A COMPARATIVE STUDY ON THE BIOLOGY OF TWO SUBSPECIES OF TREE SQUIRRELS, PARAXERUS PALLIATUS TONGENSIS, ROBERTS, 1931 AND PARAXERUS PALLIATUS ORNATUS (GRAY, 1864) IN ZULULAND

by

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ABSTRACT

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In comparing the biology of the two subspecies of tree squirrels of P. palliatus, it was found that mass and all body measurements differ significantly. The subspecies of palliatus on the Moçambique plain occur in forested islands with lighter and smaller squirrels in dry forests and darker and heavier squirrels in more moist forest.

Aspects of the other two southern African tree squirrels, Paraxerus cepapi cepapi and Funisciurus congicus congicus have been included to further investigate adaptations to niche. The two subspecies of P. palliatus occur in forests that are in more moist regions whereas cepapi and congicus inhabitat relatively dry savanna regions and are subjected to greater extremes of temperature. Vegetation density presents the most obstruction to visibility in the forests of tongensis.

Phenological observations show a seasonal pattern in all four the habitats.

and of male tongensis it was 4,33 ± 1,34 (n=3).
Home range of male ornatus was 3,18 ± 1,72 (n=12)^ Female home ranges were smaller for both ornatus and tongensis and averaged 2,19 ± 0,93 (n=6) and 0,73 ± 0,10 (n=3) respectively. Population density and biomass estimates were the highest for ornatus at 4,32 squirrels / ha or a biomass of 1 650 g / ha.

Twenty eight feeding records for each of the two subspecies of P. palliatus are included. A study of the feeding efficiency of the tree Paraxerus spp. indicate that ornatus is the most efficient feeder: on medium- and large- sized kernels it feeds in 59,5% to 66,7% of the time cf. tongensis and in 36,7% to 41,4% of the time cf. cepapi. Lengths of the different sections of the intestines, indicate that southern African tree squirrels are more insectivorous than tropical tree squirrels.

Oxygen consumption indicates that the two forest species are adapted to more moist habitat than the two savanna species.

Cepapi with the lowest oxygen consumption is particularly well-adapted to conserve energy. On the other hand, thermal conductance is the highest in *congicus* to rid it of excess heat. This is the only one of the four species which carries its tail over its head, probably thus aiding in thermoregulation.

In captivity the forest species were found to be more active (move over greater distance per day) than *cepapi* and *congicus*. This is probably related to the dispersed food resources and the greater volume and range of movement in forests. Less allogrooming is performed by the forest than by the savanna ("contact") species. Frequencies of both murmuring and tail-flicking were greater for the forest species than for the savanna species. Both these aspects are related to intraspecific communication in dense habitat.

Sonographic analyses were made for almost all the calls of all four species. The main difference between the forest and savanna species is that the fundamental frequencies are consistently higher in the latter two species. The call of extreme alarm is a low-pitched bark in the forest species, but a high-pitched whistle in the savanna species. Between *ornatus* and *tongensis* the difference lies in frequency of vocalisation, the former being more vocal. Oestrus is communicated vocally in *cepapi* but olfactorily in *ornatus* and *tongensis* in the denser habitats.

Reproduction in the two forest species is seasonal and occurs from about August to March. Murmuring by males is also seasonal and ceases when scrotal size diminishes. Gestation period is 59 d in *ornatus* (n=1) and litter size is 1,69 ± 0,48 in *tongensis* (n=13), and 1,60 ± 0,52 (n=10) in *ornatus*. The small litter size and long gestation is accompanied by a more precocial state of development at birth than and independence at almost half the age of temperate tree squirrel species.

A description of moult of *ornatus* and *tongensis* is included, as well as the identification of ecto- and endoparasites collected from *P. palliatus* in KwzZulu.

PREFACE

Certain aspects related to the present study have already been published or are in press under the following titles:

1 Notes on the western striped squirrel, Funisciurus congicus congicus (Kuhl, 1820). 1978. Madoqua 11: 119-128.
2 Environment and reproduction in tree squirrels with special reference to the genus Paraxerus. In: Gilmore, D.P. and Cook, B. (Eds.). Environmental factors in mammalian reproduction. MacMillan London. In press.

The first article has been included as an addendum to this dissertation as frequent reference is made to it. The second article is incorporated in the Chapter on Reproduction. The following articles have already been published on related aspects:

1 Aspects of the ecology, reproductive physiology and ethology of the bush squirrel, Paraxerus cepapi cepapi. M.Sc thesis. University of Pretoria.
2 Behaviour of the bush squirrel, Paraxerus cepapi cepapi. Mammalia 41: 119-166.
3 Factors affecting breeding synchronisation in an African bush squirrel, (Paraxerus cepapi cepapi). J.Reprod. Fert. 50: 125-127.
4 Aspects of reproduction of male bush squirrels Paraxerus cepapi cepapi (A. Smith, 1836) in the Transvaal. Publ. University of Pretoria. New series 97: 86-91.
5 Aspects of Phallic morphology of the bush squirrel, Paraxerus cepapi cepapi. Zool. Afr. 12: 229-231
6 Age determination in the bush squirrel (Paraxerus cepapi cepapi) Zool. Afr. 12: 89-99
7 Feeding habits of the bush squirrel Paraxerus cepapi cepapi (Rodentia: Sciuridae). Zool. Afr. 12: 459-467.

Aspects investigated in the present study but not directly related to the theme of niche separation, have been described in an appendix, and include records of ecto- and endoparasites, and moult progression.

ACKNOWLEDGEMENTS

This study was carried out under the auspices of the Mammal Research Institute of the University of Pretoria supported by grants from the Council for Scientific and Industrial Research and the Wildlife Society of Southern Africa. Permission to work in the selected study areas was granted by the KwaZulu Department of Nature Conservation, the Department of Forestry and the Natal Parks Board. In the KwaZulu study area I received continuous support from Mr and Mrs F.J. Joubert of St. Lucia Estuary and Mr & Mrs I.F. Garland of Mtunzini, and from Mr A. Odendaal at Port Durnford Forestry Station. The following people accompanied and helped with work in Ngoye forest. The late R.L. Cooper, B.H. Erasmus, A. Harris, J. Watson, Dr. C.J. Stutterheim, D. Skinner, J. van der Vegte, R.D. and M. Carr, and P.G.H. and S. Frost. Their help was much appreciated. Assistance received in S.W.A./Namibia has been acknowledged in Viljoen, 1978. J. Venter and M. Wolhuter gave assistance at Mkwakwa forest

Many colleagues of various institutions have contributed to this study. In particular, I thank Dr. I.L. Rautenbach, Mr. A. Wehmeyer, Prof. I.W. Hay, Dr. A.G.W. Steyn, Dr. S. du Toit, Dr. A. Verster, Miss J. Walker, Dr. J. Ledger, Dr. H. Keogh, Mr. G. van Urk, Dr. G.K. Theron, Mrs. A. van der Hoven, Mrs. B. Potgieter and Mr. H. de Witt. KwaZulu University made available climatic data from the Ngoye forest.

My sincere appreciation and thanks are also expressed to Prof. J.D. Skinner for his guidance, supervision and interest. Also to my husband George who gave continuous encouragement, to my father, mother, and mother-in-law for assistance duri the final stages of the work, and to Freda Murray for typing the manuscript.

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CHAPTER 1

GENERAL INTRODUCTION

MOTIVATION AND OBJECTIVES OF THE STUDY

When considering the conservation of our natural resources, smaller mammals have frequently been neglected. The priority given to larger mammals is undoubtedly due to their prominence, glamour and the greater demands that they make on the environment. However, land available for wildlife is diminishing rapidly and the conser=vation of smaller mammals will soon demand a thorough knowledge of their ecology, physiology and behaviour. Moreover, if denudation of the habitat as practised by the local native inhabitants is allowed to proceed without restraint, the two subspecies of tree sciurids occurring in KwaZulu are undoubtedly endangered. Commen=ting on the Kosi Lake region, Tinley (1964) mentioned that forests were diminishing in size due to the continued chopping, burning and cultivating by natives over the years. Hanks (*pers.comm.*)* mentions that each native requires one ton of firewood *per annum* and Acocks (1975) provides evidence to show how the forested areas have already diminished in South Africa. Knowledge of the life histo=ries of forest animals is necessary for their future conservation, and a study on any forest species could yield data which might also be relevant to other species, Despite the fact that the Ngoye forest is unique with regard to several species (see Chapter 11), no long-term studies have been undertaken in the forest. Studies in the forest could alert the KwaZulu authorities to the value of the forest.

The original objectives of the present study were to examine the biology of two subspecies of KwaZulu squirrels, *Paraxerus palliatus ornatus* (Gray, 1964) and *P.p.tongensis* Roberts, 1931 . During the course of the study it became apparent that information on two additional southern African tree squirrel species would add to

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*Dr. J.Hanks, Dept. of Biological Sciences, University of Natal, Durban 4000 the comparison of the forest squirrel species and could reveal more information on behavioural and morphological adaptations to habitats ranging from savanna and woodland to moist forest. Therefore, although directed mainly towards the KwaZulu species, relative information was obtained to compare aspects of adaptive strategies of *P.cepapi cepapi* (A. Smith, 1836) and *Funisciurus congicus congicus* (Kuhl, 1820), both of which occur in the heliophyte systems of Tinley, (1975). Figure 1 illustrates the distribution of these species and Figures 2 and 3 show the locality of the study areas for *P.p.ornatus* and *P.p.tongensis*.

Descriptions of climate, distribution and habitat preferences in the ranges of the four squirrel species have been included to define the niche of each species. And subsequently, the aspects of their biology which could be adaptive to this niche, are investigated.

COMMON NAMES OF THE KWAZULU SQUIRREL SPECIES

P.p.ornatus is known as the Ngoye red squirrel and *P.p.tongensis* as the Tonga yellow squirrel (Tinley, 1976) or the Tonga yellow-chested squirrel (Roberts, 1951). I suggest that it be designated the Tonga squirrel thus reflecting the subspecific nomenclature, even though Tongaland is now known to the KwaZulu people as Maputoland. Native names of the *P.palliatus* squirrels in different regions are the following:

P.p.swynnertoni from Mt.Selinda - Inchindana

P.p.sponsus from Malawi Hill - Tindi (this is probably *palliatus* and not *sponsus*), and from 15 miles west of Tambarra, Moçambique - Inyakafula

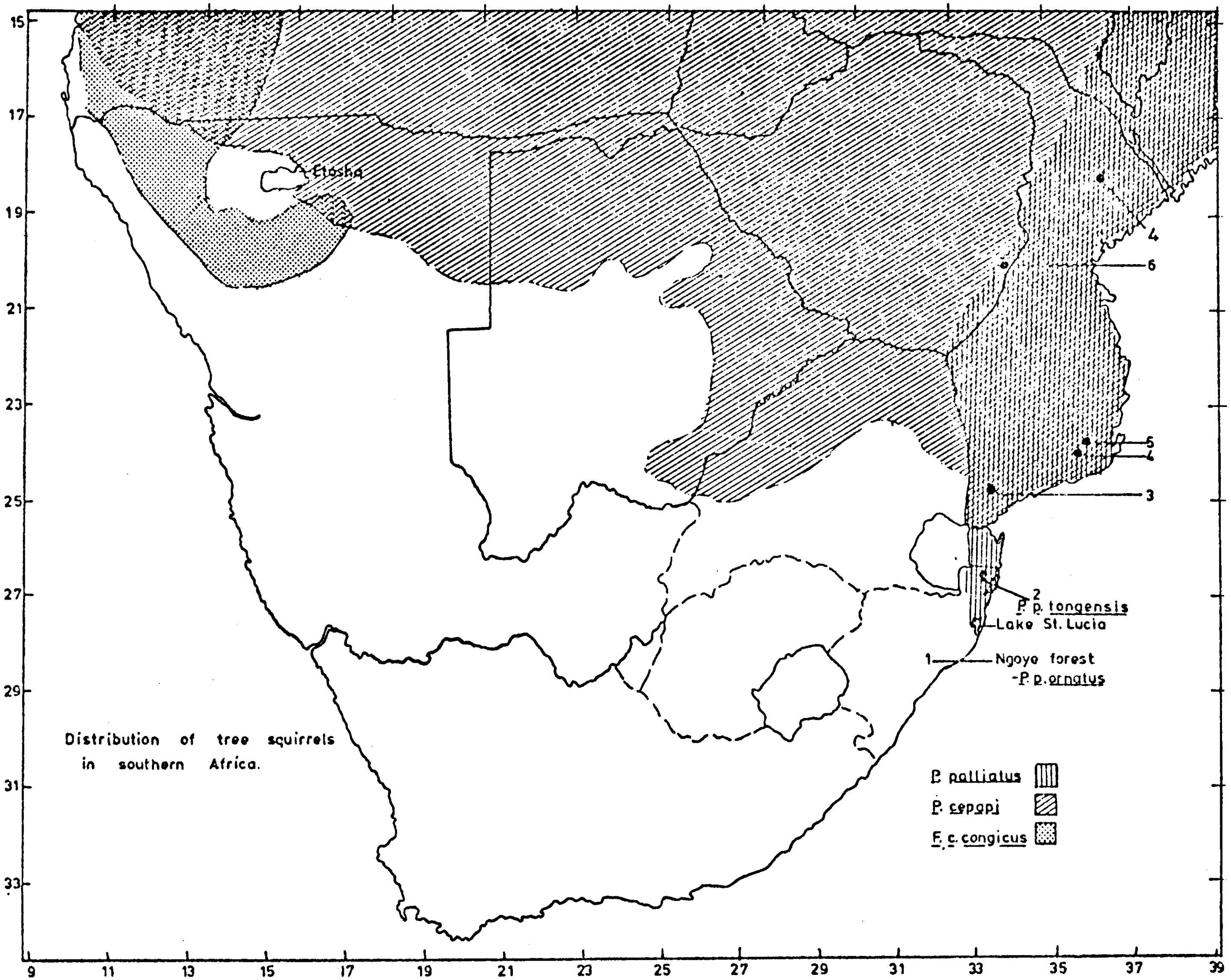
F. sponsus (Thomas and Wroughton, 1907) from Coguno - Shintsi
F. palliatus (Sclater, 1900) - Pocoluti - Zulu; Inchindau ebomvu Swazi, Tshindi - at Inhambane;

P.sponsus tongensis from Mangusi (i.e. *P.p.tongensis*) I-sheeni;

P.p.ornatus (Roberts 1951) - Intshindane, ubunt-shindane, impukuluthi, ingwejeje. *P.p.tongensis* is also known as I-somghede at Cape Vidal.

Throughout the rest of this dissertation, for the sake of brevity, the studied squirrels are referred to as squirrel species, namely *ornatus*, *tongensis*, *cepapi* and *congicus*, even though *ornatus* and *tongensis* are actually classified as subspecies of the species *palliatus*. However, wherever this terminology could result in confusion, the specific and subspecific nomenclature are added. It will be seen that *ornatus* and *tongensis* differ greatly in colour, size and certain aspects of behaviour, and there is no doubt that they will not interbreed freely. However, the present subspecific nomenclature does enlighten their origin and affinities as pointed out by Kingdon (1974).

Figure 1. Distribution of southern African tree squirrels, *Paraxerus palliatus*, *P.c. cepapi* and *Funisciurus congicus*. The numbers refer to subspecies of *P. palliatus*: 1. *ornatus* 2. *tongensis*, 3. *auriventris*, 4. *sponsus* (Inhambane to Beira), 5. *bridgemani*, 6. *swynnertoni*.



Distribution of tree squirrels in southern Africa.

Figure 2. Locality map of Ngoye forest (28° 50'S, 31°42'E), study area of *P.p. ornatus*. Numbers indicate rainfall stations within the forest reserve.

