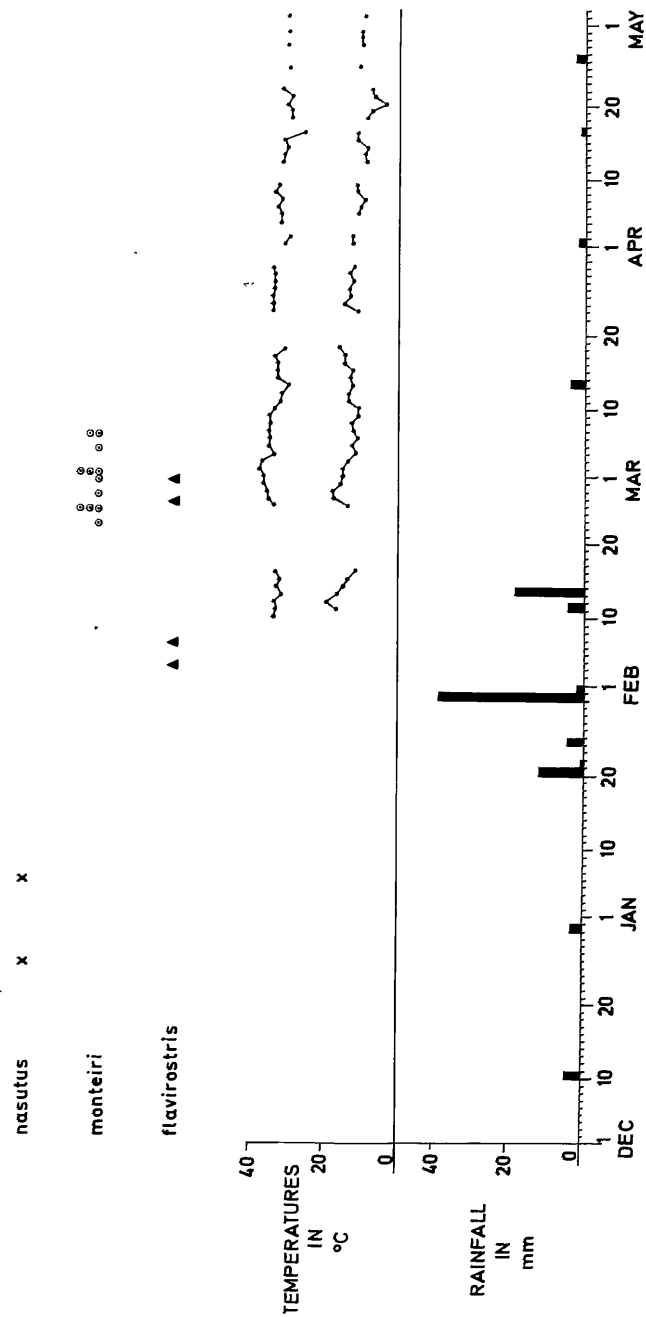


Figure 28. The rainfall prior to onset of nesting, against the ratio of the number of days since the start of the wet season to the number of days on which rain fell ("wetness"), for each nest of four species of *Tockus* hornbill. Plotted for four consecutive seasons in the central Kruger National Park (1966-67 to 1969-70), and for the 1970 season on Valencia Ranch. *T. nasutus* (n, solid line), *T. erythrorhynchus* (e, dotted line), *T. flavirostris* (f, broken line) and *T. monteiri* (m, dotted line).

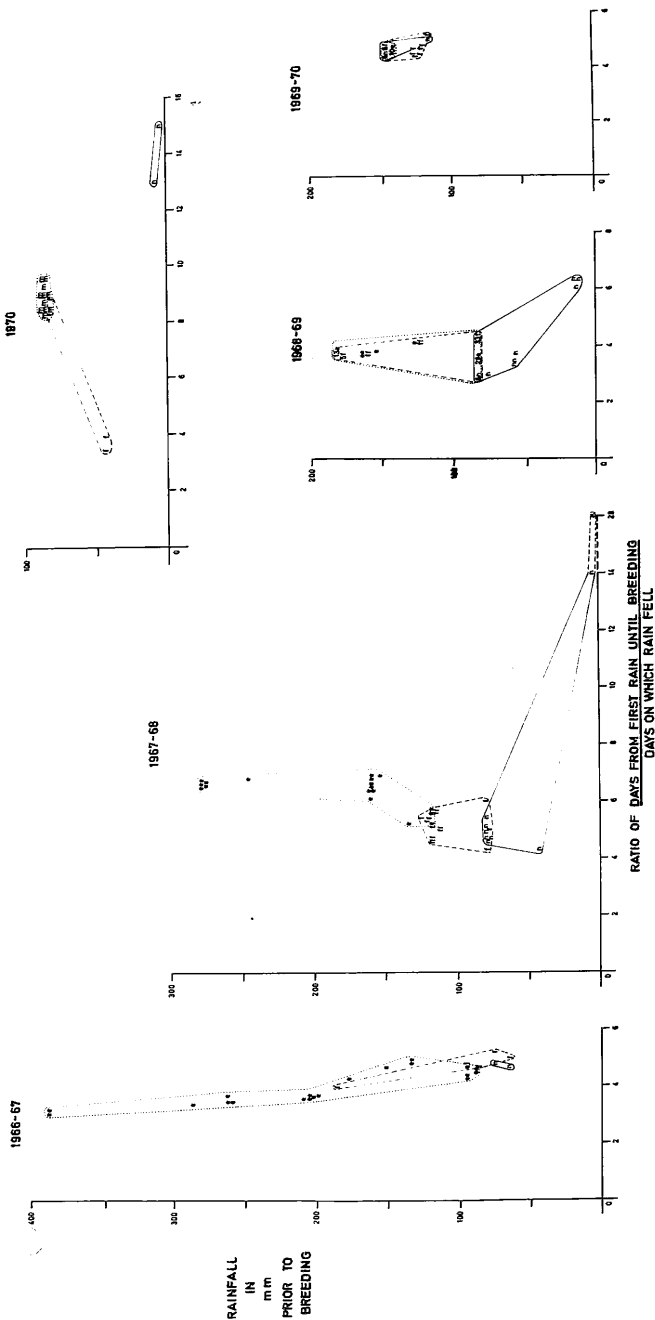


Figure 29. The average arthropod biomass recorded at three day intervals from two funnel traps, and two 100-sweep transects, near Satara, Kruger National Park. Daily rainfall, maximum and minimum temperatures, and number of nests started each day of *T. nasutus*, *T. erythrorhynchus* and *T. flavirostris*, are plotted, for the 1968-69 seasons. Open symbols indicate second broods.

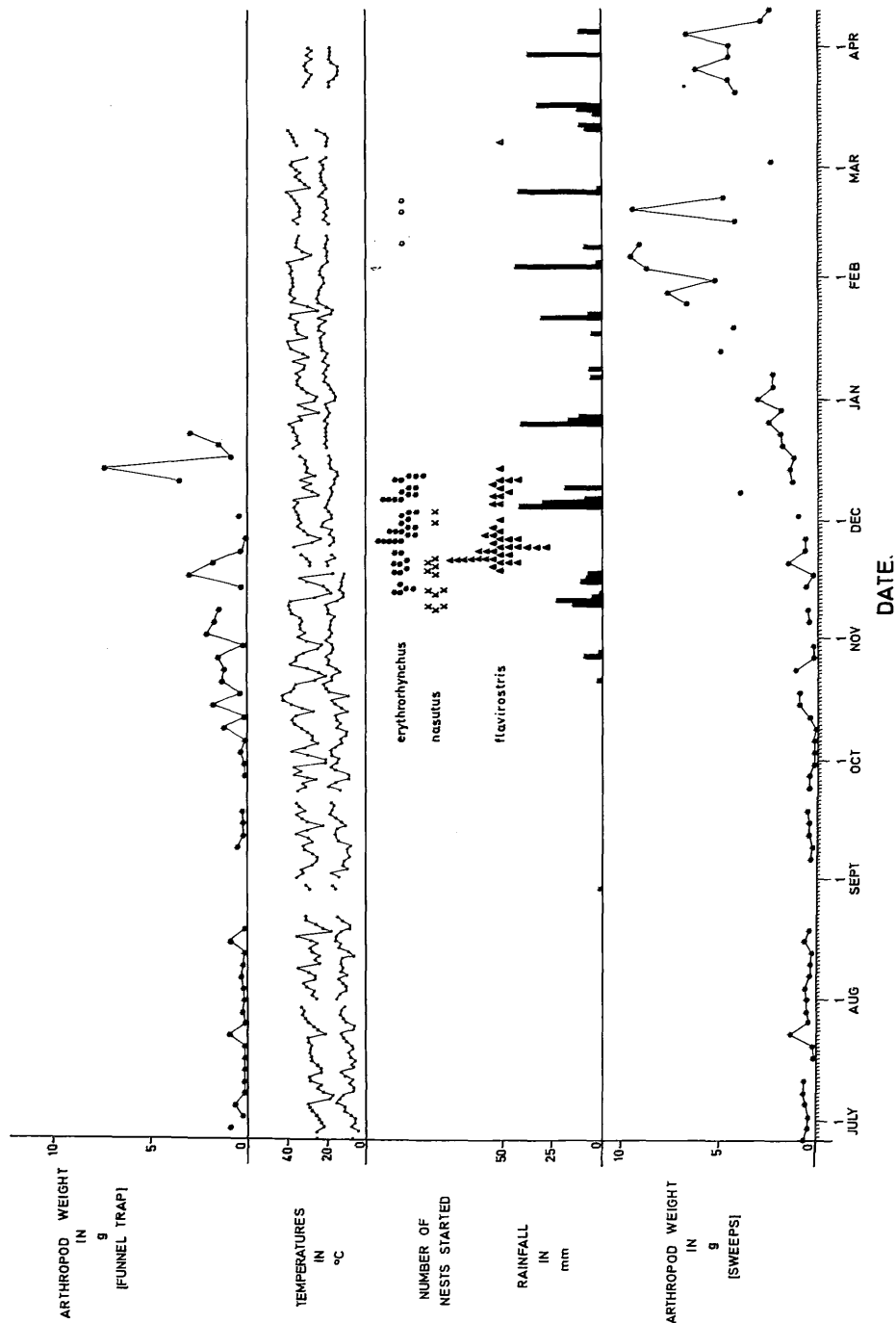


Figure 30. Gonad measurements of specimens of *I. nasutus*, *I. erythrorhynchus* and *I. flavirostris* collected in the central Kruger National Park in the middle of each month from June 1967 to October 1968. Average testis volume ( $\text{mm}^3$ ) of males, and diameter of largest ovarian follicle (mm) of females, are plotted against the rainfall since the previous collecting time (or 30 days previously if there was no collecting). The solid bar above each graph indicates the recorded span of onset of nesting for that species during the 1967-68 breeding season.

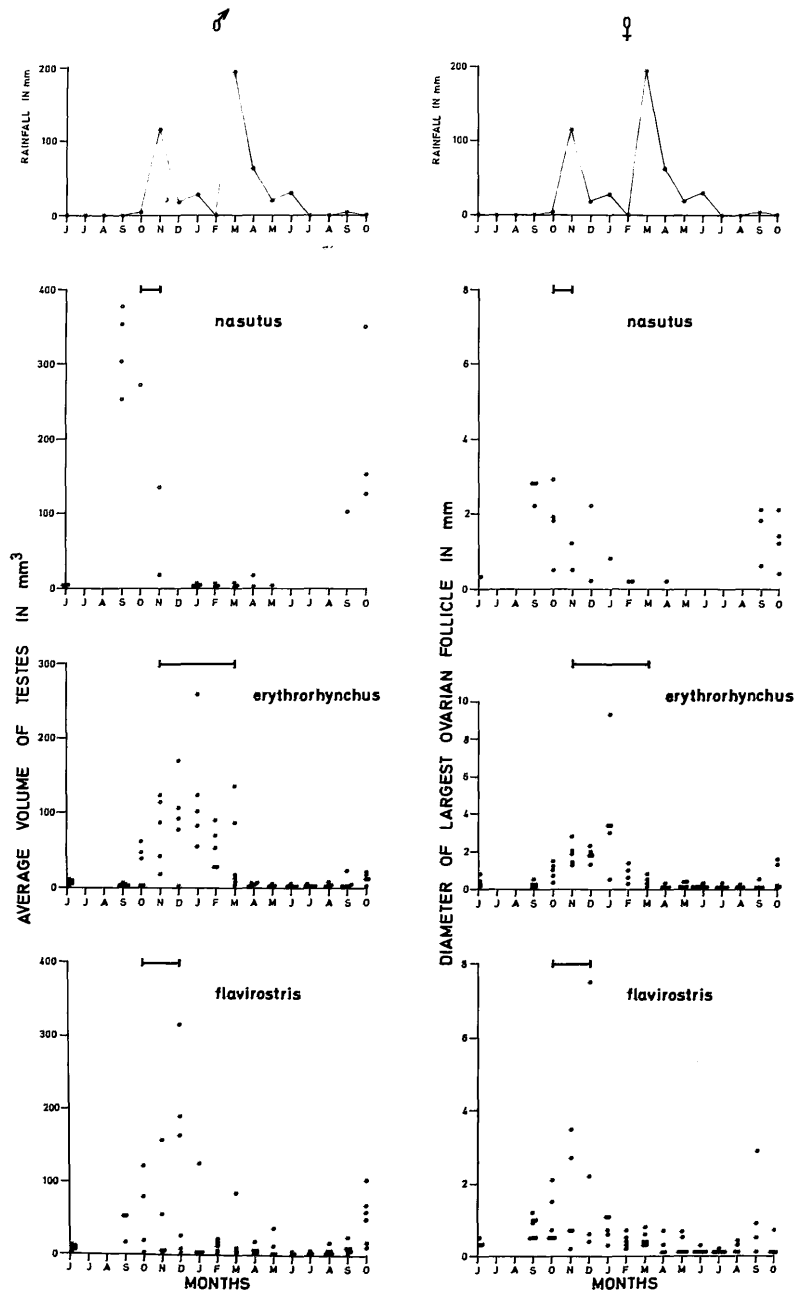


Figure 31. A map of the central regions of the Kruger National Park used for a breeding study area for three species of hornbill, showing the numbers and positions of nest holes, except for those in the Satara study area.