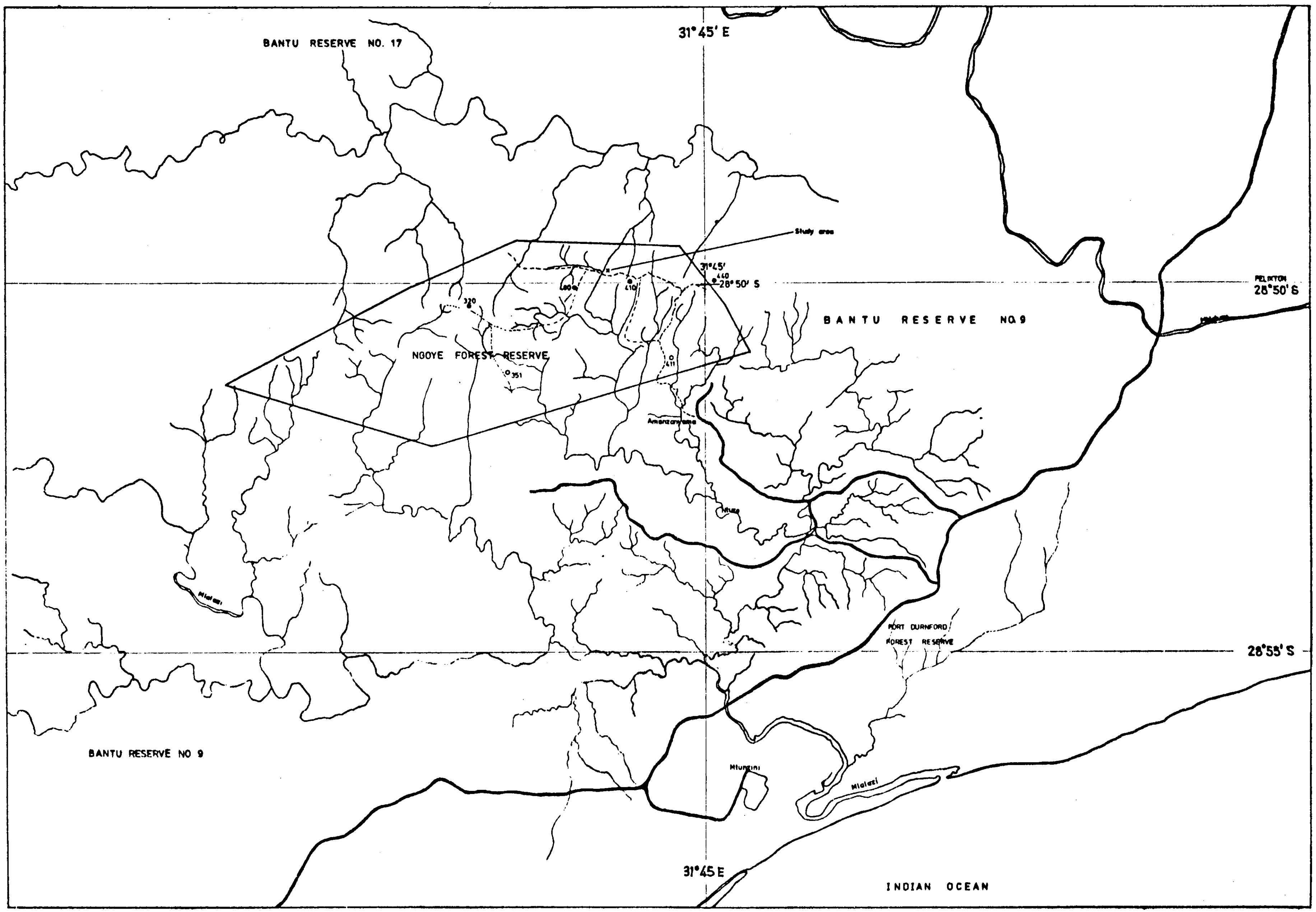
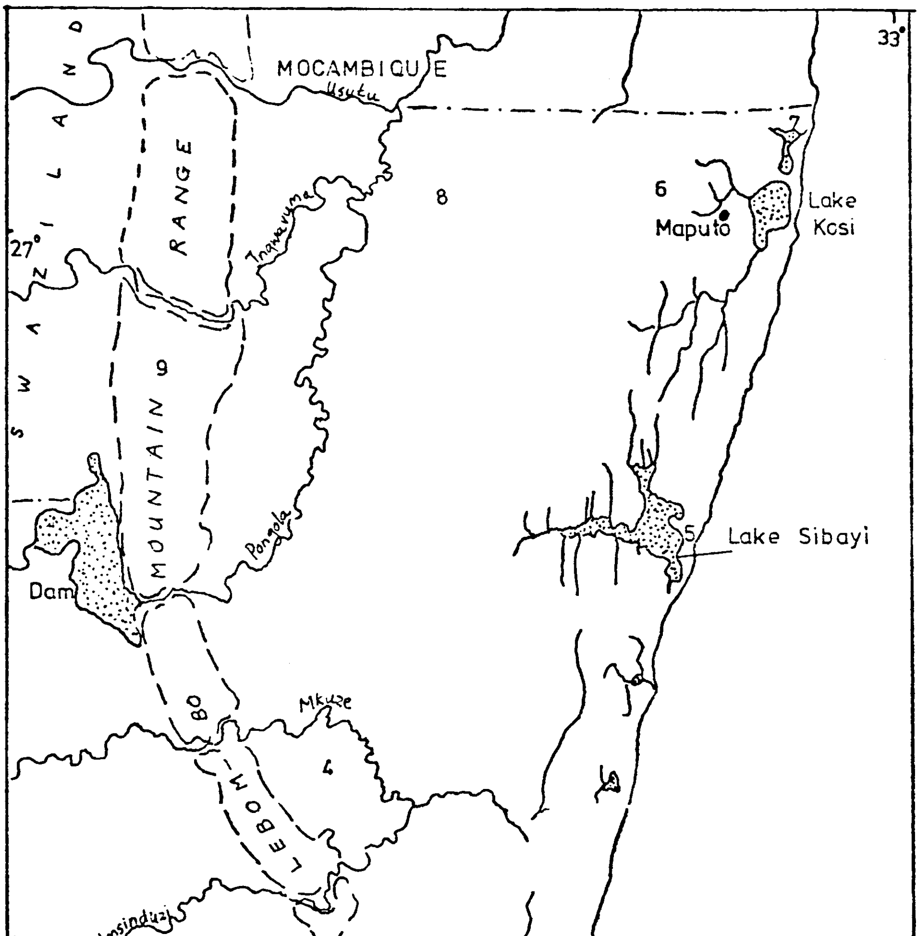

BANTU RESERVE NO. 17
31°45′ E
Study area
31°45′
440
28°50′ S
400
410
320
411
351
NGOYE FOREST RESERVE
Amanzamnyama
BANTU RESERVE NO.9
FELIXTON
28°50′ S
Ntuze
Mlalazi
PORT DURNFORD
FOREST RESERVE
28°55′ S
BANTU RESERVE NO 9
Mtunzini
Mlalazi
31°45 E
INDIAN OCEAN

Figure 3. Locality map of Mkwakwa forest (28°30'S, 32°24'E) study area of _P_._p_. _tongensis_. Numbers indicate localities visited within the distribution area of _tongensis_: 1. Dukuduku forest, 2. Charter's Creek, 3. False Bay, 4. Mkuze Game Reserve, 5. Lake Sibayi, 6. Manguzi forest, 7. Lake Kosi, 8. Sihangwane, dry forest, 9. Gwalaweni forest, 10. Maphelane.


MOCAMBIQUE
Usutu
SWAZILAND
27°
33°
RANGE
MOUNTAIN
9
8
Ingwavuma
6
Maputo
7
Lake Kosi
Pongola
Dam
5
Lake Sibayi
LEBOMBO
Mkuze
4
Umsinduzi
Umsinene
3
Lake St Lucia
Hluhluwe
Cape Vidal
Lake Bangazi
2
Nyalazi
Mkwakwa study area
St Lucia Estuary
1
Mtubatuba
Umfolozi
10

CHAPTER 2

CLIMATE, DISTRIBUTION AND HABITAT PREFERENCES

INTRODUCTION

Climate is intimately linked with, and has a major influence on the distribution and adaptation to niche of animals. Therefore, these three subjects are here considered together at the commencement of the dissertation as an introduction to the four species and to distinguish the niche of each species to an extent. However, the vegetation analyses of the specific study areas are compared separately in Chapter 4.

MATERIALS AND METHODS

To obtain information on the microclimate within the KwaZulu forests a thermo-hygrograph was placed on the ground in deep shade in the forests during visits to the study areas, and wet- and dry bulb, and maximum/minimum thermometers were placed both inside and in the shade outside the forests at a height of 1 m. Readings were taken at 06h00, 12h00 and 18h00. Climatic data were obtained from the weather bureau in Pretoria.

Areas visited to obtain more data on distribution, were Nkandhla and Eshowe forests for ornatus, and Gwalaweni forest, Sihangwane, Kosi Bay, Lake Sibaya, Mkuze Game Reserve, Sodwana Bay, False Bay, Charters Creek, Dukuduku Forest and Maphelane Dune for tongensis (fig. 3)

RESULTS

CLIMATE

Köppen's climatic designations relevant to the distribution of the four species are given in Table 1 and symbols are defined in Table 2. All four of the species occur where the mean annual temperature exceeds 18°C and where the dry season occurs in the winter. The red squirrel P.palliatus occurs in frost-free regions, either in warm temperate rainy or tropical rain climates. The bush squirrel, P.cepapi and striped squirrel, F.congicus, occur in hot and arid Steppe areas. Rainfall and temperature regimes for the different areas are given in Figs.4 and 5. According to Köppen's classification the precipitation during the driest month in Ngoye forest should be 10% of that of the

TABLE 1

THE KöPPEN CLIMATIC DESIGNATION (SCHULZE, 1947) FOR THE DISTRIBUTION AREAS OF SOUTHERN AFRICAN TREE SQUIRREL SPECIES

SPECIES	KöPPEN DESIGNATION	REGION
P.palliatus	Cwb	Melsetter
	Aw	Moçambique
P.palliatus ornatus	Cfwa	Ngoye Forest
P.p.tongensis	Cfwa & Cwa	Maputoland
	Aw	Kosi Bay
P.cepapi	Bshw	Northern parts of SWA/Namibia, Botswana and Transvaal
	Aw	Moçambique
	Cwa	Rhodesia
	Cwb	"
F.congicus congicus	BShw	Northern SWA/Namibia, Angola

TABLE 2

DEFINITION OF SYMBOLS USED IN THE KöPPEN CLASSIFICATION OF AFRICAN CLIMATES (SCHULZE, 1947)

SYMBOL	DEFINITION
A	(Tropical rain climates). Mean temperature of coldest month at least 18°C.
B	Arid climate
C	Warm temperate rainy climates; at least one month with mean temperature below 18°C and at least eight months with mean temperature > 1°C; coldest month above -3°C.
S	Steppe
a	Mean temperature of warmest month > 22°C.
b	Mean temperature of warmest month < 22°C.
h	Hot and dry, mean annual temperature > 18°C.
f	Sufficient rain during all months; for summer rainfall f denotes that precipitation during the driest month exceeds one-tenth that of the wettest month (all habitats here studied have summer rainfall)
w	Dry season in winter

Figure 4. Climatic data in the habitat of *P. palliatus* in KwaZulu at Cape St. Lucia and Otobotini for *P.p. tongensis*, and Eshowe and Ngoye forest for *P.p. ornatus*. (--- rainfall in mm, 1-7 temperatures in °C: 1 - extreme maximum, 2 - mean monthly maximum, 3 - mean daily maximum, 4 - mean daily, 5 - mean daily minimum, 6 - mean monthly minimum, 7 - extreme minimum. (Temperature range is the mean value and was not calculated for Ngoye forest as these records only cover four years. Note - altered scale for rainfall in Ngoye forest).

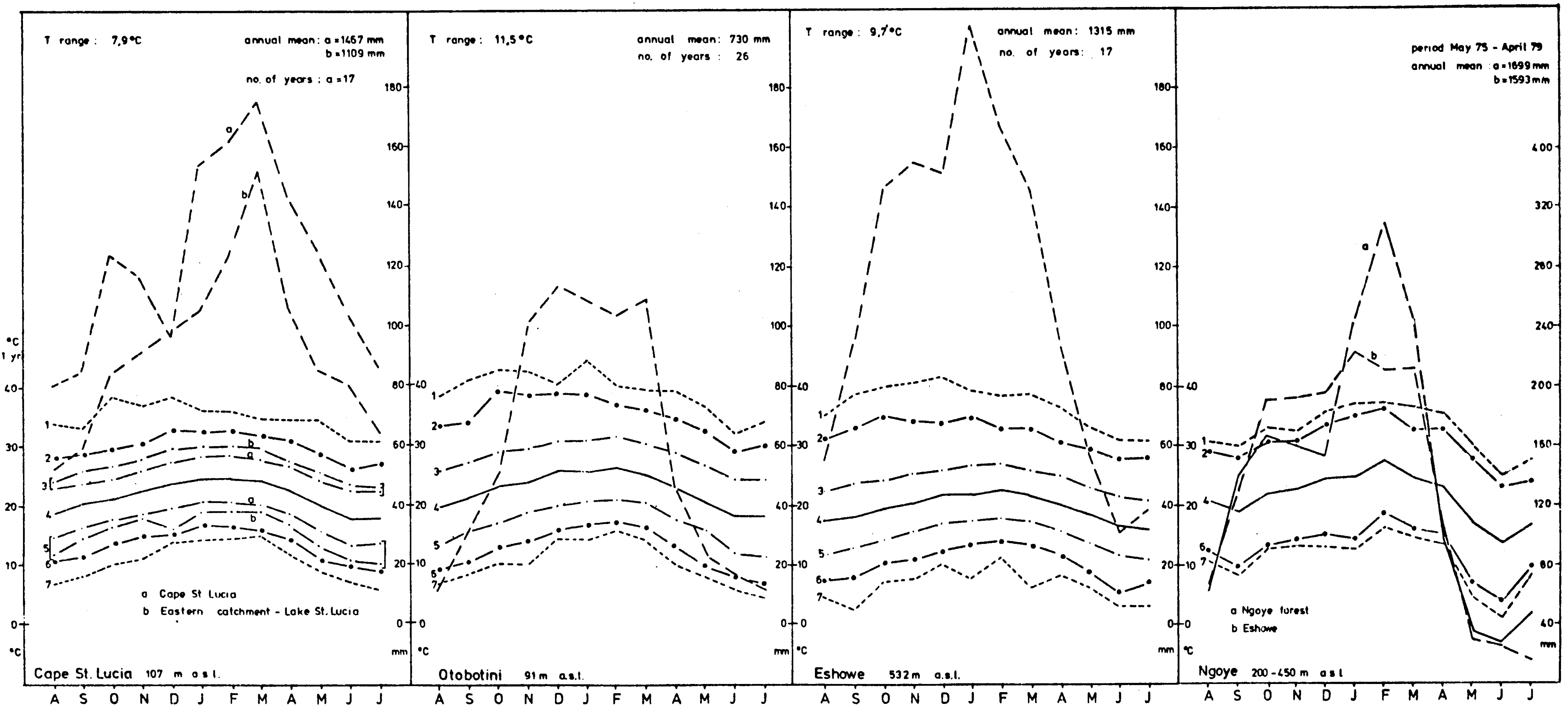
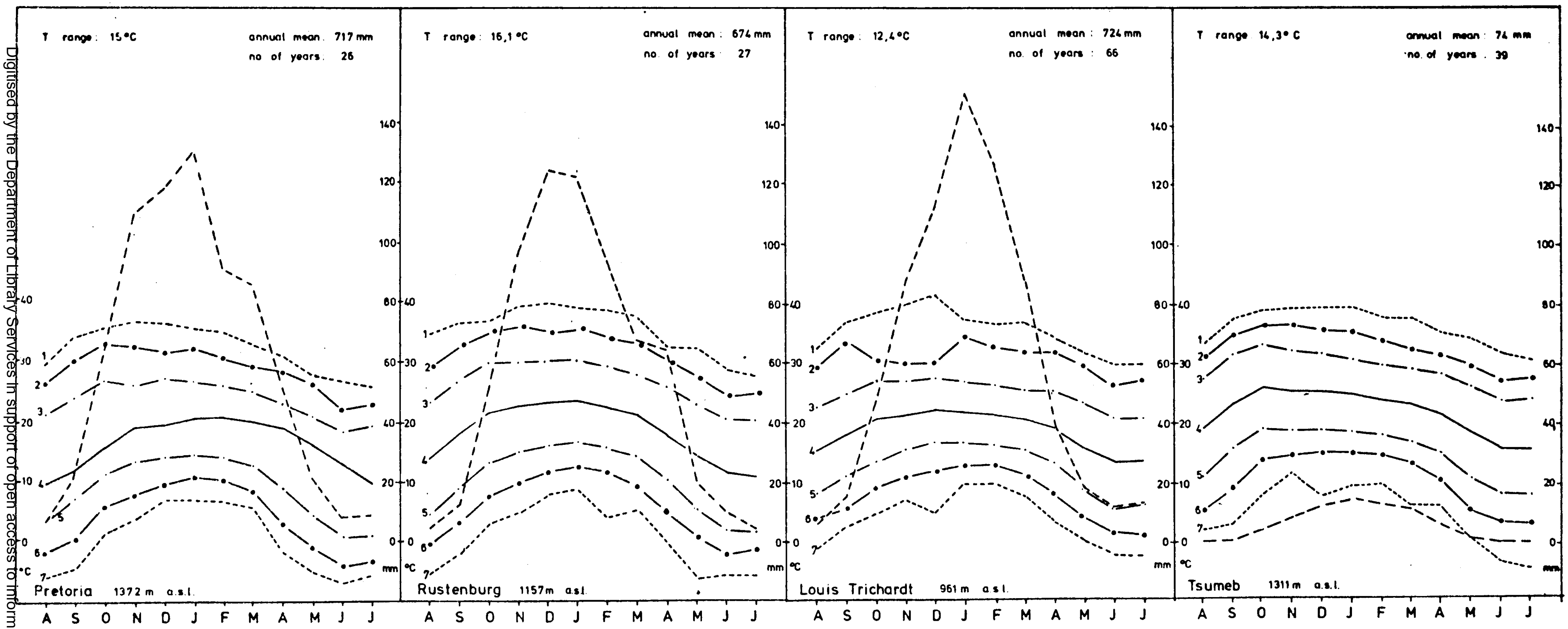

T range: 7,9°C
annual mean: a = 1467 mm
b = 1109 mm
no. of years: a = 17
°C
(31 yr)
a
b
a Cape St Lucia
b Eastern catchment - Lake St. Lucia
Cape St. Lucia 107 m a.s.l.
T range: 11,5°C
annual mean: 730 mm
no. of years: 26
Otobotini 91 m a.s.l.
T range: 9,7°C
annual mean: 1315 mm
no. of years: 17
Eshowe 532 m a.s.l.
period May 75 - April 79
annual mean: a = 1699 mm
b = 1593 mm
a Ngoye forest
b Eshowe
Ngoye 200 - 450 m a.s.l.
1
2
3
4
5
6
7
mm
°C
0
10
20
30
40
60
80
100
120
140
160
180
200
240
280
320
400
A S O N D J F M A M J J

Figure 5. Climatic data in habitat of *Paraxerus c. cepapi*, Rustenburg and Louis Trichardt, and of *Funisciurus c. congicus* Tsumeb. Pretoria data included to illustrate climatic conditions for captive squirrels. (--- rainfall in mm; 1-7 temperature in °C: 1 - extreme maximum, 2 - mean monthly maximum, 3 - mean daily maximum, 4 - mean daily, 5 - mean daily minimum, 6 - mean monthly minimum, 7 - extreme minimum. (Temperature range is of mean values).



— — — — rainfall, 1-extreme maximum; 2-mean monthly maximum, 3-mean daily maximum; 4-mean daily 5-mean daily minimum, 6-mean monthly minimum, 7-extreme minimum; 1 to 7-temperatures.

wettest month, but during the four years rainfall was measured, it was only 7,89% of that of the wettest, but this is too short a period, as at nearby Eshowe, over 17 years, rainfall has been measured as 16% of that of the wettest month (Weather Bureau, Pretoria). Mean annual rainfall has been 1 868 mm at Ngoye forest (28°50'S, 31°42'E) over the past four years (May 1975 - April 1979) and 1 315 mm at Eshowe (28°53'S, 31°28'E) at a similar altitude. Empangeni just north of the Ngoye forest lies on the 1 000 mm isohyet. The mean annual rainfall varies from 628 mm at Otobotini (27°25'S, 32°06'E) to 1 318 mm at Cape St.Lucia (28°30'S, 32°24'E) in the range of *tongensis*. According to Schulze (1947) the Lake St.Lucia mean annual rainfall is 890 mm and the isohyet of 1 100 mm passes through the study area at Mkwakwa, 700 mm through False Bay, 800 mm through Hluhluwe and 600 mm to the north west but still east of the Lebombos.

Rainfall for the distribution of *P.cepapi* in southern Africa varies from 74 mm at Tsumeb (19°14'S, 17°43'E) to 724 mm at Louis Trichardt (23°03'S 29°54'E), but in Moçambique, rainfall up to 1 024 mm at Inhaminga (Tinley, 1978) falls in its habitat. In the habitat of *F.congicus* the rainfall varies from 74 mm at Tsumeb to 495 mm at Ombalantu in western Ovambo. Rainfall is markedly seasonal with an erratic occurrence within the rainy season. (Tinley[x], *pers.comm.*). According to the isohyet map of S.W.A./Namibia (Tinley, 1969) *congicus* inhabits the region between 100 and 300 mm isohyets down the western length of its distribution, but at places they pass the 400 and 500 mm isohyets.

Climatological data are summarised in Tables 3 to 7 for the distribution range of the four species. Table 8 and Fig.6 give temperature data at the forested study areas within and outside the forests, which reveal lower minima and maxima and a lower average temperature throughout the year in the Ngoye forest than at Mkwakwa. There is a greater range of temperatures in the coastal forest than in Ngoye. Higher maxima and lower minima were recorded outside the forests, than inside. The average temperature does not differ much for the xeric and mesic pairs of squirrels.

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[x] Dr. K.L. Tinley, Poste Restante Nahoon, 5210.

TABLE 3

WEATHER DATA FOR STATIONS IN THE DISTRIBUTION AREAS OF THE FOUR TREE SQUIRREL SPECIES

	LOCALITY AND NUMBER OF YEARS	TEMPERATURE °C						RAINFALL (mm)
		MEAN MIN.	MEAN MAX.	EXTREME MIN.	EXTREME MAX.	AVERAGE TEMP.	RANGE	
*A	Otjivasandu 3 years	12,1	30,6	6,1(June)	33,5(Oct)	21,4	27,4	322,6(6years)
	Ohopoho 36 years	12,0	30,9	5,7(July)	34,2(Oct)	21,5	28,5	352,6
	Onaangua 5 years	14,8	30,8	7,5(July)	34,6(Oct)	22,8	27,1	596,6
	Uis Mine 9 years	14,0	31,1	9,8(Aug)	33,6(March)	22,6	23,8	141,9
	Outjo	12,6	29,7	-4,4	39,6	21,1	17,1	4,1
B	Tsumeb 39 years	15,0	29,2	-3,9	39,6	22,1	14,3	74,2
	Ghanzi 27 years	12,0	29,4	-8,7(July)	43,9(Feb)	20,7	17,4	53,0
	Naboomspruit 3 years	11,6	26,2	-3,2(June)	37,2(Nov)	18,9	10,2	617,0(65 years
	Louis Trichardt 44 years	12,7	25,1	-1,7(June)	41,7(Dec)	18,9	12,4	723,6(66 years
	Rustenburg 42 years	10,6	26,7	-6,1(May)	40,0(Dec)	18,6	16,1	674,0(27 years
	Pretoria 26 years	8,7	23,7	-7,0(June)	36,8(Nov)	16,2	15,0	716,9(40 years
C	Otobotini 26 years	16,9	28,4	4,4(July)	44,4(Jan)	22,7	11,5	730,0
	Cape St.Lucia 31 years	17,5	25,4	5,7(July)	38,9(Dec)	21,5	7,9	1 466,5 (17 year
D	Eshowe 35 years	14,7	24,4	3,3(June/ July)	41,7(Dec)	19,6	9,7	1 315,0 (17 year
	Empangeni 34 years	15,8	26,4	1,1(July)	45,6(Dec)	21,1	10,6	1 192,8 (65 year

* DISTRIBUTION AREAS OF:

A - *Funisciurus c.congicus*

B - *Paraxerus c.cepapi*

C - *P.palliatus tongensis*

D - *P.p.ornatus*

TABLE 4

TEMPERATURE AND RAINFALL DATA FOR THE HABITAT OF *P.p.TONGENSIS* ON THE SOUTHERN PART OF THE MOÇAMBIQUE PLAIN

	LOCALITY					
	CAPE ST.LUCIA - 339/720 111 m a.s.l; 28°30'S 32°24'E			OTOBOTINI 411/175 91 m a.s.l.; 27°25'S 32°06'E		
	JANUARY	JULY	ANNUAL MEAN	JANUARY	JULY	ANNUAL MEAN
TEMPERATURES (°C)						
Extreme maximum	36,1	30,6	38,9	44,4	34,4	44,4
Extreme minimum	14,4	5,7	5,7	14,4	4,4	4,4
Mean maximum	28,4	22,5	25,4	31,1	24,6	28,4
Mean minimum	20,8	13,5	17,5	20,8	11,6	16,9
RAINFALL (mm)	154,9	86,7	1 466,6	108	11	730

TABLE 5

TEMPERATURE AND RAINFALL DATA FOR THE HABITAT OF P.p.ORNATUS (NGOYE FOREST) AND THE IMMEDIATE VICINITY (ESHOWE AND EMPANGENI)

	ESHOWE - 303/833 532m a.s.l.; 28°53'S,31°28'E			EMPANGENI - 304/736 137 m 28°46'S, 31°55'E			NGOYE FOREST (Outside Station 411) (April 1978 to May 1979) 200 to 450 m a.s.l; 28°50'S, 31°42'		
	JANUARY	JULY	ANNUAL MEAN	JANUARY	JULY	ANNUAL MEAN	JANUARY	JULY	ANNUAL MEAN
TEMPERATURES (°C)									
Extreme max	39,4	30,8	41,7	43,3	32,8	45,6	37,0	27,9	32,4
Extreme min	7,8	3,3	3,3	12,5	1,1	1,1	12,7	8,0	11,2
Mean max	26,8	21,2	24,4	29,3	23,1	26,4	35,0	24,1	30,2
Mean min	17,7	11,0	14,7	19,5	10,4	15,8	14,4	9,5	12,8
RAINFALL (mm)	104,6	57,3	1 315,1	132,1	58,7	1 192,9	245,9	46,7	1 698,8

TABLE 6

TEMPERATURE AND RAINFALL DATA FOR THE HABITAT OF P.c.CEPAPI IN NORTHERN TRANSVAAL, BOTSWANA AND NORTHERN SWA/NAMIBIA

	NABOOMSPRUIT, 1 113 m a.s.l 24°31'S, 28°43'E			MESSINA, 549 m a.s.l. 22°20'S, 30°03'E			MAUN, 942 m a.s.l. 19°59'S, 23°25'E			GROOTFONTEIN, 1 263 m a.s.l 31°29'S, 25°02'E		
	JANUARY	JULY	ANNUAL MEAN	JANUARY	JULY	ANNUAL MEAN	JANUARY	JULY	ANNUAL MEAN	JANUARY	JULY	ANNUAL MEAN
TEMPERATURE (°C)												
Extreme max	32	22	30	42	34	43	40	32	43	38	24	38
Extreme min	16	3	7	15	4	3	9	-5	-6	0	-11	-13
Mean max	29	22	23	32	25	29	32	25	30	30	15	23
Mean min	17	4	13	21	11	17	19	6	14	12	-1	6
RAINFALL (mm)	115	5	617	78	3	340	110	0	471	47	13	377

TABLE 7

TEMPERATURE AND RAINFALL DATA FOR THE HABITAT OF F.c.CONGICUS IN NORTHERN S.W.A./NAMIBIA

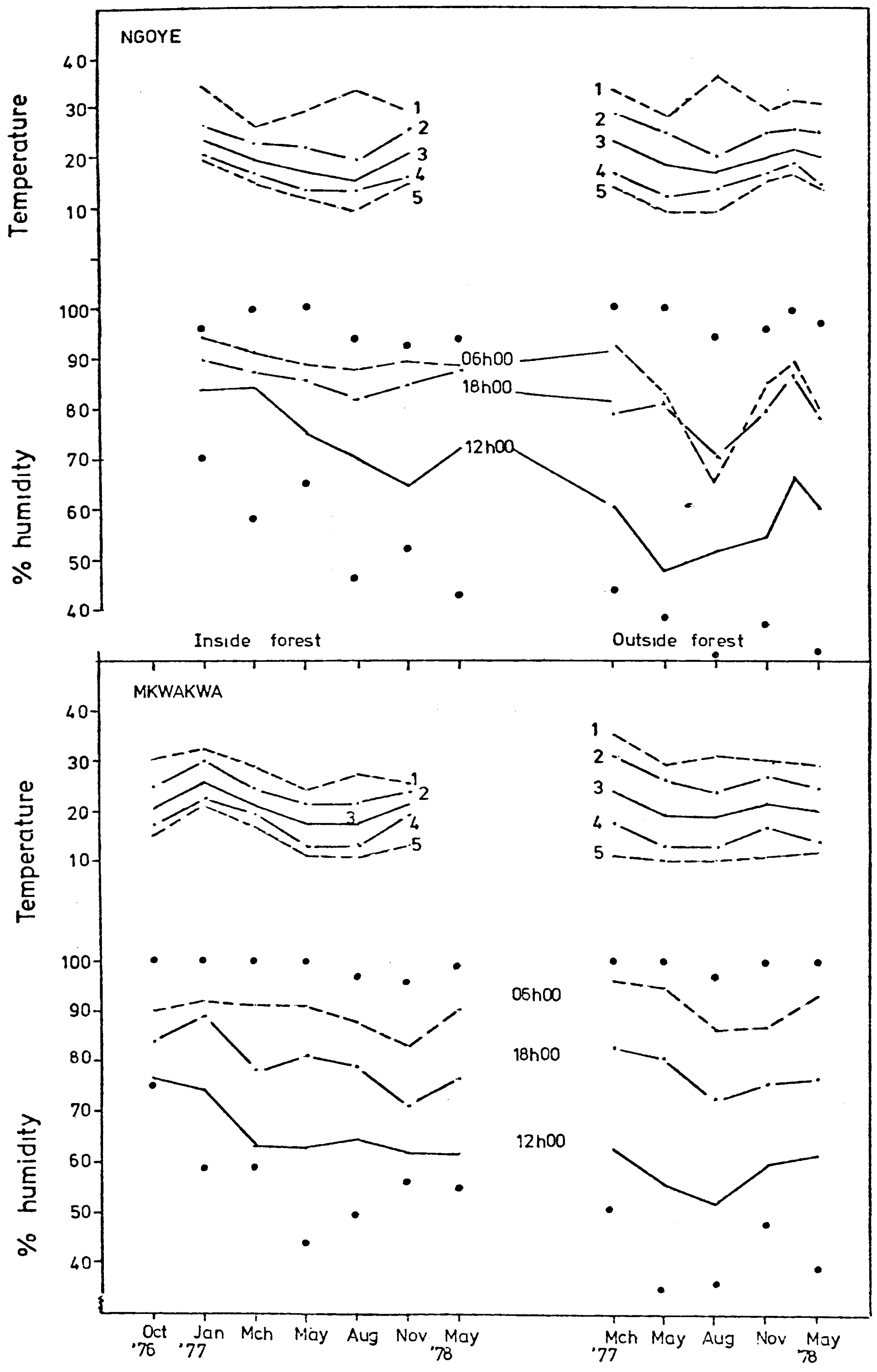
	TSUMEB, 1311 m a.s.l. 19°14'S, 17°43'E			OUTJO 1265 m a.s.l. 20°07'S, 16°09'E		
TEMPERATURE (°C)	Jan	July	Annual Mean	Jan	July	Annual Mean
Extreme max	39,6	30,8	39,6	37,3	29,0	39,6
Extreme min	9,6	-3,9	-3,9	9,7	-3,0	-4,4
Mean max	31,2	24,5	29,2	32,5	24,9	29,7
Mean min	18,7	8,2	15,0	17,1	5,7	12,6
RAINFALL (mm)	14,6	0,1	74,2	-	-	410

TABLE 8

TEMPERATURE DATA FOR NGOYE FOREST AND COASTAL FOREST AT LAKE ST.LUCIA (MKWAKWA)

MONTH	TEMPERATURE (°C)											
	MEAN MIN		MEAN MAX		EXTREME MIN		EXTREME MAX		AVERAGE		RANGE	
	NGOYE	MKWAKWA	N	M	N	M	N	M	N	M	N	M
April 1977												
Outside	16,7	17,5	28,2	30,9	14	11	33	35	22,4	24,2	11,54	13,3
Inside	16,9	18,8	22,6	24,6	15	17	26	29	19,8	21,7	5,75	5,8
January 1977												
Inside	20,9	22,7	26,6	28,9	20	21	34	32	23,8	25,8	5,65	6,2
June 1977												
Outside	12,2	12,9	25,2	26,3	9	10	32	29,5	18,7	19,6	13,0	13,3
Inside	13,5	13,3	21,5	21,3	12,5	11	29	24	17,5	17,2	8,0	7,9
August 1977												
Outside	13,8	13,0	19,7	24,2	9	10	36	31	16,6	18,6	5,5	11,2
Inside	13,3	13,1	19,0	21,8	9,5	11	33	27,2	15,9	17,4	6,1	8,6
October 1977												
Outside	16,7	16,6	24,5	26,7	15	11	29	30	20,6	21,7	7,8	10,0
Inside	16,2	18,5	25,9	23,5	15	13	29	25	21,6	21,0	9,7	5,0
November/December 1977												
Outside	18,3	-	24,9	-	16,2	-	31,2	-	21,7	-	6,6	-
May 1978												
Outside	14,9	13,9	24,7	24,8	14	11,5	30	29	19,9	19,4	9,8	10,9

Figure 6. Climatic data at the two KwaZulu study areas, Ngoye and Mkwakwa forests. Temperature: 1 - extreme maximum, 2 - mean maximum, 3 - mean daily, 4 - mean minimum, 5 - extreme minimum. Humidity taken inside and outside of forests, maximum and minimum values, as well as readings at 06h00, 12h00 and 18h00.


NGOYE
Temperature
40
30
20
10
1
2
3
4
5
% humidity
100
90
80
70
60
50
40
06h00
18h00
12h00
Inside forest
Outside forest
MKWAKWA
Temperature
40
30
20
10
1
2
3
4
5
% humidity
100
90
80
70
60
50
40
06h00
18h00
12h00
Oct '76
Jan '77
Mch
May
Aug
Nov
May '78
Mch '77
May
Aug
Nov
May '78

Percentage relative humidities as measured in- and outside the two forested study areas, are presented in Tables 9 and 10/Figure 6, revealing a higher humidity inside the Ngoye forest than inside the coastal forest at Lake St.Lucia. Throughout the day the humidity inside the Ngoye forest canopy as a percentage of the humidity outside, is consistently higher, but in the coastal forest this is only true for the midday reading (Table 10). Relative humidity is lower in the habitats of *cepapi* and *congicus* than in that of *ornatus* and *tongensis* (Table 38). √

DISTRIBUTION AND HABITAT PREFERENCES (see Table 11 for definition of habitats)

The distribution of the four species is illustrated in Figure 1. (Compiled from Shortridge, 1934; Hill and Carter, 1941; Roberts, 1951; Ellerman, Morrison-Scott and Hayman, 1953; Tinley, 1969; Smithers, 1971; Davis, 1974; Kingdon, 1974; Smithers and Lobão Tello, 1976; Sherry, 1977; and various museum records).