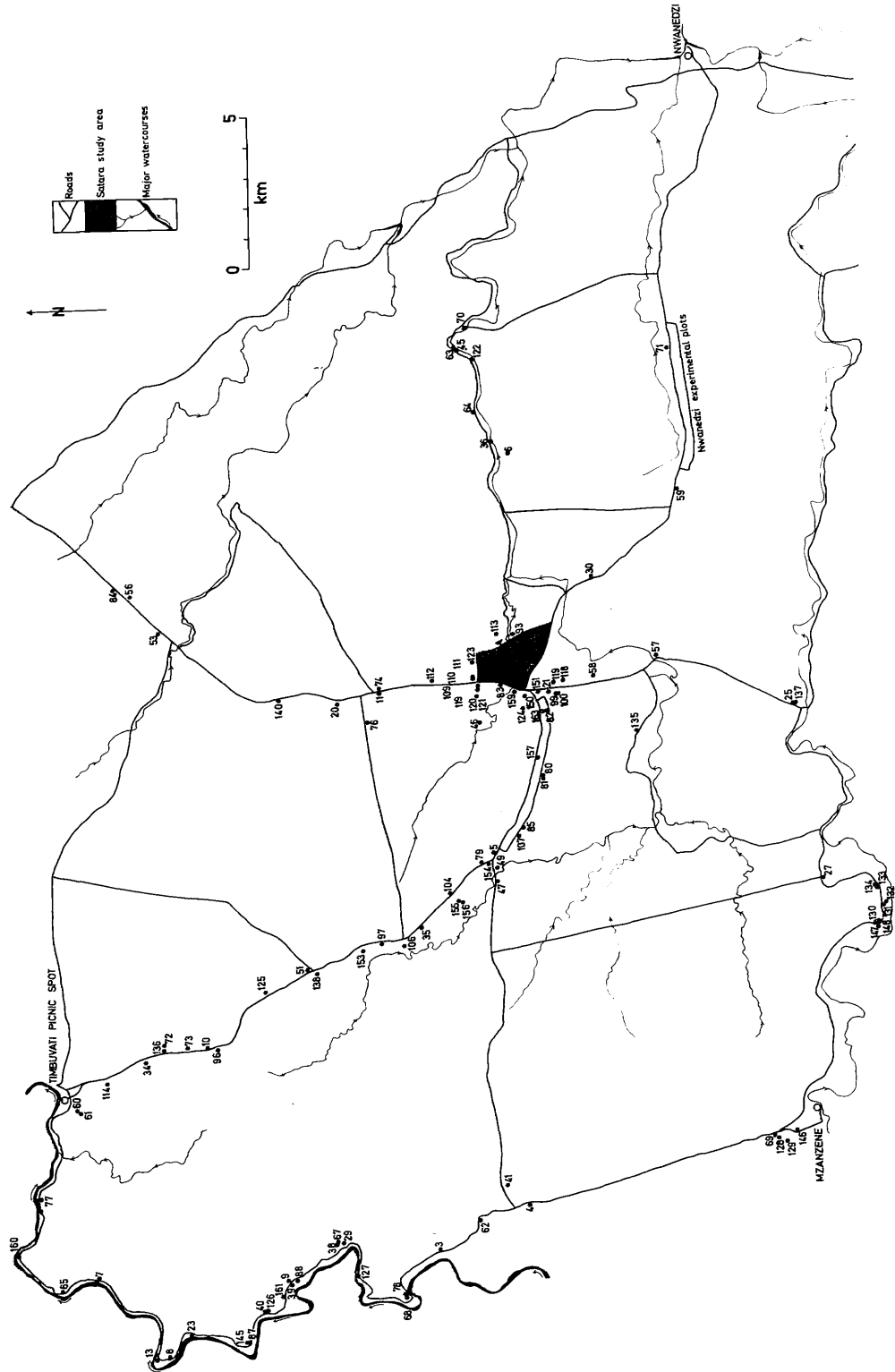


Table 18. Assessment of the habitat within about a 50 m radius of the nest of three species of Tockus hornbill in the Kruger National Park.

	Hornbill species		
	<u>T. nasutus</u>	<u>T. erythro-</u> <u>rhynchus</u>	<u>T. flaviros-</u> <u>tris</u>
Number of nests	20	85	73
Percentage in each habitat alternative			
1. Tree density			
A. Scattered parkland	80	72	83
B. Dense woodland	20	28	17
2. Grass Cover			
A. Sparse grass cover	35	72	48
B. Longer than sparse grass cover	65	28	52
3. Location			
A. In riparian association	15	27	18
B. Away from rivers and watercourses	85	73	82

Table 19. Mean dimensions of 178 hornbill nest holes examined in the Kruger National Park, used by three species of Tockus hornbills. Figures in brackets are the extremes recorded.

Dimensions recorded	Hornbill species		
	<u>Tockus nasutus</u>	<u>Tockus erythro-rhynchus</u>	<u>Tockus flavirostris</u>
Height of nest entrance from the ground(m)	3,47 (0,70-9,14)	3,20 (0,30-9,14)	3,88 (0,76-12,19)
No. of nests facing to each compass quarter			
N	7	15	13
NE	0	6	11
E	2	9	14
SE	1	7	7
S	3	12	6
SW	1	8	4
W	4	13	7
NW	2	15	6
Maximum width of nest chamber (cm)	23,2 (15-32)	20,6 (5 -38)	20,5 (7 -35)
Depth of nest floor below lip of entrance (cm)	8,2 ( 0-20)	9,1 (0 -28)	11,5 (0-27 )
Percentage of nests with a "funkhole" above the chamber	85%	72%	77%
Height of the entrance hole (cm)	8,5 (5,0 - 20,0)	8,5 (3,5 -62,0)	7,0 (3,5 -19,0)
Width of entrance hole at widest point(cm)	4,0 (2,5 - 8,0)	4,0 (2,5 - 9,5)	4,0 (2,5 - 6,5)
Number of nests in sample	20	85	73

Table 20. Tree species in which three species of hornbill occupied nest holes in the Kruger National Park.

	Hornbill species		
	<u>T. nasutus</u>	<u>T. erythro-</u> <u>rhynchus</u>	<u>T. flaviros-</u> <u>tris</u>
Number of nests recorded	20	85	73
Percentage of nests in:			
<u>Sclerocarya birrea</u>	25	27	25
<u>Acacia nigrescens</u>	30	22	27
<u>Combretum imberbe</u>	15	11	27
<u>Lonchocarpus capassa</u>		6	
<u>Lanea stuhlmanii</u>	10	2	3
<u>Peltophorum africanum</u>			1
<u>Diospyros mesptiliformes</u>	5	2	1
<u>Acacia robusta</u>	5		1
<u>Acacia delagoensis</u>	10	22	4
<u>Acacia burkei</u>		2	1
<u>Acacia tortilis</u>		1	
<u>Combretum transvaalense</u>		1	
<u>Kigelia pinnata</u>			1
<u>Albizzia harveyi</u>		2	6
<u>Colophospermum mopane</u>			3
<u>Lanea bicolor</u>		1	
<u>Terminalia prunoides</u>			1
<u>Schotia brachypeltata</u>		1	

Table 21. The number of trees large enough to contain a hornbill nest hole counted in the Nwanedzi experimental plots of approximately 125 hectares; an area of typical Acacia nigrescens - Sclerocarya birrea parkland.

Tree species	Number	Percentage of total
<u>Sclerocarya birrea</u>	86	41,5
<u>Acacia nigrescens</u>	62	32,0
<u>Combretum imberbe</u>	36	18,5
<u>Lonchocarpus capassa</u>	4	2,5
<u>Lannea stuhlmanii</u>	3	2,0
<u>Peltophorum africanum</u>	1	1,5
<u>Cassia abbreviata</u>	3	2,0
Total:	195	100,0

Appendix 5.

Use of nest holes examined for more than one season or brood, used by three species of hornbills in the Kruger National Park, during four consecutive breeding seasons. Occupation is indicated by N for T. nasutus, E for T. erythrorhynchus and F for T. flavirostris.

Hole No.	Breeding season			
	1966-67	1967-68	1968-69	1969-70
1	N	not used	not used	
2	N	occupied by bees	not used	
3		N	F	
4		N	N	
5		N then E	N	N
6		N, ♀ cut out for specimen	not used	
7		N	not used	
8		N	F	
9		N	E	
10		N	N	N
11		N then E	N	N
12	E	not found	F	
13	E	not used		
14	E	E, ♀ caused to desert before laying	examined by E but not used	
16	E	E	pair move to hole 91 due to building operations at old hole	
20	E	tree broken by elephants		
21	E	E	tree broken by elephants	
22	E	E	E	E
23	E	occupied by bees	not used	
24	E	not used	E	
25	E	not used	pair in adjacent tree in hole 137	
26	E	E	E, ♀ dead on nest floor, before laying started	
27	E	not used	EE (two broods)	

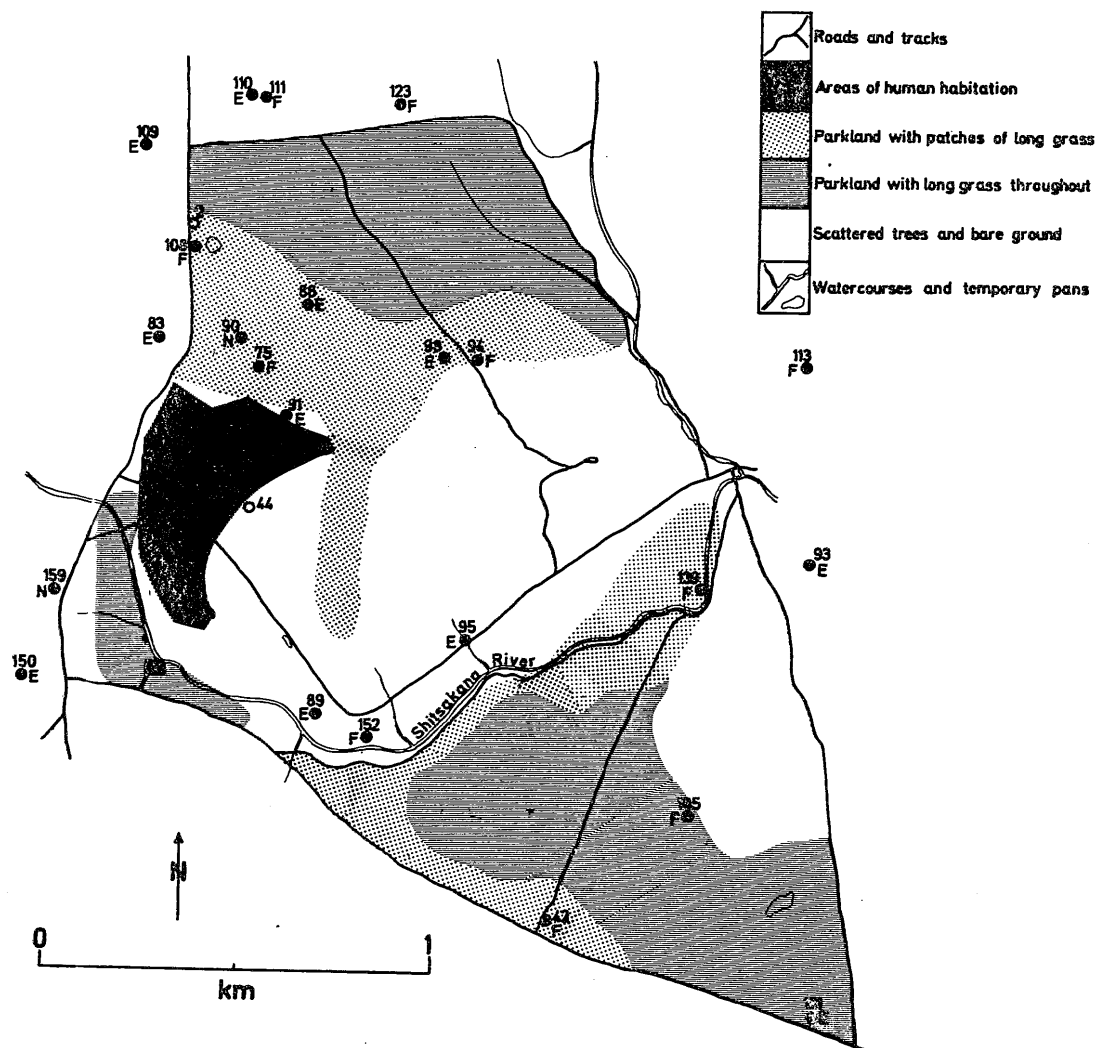
Appendix 5. (Cont.)

Hole No.	Breeding season			
	1966-67	1967-68	1968-69	1969-70
29	E	not used	not used	
30	E	tree broken by elephants		
31	E	not found	E	E
32	E, chopped open to take chicks	not used	F	
33	E	not found	E	
34	E	E, chopped open to take chicks	not used	
35	E	E	E	
36	E	not used	tree broken by elephants	
37		EE(two broods)	E	
38		E	E	E
39		E	E	
41		E	examination wedge fallen out	
42		F then E	F	
43		E	EE(two broods)	
44		E, chicks all die ?due to death of parents	not used	
45		E	E	
46		E	not used	
47	F	F	F	F
48	F	not used		
49	F	inspected by E, but not used		
50	F flooded out	not used		
51	F	not used	not used	
52	F	F	F, ♀ dead on nest floor, before laying started	
55	F	inspected by E, but not used		
57	F	not used	F	

Appendix 5. (Cont.)

hole No.	1966-67	1967-68	1968-69	1969-70
92		mud sealing by F, but not used	F	
95		E	E	
99			F	F
102			F	F
105			F	F
125			N	N
135		used by <u>Glau-</u> <u>cidium perlatum</u>	F	
136			N	F
138			F then F with second brood	F
141			E	E
144			E	E
150			E	E
157			F	F
159			N	N
160			E	E

Figure 33. The Satara breeding area, showing the position of the nest holes, and the main vegetation features of the area. The nests occupied by these hornbill species during the 1968-69 season (solid circle) are marked as N - Tockus nasutus, E - T. erythrorhynchus and F - T. flavirostris. Unoccupied holes are marked with open circles.



**Figure 34.** The extent of nesting territories of three species of hornbill within the Satara study area, indicated by the maximum distances at which hornbills were seen from the nest (radiating lines). Position of territorial conflicts are marked  $\otimes$ . Pairs suspected to be resident in the area, but whose nests were not found, are marked S. A - T. nasutus; B - T. erythrorhynchus; C - T. flavirostris.