Davis (1974) mentioned that the east African red squirrel, *P.palliatus* occurs on the eastern belt of the southern savanna woodlands from Ngoye forest northwards, east of the great escarpment except at Mt.Chirinda. The two KwaZulu subspecies of this species in xeric to mesic forested habitat are the Ngoye red squirrel, *P.palliatus ornatus* (Gray 1864) found only in the Ngoye forest, and the Tongaland orange-chested squirrel, *P.p,tongensis* Roberts 1931, found in coastal and coastal dune forests in Tongaland. The southernmost distribution record for the latter species is at St.Lucia (28°30'S, 32°30'E).

Kingdon (1974) mapped the distribution of *P.palliatus* throughout Africa and described their habitat as forest and thicket formations where a shaded leafy microclimate is formed at the lower levels of the forest and in thick undergrowth. Smithers and Lobão Tellò (1976) found them in Moçambique in tropical forest or moist thicket, utilising the forest or thicket floors; they also occur in dry forest and miombo savanna.

TABLE 9

HUMIDITY DATA FOR NGOYE FOREST AND COASTAL FOREST AT LAKE ST.LUCIA (MKWAKWA)

MONTH	% HUMIDITY									
	06h00		12h00		17h00		AVERAGE		RANGE	
	N	M	N	M	N	M	NGOYE	MKWAKWA	NGOYE	MKWAKWA
January 1977										
Inside	94,6	92,3	83,9	74,1	89,8	88,6	88,28± 7,93	76,15±19,93	71 - 96	59 - 100
April 1977										
Outside	92,0	96,1	60,9	63,3	79,0	82,9	76,5 ±17,79	80,77±15,74	44 - 100	51 - 100
Inside	91,2	90,9	84,0	76,0	87,0	77,8	87,14± 9,83	81,66± 9,46	58 - 100	59 - 100
June 1977										
Outside	82,5	95,2	47,8	55,9	81,0	81,1	69,88±20,96	71,0 ±19,17	38 - 100	35 - 100
Inside	88,6	91,3	75,3	62,8	86,5	74,4	83,69± 8,85	77,43±14,42	65 - 100	44 - 100
August 1977										
Outside	65,0	86,7	51,7	52,1	69,0	72,5	64,28±18,73	71,0 ±18,09	27 - 94	36 - 97
Inside	87,8	87,9	70,2	64,5	81,7	78,9	79,88±12,72	74,67±17,77	53 - 94	49 - 97
October 1977										
Outside	84,7	87,1	54,6	59,9	80,2	75,9	74,24±16,76	75,09±13,81	37 - 94	48 - 100
Inside	89,0	83,0	64,8	61,8	84,0	71,2	79,93±13,20	72,97±12,17	52 - 92	56 - 96
December 1977										
Outside	88,8	-*	66,2	-	85,6	-	80,14±14,32	-	48 - 99	-
May 1978										
Outside	79,3	93,4	59,3	61,7	78,7	76,8	67,04±22,05	78,57±15,39	19 - 97	39 - 100
Inside	88,0	90,4	71,9	71,5	87,7	76,3	83,03±13,11	79,76±12,71	43 - 94	55 - 99
Levels of significance for measurements inside the forests (t-tests for paired statistics)										
	NS		$p < 0,05$		$p < 0,025$					

*There was no visit to Mkwakwa forest in December 1977

TABLE 10

HUMIDITY INSIDE NGOYE FOREST AND COASTAL FOREST AT LAKE ST.LUCIA, (MKWAKWA) AS A PERCENTAGE OF HUMIDITY OUTSIDE THE FOREST IN SHADE

MONTH	06h00		12h00		18h00	
	NGOYE	MKWAKWA	NGOYE	MKWAKWA	NGOYE	MKWAKWA
March 1977	99	95	138	120	110	94
May	107	96	158	112	107	92
September	135	101	136	124	118	109
November	105	95	119	103	105	94
May 1978	111	97	121	116	111	100

TABLE 11

DEFINITION OF THE HABITATS OF THE FOUR SQUIRREL SPECIES (HABITATS FOLLOWING TINLEY, 1975)

FOREST

Stratified, closed woody plant community dominated by trees, usually with two woody plant strata including the upper canopy of trees, and containing many synusiae. Seedling stages of canopy trees, subordinate tree and shrub layers, and understorey including some specialized grasses are typically sciophytes. Mostly ever= green but Dry Forest types are semi-deciduous. Fire does not pass through forest.

THICKET

Usually stratified, very dense, almost impenetrable tree and/or large shrub community. Climbing and scandent plants are often common. Grass usually discontinuous or absent. Thicket can be primary or secondary, tall or short, non-thorny e.g. coast bush, or thorny. Shorter than 3-4 m should be referred to as scrub-thicket. Secondary thicket is the typical mature cover of post-cultivation sites and on overstocked areas. In moist areas thicket is seral to forest. Fire passes through deciduous thicket but not through evergreen thicket.

WOODLAND

Stratified or singly storey stands of trees with crown of trees spaced from less than one crown diameter apart, to crowns interlocking or overlapping. With shrubs, grassland and/or forb groundlayer. Components of this and savanna types are mostly heliophytes. Fire passes through most of these types. Tropical examples include Brachystegia savanna woodland, C.mopane savanna woodland. Woodlands also occur in riverine sites.

SAVANNA

Stratified stands of trees spaced from about three crown diameters apart to crowns overlapping where aggregations occur. With shrubs, grass and/or herb groundlayer. The spacement of trees is intermediate between woodland and open tree savanna.

Sherry (1977) reports from south east Rhodesia that the typical squirrel of the drier parts is. P.cepapi① and that P.palliatus② inhabits the following habitats: Brachystegia glaucescens woodland; Androstachys johnsonii woodland/thicket; riverine and alluvial woodland. He found the common feature in these latter habitats to be: a dense upper storey of mature trees, giving shade, and an understorey of dense shrubs often forming a thicket. He was working outside the range of evergreen montane forest in a 400 - 600 mm mean annual rainfall regime. In the hot season daily temperatures frequently exceeded 40°C. He suggests that the red squirrel is primarily a low altitude woodland/thicket species and that the montane evergreen forests of eastern Rhodesia (≥ 1 000 mm of rain/year) provide suitable habitats on the edge of the species range. Tinley (1976) in his reconaissance of Tongaland recorded the species from coastal dune forest, coastal forest, sand forest and also in open and closed woodland. They also occur in dune scrub and dry sand forest.

The Ngoye red squirrel P.p.ornatus inhabits the Ngoye forest which comprises 2 900 ha at 300 to 450 m a.s.l. It is a humid, coastal, subtropical floristic type (Venter, 1969) and the Köppen designation of climate is Cfwa - see Table 1 (Schulze, 1947). Axelrod and Raven (1978) mention Ngoye forest as a particularly fine example of subtropical evergreen forest and Huntley (1965) states that it has affinities with tropical rain forest, evident from the climax forest physiognomy (buttressed roots, fluted stems, drip tips to leaves, cauliflorous flowers, and five recognisable strata: upper canopy 13,7 m to 19,8 m with the climax areas reaching up to 21,3 to 27,4 m. The canopy is continuous except for openings caused by fallen trees. Shrub and file layers are poorly developed, and there is a paucity of lianes and an abundance of epiphytes). Qudeni, the forested area only 42 km from Ngoye, is termed as a mistbelt mixed Podocarpus forest (Moll, 1972). He mentions two other types of montane forests, namely the montane Podocarpus and inland subtropical forest types of Acocks (1953), the latter at lower altitudes and further to the north and having a greater affinity with the tropical forests. Presumably he allocates Ngoye forest to this latter category. The Ngoye forest is unique in that it contains tropical elements which are only encountered at a much higher latitude in Africa, often only at the level of Melsetter but occasionally also a considerable distance further south in Pondo=land (see Chapter 11).

P.p.ornatus is confined to Ngoye forest but a similar although slightly darker squirrel is encountered at Melsetter (20°30'S, 32°40'E) and a slightly lighter one at Gorongoza (18°30'S, 34°50'E). Both the latter squirrels have been classified as separate subspecies, namely *swynnertoni* and *sponsus*.

✓

The Tonga yellow-chested squirrel *P.p.tongensis* occurs in Maputoland on the soutern tip of the Moçambique plain. The region is at the extreme north eastern end of the Republic of South Africa and is bordered by the Lebombo Mountains on the west, the Indian Ocean on the east, Lake St.Lucia in the south (28°S latitude) and the Moçambique border in the north - an area of about 6 400 km^2 (Tinley, 1976). Tinley also states that the major part of this area lies between 75 and 92 m a.s.l. and 69% is composed of deep loose, acid sand, covered mainly in a savanna and dry forest mosaic. The forest patches are of variable siz often longitudinal in shape - a tropical element unique in South Africa. Where subsurface impermeable horizons occur, enough moisture is trapped for the dense forests to exist. The hardpan horizon must not be at the surface which causes tremendous rainwater loss by sheet wash in mopane and tamboti clay soils. These stands of dense dry forest typically on the crests of rises meet the open savanna abruptly. Bayer (1938) describes the Tongaland forests as evergreen sub-tropical forest - or evergreen coast forest representing the climax of the coast belt vegetation.

Tinley (1976), classified these forests as follows:

(a) Forests on the Lebombos - transitional mountain evergreen forest (mixed tropical and temperate)
(b) Tropical dry forest and thicket on the sandveld
(c) Transitional coast evergreen forest, mixed temperate and

tropical, also on the sandveld and dunes.

Only a small portion of this distribution area supports forests suitable for <u>tongensis</u> habitation. An estimate of the proportion of squirrel habitat can be obtained from the classification of habitat on the eastern shores of Lake St.Lucia south of Lake Bangazi and north of the St.Lucia Game Park:

	Ha
Open water	6,34
Pine plantations	2736,22
Vleis within pine plantations	362,76
Indigenous forest patches within pine plantations	166,36
Dune forest	1081,33
Mesic forest (excluding patches within pine plantations)	563,05
Forest precursor	1243,07
Hygrophilous grassland	2712,78
Mangroves	4,61
Reedswamps and vegetated pans	3215,93
Swamp forest	455,73
Secondary grassland	2436,63
Clearings within forest area	50,76
Fire breaks	66,86
Sand blows	109,81

(This breakdown excludes the beach and the area of Lake Bangazi)

The area of habitat suitable for <u>tongensis</u> comprises the indigenous forest patches, forest precursor, dune and mesic forest areas, i.e. 3 053,81 ha or 20,07% of the total area above. But forest patches in pine plantations would probably not harbour squirrels, leaving 2 887,45 ha or 18,98% of the total area. If forest precursor is also excluded, 1 644,38 ha or 10,81% remains. If the dune and mesic forest habitats are calculated for a larger area along the eastern shores, i.e. up to Sengwane in the north, habitat suitable for <u>tongensis</u> then totals 4 878,53 ha or 20,08% of this area of 24 293,32 ha. The dune forest occurs as a continuous belt hugging the coast line, but the mesic forest is distributed in patches with an average size of 21,72 ± 19,09 ha (n = 40).

The yellow-footed bush squirrel *P.cepapi* occurs from Zambia and Tanzania (Amtmann 1966) in the north and almost reaches the Angolan coast in the west (Kingdon 1974). In the south west it sometimes overlaps with *F.c.congicus* in S.W.A./Namibia but is mainly distributed along the east of the Etosha saline (Viljoen, 1978). In Moçambique according to Smithers and Lobao Tello (1976) the species has a wide distribution in savanna of the central parts of the Lourenço Marques District (although absent from the Incomati River southwards in the Lebombo range of hills), to the Tete district and into the southern parts of the Zambezia district; it occurs throughout the central and southern provinces of Malawi and it might, therefore, be expected to occur more widely in the Zambezia district and into the western parts at least of the Moçambique district. However, Kingdon (1974) points out that in the latter regions *P.flavivittis* most probably occupies the niche of *P.cepapi*. In Botswana *P.cepapi* is widely distributed throughout the northern parts of the territory, wherever there is suitable woodland habitat (Smithers, 1977), but it is absent in the open grassland of the southern part of the Makgadikgadi pans. In the Transvaal it occurs widely in the north down to Rustenburg (25°38'S, 27°16'E) in the south west and to the Olifantsriver in the east. They do not occur in Swaziland or south of Maputo on the Moçambique plain. The subspecies studied here is restricted to the Transvaal southern Botswana and the southern part of Rhodesia (Roberts, 1951).

Kingdon (1974) found that in East Africa the species is numerous in mixed woodland and thicket that grows on stony, hilly country and found that they must be either limited or encouraged by absence or presence of holes in trees. Wherever annual fire is a hazard (as occurs over most of their range) this consideration must be particulary limiting. In Botswana, Smithers (1971) indicates the habitat as woodland, includin *Colophospermum mopane*, riverine, *Acacia* and miscellaneous woodland with *Acacia*, *Terminalia* and *Combretum*, including *Sclerocarya caffra*, Combretum imberbe, etc. They were absent in Baikiea woodland which covers a large area on Kalahari sand immediately south of the Chobe River. In the Transvaal the species is widely distributed in the north in woodland and thicket but is limited by the number of suitable nest-holes. In Moçambique Tinley (pers.comm.) found the species in the woodland and savanna regions, but in the thickets and forested areas it is replaced by P.palliatus.

F.c.congicus, the western striped squirrel, is distributed in the Arid Savanna moisture province of the Interior Plain of S.W.A./Namibia (Tinley, 1971), and has been mapped by Tinley (unpubl., 1970 - included here in Figure 1). He shows that the bush squirrel intrudes from the east (Botswana) reaching its most westerly distribution points at Otavi (19°45'S, 17°20'E) in the south and at Ruacana falls (17°20'S, 14°15'E) in the north. At these two localities the bush squirrel overlaps with the striped squirrel. However, inbetween, the bush squirrel occurs around the east of the Etosha saline, and the striped squirrel along the west. There is a large amount of overlap in western Ovamboland, where the striped squirrel extends as far south as the forest belt between Ondongua and Ukuambi (Shortridge, 1934) and also just north of the S.W.A. border where the striped squirrel follows the Kunene River and the bush squirrel occurs up to Mossamedes and Capelongo close to the coast (Hill and Carter, 1941). In regions of overlap, the two species can be found in the same tree (Shortridge, 1934).

The genus Funisciurus ranges as far north as Southern Tanganyika and Sierra Leone, and through the Northern Congo to Lake Tanganyika and Ruwenzori in the east; the species which concerns us here, occurs up to the Congo River where the type specimen was collected (Shortridge, 1934). Amtmann (1966) mentions them in the Katanga district of the Congo and says that they are probably to be found in eastern and north-eastern Angola. The species is numerous in the west of Angola (Hill and Carter, 1941) and it occurs right up to the seaboard as far south as Benguela and then south-eastwards down the mountain range in Kaokoland to the Ugab River (20°45'S, 15°15'E) (Coetzee*, pers.comm.)

From there is follows the mountain range eastwards with the C.mopane and Commiphera/Kirkia vegetation types mapped by Tinley (1969).

Walker (1964) notes the genus in palm groves, palm scrub, savanna and in forests up to 2 175 m. Hill and Carter (1941) describe the striped squirrel from plateau country in Angola but also right up to the edge of the desert. On the coast, he notes them as common in the palm groves, in the bushes of the savanna and also in the trees on the sides of the cliffs. Shortridge (1934) notes that they prefer mopane and mixed forest, as well as dry river courses where the trees attain a larger size than elsewhere. Tinley (pers.comm.) associates them with granite outcrops, and not with open plains; and Schlettwein[x] (pers.comm.) has also seen them frequently along dry water courses and on rocky out=crops, especially where some large trees are to be found close to these koppies. Both Schlettwein and Tinley surmise that the animals move seasonally, occurring in the wet season on the koppies and in the dry season along the river courses.

Giess (1971) maps mopane savanna (his vegetation type 5) and mountain savanna and karstveld (his type 6) over this region; and the more detailed description of De Sousa Correia (1976) of the Kaokoland, indi=cates Colophospermum/Spirostachys savanna; C.mopane/Terminalia prunioides/Acacia spp. savanna with Terminalia sericea, Lonchocarpus nelsii, Combretum apiculatum, C.imberbe and Kirkia acuminata; C.mopane/T.prunioides savanna, sub-desert steppe with C.mopane and T.prunioides; and escarpment area with rocky hills (his types 9,10,12, 13&14). Overlap between the two squirrel species occurs in his vegetations types 2,3&4.

DISCUSSION

It is apparent that the two subspecies of P.palliatus occur in a more moist habitat (higher rainfall and greater humidity) and that the extre=mes of temperature are not as great as in the open habitats of P.cepapi and F.congicus. The latter species inhabits a region which is more arid than that of P.cepapi even though they do overlap in certain areas.

[x] Mr C.A. Schlettwein, Otjitambi, P.O. Outjo, S.W.A.

(See Chapter 7 for a discussion of climatic adaptation of the four species).

Establishment of the subspecies of P.palliatus on the eastern seaboard relative to prehistoric geology and climate:
There is a precipitous falling off of the tropical fauna in the Lake St.Lucia area and the appearance of non-tropical elements for which nothing in the way of habitat, rainfall, temperature, predators or prey can account per se; it can only be interpreted in the light of the faunal pattern shifting with oscillations in the general thermal pattern (Poynton, 1961). When considering the present fauna of the KwaZulu region, both geological and climatological (temperature and rainfall) changes of past periods indicate restriction of fauna and flora to certain areas. The extant families of mammals arose in the Tertiary (Cracraft, 1974) and the present biotic pattern of South Africa is of Pleistocene origin (Balinsky, 1962; Stuckenberg, 1969). Stuckenberg (1969) concludes that it must have been established in the 14 000 years since the recession of the last glacial, when the tropical fauna could extend back into country from which it had previously retreated.

GEOLOGY

King (1963) states that there has been little physiographic change in Africa since the mid-Miocene (25 million years B.P.). The last great tectonic movement occurring in the late Pliocene, was a powerful outward tilting of the whole province of Natal. The Cretaceous and Pleistocene marine formations on the KwaZulu coast, extend inland as far as Mtubatuba and the foot of the Lebombos (King and Belderson, 1961). Hobday (1965) mentions that during the Eo- and Oligocene the sea presumably retreated beyond the present coastline; the early Miocene marine incursion was followed by renewed end-Miocene uplifting and tilting. The Pliocene sea extended far inland, bevelling the whole Zululand plain. During the maximum retreat of the sea corresponding to the Wurm Glacial stage (last Glacial) the shoreline was probably close to the edge of the continental shelf. Then again there followed advance and recession of the sea. Advance-retreat oscillations of the sea on the coastal plain also occurred 130 000 to 75 000 years ago and the St.Lucia barrier originated in the penultimate Saalian glaciation. To the east of Lake St.Lucia, the topographical features appear consistently younger than to the west.

As the Miocene sea transgressed, a deltaic sandbank is believed to have formed at the mout of the ancestral Umfolozi River (Hobday, 1965). There was a bay six miles wide at the mouth of the Umfolozi River 4 800 years ago. Some tropical species of plants extend only to the northern side of what was, until the agricultural era, a vast marshy area around the lower length of the Umfolozi River on the coastal plain just south of Lake St.Lucia (Stuckenberg, 1969). This is also the area where the distribution of tongensis ends abruptly on the Maphelane dune, to the south of which the Umfolozi River must have emptied into the sea. The rivers to the north (Mkuze, Mzenene, Hluhluwe and Nyalazi) did not alway cross the dune barrier but the Umfolozi River flowed strongly enough to do so (Hobday, 1965). The distribution of tongensis on the coastal plain is determined by the marine incursions, the last time that the sea receded being late in the Pleistocene. During the Wurm Glacial 20 000 years ago, the shoreline would have retreated far out on the continental shelf. (± 20 ft drop in s.l. 5 000 to 7 500 B.P.). There was a subsequent post-glacial rise of sea-level and when the sea-level receded again and the lagoon system became entirely sealed off from the sea. This is probably when the forest spread to Maphelane.

However, ornatus very probably entered the Ngoye forest during an earlier period. Ngoye forest lies on pre-Cretaceous rocks (Orme, 1973), and Van Wyk (1963) mentions that the oldest rocks of Natal in the south lie in the Nkandhla region (just south of Ngoye). Frankel (1960) also states that the major fault to the north of Empangeni (which is just north of Ngoye), the Eteza fault, between the Basement rocks and the Stormberg basalts, which trends north-east from near Empangeni into the Umfolozi area, is post-basalt and probably pre-Cretaceous in age. In this region the coastline has not shown major shifts since the Cretaceous period.

CLIMATE AND VEGETATION

As regards temperature, Stuckenberg (1969) considered the drop in mean temperature during the last hypothermal to be 5°C and calculated Effective Temperature (ET)throughout southern Africa. ET takes into consideration mean annual range of temperature and the length of the warm season or breeding period. The probable 15°C ET isoline of the previous hypothermal includes the distribution of *P.palliatus* where today the 17°C ET isoline encompasses the *palliatus* distribution. He considers ET as a more important measure of limiting factors than mean temperature as do Poynton (1964) and Bass (1966). The latter also considers frequency of breeding nights (temperature above 20°C) crucial for survival of Amphibians and find a considerable reduction from St.Lucia southwards. The distribution of tropical snakes is also determined by the 15°C ET isoline of the hypothermal (Stuckenberg 1969) which would have restricted them to the Limpopo Valley, eastern Lowveld and Zululand in the hypothermal. The present 15° ET isoline as mapped by Stuckenberg could be the factor determining distribution of *P.cepapi* in southern Africa.

Northern Africa, which was near the equator in the Cretaceous, was covered in forest from coast to coast. Since many of the taxa of subtropical evergreen forest range widely to the north, contributing to tropical forests, a wider, more continuous distribution is implied for them prior to the spread of dry climate (Axelrod and Raven, 1978). Moreau (1952) infers from avifauna that the differentiation of the lowland forest biome from savanna is probably the oldest on the continent (at least Miocene) and the differentiation of lowland from montane forest almost as old. He finds that the relationships between the Usambara Mountains in Tanzania and Namuli Mountain in northern Moçambique (dark forms of *palliatus* occur on both these mountains) indicate unavoidably that there was free interchange of montane forms at some stage of the Pleistocene. In both bird and plant species there are similarities between West and East African lowland forest at the generic level and the extensive differences at the specific level sugges that the original free interchange stopped perhaps early in the Pleistocene giving a period of half a million years and upwards for the specific differentiation of avifauna. Moreau states that this is in accord with estimates for differentiation of mammals and insects.

Carcasson (1964) states that the South African forest fauna suggests that forests have not covered any significant portion of the country since the Miocene. He also dates the connection between East and West African forests to the Miocene whereas Misonne (1963) takes this connection back to the Oligo-Miocene. Wild (1967) states that 46% of the flora of the Chimanimani Mountain is endemic, and that the period during which the Cape flora was continuous, is thrown back to the early Tertiary. Axelrod and Raven (1978) date the isolation of the Knysna forest to the Miocene, and Stuckenberg (1962) concludes that the last occasion when the Lesotho Highlands and Cape Fold Mountains were continuous to share a common fauna, must have been during the mid-Miocene at the latest. But Axelrod and Raven (1978) say that even during Pleistocene pluvials, temperate rainforest expanded greatly in southern Africa as shown from records near Cape Town.

Bigalke (1968) says that no mammals are endemic to any of the relict lowland forest islands on the east coast, and the relicts can only have been in contact with the main body for short periods during the Pleistocene. However, the subspecies of *P.palliatus* isolated on these lowland islands differ widely e.g. on the Usambaras (*Paraxerus vexillarius*), Namuli Mountain (*P.vincenti*), Chimanimani Mountain (*P.p.swynnertoni*) and Ngoye forest (*P.p.ornatus*); and Carcasson (1964) with regard to butterfly distribution, found most of the species in the eastern forests were either endemic species or very distinct subspecies representing genera which are much better developed in the western forests. He concluded that this situation arose as a result of:

1 No broad connections since the uplifting of the eastern plateau some time in the Miocene;
2 Subsequent connections, particularly the more recent ones of the Pleistocene, must have been short-lived and on a narrow front (probably between Lake Tanganyika and Lake Nyassa);
3 The forest refuges on the east coast (Usambara, Uluguru and Nguru Mountains) were probably much smaller than the western refuges.

There is also a much greater diversity of squirrels in West Africa, where e.g. nine species occur in a Gabon rain forest (Emmons, 1975).

Squirrels are known in the fossil records of Eurasia and North America from the late Miocene, and forest connections between Africa and Eurasic existed in the late Oligocene and early Miocene, but this region then became relatively dry. Kingdon (1974) therefore concludes that squirrels probably invaded Africa in the Miocene. Miocene records do exist of sciurids from east and central Africa (Vrba*, pers.comm). Tinley (1967) states that it is probable that a high rainfall route was available on the KwaZulu coastal plain since Mio-Pliocene or early Pliocene, but after this period the climate became drier or more variable disrupting the Evergreen forest cover, allowing a long enough time for endemism to occur. And since the arid Limpopo and Zambezi intervals are older than the Quaternary (King, 1951; Stuckenberg, 1962) it seems probable that the forest connections were of Mio-Pliocene time:

Axelrod and Raven (1978) conclude that there was a spread of drier climate in the early Miocene and state that there were at least two periods of rapid speciation in South Africa. The first in the Miocene with broad warping and uplifting of Africa and the second resulting fron Plio-Pleistocene deformation, and fluctuation in climate. Africa emerged from the last hypothermal 10 to 20 000 years ago (Morton, 1967; Coe, 1967; Livingstone, 1975; Axelrod and Raven, 1978; Simpson and Haffer, 1978). There is some dispute over whether this hypothermal coincided with the pluvial (Carcasson, 1964; Cooke, 1964; Livingstone, 1975). And it seems probable that there were major regional differences in climate and hence in vegetation following the early Miocene.

Axelrod and Raven's (1978) map of the Oligo-Miocene African vegetation

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*Dr E.S. Vrba Transvaal Museum, Paul Kruger St., Pretoria 0002 shows subtropical laurel forest from the Cape to northern Moçambique whereas their map of the late Mio- early Pliocene shows forest cut off at the bight of Maputo extending south of this. To the north in Moçambique, was savanna-woodland as at present. Could this possibly be why P.cepapi is distributed up to the bight of Maputo and no further south?

In the light of the climatological evidence, Ngoye forest has probably also been isolated since Miocene. Qudeni forest (±42 km west of Ngoye) is considered the northernmost temperate mistbelt forest (Afro-montane forest) by Moll (1972), and Ngoye forest as the southwestern limit of lowland subtropical forest (Werger, 1978). Ngoye, which has many endemics or clear subspecies, and the forests to the west (Nkandhla and Qudeni) were probably not connected since the Mio-Pliocene. Any possibl connection during the Pleistocene to the coastal plain must have been short-lived. It is also probable that the evergreen forest is not as Sherry (1977) suggests habitat on the edge of the range of the specie but rather that it is the original habitat of the species. And that the "low altitude woodland/thicket" subspecies are probably separate species that have evolved from the forest stock.

CHAPTER 3

DESCRIPTION AND MEASUREMENTS OF SOUTHERN AFRICAN TREE SQUIRREL SPECIES

INTRODUCTION

Eleven subspecies of P.palliatus have been described from the Moçambique plain by Amtmann (1966) (i.e. auriventris, barawennsis, bridgemani, frerei, ornatus, palliatus, sponsus, suahelicus, swynnertoni, tanae and tongensis). In addition, there are three species, P.lucifer, P.vexillarius and P.vincenti which have close affinities with, and which have on occasion been included in the palliatus group (Kingdon, 1974). Identification of P.palliatus subspecies has presented difficulties to various authors (Roberts, 1931; Kingdon, 1974; Smithers and Lobão Tello, 1976). The colour and size differences of the forest-isolated local populations have been the reason for the prolifically named subspecies. Wherever possible, descriptions and measurements of these have been included where relevant to clarification of the adaptations to habitat. Other species-specific characteristics of the four southern African tree squirrel species are included in this chapter.

MATERIALS AND METHODS

DESCRIPTION AND BODY MEASUREMENTS

Descriptions and body measurements were taken from museum skins (South African museum - 4, Queen Victoria museum, Salisbury - 36, Natal Museum, Pietermaritzburg - 4, Transvaal museum, Pretoria - 24, Blantyre museum - 2, Maputo museum - 13, Buluwayo museum - 4.), and various references (Roberts, 1951; Sclater, 1900; Ellerman, Morrison-Scott and Hayman, 1953; Amtmann, 1966 ; Smithers and Lobão Tello, 1976; Kingdon, 1974). Body measurements and distribution records from the present study for P.p.ornatus and P.p.tongensis have been included. Body measurements taken were ear, hindfoot (c.u.),total and tail lengths (Cockrum, 1955).

CRANIAL MEASUREMENTS

Cranial measurements taken from museum skulls and from skulls collected during the present study were according to Cockrum (1955), as follows:

1 Maximum length of cranium - The overall length from the anterior tip of the nasals to the posterior bulge of the brain case, mastoid bullae, or other structure making up the most posterior part of the skull.

2 Minimum interorbital constriction - The least distance across the top of the skull between the orbits.

3 Zygomatic breadth - The greatest distance across the zygomatic arches of the cranium perpendicular to the long axis of the skull, or the greatest distance between the outsides of the zygomata.

4 Cranial breadth - The greatest distance across the braincase immediately posterior to the zygomatic arches.

5 Nasal length - From a line connecting the anterior-most parts to a line connecting the posterior-most extensions of the nasal bones

6 Nasal breadth - Distance from most lateral point of one nasal to the corresponding point of the other.

7 Depth of cranium - Vertical distance from a line connecting the tips of the upper incisors with the most ventral portion of the posterior part of the cranium to the highest part of the cranium (taken with the help of a glass slide beneath the skull).

8 Length of the maxillary molar series - Distance from the anterior alveolus of the first premolar to the posterior alveolus of the posterior molar.

9 Mandibular toothrow - Same as for the maxillary tooth row.

MEASUREMENTS OF BACULA AND CLITORIDES

Phalli of three ornatus, two tongensis and two congicus and vulvae of four ornatus and three tongensis, which had been preserved dry with sodium fluorosilicate, were processed in two per cent KOH solution & stained with 0,003% Alizarin Red S dye according to Lidicker (1968). Measurements and sketches were made with an ocular micrometer using a stereoscopic microscope. Measurements taken were:

Bacula: Lateral width and length, ventral length and width and crest length and width

Clitorides: Lateral length and width, and ventral length and width.

INTESTINAL TRACT MEASUREMENTS

Lengths of stomach, caecum, large and small intestines could indicate degree of herbivory/insectivory (Rahm, 1972) and thus be species-specific, and were measured on freshly collected specimens (see Chapter 6).

HAIR SCALE PATTERNS

The scale patterns and cross-section appearances of hairs have been used to identify small mammals *(Keogh, pers.comm.). These aspects were investigated for tongensis, ornatus and cepapi.

RESULTS

Description and identification of the two South African subspecies of P.palliatus:

Roberts (1951) describes the Tonga squirrel as follows: "The dorsal general coloration from the forehead to root of tail is freckled brown and yellowish, owing to the admixture of annulations of dark brown or blackish and pale yellowish on all the hairs; the orange-yellow of the face embraces the snout and the area around and behind the eyes to the base of the ears; the hands and feet are yellowish above and below, the fore-arms with an external brighter patch as an extension from below, and similarly on the hind-limbs there is a brighter red patch the edges of the tail are decidedly redder than the underparts of the body; the orange about the face and under parts intensifies to orange reddish about the hind limbs and tail; the centre of the throat is whitish". According to Roberts, tongensis has more black-tipped hairs above and the red of the tail a darker shade than in auriventris (from three available specimens) in size rather larger, but the tail equally short. P.p.auriventris is described as having the colour of bridgemani (described from two specimens from Panda, near Inhambane) but that it is slightly smaller and with a much shorter tail. P.p.bridgemani is distinguished from sponsus by its paler colour and orange-bordered tail but the general body dimensions are as in sponsus (Roberts, 1951). P.p.sponsus has the tail a general rufous appearance

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*Mrs H. Keogh, Dept. of Medical Ecology, South African Institute of Medical Research, Johannesburg owing to rufous hair tips rather than a richly-coloured border. Colouring of specimens of *sponsus* from Bunga in the Gorongoza National Park closely resemble the colouring of *ornatus* which is described by Gray (1964) as follows: "back dark blackish grizzled; hairs red, with a broad black subterminal band and a white tip; head, legs, thighs, underside, and tail very bright red-bay; the hairs of the head, limbs and belly are red to the base and of the tail very vivid and dark red for more than half their length, the base, especially of those near the lower end of the tail, black, with two broad greyish bands". Roberts (1951) also adds that *ornatus* bears a close resemblance to *swynnertoni*, on the one hand, and *sponsus* on the other, the upper parts more rufous-tinted and lighter than in the former and much darker than in the latter, the red parts intermediate between the two; the tail wine-red, but the skull and general dimensions larger in nearly every respect; the hairs of the tail with three black bands as in *sponsus*.

During the present study it became clear that *ornatus* and *tongensis* are two different species, both ethologically (see e.g. Chapter 9), as well as with regard to size (Table 12) and colour. From examination of museum skins it seemed probable that *auriventris* should not be separated from *tongensis*. Thus, the artificial distribution limit of the Moçambique border will be eliminated It is also improbable that *bridgemani* is a different subspecies. Smithers and Lobão Tello (1976) group *auriventris*, *bridgemani* and *sponsus* together "in the mean time". However, it is apparent that *bridgemani*, *auriventris* and *tongensis* bear a close resemblance to one another and that *sponsus* is much darker and similar to *ornatus* and *palliatus*.