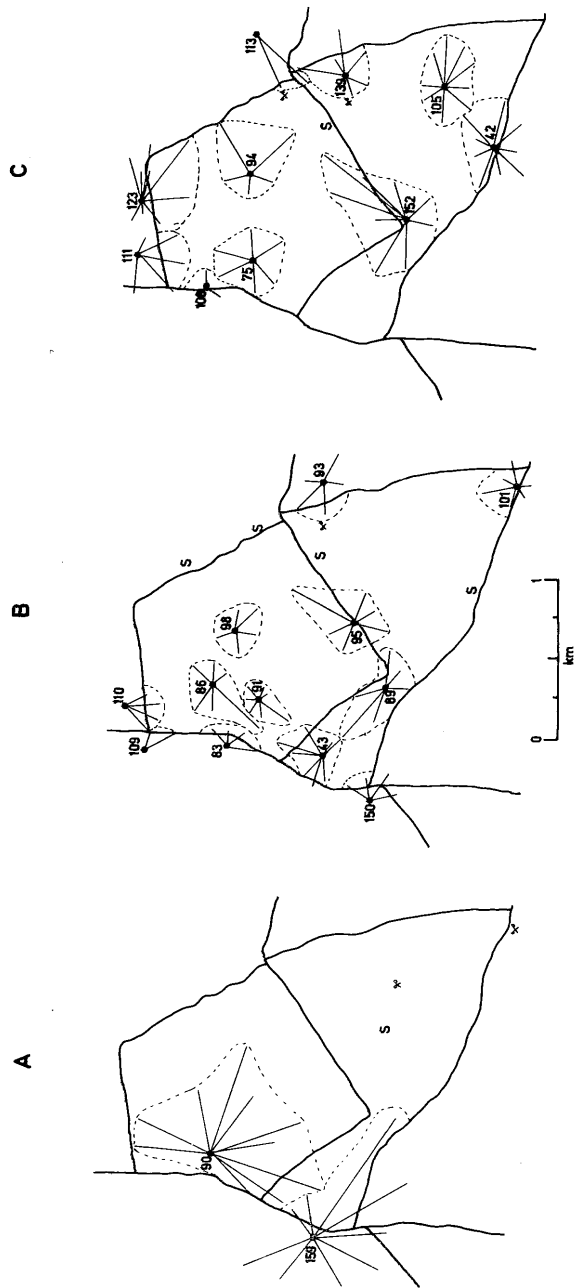


Table 22. Territory sizes for three species of hornbill in the Satara study area of the Kruger National Park.

Hornbill species.					
<u>T. nasutus</u>		<u>T. erythrorhynchus</u>		<u>T. flavirostris</u>	
Nest no.	Territory size in hectares	Nest no.	Territory size in hectares	Nest no.	Territory size in hectares
90	64	86	10	111	14
159	62	98	7	123	22
Average:	<u>63</u>	91	5	75	12
		43	9	94	16
		89	12	152	27
		95	14	139	13
		93	12	105	13
		101	9	42	20
		Average:	<u>10</u>	Average :	<u>17</u>

Table 23. Some distances between simultaneously active nests of different species of Tockus hornbill in the Kruger National Park.

Species involved	Respective hole numbers	Distance apart m
<u>T. nasutus</u> and <u>T. flavirostris</u>	11 and 74	50
<u>T. erythrorhynchus</u> and <u>T. flavirostris</u>	38 and 67	50
	80 and 81	40
	133 and 134	30
	110 and 111	20
	100 and 99	5
	121 and 120	0, both nests in the same tree

Table 24. The time, to the nearest day, from hornbill females entering the nest and the commencement of laying, for three species in the Kruger National Park.

Species	Days elapsed	Number of records
<u>T. nasutus</u>	5	2
	9	1
<u>T. erythrorhynchus</u>	6	2
	6+	2
<u>T. flavirostris</u>	4	1
	5	1
	6	1
	—	
Average:	6	

Table 25.

Observations on the interval, to the nearest day, between laying of the eggs of a clutch, or hatching of chicks of a brood, for three species of hornbill in the Kruger National Park.  
 nh - eggs did not hatch.

Hornbill species	Clutch size	Days to lay the clutch	Laying interval between eggs				Days to hatch a brood	Hatching interval between chicks				
			1 & 2	1 & 3	1 & 4	1 & 5		1 & 2	1 & 3	1 & 4	1 & 5	
<u>I. nasutus</u>	5	6 -10										
	5	7 -10	1	under 5	6	under 11	8	2	3	3	8	
	4	5+										
	4	4+										
	4						5	1	3	5		
<u>I. erythrorhynchus</u>	5	8+										
	4						7	3	5	7		
	4	6 -11	2	4 - 6	under 12							
	4	9+										
	4						6	1	3	6		
	5						6+	1	4	6	nh	
	4	6	1	3	6		6	1	4	6		
<u>I. flavirostris</u>	4	8+										
	4	8 - 9					6+	2	6	nh		
	5	9+										
	4	9+										
	4	9					9	1	6	9		

Table 26.

Comparison of the ratios of egg sizes and the ratio of body weights for three species of hornbill ; all data from the central region of the Kruger National Park.

Hornbill species	Average egg length, mm	Ratio	Average egg width, mm	Ratio	Average ♀ body weight, g	Ratio
<u>T. nasutus</u>	37,0	1,10	36,2	1,09	146,2	1,16
<u>T. erythrorhynchus</u>	33,6	1,00	24,1	1,00	126,4	1,00
<u>T. flavirostris</u>	36,6	1,09	25,5	1,06	167,9	1,33

Table 27. Clutch sizes for three species of hornbill in the Kruger National Park in three consecutive breeding seasons.

Hornbill species	Breeding season			Overall
	1966-67	1967-68	1968-69	
<u>T. nasutus</u>				
Complete clutches				
of: 1 egg				
2 eggs				
3 eggs		1		1
4 eggs		1	3	4
5 eggs		1	3	4
Average:		4,0	4,5	4,3
<u>T. erythrorhynchus</u>				
Complete clutches				
of:				
1 egg				
2 eggs		1		1
3 eggs	2	4	1	7
4 eggs		4	15	19
5 eggs			14	14
Average:	3,0	3,3	4,4	4,1
<u>T. flavirostris</u>				
Complete clutches				
of 1 egg				
2 eggs		1		1
3 eggs		4	8	12
4 eggs		2	14	16
5 eggs		2	3	5
Average:		3,6	3,8	3,7

Table 28. Incubation periods, to the nearest day,  
for three species of hornbill in the Kruger  
National Park.

Species	Incubation period in days	Number of records
<u>T. nasutus</u>	24	2
	25	2
	26	1
<u>T. erythrorhynchus</u>	23	2
	24	2
	25	2
<u>T. flavirostris</u>	24	1
Overall average :	<u>24,3</u>	

Appendix 6. Details for nests of three species of hornbills in the Kruger National Park, of clutch size, number of chicks hatched and number of chicks leaving the nest, where these figures are accurately known.

A. Tockus nasutus

Nest hole number	Season	Clutch size	Number of chicks hatched	Number of chicks to leave nest	Remarks
2	1966-67		3		
3	1967-68	3	3	3	
4	1968-69	5	5		
	1967-68	4	1		
5	1967-68	5	5		
	1968-69	5	5		
6	1967-68		3		
7	1967-68		3		
8	1967-68		3		
10	1967-68		3		
	1968-69	4	3	3	
11	1968-69	4	3	3	
19	1967-68		4		
60	1968-69	5	4	4	
90	1968-69	4	4	4	
103	1968-69		3		
117	1968-69		4		
125	1968-69		3	0	Tree growth closed nest entrance prematurely.
130	1968-69		3	0	Tree growth closed nest entrance prematurely
	Average :	4,3	3,5	2,4	(or 3,4 discounting total failures)

Appendix 6. (Cont.)

B <u>Tockus erythrorhynchus</u>					
Nest hole number	Season	Clutch size	Number of chicks hatched	Number of chicks to leave nest	Remarks
5	1967-68	3			
9	1968-69	5	4		One egg lost during incubation period
11	1967-68		3		
13	1966-67		3		
16	1967-68	4	4	2	Two chicks die of starvation.
21	1967-68	4			
22	1968-69	4			
24	1966-67	3	3		
27	1966-67	3	3		
	1967-68		4		
	1968-69		3		
31	1966-67		3		
32	1966-67	3	2	2	One egg failed to hatch
34	1967-68	3	3		
35	1968-69	4	3	0	One egg lost during incubation, chicks all dead, due to death of parents?
36	1966-67	4			
38	1967-68	2	2	2	
	1968-69	5	5		
39	1967-68	3			
	1968-69	4			
42	1967-68	4	4	2	Two chicks die of starvation.
43	1968-69	5			
44	1967-68		4	0	Chicks all dead, due to death of parents?

Appendix 6. (Cont.)

Nest hole number	Season	Clutch size	Number of chicks hatched	Number of chicks to leave nest	Remarks
78	1968-69	5			
79	1968-69	4	4		
		3	1		Second brood. One egg in nest dried up.
80	1968-69	4			
82	1968-69	4			
85	1968-69	5			
86	1968-69	4			
88	1968-69	5	5	0	Rotting chicks on nest floor, flooded out.
89	1968-69	4	3		One egg broken by observer.
91	1968-69	4			
93	1968-69	4	4		
95	1968-69	5	4		One egg failed to hatch.
98	1968-69	5			
100	1968-69	4	4	4	
101	1968-69	5			
110	1968-69	5			
115	1968-69	5			
116	1968-69	5			
118	1968-69		2		
121	1968-69	4			
122	1968-69	4			
124	1968-69	4			
127	1968-69	5			
132	1968-69	4	4		
137	1968-69	4			
144	1968-69		2		
151	1968-69		4		
153	1968-69		4		
160	1968-69		2		
166	1968-69		4		
	Average :	4,1	3,3	1,5	(or 2,4 discounting total failures)

Appendix 6. (Cont.)

C. <u>Tockus flavirostris</u>					
Nest hole number	Season	Clutch size	Number of chicks hatched	Number of chicks to leave nest	Remarks
3	1968-69	4	4		
8	1968-68	4	3	0	Nest broken open by elephant and then preyed on.
32	1968-69		3		
42	1967-68	5	5	3	Two chicks die of starvation;
	1968-69	4	2	2	Two eggs lost during incubation.
47	1967-68	3	2		
	1968-69	4	3		One egg lost during incubation.
53	1966-67		3	2	Dead chick on nest floor, due to starvation?
56	1966-67		2		
57	1966-67		3		
	1968-69		3		
58	1967-68	3	2	2	One egg failed to hatch.
60	1967-68	4			
61	1967-68	2	2		
	1968-69	4			
62	1967-68	3			
	1968-69	3	3		
63	1967-68	3			
64	1967-68		2		
65	1967-68	4			At least one egg failed to hatch.
	1968-69	4			
66	1967-68	5			
67	1967-68		3		
	1968-69	5	3		At least one egg infertile;
68	1968-69	4	3		
73	1968-69		3		
74	1968-69	5	1	1	4 eggs with dead embryos.
75	1968-69	4	4	3	

Appendix 6. (Cont.)

Nest hole number	Season	Clutch size	Number of chicks hatched	Number of chicks to leave nest	Remarks
76	1968-69		4		
77	1968-69	4	4	0	One emaciated chick in nest with rotting remains of rest.
81	1968-69	3	3		
84	1968-69		4		
87	1968-69	3	0		Hole flooded.
92	1968-69	4			
94	1968-69	5			Hole flooded, due to work of observer.
99	1968-69	3	2		
102	1968-69	3			
104	1968-69	3	3		
105	1968-69		4		
106	1968-69		4		
108	1968-69	4	1	1	3 eggs failed to hatch.
111	1968-69	4	3		
112	1968-69	4			
113	1968-69		4		
119	1968-69	4			
120	1968-69	3			
134	1968-69		4		
135	1968-69		4		
138	1968-69	3			
	Average :	3,5	3,0	1,4	(or 2,0 discounting total failures).

Table 29. Hatching success for three species of hornbill in the Kruger National Park.

Hornbill species	No. of eggs laid	No. of eggs hatched	Percentage hatched	Average size of clutch	Average size of newly hatched brood	Average % hatched
<u>T. nasutus</u>	39	33	85	4,3	3,5	81
<u>T. erythrorhynchus</u>	76	62	82	4,1	3,3	80
<u>T. flavirostris</u>	72	53	74	3,7	3,0	81

Table 30. Time, to the nearest day, of the females' emergence after the hatching of the first egg of a clutch, and the youngest chick recorded left in a nest, for three species of hornbill in the Kruger National Park.

Hornbill species	Records of days from hatching of first egg to emergence of female.	Age, in days, of youngest chick left in a nest.
<u>T. nasutus</u>	19 21 24	13
<u>T. erythrorhynchus</u>	20 23	14
<u>T. flavirostris</u>	20 20-22 21	20
	<hr/>	<hr/>
Overall average:	21,1	16

Table 31.

The age of chicks when they leave the nest for three species of hornbill, and their position within the brood. ds - died of starvation before leaving.

Hornbill species	Age on leaving nest in days, and position in brood.				
	1st chick (eldest)	2nd chick	3rd chick	4th chick	5th chick (youngest)
<u>T. nasutus</u>	43	45	44	47	48
			43		
	45	44	47	49	
<u>T. erythrorhynchus</u>	45	48	ds	ds	
	45	50	ds	ds	
	44	49			
	39	41	44	44	
<u>T. flavirostris</u>	45				
	42				
	45	45			
		42			
	47				
	47				
Overall average	44,3	46,0	45,2	46,7	48

Appendix 7. The development of chicks of three species of Tockus hornbill.

INTRODUCTION: The development of plumage and colouration of three chicks of I. nasutus, I. erythrorhynchus and I. flavirostris is described. Development of Tockus chicks has been described for a hand-reared I. flavirostris chick (Prozesky 1965), and for a wild I. monteiri chick (Kemp and Kemp 1972; Section 5).

The growth curves for wing, tail, ulna, bill and tarsus are given in Section 7. They compare exactly with the curves for I. monteiri (Section 5). So similar is the development of the chicks that a general description is given, with specific variations given only where necessary. The various parts of the body are considered separately, but the colours of the plumage are not described because they are covered by Sanft (1960). Finally, photographs of stages in the growth of an individual I. erythrorhynchus chick are appended.

THE DAY-OLD CHICK: At hatching, chicks are naked, pink all over but for a white tip to the upper mandible, a grey colour in the area of the eyes and at the claw buds. The eyes are closed. The upper mandible is about 2 mm shorter than the lower. Dried up egg membranes are still attached to the belly.

PLUMAGE DEVELOPMENT; Rectrices - In the second day the rectrices are visible through the skin as a dark area, and tufts where they will appear develop by the third day. The quills appear on the fourth day, and the feathers begin to break out of the quills on about the 15th day after hatching. Rectrix growth is completed about two weeks after the chick has left the nest, when about 60 days old.