The original description of subspecies was based on very few specimens and it is doubtful whether nutritionally influenced parameters such as size are valid in such small samples. In addition, individuals were allocated to subspecies on colour differences which can be more obscure than changes due to moult which have been found to exist (e.g. in *ornatus*, see Appendix 1). Furthermore, the number of black bands on tail hairs was also used as a distinguishing characteristic, but it is not clear

TABLE 12

BODY MEASUREMENTS OF P.PALLIATUS FROM KWAZULU (SAMPLE SIZE IN PARENTHESIS, MEASUREMENTS IN mm, AND MASS IN g)

	HEAD AND BODY	TAIL	HINDFOOT (c.u.)	EAR	MASS	EVISC. MASS.
P.P.ORNATUS						
Adult	219,17(18)± 6,98	203,48(53)± 7,08	51,83(61)± 1,61	20,22(43)± 1,07	360,91(62)±18,30	
	225,08(12)±11,08	204,24(33)±10,64	51,79(42)± 1,89	21,15(32)± 2,48	378,93(42)±23,68	
Adult Total	221,53(30)± 9,16	203,77(86)± 8,57	51,81(103)±1,72	20,62(75)± 1,42	368,19(104)±22,37	306,1 (6)±20,29
Subadults	211,88(8)± 7,40	204,59(24)± 8,08	51,54(26)±2,18	19,98(22)± 0,72	313,6 (24)±32,25	271,75(2)± 0,35
Juveniles	196,0 (2)±22,63	197,67(3)± 6,81	44,75(5)±14,69	19,36(4)± 0,78	222,62(5)±44,29	
P.P.TONGENSIS						
Adult	184,0 (5)±12,63	176,02(13)± 7,87	43,49(18)± 1,58	19,63(16)± 1,50	207,45(29)±16,48	187,72(5)±17,45
	190,83(6)± 6,46	175,53(15)±10,23	44,26(18)± 2,0	19,26(16)± 1,47	210,60(31)±21,62	177,72(4)± 6,60
Adult Total	187,73(11)± 9,87	176,83(28)± 9,08	43,88(36)± 1,80	19,44(32)± 1,47	209,06(60)±19,24	183,28(9)±14,01
Subadults	185,33(6)± 9,85	172,20(10)± 8,47	43,23(19)± 0,91	20,18(8)± 1,12	178,63(24)±12,24	164,27(6)± 6,87
Juveniles	152	161,0 (6)± 6,96	42,47(14)± 1,66	18,40(11)± 1,60	139,69(13)±22,12	

whether the authors included the terminal black band which would give both ornatus and tongensis four instead of the three black bands recorded by Roberts (1951). Moreover, the black bands differ between juvenile and adult fur and can be counted wrongly in moulting adult.

In the comparison of mass and body measurements (Table 13), measurements from Roberts (1951) are not included as it was found on re-examining museum specimens, that he considered some subadults (obvious from juvenile fur) as adults. Furthermore, measurements from museum labels differed from those given in his publications, and cranial measurements also measured differently from those used in the present study.

The lighter shades of P.palliatus occur on the coastal plain and show a considerable variation in colour. Tinley* (pers.comm) separates the localities of the museum specimens from the Moçambique-plain into moist and dry habitat as follows:

Moist: Chipata lighthouse
Chitengo
Inhamitanga
Bunga, an Inselberg in the Gorongoza National Park
Coguno
Dry: Mabenje and Maringa on the north bank of the Save River
Zinave
Chiniziwa
Panda

The range of specimens from the above 'moist' forests consistently contain darker and slightly larger individuals. In Tables 13 and 16 the squirrels are arranged according to moistness of habitat and show a clear continuum of size from Ngoye forest with the dark ornatus to tongensis, the smallest. The colour variation is also exemplified in Maputoland where P.p.tongensis from the dry sand forest such as at Sihangwane and the shores of Lake St.Lucia, as well as from the Mseleni Mission station on the western shores of Lake Sibaya, are lighter in colour and mass than the specimens from the moist coastal forest as at Manguzi forest, Kosi Bay and Lake Sibaya's eastern shores.

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* Dr. K.L. Tinley, Poste Restante Nahoon, 5210

TABLE 13

BODY MEASUREMENTS OF THE *P.PALLIATUS* GROUP OF SQUIRRELS FROM MUSEUM SKINS (mm)

SPECIES	DISTRIBUTION	SAMPLE SIZE	HEAD/BODY	TAIL	HINDFOOT (c.u.)	EAR	MASS
P.vincenti	Namuli Mountain Moçambique Central	5	212,0 ± 5,87	209,0 ± 8,94	46,6 ± 1,95	21,1 ± 0,55	-
P.p.sponsus	Rhodesia, Southern Malawi						
	(a) Moist localities	11	202,45±13,31	210,29±13,35	50,73± 2,15	21,0 ± 1,12	280,83±38,33 (n = 10)
	(b) Dry localities	12	202,42±14,49	198,60±10,93	49,45± 2,30	20,04± 1,29	269, 5±46,65 (n = 4)
P.p.ornatus	Ngoye Forest	4	216,25± 6,5	221,5 ±11,96	50,75± 2,22	20,75± 0,96	-
P.p.swynnertoni	Mount Selinda	9	201,11±14,61	204,88±20,1	51,5 ± 2,88	19,80± 1,30	291,5 (n = 1)
P.p.auriventris	Magude, Lower Limpopo	4	192,50± 9,57	172,50±21,02	42,83± 1,89	-	-
P.p.tongensis	Manguzi Forest at Maputa	6	181,67± 4,08	175,0± 7,07	44,72± 1,34	15,38± 2,67	-

When comparing mean body measurements and mass of adults of the *Paraxerus spp*. from Table 13, it was found that *ornatus* is significantly larger than *tongensis* in all the measured parameters. On the head-body length and the eviscerated mass, t-tests for difference between two means were employed as the sample size is less than 30. The means differed significantly in both instances ($P < 0,01$). For the remaining measurements i.e. tail, ear and hindfoot lengths and mass, a z-test for difference between the two species was significant in all these parameters ($p < 0,01$). A similar situation exists between *ornatus* *cf*. *cepapi* and the three *Paraxerus* species *cf*. *congicus*. However, *cepapi* and *tongensis* are not very different in measurements. Indeed, measurements from populations of these two species from different localities e.g. *tongensis* from Lake Sibaya and from Lake St.Lucia (marginally larger and smaller populations, respectively) and of *cepapi* from the Limpopo River and from Naboomspruit (marginally smaller and larger populations, respectively) show that these two species do overlap (unpublished information). The difference between calculations of the tail length as a percentage of the total length was non-significant when comparing the *Paraxerus* spp, but significant when comparing the *Paraxerus* spp. with *congicus* (48:52% of total length) which uses it in thermoregulatory behaviour (see Chapter 7).

BACULA AND CLITORIDES

Sample size is small for *ornatus*, *tongensis* and *congicus*, and measurement cannot be tested statistically, but do suggest certain differences. (Table 14). The baculum of *Funisciurus* is more slender and slightly shorter than that of *Paraxerus* (Figure 9). However, the main difference lies in the appearance of the crest which runs with parallel sides and not with the curved lines of *Paraxerus*. Measurements from *cepapi* are consistently smaller than those of *P.palliatus*, but appearance in the latter squirrel is similar to that described for *P.c.cepapi* in Viljoen (1977b).

TABLE 14

MEASUREMENTS OF BACULA AND CLITORIDES OF SOUTHERN AFRICAN TREE SQUIRREL SPECIES (mm)

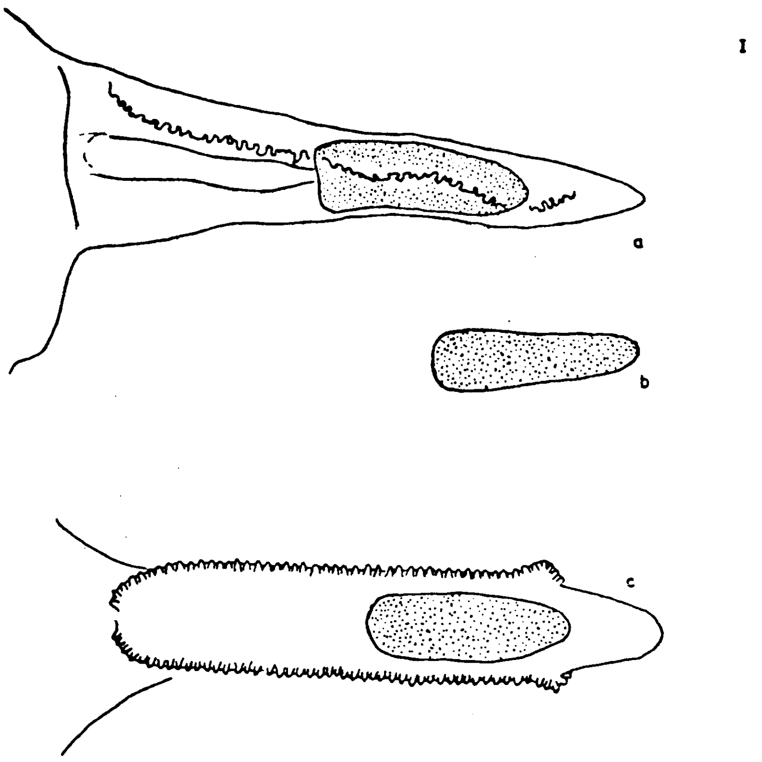
SPECIES		BONE				CREST	
		1*	2	3	4	5	6
BACULA							
Funisciurus congicus congicus		1,043	1,806	0,987	1,860	0,868	3,745
		0,062	1,240	0,072	1,872	0,955	3,329
P.c.cepapi (n = 12) (from Viljoen, 1976)		0,728	1,324	1,328	0,732	1,112	2,930
Paraxerus palliatus tongensis	T1	1,116	2,145	0,707	2,151	1,438	3,912
	T3	0,880	1,755	1,240	1,810	1,395	3,348
P.p.ornatus	N2	0,930	1,854	0,936	1,736	1,414	3,763
	N3	1,203	1,693	0,918	1,662	1,228	3,553
	N6	1,135	2,164	1,203	2,052	1,550	3,782

1* Lateral width, 2 Lateral length, 3 Ventral width, 4 Ventral length, 5 Crest width, 6 Crest length

CLITORIDES		1*	2	3	4
P.palliatus tongensis	T4	0,868	0,527	0,868	0,527
	TV	1,017	0,564	1,066	0,856
	T6	0,868	0,422	0,856	0,533
P.p.ornatus	N1	1,327	0,769	1,314	0,589
	N4	1,358	0,707	1,550	0,744
	N5	1,234	0,694	1,228	0,694
	N7	1,296	1,488	1,259	1,308

1* Lateral length, 2 Lateral width, 3 Ventral length, 4 Ventral width

Figure 7. Bony elements of the penis - baculum and bony ridge surrounding the phallus dorsally: I *Funisciurus c. congicus*, II *Paraxerus p. ornatus* - lateral (a), ventral (b), and dorsal (c) views. (enlargement 3 x 10^3).



Bony elements in the penis: I *F. c. congicus*, II *P. p. ornatus*
[a - lateral, b - ventral, c - dorsal view]

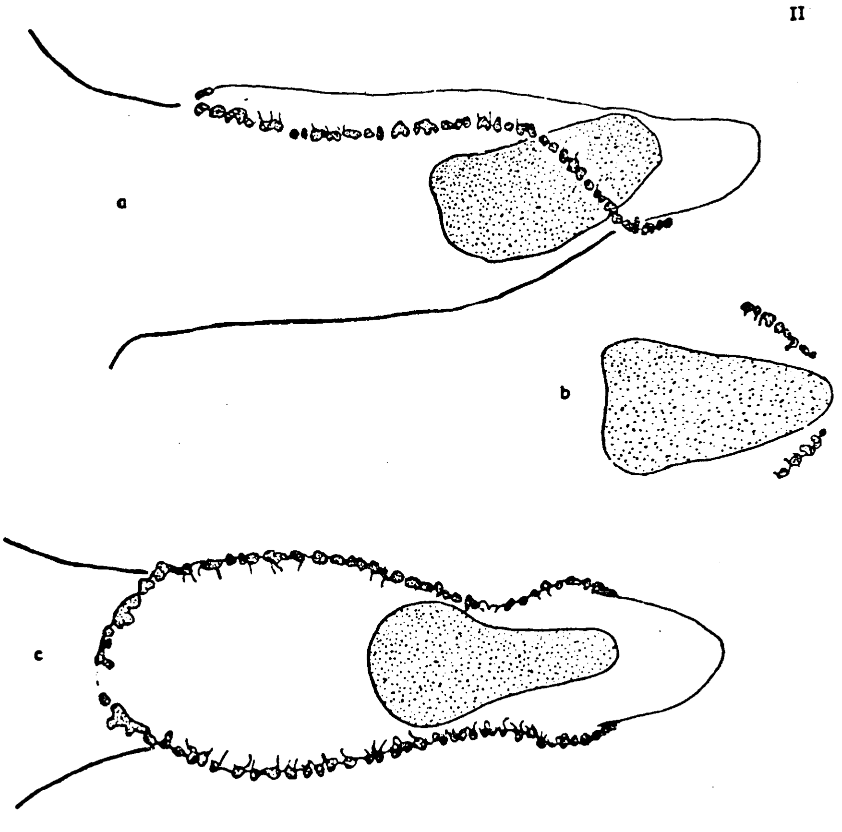
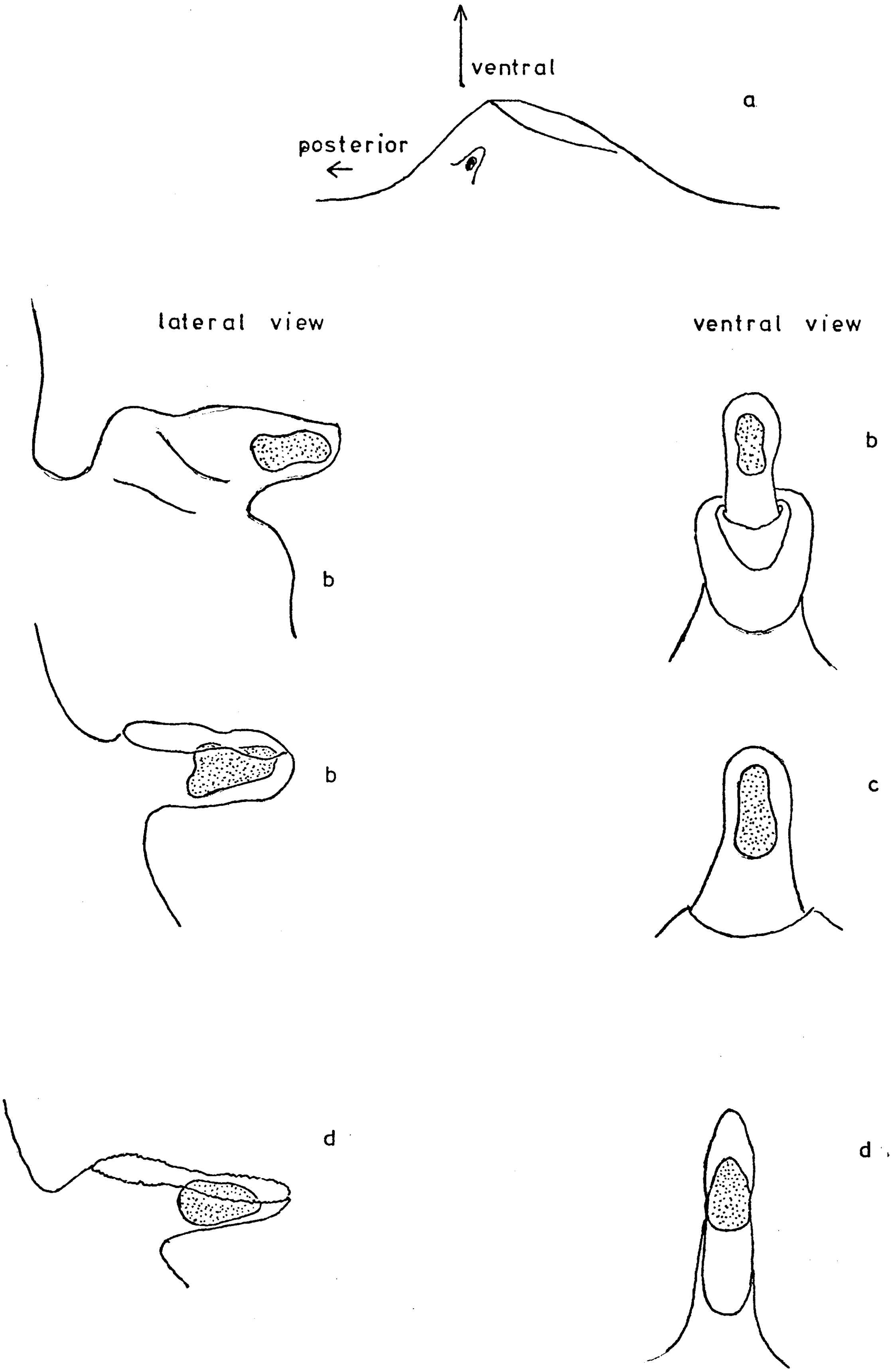


Figure 8. Position of clitoris (a), and clitorides of *Paraxerus p. tongensis* (b), *P.p. ornatus* (c), and *Funisciurus c. congicus* (d). (enlargement 1,5 x 10^3)


ventral
posterior
a
lateral view
ventral view
b
b
b
c
d
d

Clitorides (Figure 10) measured and sketched for tongensis and ornatus are larger in the latter squirrel.

INTESTINAL TRACT MEASUREMENTS

Measurements for P.p.tongensis and P.p.ornatus differed significantly, and are shown and discussed in Chapter 6.

HAIR SCALE PATTERNS

Descriptions of cross-sections and cuticular scales are illustrated in Table 15. The small medulla in the cross-sections and the difference in the scale margins distinguishes P.c.cepapi from P.palliatus but ornatus and tongensis cannot be separated on hair scale patterns alone.