Remiges - The same growth sequence as the rectrices, the primaries and secondaries

Appendix 7. (Cont.)

emerging at the same time although the inner secondaries emerge about a day before the other remiges.

Wing coverts - Show first over the elbow on the second day, emerge on the sixth day and the feathers begin to break out of the quills on the 13th day after hatching. Emergence of the feathers from the quills is delayed in all Coraciiformes chicks, giving them a spiky appearance for a time. This spiky stage ("porcupine stage" of Prozesky 1965) lasts from about the tenth to the 20th day after hatching in Tockus hornbill chicks. The wing coverts cover the wings by the 22nd day, are about three quarters grown by the 25th day, and completely grown when leaving the nest on the 45th day after hatching.

Breast and thighs - Are considered together due to similar rates of development. They show under the skin on the second day, the quills emerging on the fourth day and beginning to break open on the ninth day. The breast, abdomen and thighs are covered by feathers by the 20th day, being the first area to be covered by feathers.

Back - Tail coverts show under the skin by the second day, and on the back by the fourth day. The back feathers develop out of phase, those at the posterior being about two days more advanced than those at the anterior. Quills emerge on the lower back and tail coverts on the sixth day and the feathers begin to break out on the 12th day. The feathers are about half out on the lower back by the 22nd day, cover the lower back by the 30th day, and are completely grown by the time of leaving the nest.

Neck - The feathers on the tract down the throat and front of neck are the most retarded of the feather areas. The quills are visible under the skin by the fourth day, emerge on the seventh day, and the feathers begin to break out on the 11th day. However, the feathers only completely cover the front

Appendix 7. (Cont.)

of the neck by about the 35th day after hatching. The feathers at the shoulders and very top of the back are in phase with the neck feathers.

Head - The quills are visible under the skin by the second day, especially at the lores which is more advanced than the rest of the head. The quills emerge by the fourth day and the feathers begin to break out on the 18th day. The feathers cover the head by the 25th day, but the quills are visible on the sides of the head until at least the 32nd day. This is due to the slow development of the ear coverts. The eyelashes are visible under the skin by the ninth day after hatching, emerge on the 11th day, but are not quite completely grown even by the time of leaving the nest.

ORGAN DEVELOPMENT: Air sac - At the end of the first day the air sac is visible as two bodies over the scapulars. By the second day these have joined to form a single sac which increases in extent until the 15th day. The air sac development is about a day later for I. nasutus. By the fourth day the air sac extends down the sides to the ribs and down the back to the anterior end of the pelvis. On the fifth day extensions begin along the top of the wing and neck, and as far back as the acetabulum on the pelvis. By the fifth day the air sac extends around the lower jaw to the base of the bill. By the seventh day the sac extends over the shoulders and by the eighth day joins at the point of the sternum. By the ninth day it has reached the base of the tail. By the 15th day, the air sac covers the whole back, back of neck and bottom of lower jaw, top of humerus, ribs and furcula and part of upper sternum.

## Appendix 7 (cont.)

Legs and claws - The claw buds are evident at hatching. They begin to grow immediately, and to darken from light grey to black, being fully developed by the 20th day. The legs are pink at hatching, a pale grey by four days, purplish by the ninth day, dark grey by the 12th day, and black by the 18th day. The "knee" has a calloused area, evident by the second day after hatching, but no special tubercles or pads as are present in chicks of several Piciformes families.

Bill - The bill is pinkish in all species at hatching, but develops specific colours thereafter. In I. erythrorhynchus the bill deepens to a yellow-orange colour by about the 20th day, at which time a black line develops along the bottom of the lower mandible. The black line intensifies, as does the orange colour, until emergence from the nest. In I. nasutus the bill becomes black and develops a pale cream line along the middle of the upper mandible. In I. flavirostris the bill becomes a dusky black-brown, somewhat mottled, until about two weeks after emergence from the nest when a yellow similar to the adults appears. The bill has not attained the adult size by emergence, and may grow for at least a year, by which time the colours of the bill are the same as the adult. Possibly the birds are mature and breed within a year i.e. by the following season after they were hatched.

At hatching the upper mandible is several millimeters shorter than the lower, but they have grown to equal length by the fifth day. The bill is also straight at hatching, and the curve only becomes apparent by the eighth day. The white egg tooth on the tip of the upper mandible has disappeared by the 28th day.

Appendix 7. (cont.)

Eyes - The eyes are closed at hatching, and the future opening is only evident as a line on the skin. The ridges of the eyelids are obvious by the fourth day and slowly develop and move apart. The eyes can only be considered truly open and functional by about the 12th day after hatching. The eyes, as for all Tockus hornbill chicks, where it is documented, are a light blue-grey colour. They develop into the adult colour within about a year of leaving the nest.

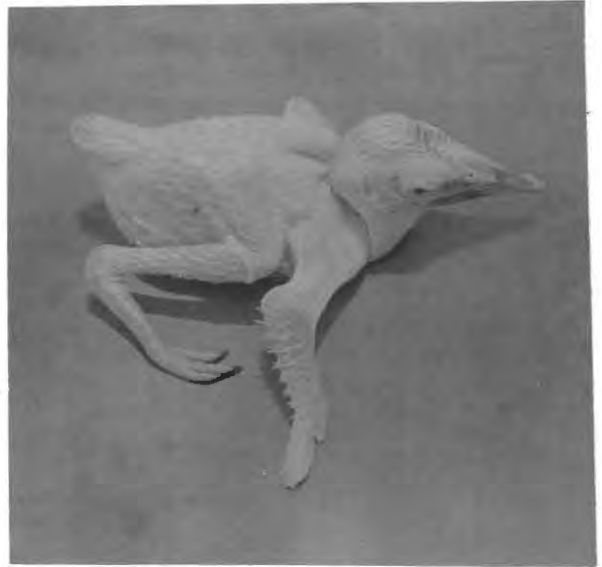
N.B. The duration of the stages of development are averages from several broods and all three species and must not be taken as exact.

Appendix 7 .  
cont.

Stages in the development of a Tockus erythrorhynchus chick. Age is given in days, and the tarsus measurement is given to indicate the size of the chick.



1 day old; Tarsus 10,7 mm



5 days old; Tarsus 13,3 mm



9 days old; Tarsus 20,2 mm



14 days old; Tarsus 30,7 mm

Appendix 7.

Cont.



18 days old; Tarsus 33,1 mm



22 days old; Tarsus 36,0 mm



26 days old; Tarsus 38,0 mm



30 days old; Tarsus 38,7 mm

Appendix 7.  
Cont.



34 days old; Tarsus 39,5 mm



38 days old; Tarsus 39,5 mm



42 days old; Tarsus 39,5 mm

Figure 35. Growth curves from daily measurement of eldest chicks of three *Tockus* species. A. - *T. nasutus* from nest 90 ; B. - *T. erythrorhynchus* from nest 100 and C. - *T. flavirostris* from nest 42. All were in the nest at approximately the same time during the 1968-69 breeding season, and the nests are in close proximity to each other.

A

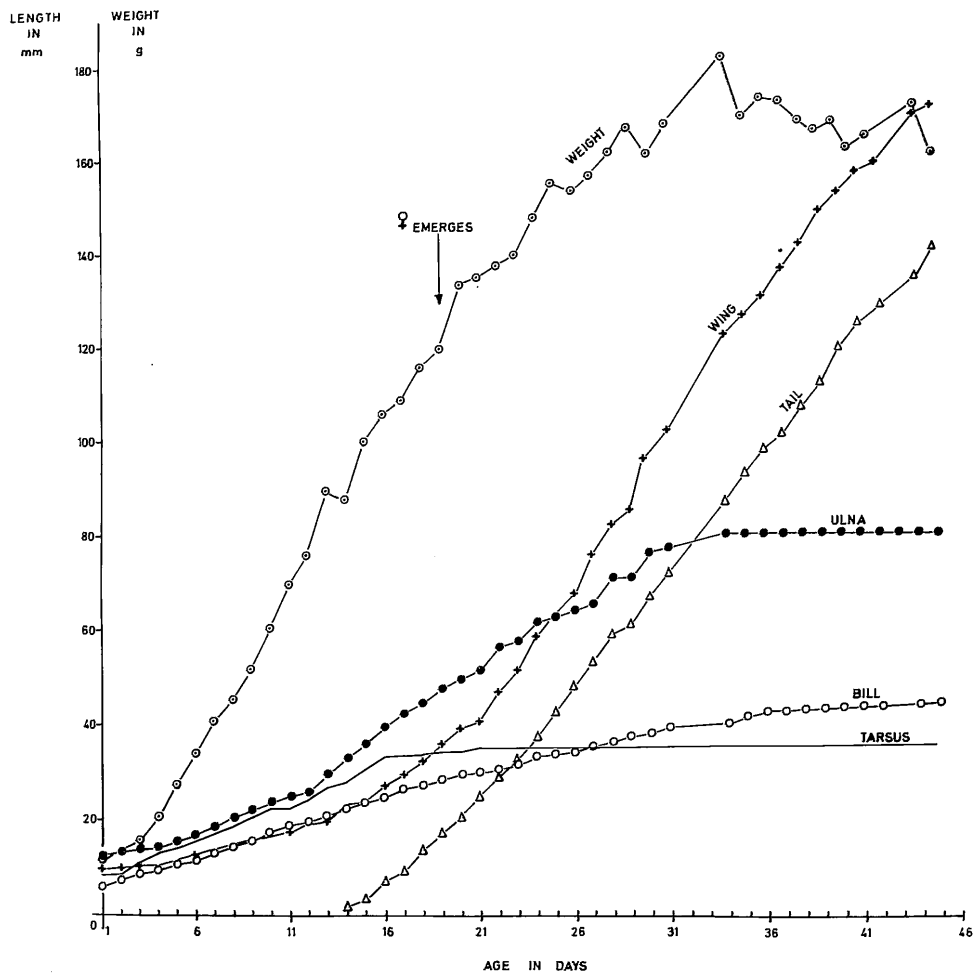


Figure 35. (Cont.)

B

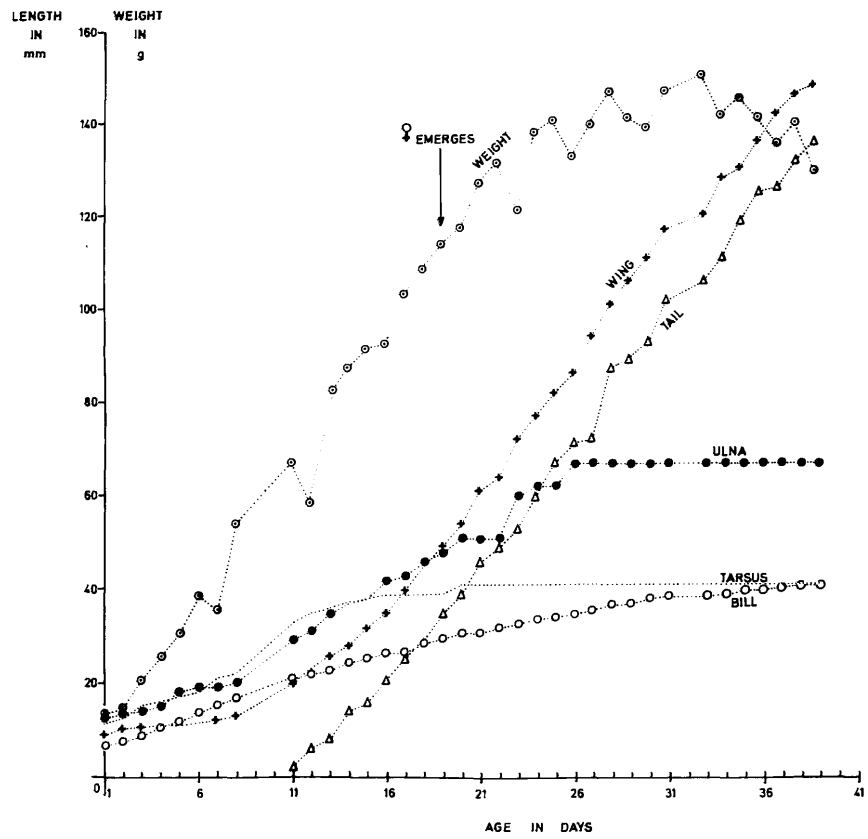


Figure 35. (Cont.)

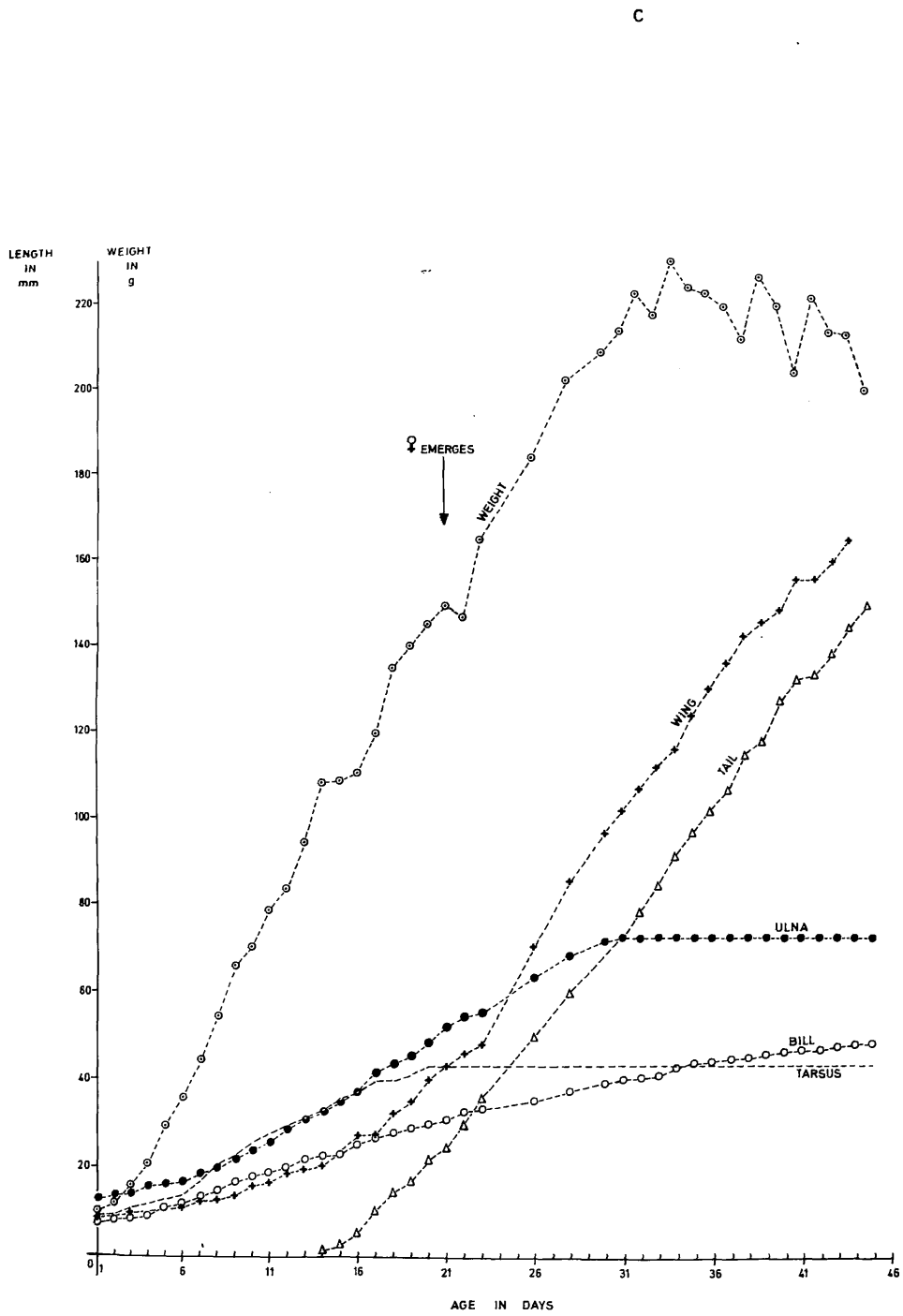


Figure 36. Weight curves for all members of broods of three *Tockus* hornbill nesting within 1,5 km of one another during the 1968-69 breeding season. The daily rainfall and maximum temperature are also plotted for the nesting period. N chicks 1 - 4, *T. nasutus* nest 90; E chicks 1 - 4 *T. erythrorhynchus* nest 100; F chicks 1 and 2, *T. flavirostris* nest 42; F chick 1b, *T. flavirostris* nest 108.