DISCUSSION

Identification and description of the other species and subspecies of the East African red squirrel group is relevant here, to place the two southern African subspecies in perspective. The tree squirrels of southern Africa are represented by the genuses Heliosciurus, Paraxerus and Funisciurus. Heliosciurus rufobrachium occurs in Moçambique and part of Rhodesia, and is distinguished from Paraxerus by having 4/4 cheekteeth instead of 5/4. Paraxerus is represented by the bush squirrel P.cepapi (10 subspecies have been described) which is widely distributed in woodland across southern Africa. (Figure 1), by P.flavivittis (four subspecies) the eastern striped squirrel in north-eastern Moçambique (where it possibly replaces P.cepapi) and P.palliatus, the east African red squirrel, in dense vegetation on the Moçambique plain. The third genus Funisciurus penetrates southern Africa in the west in S.W.A./ Namibia and Angola - i.e. F.congicus congicus, the western striped squirrel, which has a similar separation on cheekteeth from Heliosciurus, but is distinguished from Paraxerus by the cheekteeth being more specialised, those of both upper and lower jaws being more or less flat-crowned in adults; females of Funisciurus have two pairs of mammae whereas those of Paraxerus and Heliosciurus have three pairs (Amtmann, 1966). Kingdon (1974) argues that the distinction of "more or less" flat-crowned teeth is not acceptable for differentiating between Funisciurus and Paraxerus and that nipple counts are

TABLE 15

IDENTIFICATION OF HAIR OF TREE SQUIRRELS, PARAXERUS SPP.

PARAMETER	P.C.CEPAPI	P.PALLIATUS ORNATUS	P.P.TONGENSIS
Cross-sections Rump Tail	Round. Small medulla. Round and some oval. Small medulla	Round. Large medulla. Round. Large medulla.	Round. Large medulla. Round and some oval. Large medulla
Cuticular scale pattern at 1/2 way mark (All hairs)	Irregular waved mosaic. Haphazard appearance.	Irregular waved mosaic. Scales placed in horizontal axis.	Irregular waved mosaic. Shorter thicker hair than P.palliatus ornatus
Scale margins	Rippled-crenate	Smooth	Smooth crenate towards tip
Distance apart of scales	Near	Near	Near

The small medulla in the cross-sections and also the difference in the scale margins distinguish cepapi from palliatus

TABLE 16

CRANIAL MEASUREMENTS*OF SUBSPECIES OF TREE SQUIRREL, P.PALLIATUS (mm)

SAMPLE SIZE	SPECIES	1*	2	3	4	5	6	7	8	9
11	P.p.ornatus	50,94±1.63	15,06±0,76	29,35±1.34	21,74±0,43	7,39±0,40	14,95±0,66	20,72±0,67	9,89±0,68	9,82±0,25
5	P.p.vincenti (from Hayman, 1950)	50,44±0,38	15,64±0,23	29,82±0,33	-	-	14,33±0,67	-	9,12±0,13	8,92±0,13
9	P.p.swynnertoni	48,44±0,90	14,35±0,91	28,38±0,48	21,06±0,45	7,04±0,39	14,00±0,61	20,31±0,37	9,02±0,14	9,30±0,34
1	P.p.frerei	51,20	15,40	29,50	22,75	7,25	16,45	21,85	-	-
1	P.p.lucifer	55,03	14,85	31,60	22,95	8,15	16,25	22,95	10,35	11,10
7	P.p.sponsus °a	47,91±1,46	13,65±0,59	27,95±1,26	20,72±0,34	7,11±0,43	14,23±0,84	19,98±0,67	-	-
5	°b	49,52±1,15	14,17±0,45	28,73±0,55	20,87±0,64	7,64±0,52	14,82±0,41	20,84±0,59	-	-
13	P.p.tongensis	45,3 ±0,83	13,23±0,35	26,27±0,61	20,45±0,27	6,62±0,32	13,04±0,21	19,08±0,53	8,55±0,53	8,15±0,25
	TM6084	44,95	13,55	26,00	20,25	6,90	12,70	19,45	8,20	
	TM2367	-	12,70	25,75	19,90	-	-	18,95	7,80	

*1 Maximum length of cranium
2 Minimum interorbital constriction
3 Zygomatic breadth
4 Cranial breadth
5 Nasal breadth
6 Nasal length
7 Depth of cranium
8 Maxillary toothrow
9 Mandibular toothrow

°a= from dry forest at Chiniziwa, Zinave, Beira, Maringa and Mobenje on north bank of Sabi River
°b= from moist forest at Gorongoza, Inhamitanga, Chitanga, Chipata Light House

The measurements of two type specimens in the Transvaal Museum were : TM6084 - P.sponsus tongensis,
TM2367 - P.bridgemani auriventris
indicates the latter slightly smaller than the typical P.p.tongensis

often inconsistent. However, sciurid cheekteeth show conservatism (Moore, 1959) and in the generic arrangement Thomas (1909) states the following:
"*Funisciurus*: Lower molars regularly and deeply ridged, without high cusps; cheekteeth are hypsodont, rounded in section; lower molars consisting of four well-marked transverse ridges, subequal in height, with well-defined (usually blackened) clefts between them; no individual cusps much surpassing the general level of the teeth; the teeth of *Funisciurus* are very highly specialised, far more so than in *Paraxerus* and may be readily recognised by these characters and by the elongated skull with long muzzle;
Paraxerus: Lower molars irregularly ridged with high cusps; molars rather hypsodont and with a tendency to the development of transverse ridges found in *Funisciurus*, but less specialised than those of the latter; lower molars similarly with four transverse ridges, but these are irregular in development and shape, and are considerably surpassed in height by the lateral cusps, especially that at the antero-internal corner of each tooth. Skull less elongate and rounded with the muzzle intermediate between that of *Funisciurus* and normal squirrels. Ante-orbital foramen and zygomatic ridge as in *Funisciurus*". Indeed, Kingdon (1974) also shows the elongation of the skull of *Funisciurus* in his sketches, and the discrepancy in the number of nipples that he found, occurred in one specimen of *F.carruthersi*, which certainly does resemble *Paraxerus palliatus* in voice, colour, tail length and shyness, rather than *Funisciurus*. This one species should possibly have been classified as *P.palliatus*.

Kingdon classifies *Paraxerus* as a subgenus of *Funisciurus*. I have retained it generically separate as a result of the extreme differences between them in our region. But Kingdon's classification and explanation of the evolution and hybridisation is probably close to the truth.

A closer look at the subspecies of *Paraxerus* elucidates aspects of the two KwaZulu squirrel species. In *Paraxerus* there is much confusion between species and subspecies which is evident from the nomenclature:

Heliosciurus lucifer of Ellerman (1940) is now *Paraxerus lucifer* (Amtmann, 1966; Kingdon, 1974). *Paraxerus cepapi auriventris* (Roberts 1931, is now accepted to be *P.palliatus auriventris* (Roberts 1951, Amtmann, 1966). *P.p.auriventris* has a pale orange belly with a back almost like the dark *cepapis* from Zinave - it does indeed look like a hybrid between *cepapi* and *palliatus tongensis* and has unpigmented foot-soles (excluding the pads) similar to those of *cepapi*, whereas *palliatus* has pigmented footsoles (See Figure 19, Chapter 9). Smithers and Lobão Tello (1976) suggest that *Paraxerus vincenti* should be *P.palliatus vincenti*, whereas Amtmann (1966) states that *vincenti* is possibly inclusive in the species *P.vexillarius* and *P.v.byatti* (the latter two from the mountain forests in central and eastern Tanzania). It is a pity that no indication of habitat is given on museum labels. *P.p.bridgemani* is described inland from Inhambane (Swynnerton and Hayman, 1950) and also from south-eastern Tanzania (Amtmann, 1966) This latter locality is disputed by Smithers and Lobão Tello (1976) who state that this must surely be incorrect as the type of locality of the nominate form is just south of the Rovuma River, the border with Moçambique in this sector, and they therefore restrict the lighter coloured *bridgemani* and all the light coloured subspecies to the south of the Save River. However, the two specimens in Tanzania (i.e. *palliatus* and *bridgemani*) could have come from two completely different habitats, and one specimen from the museum collected at Pinda Peninsula on the coast (14°10'S), by J.L.B. Smith is extremely light-coloured albeit bright. In addition, one of the darkest forms, *ornatus*, is the most southerly species in Ngoye forest. Specimens of the nominate *P.p.palliatus* were not available for this study, but are listed from north-eastern Moçambique (Amtmann, 1966) and central and southern Malawi (Sweeney, 1959). Lawrence and Loveridge (1953) describe *P.p.palliatus* from Malawi as probably being the same as that described previously from north-eastern Moçambique at 11°S and 15°S, but state that the Malawi specimens are markedly more ochraceous, or less red, and Neumann (1902) describes *palliatus* as having a chestnut red ventrum and tail. Evidence therefore seems to signify that *palliatus* is a dark form, and it is more likely that it should be grouped with *sponsus* than with *bridgemani* and *auriventris* as by

Smithers and Lobão Tello (1976).

P.p.sponsus is described from Coguno, Inhambane district (this is a moist forest) but is said to occur up to Beira. Thomas and Wroughton (1907) describe sponsus as a Funisciurus intermediate in size between cepapi and palliatus with the colour pattern of the former and the bright colouring of the latter. The size, particularly the skull, is rather smaller than in palliatus. They include tongensis in the species sponsus as it "agrees in all essential characters with the present species (i.e. sponsus) to which we have no hesitation in assigning it". They separate ornatus from the above two species.

On the Moçambique plain the suitable P.palliatus habitat (i.e. dense thickets or forests) occurs in isolated geographic islands of vegetation completely separated from neighbouring islands (see Chapter 2). They exhibit an amazing spectrum of colour variation on the ventral surfaces, face and hands, from very pale orange, through varying shades of yellow and orange to red. Near Inhambane two subspecies have been described within 40 km. If habitat is brought into consideration this colour variation can be better understood. It seems a clearcut case of dry and moist habitat influencing colour and size, with the light-coloured and smaller squirrels (tongensis and auriventris) found in dry forest; the two populations of sponsus being intermediate in the dry and moist forest; while the largest forms are present in the ever=green forest, i.e. P.p.ornatus, P.p.swynnertoni, P.vincenti, P.lucifer and P.vexillarius. (Ngoye forest, the Mt.Chirinda forest and Gorongoza where the Bunga Inselberg occurs, are all on old soil - Jurassic/Cretaceous, whereas the coastal plain is on early sands - Pleistocene, and could be swamped again by a rise of 100 m of sea level (Tinley, pers.comm.)* Therefore, the lighter forms have probably evolved from the darker species. As a result of being completely isolated for long

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*Dr K.L. Tinley, Poste Restante, Nahoon, 5210 periods, these darker squirrels are easily distinguishable and have occasionally been accorded specific status. If they had all been classified as *P.palliatus* subspecies one would have had a clearer pictur of the original radiation during pluvials when forest vegetation was mor widespread. With the subsequent disappearance of forest connections, the squirrels were isolated in forest refuges, but simultaneously spread down the coastal plain as the sea receded.

Ingoldby (1927) illustrated a very similar colour range related to habitat in *Heliosciurus*. He found that from inspection of a specimen he could in many cases not infer the geographical locality, but the type of country from which it came, i.e. regarding rainfall, vegetation, temperature and altitude. The same form had been ascribed several different names in various parts of its distributional range, merely because the patches inhabited were not continuous. The deeply coloured, large forms occurred in patches corresponding well with distribution of heavy rainfall and rain-forest, and wherever the bush was thinner and the ground lower, forms were slightly smaller and paler, and on the savanna little pale squirrels were to be found.

CHAPTER 4
HABITAT ANALYSES

INTRODUCTION

A description of habitat is essential to clarify the adaptive strategies of the four squirrel species being compared. In order to study the vegetation on a comparative basis, three different plotless methods of vegetation analyses were applied. Behaviour and niche occupation of the species are directly dependent on visibility and vegetation density and therefore, in the analysis of vegetation, differences in density were of prime importance. Absolute plant density (plants/m^2) was measured, as well as horisontal density or vegetative obstruction to visibility. Other aspects of the habitats that were sampled, were the climate (Chapter 2), soil and plant phenology.

MATERIALS AND METHODS

DESCRIPTION OF THE STUDY AREAS

The Ngoye squirrel occurs only in the Ngoye forest. A study area was initially selected on the western edge on the forest road. However, to cut down on travelling time (30 min for 6 km), and possible bog-downs on the laborious road in the rainy season, the area of study, was changed after the first six months during which enough squirrels had been caught for captivity studies. The location of the eventual study area was situated where the forest road enters the main body of forest on the western edge, after passing through two forest tongues. The area is hilly and includes areas of climax forest as well as secondary growth so as to contain habitat that is representative of the whole forest. (Fig. 9)

The tongensis study area was more difficult to select. These squirrels are extremely shy and their habitat being very dense with much leaf litter, is unaccommodating to the observer. November 1975 was spent at Lake Sibaya to investigate the feasibility of a study area there, but the area was subsequently flooded by a rising lake level. At Lake St.Lucia the squirrels are relatively tame as a result of the many tourists (Taylor,[x] pers.comm). However, these visitors as well

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*R.H. Taylor, Natal Parks Board, P.O. St.Lucia Estuary, 3936

Figure 9. Map of the study area in Ngoye forest (for *P.p. ornatus*) Symbols indicate: x - vocalisation clashpoints, ● - nest trees, and maximum distance of movement of tagged males, △-toe 1, □-toe 7, and ○-toe 20. Numbers indicate 1-9 trapping stations. Dense patches of vegetation within the forest are shadowed.

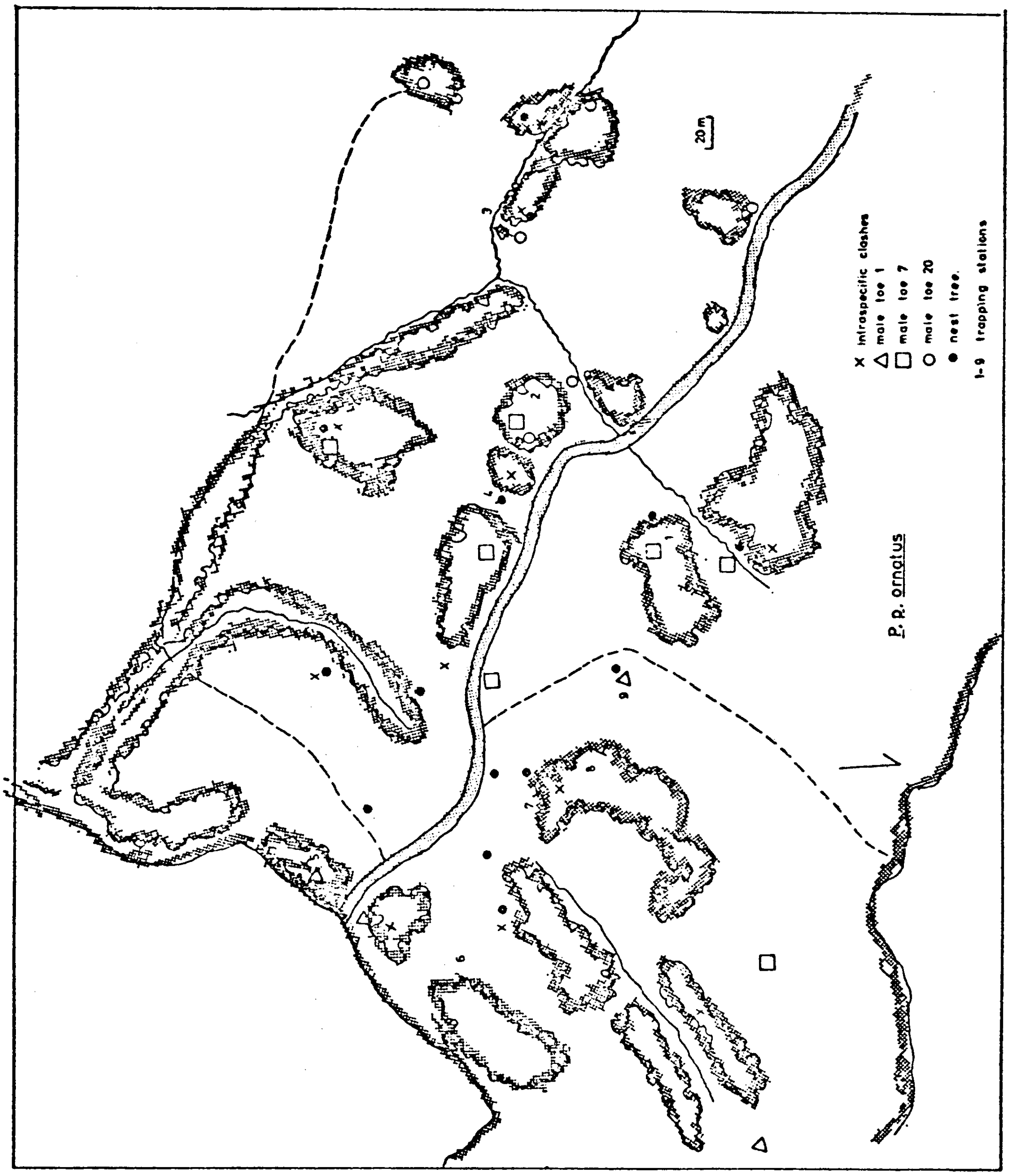
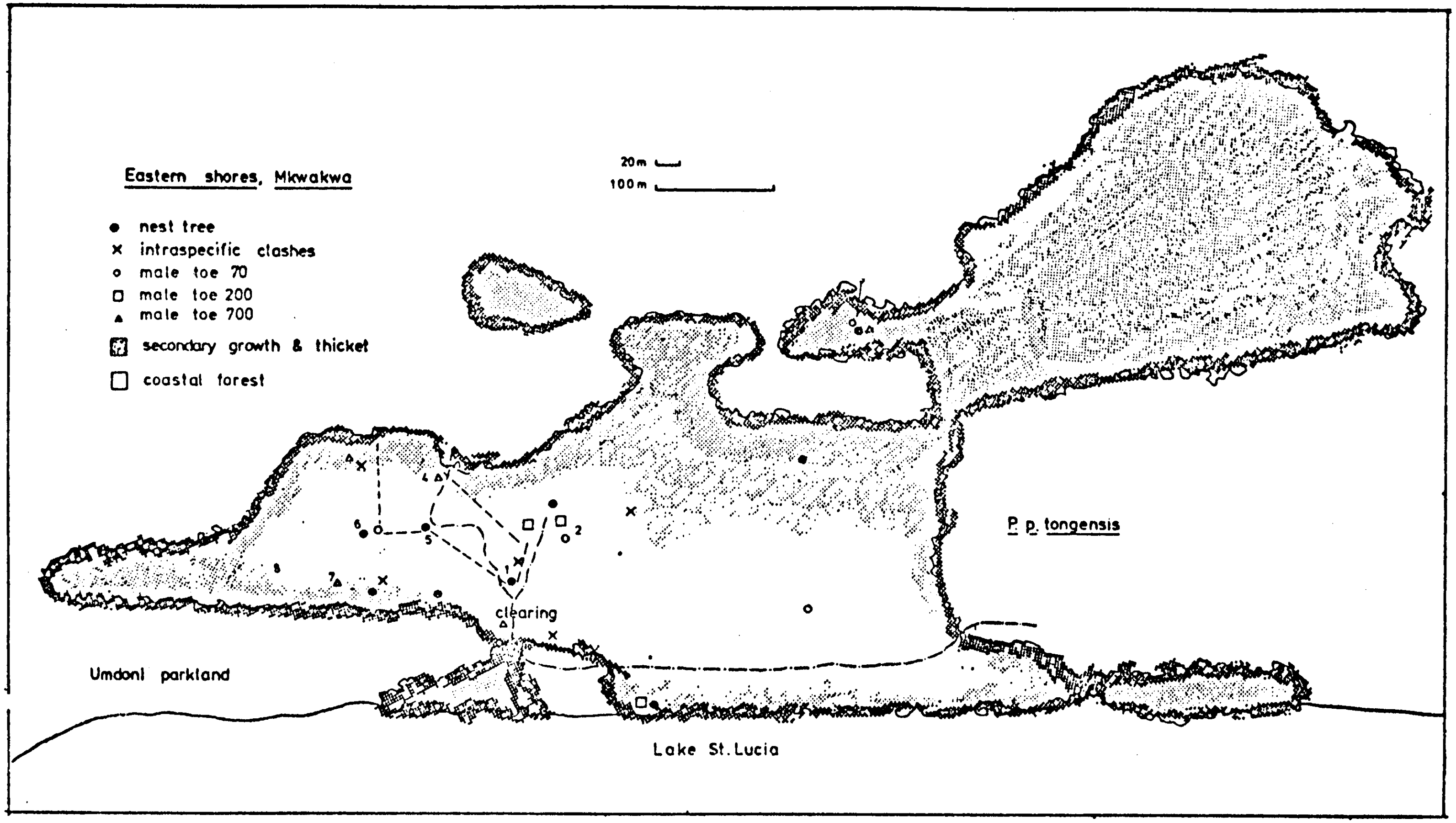