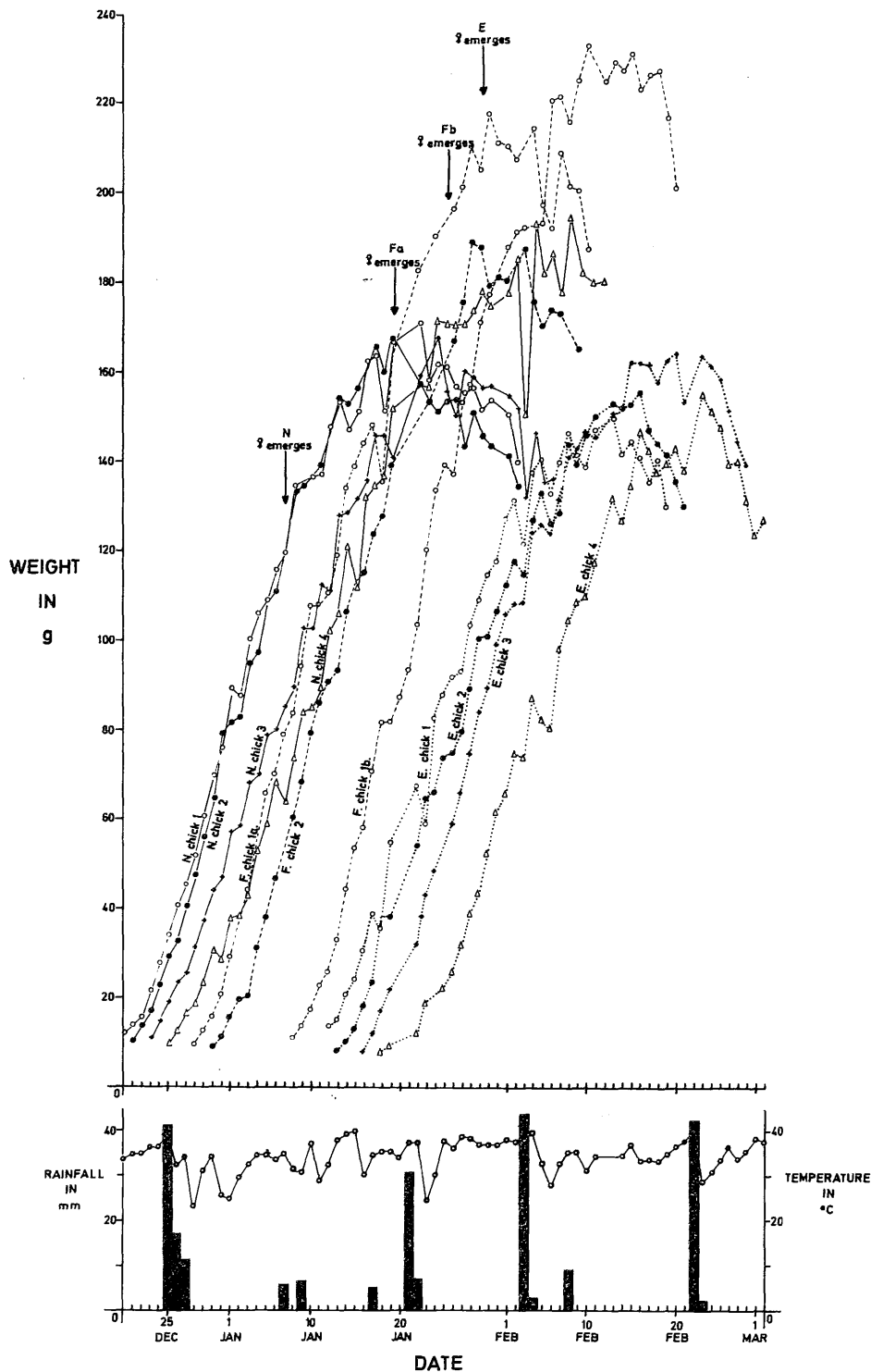


Figure 37. Weight curves for all chicks in two broods of Lockus erythrorhynchus, in nests 42 (upper) and 16 (lower) started late in the 1967-68 breeding season. The daily rainfall and maximum temperature are also plotted for the nestling period.

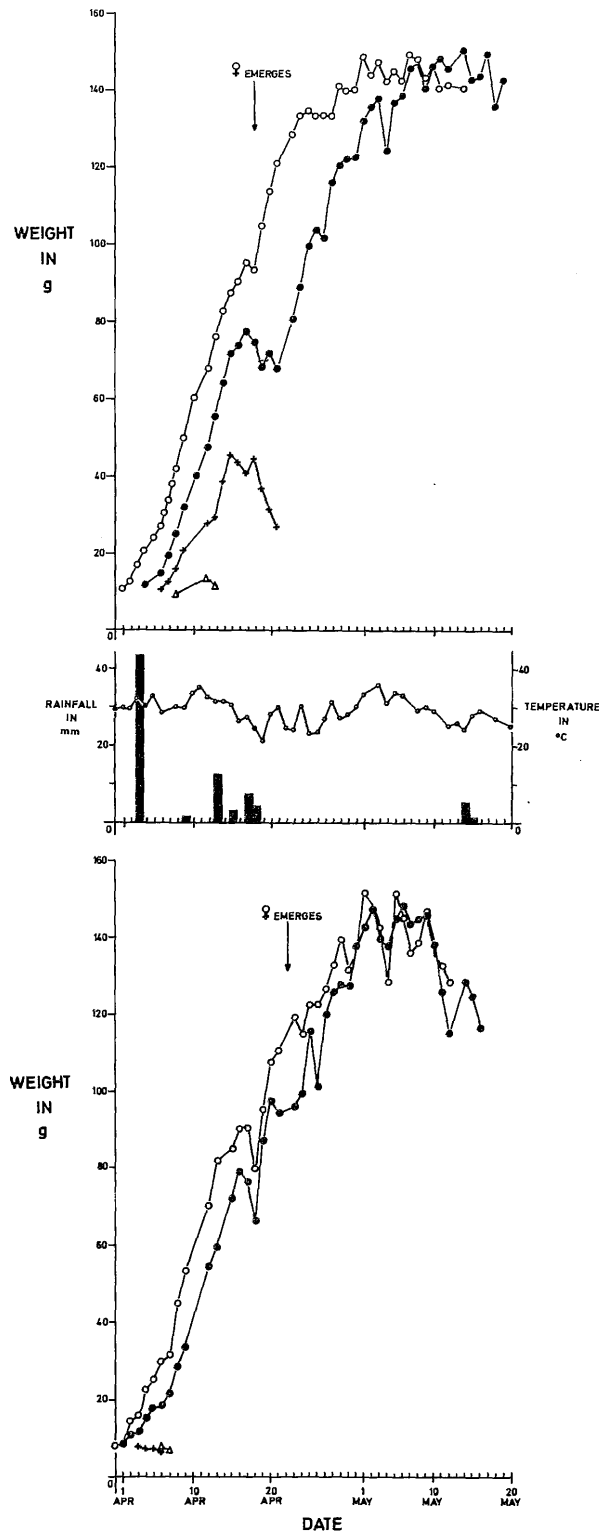


Table 32. Feeding rates recorded at nests of three species of hornbill in the Kruger National Park.

Hornbill species and nest number	Contents of nest	Stage of nest	Duration of watch Hrs/Mins	Feeds	Feeding rate feeds/hr
<u>T. nasutus</u>	10 ♀ 3 eggs	3 days after laying started	8.15	44	5,3
	8 ♂ 4 chicks	Eldest chick 38 days old	11.15	14 ♂ 17 ♀ <hr/> 31 ♀	1,2 1,5 <hr/> 2,7
<u>T. erythro-rhynchus</u>	♀ 4 eggs	10 days after laying started	5,35	24	4,3
	43 ♀ 4 chicks one egg	Eldest chick 5 days old	5,45	488	8,3
	♂ 4 chicks	Eldest chick 9 days old	6,00	70	11,7
	♀ 4 chicks	Eldest chick 16 days old	6.00	65	10,8
	4 chicks	Eldest chick 23 days old	6.00	91 ♂ 6 ♀ <hr/> 97	15,2 1,0 <hr/> 16,2
	4 chicks	Eldest chick 27 days old	6.00	61 ♂ 4 ♀ <hr/> 65	10,2 0,7 <hr/> 10,9
	4 chicks	Eldest chick 36 days old	6.00	94 ♂ 6 ♀ <hr/> 100	15,7 1,0 <hr/> 16,7
	86 ♀	Laying not started (24 extra visits made by ♂ with lining)	5,45	46	8,0
	89 ♀	Laying not started	6.00	28	4,7
	93 ♀ 4 eggs	17 days after laying started (♂ defending mainly)	6.00	4	0,7 territory
101 ♀ 5 eggs	On point of hatching	6.00	15	2,5	
95 ♀ 4 chicks	Eldest chick 15 days old	6.00	31	5,2	
38	3 chicks	Eldest chick 25 days old	4.55	22 ♂ 10 ♀ <hr/> 32	4,5 2,0 <hr/> 6,5

Table 32 (Cont.).

Hornbill species and nest number	Contents of nest	Stage of nest	Duration of watch Hrs/Mins	Feeds	Feeding rate feeds/hr
<u>T. flavi-rostris</u>					
75	♀	2 days before laying starts	6.11	17	2,8
42	♀ 2 eggs 3 chicks	Eldest chick 3 days old	2.06	8	3,8
	♀ 5 chicks	Eldest chick 8 days old	9.10	52	5,7
67	♀ 3 chicks	Eldest chick 12 days old	10.05	94	9,3
67	2 chicks	Eldest chick 25 days old	9.48	34 ♂ 35 ♀	3,5 3,6
				69	7,1
105	♀ 4 chicks	Eldest chick 13 days old	5.40	64	11,3
123	♀ at least 2 chicks	Eldest chick 17 days old	6.00	29	4,8
152	4 chicks	Eldest chick 40 days old	6.00	14 ♀&♂	2,3

Table 33. Factors causing total loss of all chicks or eggs in nests of three species of hornbill in the Kruger National Park.

Details	Hornbill species.		
	<u>I. nasutus</u>	<u>I. erythrorhynchus</u>	<u>I. flavirostris</u>
Number of nests examined	22	73	54
Percentage where adults were probably preyed on	0	5,5	3,7
Percentage where nest contents were preyed on	0	0	0,9
Percentage where tree growth closed off the entrance hole	9,1	1,4	0
Percentage flooded	0	2,7	3,7
Percentage that reared some chicks to fledging	90,9	90,4	91,7

Table 34.

Nestling success for hornbills in the Kruger National Park.

Hornbill species	Eggs laid	Chicks to leave the nest	% leaving of eggs laid	Eggs hatched	Chicks to leave the nest	% leaving of eggs hatched	Reasons for chick loss
<u>T. nasutus</u>	16	13	81	19	13	68	Six chicks lost in two nests by tree closure
<u>T. erythrorhynchus</u>	26	12	46	28	12	43	Four chicks died of starvation, seven due to death of parents, five in one flooded nest
<u>T. flavirostris</u>	29	10	34	25	14	56	Three chicks were predated four died due to death of parents, two starved, two unknown.

Table 35. Nestling success of hornbill nests in the Kruger National Park, estimated overall, and then excluding those nests where all chicks were lost.

Hornbill species	Treatment	Average size of clutch	Average Nos. hatched	Average Nos. leaving the nest	Average percent of chicks leaving <sup>of</sup> :	
					Eggs laid	Chicks hatched
<u>T. nasutus</u>	Overall	4,3	3,5	2,4	56	69
	Less total losses	4,3	3,5	3,4	79	97
<u>T. erythrorhynchus</u>	Overall	4,1	3,3	1,5	37	45
	Less total losses	4,1	3,3	2,4	59	73
<u>T. flavirostris</u>	Overall	3,7	3,0	1,4	38	47
	Less total losses	3,7	3,0	2,0	54	67

Table 36. Predation on three hornbill species in the central Kruger National Park recorded from 1966-1969.

Predator	<u>T. nasutus</u>	<u>T. erythrorhynchus</u>	<u>T. flavirostris</u>	<u>T. erythrorhynchus</u> or <u>T. flavirostris</u>	Overall
<u>Aquila fasciata</u>	0	5	7	31	43
<u>Aquila rapax</u>	0	3	3	8	14
<u>Aquila wahlbergi</u>	1	2	0	5	8
<u>Terathopus ecaudatus</u>	0	4	6	23	33
<u>Polemaetus bellicosus</u>	0	2	1	1	4
<u>Bubo lacteus</u>	0	3	0	20	23
<u>Falco biarmicus</u>	0	0	1♀	0	1
Unidentified small cat or mongoose.	0	0	1	0	1
	—	—	—	—	
Total :	1	19	18	81	

Table 37. The percentage of examinations of nests of six large raptors when hornbill prey was found in the nest, out of visits when any prey was found, for three consecutive years in the central region of the Kruger National Park.

Raptor species	Year	Number of visits when prey recorded.	Percentage of visits when hornbills among prey in nest				Overall
			<u>I. nasutus</u>	<u>I. erythro-</u> <u>rhynchus</u>	<u>I. flavirostris</u>	<u>I. erythro-</u> <u>rhynchus</u>	
<u>Aquila fasciata</u>	1967	39		8	10	21	39
	1968	34				26	26
	1969	28		7	11	50	68
	Average overall:	101		5	7	31	42
<u>Aquila rapax</u>	1967	28		4	4	21	29
	1968	15		7		7	14
	1969	19		5	11	5	21
	Average overall:	62		5	5	13	23
<u>Aquila wahlbergi</u>	1967	10		10		10	20
	1968	69	1	1		4	6
	1969	9		11		11	11
	Average overall	88	1	2		6	9
<u>Terathopius ecaudatus</u>	1967	34		3		3	6
	1968	35		6	9	37	52
	1969	41		2	7	22	31
	Average overall	110		4	5	21	30
<u>Polemaetus bellicosus</u>	1967	8			13		13
	1968	9					
	1969	10				10	10
	Average overall:	27			4	4	8
<u>Bubo lacteus</u>	1967	23		9		78	87
	1968	2					
	1969	20		5		10	15
	Average overall:	45		7		44	51

Figure 38. My assistant (in tree) and wife (on vehicle) pointing to the position of two simultaneously active hornbill nests, of T. flavirostris and T. erythrorhynchus respectively.



Table 38. The extremes of the duration of various phases of the nesting cycle of three species of Tockus hornbill in the Kruger National Park.

Nesting phase.	Duration in days.		
	Maximum	Average	Minimum
Pre-laying period	9	6	4
Laying period	10	8	6
Incubation period	26	25	23
Nestling period	50	45	39
	<hr/>	<hr/>	<hr/>
Total	95	84	72

Figure 39. A brood of four I. nasutus chicks taken from the nest for examination, to show the gradation in size of the members, typical of Tockus hornbills.

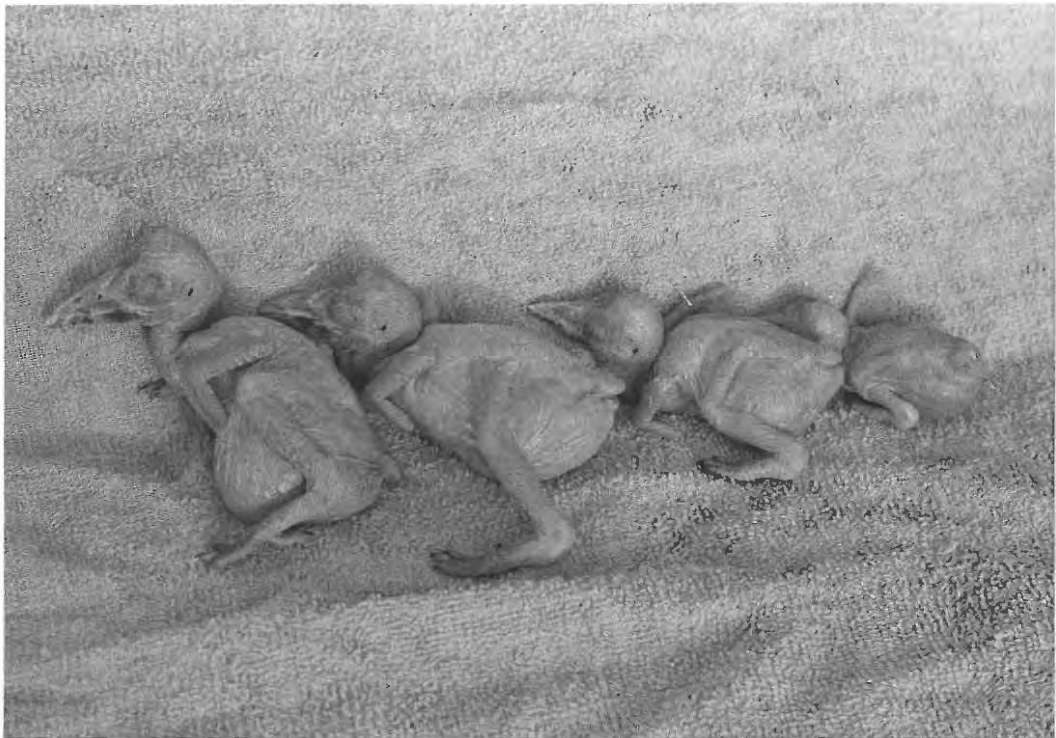


Figure 40. Site of the only recorded predation of a Tockus hornbill nest, where a branch containing the nest (arrowed) was bent and split by an elephant, rendering it unsealed.



Table 39.

The percentage of specimens collected each month with any active moult in progress, for three species of hornbill in the Kruger National Park.

Month	Hornbill species.					
	<u>T. nasutus</u>		<u>T. erythrorhynchus</u>		<u>T. flavirostris</u>	
	No. in Sample	%moulting	No. in Sample	%moulting	No. in Sample	%moulting
June 1967	3	100	10	100	10	100
July						
August						
September	7	14	10	10	10	0
October	5	40	10	60	10	10
November	4	100	10	40	10	50
December	2	100	10	100	10	100
January 1968	5	80	10	90	10	90
February	5	100	10	90	10	90
March	3	100	10	100	10	90
April	3	100	10	80	10	90
May	2	100	10	100	10	100
June			10	0	10	20
July			10	10	10	10
August			10	10	10	0
September	4	25	10	20	10	10
October 1968	7	0	10	20	10	0

Table 40.

Tail moult index (average number of rectrices growing in per specimen for each month) for three species of hornbill in the Kruger National Park.

Month	Tail moult index for each hornbill species		
	<u>I. nasutus</u>	<u>I. erythrorhynchus</u>	<u>I. flavirostris</u>
June 1967	0,0	0,0	0,3
July			
August			
September	0,1	0,1	0,0
October	0,0	0,0	0,0
November	0,0	0,2	0,3
December	2,0	1,1	3,4
January 1968	2,8	1,5	4,0
February	2,2	1,7	2,8
March	1,3	3,6	1,6
April	0,0	1,2	0,8
May	0,0	0,6	0,0
June		0,0	0,0
July		0,1	0,2
August		0,1	0,0
September	0,3	0,1	0,1
October 1968	0,0	0,0	0,0

Table 41.

Wing moult index (average number of remiges growing in per specimen each month) for three species of hornbill in the Kruger National Park.

Month	Wing moult index for each hornbill species		
	<u>T. nasutus</u>	<u>T. erythrorhynchus</u>	<u>T. flavirostris</u>
June 1967	0,7	1,5	1,1
July			
August			
September	0,0	0,0	0,0
October	0,0	0,2	0,0
November	1,8	0,3	0,8
December	7,0	2,1	4,7
January 1968	2,6	2,1	6,2
February	4,8	3,8	5,2
March	2,3	9,4	6,4
April	3,0	4,2	5,7
May	2,0	4,8	2,9
June		0,1	0,0
July		0,0	0,0
August		0,0	0,0
September	0,0	0,0	0,0
October 1968	0,0	0,3	0,0

Table 42.

Index of the body moult each month for samples of hornbills collected in the Kruger National Park. Areas of body moult (head, neck, back, flanks, breast) were scored 1 - 3 according to degree of moult. Average score for the sample gives the body moult index.

Month	Body moult index for each hornbill species.		
	<u>I. nasutus</u>	<u>I. erythrorhynchus</u>	<u>I. flavirostris</u>
June 1967	2,0	1,5	1,2
July			
August			
September	0,0	0,0	0,0
October	0,4	0,7	0,2
November	1,8	0,5	0,8
December	5,0	2,6	2,3
January 1968	2,0	1,4	3,2
February	4,8	1,0	4,8
March	7,3	5,9	5,9
April	7,7	4,4	5,3
May	5,0	4,8	4,0
June		0,0	0,2
July		0,0	0,0
August		0,0	0,0
September	0,0	0,0	0,0
October 1968	0,0	0,0	0,0

Figure 41. Tockus flavirostris female taken from nest 3 for examination when found with one egg, all rectrices moulted, but none of the remiges.



Figure 42. Tockus flavirostris female taken out of nest 58 for examination, five days after completing laying of a clutch of three eggs. The even growth of the new primary and tail feathers is evident.



Figure 43. Tockus flavirostris female from nest 58, removed for examination 10 days after completing the clutch. The simultaneous moult of the rectrices and remiges, shown by their growing in evenly, is evident.



Figure 44.  
a seed.

A female Tockus erythrorhynchus regurgitating



Figure 45. A male Tockus flavirostris scratching indirectly.



Figure 46. A female Tockus erythrorhynchus rubbing the head over the scapulars and upper wing coverts during oiling preening.



Figure 47. Characteristic position for preening the primaries, shown by a female Tockus erythrorhynchus.



Figure 48. An immature Tockus flavirostris dustbathing, the head lowered, and the wings scooping dust over the back.



Figure 49. Sunbathing postures. Upper: the sitting posture used by I. erythrorhynchus, and Lower : the all-out sprawl of an immature I. nasutus.



Figure 50. Extreme heat-loss posture of an immature Tockus nasutus, panting, with the feathers flattened and the wings held away from the body.



Figure 51. Territorial displays of Tockus hornbills in diagrammatic form. A - T. bradfieldi type of display; B - T. nasutus type of display; C - T. hemprichii type of display; D - T. monteiri type of display; E - T. flavirostris type of display.

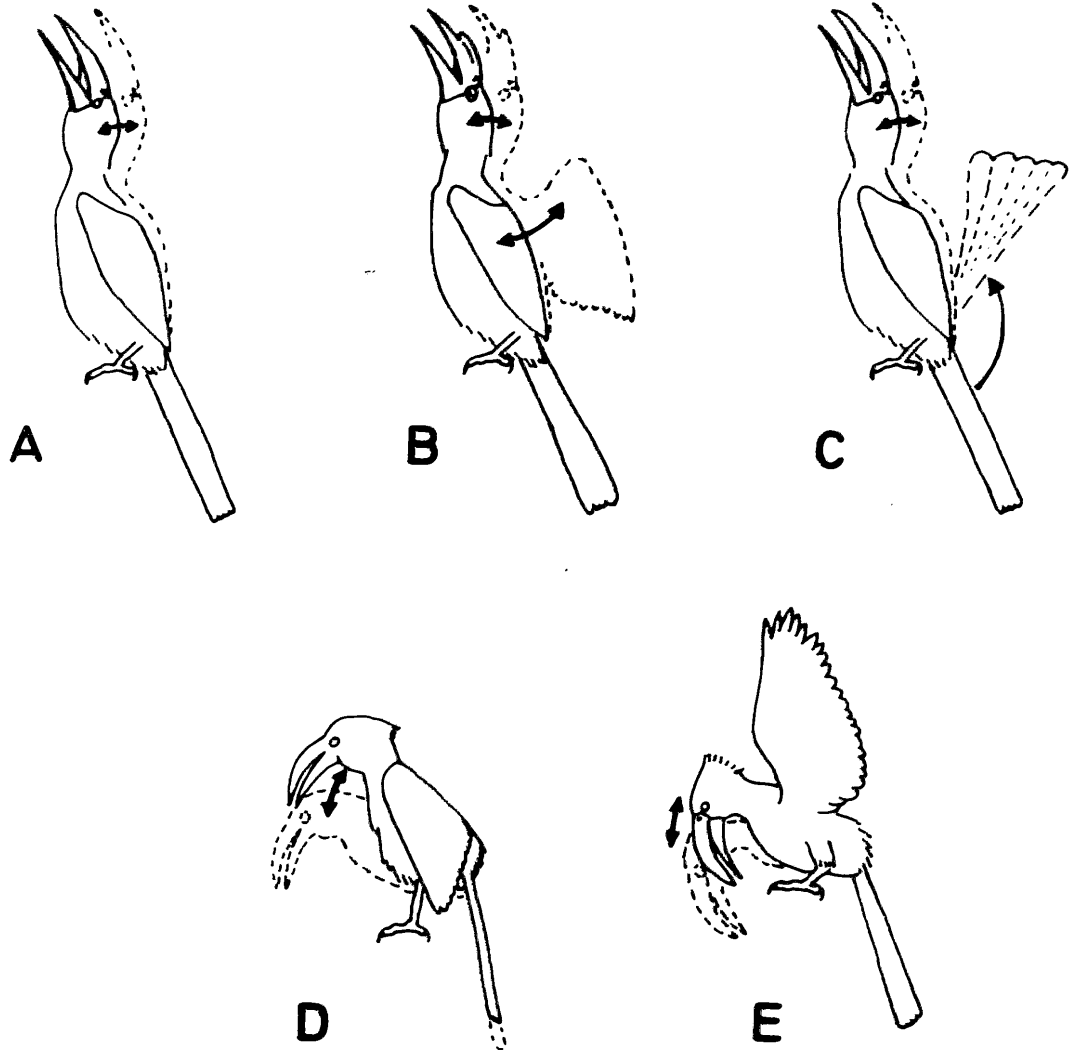


Figure 52, Threat position peculiar to chicks, also with fear elements, shown here by a Tockus nasutus chick.



Figure 53. Inquisitive posture of a tame immature Tockus  
nasutus.



Figure 54. A male Tockus flavirostris clings at the nest hole, bracing on the tail, while the female waits with mud to continue sealing.



Figure 55. A female Tockus flavirostris bringing a lump of mud for sealing up the nest hole.



Figure 56. Squatting position of Tockus flavirostris chick as in the nest, resting on the tarsometatarsus, and with the tail sticking vertically upwards.



Abdomen colour	Colour of bill	Colour of circum-orbital skin	Colour of gular skin	Eye colour
White	Cream with black and maroon tip	Dark blue to black	♂ dark blue, ♀ orange to yellowish	Brown
White	Red	Dark brown to black	♂ black, ♀ yellow to greenish (blue-green Ranger 1949)	Yellow
Whitish	Dark red and black	Black	♂ black, ♀ pale green	Dark brown
White	Orange	Black	♂ grey, ♀ pale blue green to yellow-green	Yellow
Whitish	Black	Blackish	Flesh coloured to bluish	Dark red brown
Whitish	Yellowish-white	?	?	Red-brown
Whitish	♂ black with white stripes, ♀ maroon and cream <sup>†</sup>	Blackish	♂ dark grey, ♀ light green	Red-brown
Very pale grey	Cream	Black	?	Red-brown
Whitish	Black with cream tip	?	?	Red-brown
Whitish	Red and black	Dusky flesh	Dusky flesh	Pale yellow
White	Yellow-orange	Dark pink (black in ♀ <u>I. f. flavirostris</u> )	Dark pink (black in ♀ <u>I. f. flavirostris</u> )	Yellow
White	Red, black stripe on base of lower mandible in o	Pink	Pink	Yellow in <u>T. e. rufirostris</u> , brown in <u>T. e. erythrorhynchus</u>
White	♂ orange and yellow, ♀ black	Black	Flesh to rose (Moreau & Moreau 1937)	either in <u>T. e. damarensis</u>
White	Dark red	Blackish	♂ dark grey, ♀ blue-green	Yellow Dark brown

of the colouration of Tockus hornbills.  
 tion from skins, and Sanft(1960), unless  
 se stated.

Foraging niche	Size	Overall appearance	Number of dark central rectrices	Colour of outer rectrix pairs	Colour of back	Marking of upper wing coverts
arboreal	Large	Black & white	4	Outer pair black rest white	Black	All black
arboreal	Large	Black & white	2	White-tipped	Black	Black with light edge
arboreal	Large	Sooty-brown & white	4	Outer pair black rest white	Dark brown	Dark brown edged white
arboreal	Large	Brown & white	2	White-tipped	Grey-brown	Brown with light edge
arboreal?	Small	Black & white	4	White-tipped	Black	All black
arboreal	Medium	Grey-brown & white	2	White-tipped	Brown	Brown edged white
arboreal	Medium	Grey-brown & white	2	White-tipped	Pale brown with white stripe	Brown edged light brown
arboreal?	Very large	Grey & white	2	White-tipped	Grey	Ashy-grey with black tips
arboreal?	Very large	Grey & white	2	All rectrices white-tipped	Grey	All grey
terrestrial?	Small	Brown & White	2	White-tipped	Brown	Brown with white tips
terrestrial	Medium	Black & white	4	Black with broad white band	Black with white stripe	White edged black
terrestrial	Medium	Black & white	4	Black with broad white band	Black with white stripe	White edged black
terrestrial	Medium	Black & white	4	Distal half white	Black	All black or white
terrestrial			4	White	Brown-black	White edged

Figure 57. Diagrams of the dorsal aspect of all species of Tockus hornbill to show the plumage patterns, especially of the primaries, secondaries, upper wing coverts and tail, grouped into species that have similar behaviour and ecology.

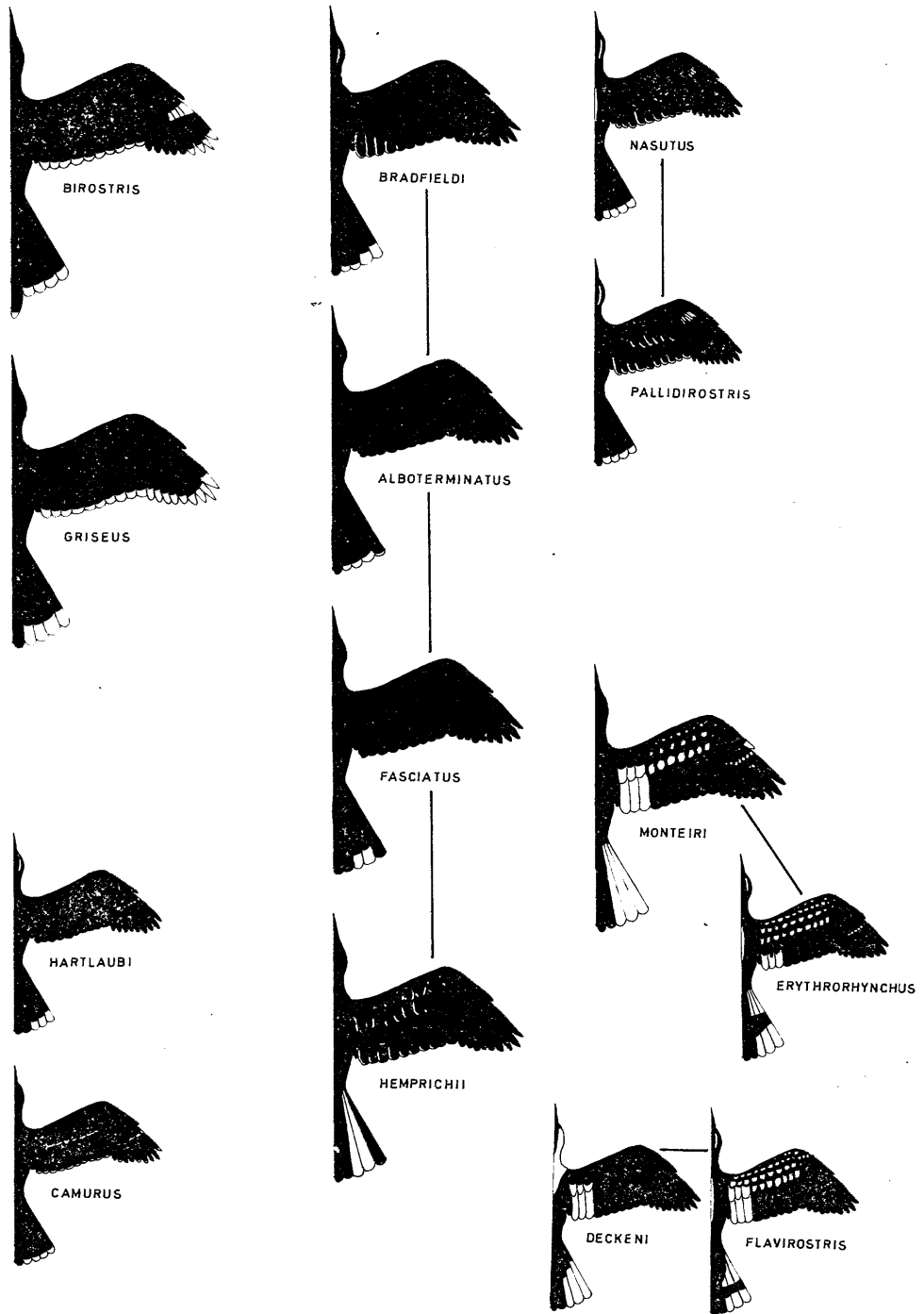


Table 4A. Table of the average wing length/tarsus ratio for each species of Tockus hornbill, arranged in descending order of magnitude. Calculated from measurements given in Sanft (1960).

Tockus species

<u>I. fasciatus</u>	7,49		
<u>I. albeterminatus</u>	7,29		
<u>I. hemprichii</u>	6,88		
<u>I. bradfieldi</u>	6,53	arboreal-	
<u>I. hartlaubi</u>	6,27	foraging	
<u>I. pallidirostris</u>	6,22		
<u>I. nasutus</u>	6,07		
<u>I. griseus</u>	5,29		
<u>I. birostris</u>	4,98	-arboreal?	
<hr/>			
<u>I. camurus</u>	4,90	terrestrial?	
<u>I. flavirostris</u>	4,75		
<u>I. erythrorhynchus</u>	4,67	terrestrial-	
<u>I. deckeni</u>	4,61	foraging	
<u>I. monteiri</u>	4,49		

TREE DWELLING

TREE

GROUND DWELLING

Table 45. A list of characters of the two species groups that form a dichotomy within the hornbill genus Tockus.

- |     |  |  |
|-----|--|--|
| 1.  | Forage mainly on the ground  | Forage mainly in trees and bushes.           |
| 2.  | Clucking calls   | Whistling calls.                             |
| 3.  | Head-down territorial display  | Head-up territorial display.                 |
| 4.  | Walk or run on the ground (except for <u>I. monteiri</u> which bounds)               | Hop on the ground.                           |
| 5.  | Direct, flap-and-glide flight  | Undulating, floppy, but dextrous flight.     |
| 6.  | Concealed roosting sites   | Open roosting sites.                         |
| 7.  | Lack of contact call   | Well developed contact call.                 |
| 8.  | Grass, leaf and twig nest lining   | Bark nest lining.                            |
| 9.  | Outer pair of rectrices largely white  | Outer pair of rectrices only with white tip. |
| 10. | Primaries with small white spots half way along their length                         | Primaries lacking white spots.               |
| 11. | Up to three inner secondaries largely white  | No secondaries predominantly white.          |
| 12. | Upper wing coverts mostly white edged with black (except in some <u>I. deckeni</u> ) | Upper wing coverts dark with paler edging.   |
| 13. | Wing/tarsus ratio less than 4,8  | Wing/tarsus ratio more than 6,0              |

Species concerned:

I. erythrorhynchus  
I. monteiri  
I. flavirostris  
I. deckeni

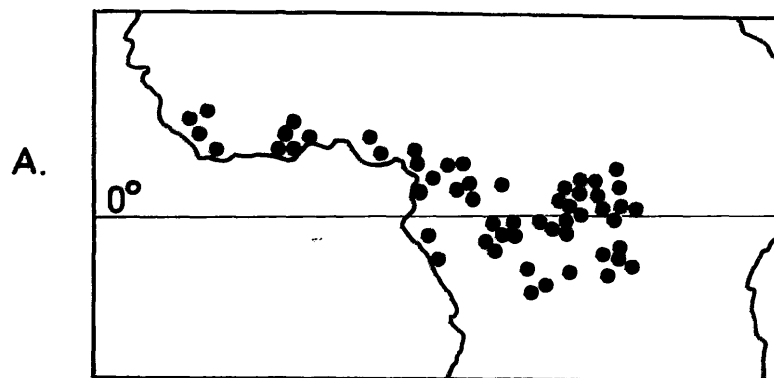
Species concerned:

I. alboterminatus  
I. fasciatus  
I. bradfieldi  
I. hemprichii  
I. nasutus  
I. pallidirostris

Species of undetermined position, because of lack of data:

I. birostris  
I. griseus  
I. hartlaubi  
I. camurus

Figure 58. The total distribution of A - I. hartlaubi and B - I. camurus. (After Sanft 1960).



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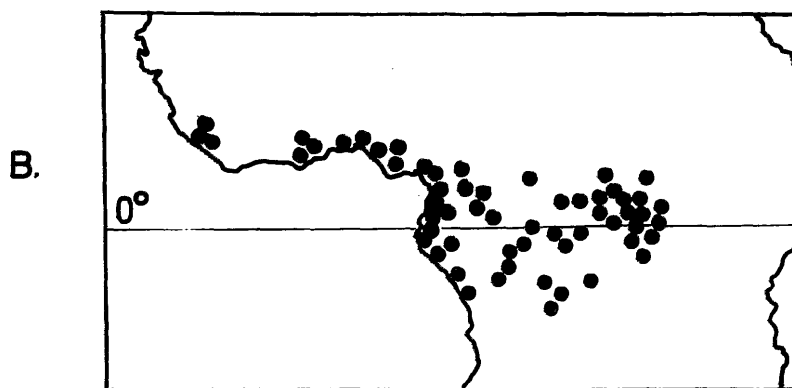


Figure 59. Distribution, in India and Ceylon, of the two non-African species of *Toxus*; solid circles, *I. birostris* and open circles *I. griseus*. From Sanft (1960).

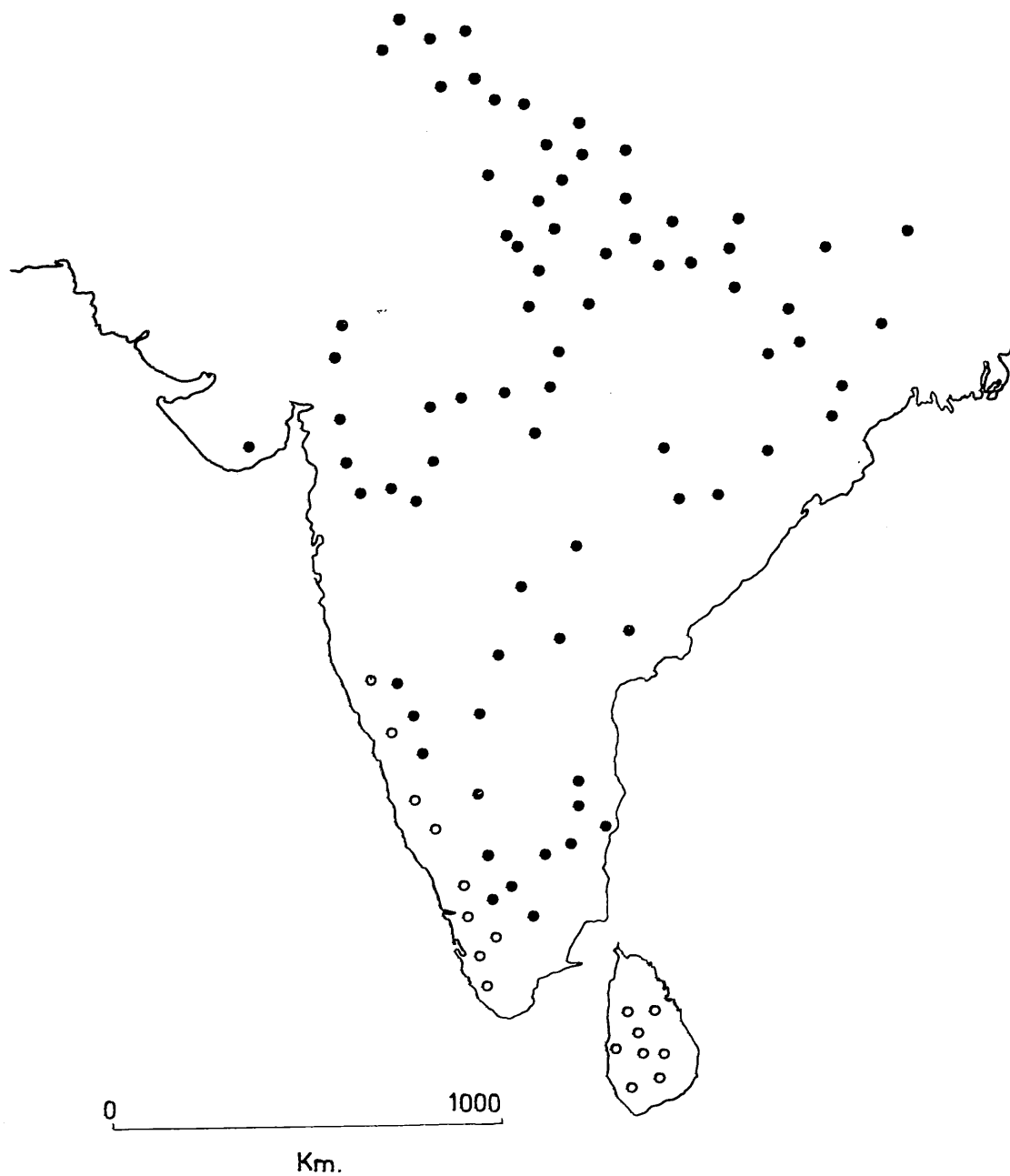


Figure 60. Distribution, in Africa, of the bradfieldi species-group. Solid circles, T. alboterminatus; open circles, T. fasciatus; crosses, T. bradfieldi; solid triangles, T. hemprichii. From Sanft (1960).

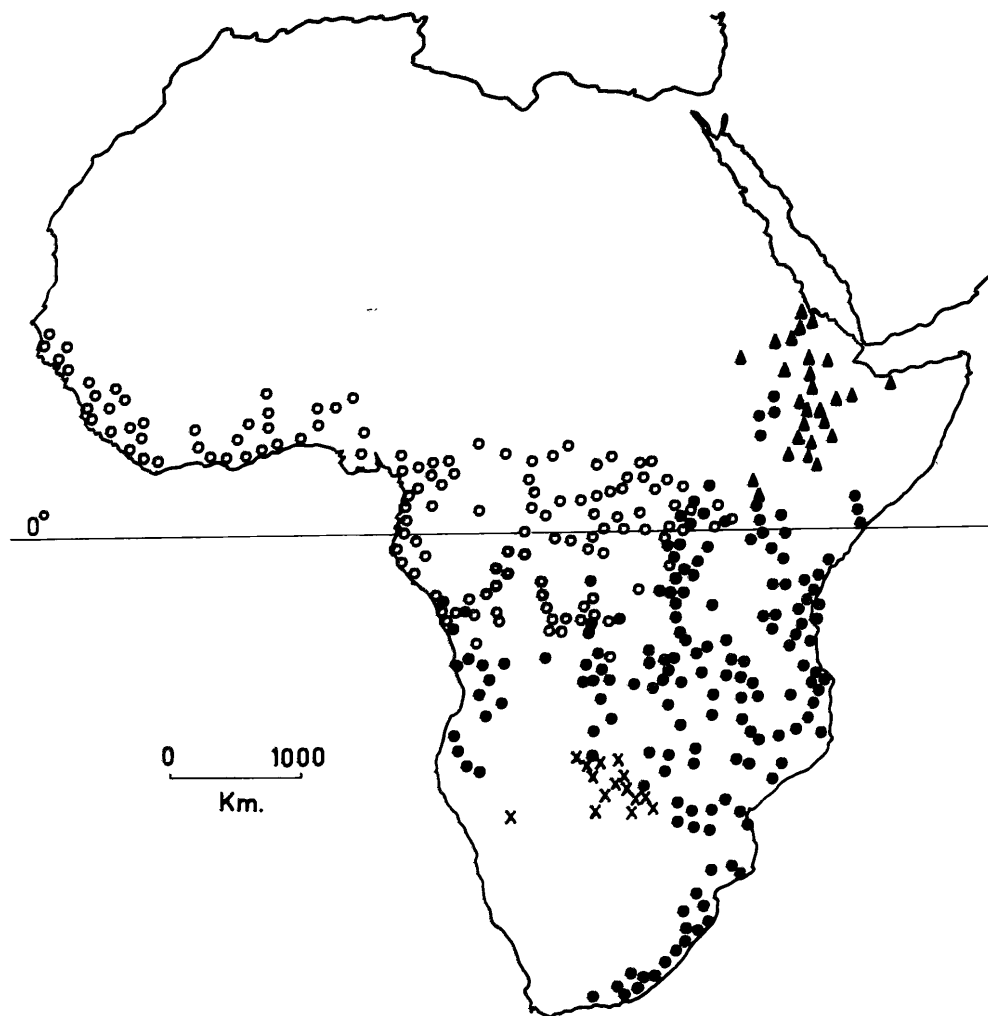


Figure 61. Distribution, in Africa, of the nasutus species-group. Solid circles, I. nasutus; open circles I. pallidirostris. From Sanft (1960).

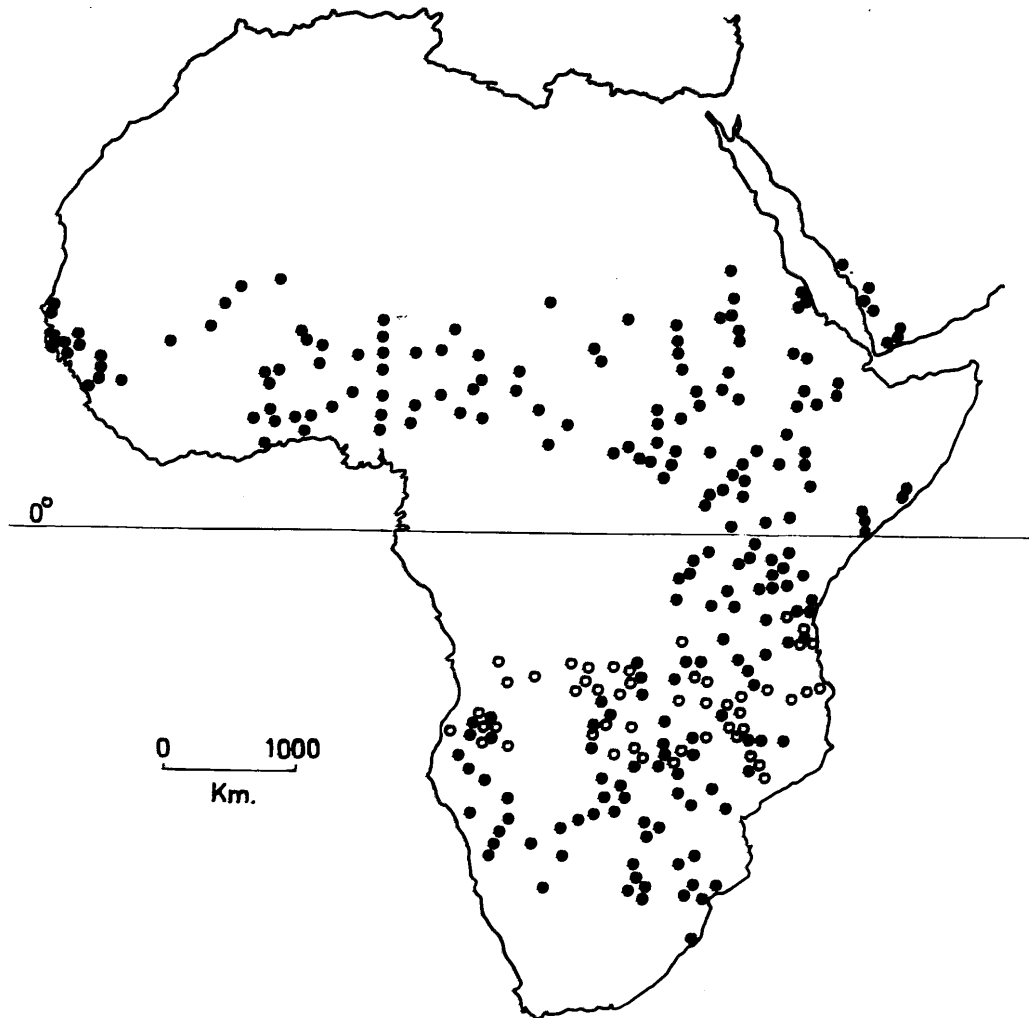


Figure 62. Distribution, in Africa, of the monteiri species-group. Solid circles, I. erythrorhynchus; open circles, I. monteiri. From Sanft (1960)

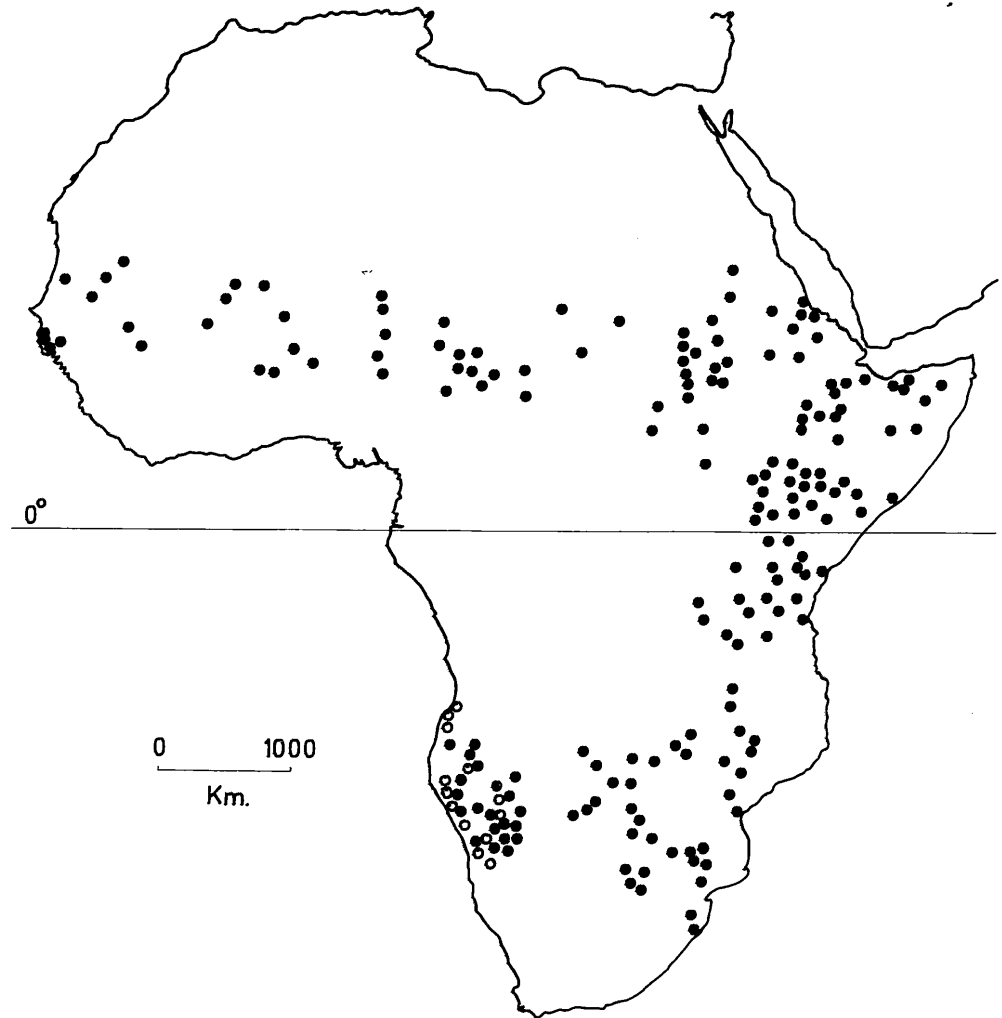


Figure 63. Distribution, in Africa, of the flavirostris species-group. Solid circles, I. flavirostris; open circles, I. deckeni. From Sanft (1960).

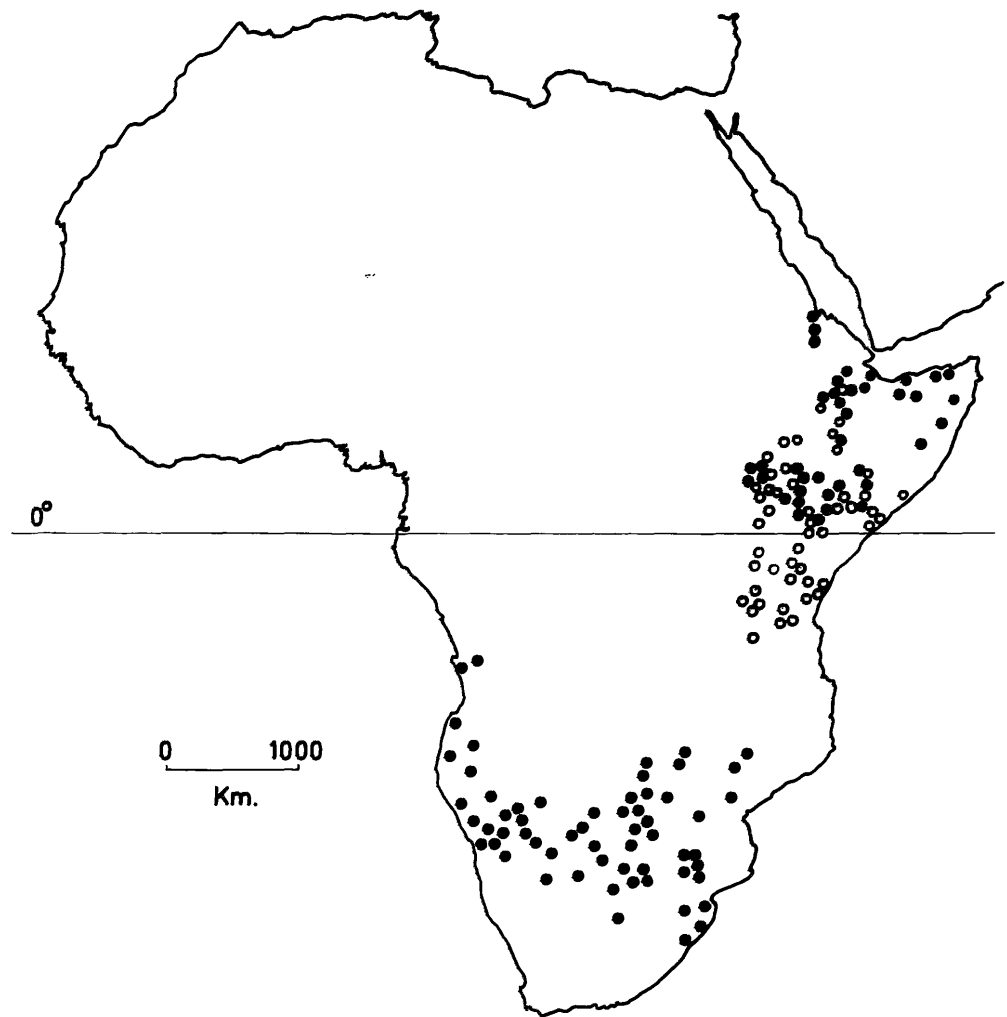


Figure 64. A diagram showing the suggested methods of radiation of the species and species groups of the hornbill genus Tockus.