20 m
X intraspecific clashes
△ male toe 1
□ male toe 7
○ male toe 20
● nest tree.
1-9 trapping stations
P. p. ornatus
1
2
3
4
5
6
7
8
9

Figure 10. Map of the study area, Mkwakwa forest (for *P.p. tongensis*) Symbols indicate: x - vocalisation clashpoints, ● - nest trees; and maximum distance of movement of tagged males, ○-toe 70, □-toe 200, △-toe 700. Numbers indicate 1-8 trap stations. Dense secondary growth is shadowed.


Eastern shores, Mkwakwa
20m
100m
● nest tree
× intraspecific clashes
○ male toe 70
□ male toe 200
▲ male toe 700
▨ secondary growth & thicket
☐ coastal forest
P. p. tongensis
clearing
Umdoni parkland
Lake St. Lucia
2
4
5
6
7
8

as incredibly numerous mosquitoes, ruled out this area. It was eventually decided to establish the study area on the eastern shores of the lake 14 km to the north of St.Lucia Estuary in Mkwakwa forest, a small forest island of about 11 ha. (Fig. 10) The squirrels there are also relatively tame as they are used to, and feed from the refuse of, the game guards (Breytenbach*, *pers.comm.*) and mosquitoes are not as numerous. The forest is on a slight rise and the plant cover is exceedingly dense but no *Isoglossa* sp., a ground cover, which obstructs vision up to 1 m, is present. Owing to the smallness of the forest patch, squirrel density figures and feeding observations are probably non-representative for the species as a whole in its distribution area. However, this would no doubt have been so for any *tongensis* study area, as their habitat is by no means uniform, i.e. varies from thickets on coastal dunes to mesic forest at Manguzi, to dry forest at Sihangwane.

The study area for *cepapi* was at Naboomspruit on the farm, Mosdene, as described in Viljoen (1975). However, to obtain a comparison of this termitaria-thicket study area, habitat analyses and density estimates were additionally made in an area of *Burkea/Terminalia* woodland on the same farm. The study area of *congicus* has been described in Viljoen (1978).

SOIL ANALYSIS

Soil samples were taken at ten different locations in the two forests and a sub-sample from each made up the sample that was analysed for pH, resistance (potential), water retaining capacity, and various elements.

* J Breytenbach, Dept. of Forestry, Saasveld, Private Bag 531, George 6530

POINT-QUARTER ANALYSIS (Curtis and Cottam, 1964)

A 32-point grid with 10 m spacing was layed out next to the study areas of both tongensis in coastal forest at Lake St.Lucia and also of ornatus in the Ngoye forest. In each quarter at each point, the nearest individuals of both the canopy (dbh $\geq$ 10 cm) and the subcanopy layers (dbh 2,5 - 10 cm) were established. The species, distance from the point, dbh (diameter at breast height, i.e. 1,5 m high) and diameter of crown coverage were measured for each individual of the canopy layer; species, distance from the point, and crown coverage, were measured for the subcanopy plants. From these data the following was calculated:

Relative frequency (F): Number of times that a plant species is present, expressed as a percentage of the number of times that the total number of plant species are present;

Relative density (D): Number of individuals of a plant species as a percentage of the total number of individuals of all plant species;

Relative dominance (Do): Total basal area of a plant species as a percentage of the total basal area of all plant species;

Importance avlue (I.V.) (Venter, 1969):

$\frac{F + D + Do}{3}$ for the canopy layer;

$\frac{F + D}{2}$ for the subcanopy layer.

THIRD-NEAREST INDIVIDUAL METHOD (McNeill, Kelly and Barnes, 1976):

This method gave the best estimate of overall plant density in woodland habitat in Rhodesia, where eight plotless methods and the quadrat method were tested against a known plant density. The third-nearest individual in each of the two 180° sectors at each of 50 points, 15 m apart along a straight line of travel were established. The distance from the point, dbh and identification were recorded for all individuals with a dbh $\geq$ 2,5 cm, as well as whether the individual was of the canopy or subcanopy layer. This method was used in all four of the habitats and at Mosdene it was used in two different vegetation types. Density was calculated according to the formulae of Morisita (1957):

$$D_1 = \frac{2}{\pi \times N} \times \sum_{i=1}^{N} \sum_{k=1}^{2} \frac{1}{r_{ik^2}} \; ; \text{ and}$$

$$D_2 = \frac{5}{\pi \times N} \sum_{i=1}^{N} \frac{2}{\sum_{i=1}^{2} r_{ik^2}} \; ; \text{ where}$$

k = number of equiangular sectors around the sampling station i.e. 2;
r = distance measured at a given station;
D = plant density per m^2
N = number of sampling station i.e. 50

If D_1 is smaller than D_2 then the best estimate of density is

$$\frac{D_1 + D_2}{2} \; ; \text{ if}$$

D_1 is larger than D_2, then D_1 is the best estimator. F, D, Do and I.V. were also calculated for the third-nearest individual method in the four habitats.

Height of at least ten canopy trees were additionally measured by a triangulation method (Husch, 1963) in each habitat.

DENSITY POLE MEASUREMENT OF PERCENTAGE COVER

This method was used to obtain an estimate of visibility in the two KwaZulu forests as well as in both the open woodland and termitaria thickets at Naboomspruit. The pole was 360 cm long with 12 divisions of 30 cm each. Percentage cover in each division was estimated from a distance of 10 m from both sides along the line of travel, at 10 points, 20 m apart. Additionally, the distance from which the pole was visible, along this line, was measured at each point from both directions.

LIGHT INTENSITY MEASUREMENT

Measurement of the incident light (linear scale converted to Lux) were taken towards the sky, in the four wind directions and vertically down, with a Luna Six 3 light meter in all four habitats at two-hourly intervals throughout the day. Light was similarly measured outside the forest, or shade cover in woodland of *cepapi* and *congicus*, and a calculation of the percentage light present in the habitat was made. This was used as an additional comparative estimate of vegetation density.

Distance at which squirrels realize an observer were recorded throughout the study as an additional indication of visibility.

PHENOLOGY

Presence of flowers, green and ripe fruit and absence of leaves were noted for the two forested habitats for trees that produced possible squirrel food and for other known plants separately. Owing to the fact that these trees could not all be identified at first, the records for the first year are incomplete. Therefore, an additional list of KwaZulu forest trees with flowering and fruiting times was compiled from Coates-Palgrave (1977). Very little time could be spent in the savanna habitat of *congicus* or the woodland of *cepapi* and therefore, a similar list was compiled for these two habitats to determine main fruiting and flowering periods (Coates-Palgrave, 1977).

Statistical tests were done to determine whether there are differences between the habitats: t-tests for difference between two means were used, as well as two separate analyses of variance, the one on the results of the point-quarter method and the other on the results of the third-nearest individual method.

RESULTS

SOIL ANALYSES

Table 17 gives a breakdown of soil analysis in the two KwaZulu forest study areas. Soils in both forests were very acid. Venter (1969) found a slightly more alkaline pH of 5,7 to 6,1 in the Ubisana valley adjacent to the Ngoye forest. The electrical potential gives an indication of the concentration of salts in the soil and when it reaches 250 ohm, the soil is brackish, and at 1 000 ohm, it is highly leached. Potential showed soil more leached at Lake St.Lucia than in Ngoye forest. Moisture retention was measured at $^1/3$ Bar (saturated moisture) and at 15 Bar (where wilting of plants occurs), and the difference between these two figures gives the moisture retention which was 4,11 in the Ngoye forest and much lower at 0,16 in the coastal forest at Lake St.Lucia.

POINT-QUARTER METHOD

Absolute density in this method = the sum of the individual point-to-plant distances/4x no. of points used = square root of the mean area/plant. Therefore the average distance squared, divided into 10 000 (i.e. the unit area of 100 x 100 m) gives the number of individuals per hectare = total density of all plant species (Curtis and Cottam, 1964). The average point-to-plant distance in the Ngoye forest canopy layer is significantly smaller than in the coastal forest at Lake St.Lucia ($P < 0,001$). Therefore the density is higher in the Ngoye canopy than in that of the coastal forest at Lake St.Lucia. The basal area is also greater in Ngoye forest than in the coastal forest. However, in the subcanopy layer, there is a greater average point-to-plant distance in the Ngoye forest and therefore a greater density in the coastal forest ($P < 0,2$).

Canopy cover per tree is smaller on average in the Ngoye forest than in the coastal forest ($P < 0,001$). With a greater density of canopy trees and subsequently greater competition for light, this smaller cover per tree is to be expected. Subcanopy cover per plant does not differ significantly between the two areas ($P < 0,5$).

TABLE 17

SOIL ANALYSES FROM NGOYE FOREST AND COASTAL FOREST ON EASTERN SHORE OF LAKE ST.LUCIA

	pH	POTENTIAL (ohm)	MOISTURE RETENTION		ELEMENTS (ppm)				
			AT 1/3 BAR	15 BAR	PHOSPHATE	Ca	Mg	Na	P
Ngoye Forest	3,90	580	21,99	17,88	1	390	112	30	60
Lake St.Lucia coastal forest (Mkwakwa)	4,75	860	7,62	7,46	1	360	135	28	75

F,D,Do and I.V. values for the trees in the two regions are given in Tables 18 and 21 and a comparison between the two areas with regard to cover, height, density, is given in Table 22.

Analysis of variance also reveals a significant difference between point-to-plant distances of the canopy layers ($P < 0,001$, F ratio = 21,634 F-table = 6,76); but that there was not a significant difference for point-to-plant distances of the subcanopy layers.

THIRD-NEAREST INDIVIDUAL METHOD

A higher density estimate was obtained for the Ngoye forest (0,29 plants/m^2) than for the Lake St.Lucia coastal forest (0,16 plants/m^2). However, this method is not directly comparable to the point-quarter method, as the former method includes individuals of both the canopy and subcanopy layers. In the savanna and woodland habitats of congicus and cepapi, the density was significantly lower at 0,05 and 0,04 plants/m^2 respectively, than in the forests. The open habitat areas of cepapi and congicus do not differ significantly (t-test for means of point-to-plant distances) and in the distribution area of cepapi the two different vegetation types sampled, do not differ either (Table 23). F,D,Do and I.V. values for the open habitats that had not been point-quarter sampled are given for the third-nearest individual method (Tables 24 to 26). The analysis of variance between the results of the third-nearest individual method for the four habitats revealed non-homogeneity of the means. Tukey's procedure (Snedecor and Cochran, 1976) at the 5% level revealed a significant difference between the open habitats (two at Naboomspruit and one at Otjitambi) and the two forests of P.palliatus (each separately tested). The three open habitats did not differ significantly from one another, although the vegetation at Otjitambi was slightly more dense than at Naboomspruit. The two forests were also found to have a similar plant density.

TABLE 18

POINT-QUARTER ANALYSIS OF THE CANOPY LAYER IN THE STUDY AREA OF P.p.ORNATUS IN THE NGOYE FOREST

SPECIES	NO.OF TREES	NO.OF POINTS OF OCCURRANCE	TOTAL BASAL AREA (m^2)	RELATIVE FREQUENCY (F)	RELATIVE DENSITY (D)	RELATIVE DOMINANCE (Do)	IMPORTANCE VALUE (I.V.)
Millettia sutherlandii	28	19	323062,6	15,83	18,42	31,48	21,62
Drypetes gerrardii	19	14	88062,3	11,67	12,50	8,58	10,84
Macaranga capensis	13	9	97110,7	7,5	8,55	9,46	8,42
Tabernaemontana ventricosa	13	11	57789,7	9,17	8,55	5,63	7,73
Harpephyllum caffrum	3	3	149798,0	2,50	1,97	14,60	6,22
Garcinia gerrardii	10	10	17585,9	8,33	6,58	1,71	5,53
Rinorea angustifolia	10	9	14168,2	7,50	6,58	1,38	5,14
Canthium inerme	5	4	42917,2	3,33	3,29	4,18	3,56
Olea capensis	5	4	32115,2	3,33	3,29	3,13	3,22
Nectaropetalum zuluense	6	5	11055,3	4,17	3,95	1,08	3,06
Syzygium guineense gerrardii	3	3	34010,9	2,50	1,97	3,31	2,56
Cryptocarya myrtifolia	4	3	15031,1	2,50	2,63	1,46	2,18
Croton sylvaticus	4	2	22282,0	1,67	2,63	2,17	2,14
Tricalysia capense	3	3	3702,9	2,50	1,97	0,36	1,61
Rhus chirindensis	3	2	9104,9	1,67	1,97	0,89	1,50
Combretum krausii	3	2	8596,7	1,67	1,97	0,84	1,48
Fagara davyi	2	2	13884,3	1,67	1,32	1,35	1,44
Schefflera umbellifera	2	2	11688,7	1,67	1,32	1,14	1,37
Bequaertiodendron natalense	2	1	11543,5	0,83	1,32	1,12	1,08
Oxyanthus speciosus	1	1	18285,8	0,83	0,66	1,78	1,07
Allophylus dregeana	1	1	16200,0	0,83	0,66	1,58	1,01
Millettia grandis	2	1	8991,7	0,83	1,32	0,88	1,00
Celtis gomphophylla	1	1	14967,2	0,83	0,66	1,46	0,97
Xymalos monospora	2	1	5836,3	0,83	1,32	0,57	0,90
Strychnos henningsii	1	1	7807,1	0,83	0,66	0,76	0,74
Cassipourea gerrardii	1	1	5933,4	0,83	0,66	0,58	0,68
Ficus natalensis	1	1	5589,6	0,83	0,66	0,54	0,67
Phyllanthus discoideus	1	1	3660,4	0,83	0,66	0,36	0,61
Teclea natalensis	1	1	2158,2	0,83	0,66	0,21	0,56
Oricia bachmanii	1	1	1313,9	0,83	0,66	0,13	0,54
Rawsonia lucida	1	1	739,2	0,83	0,66	0,07	0,52
TOTAL	152	120	1054992,9	99,97	100,02	99,97	99,99

TABLE 19

POINT-QUARTER ANALYSIS OF THE SUBCANOPY LAYER (dbh: 2,5 TO 10 cm) IN NGOYE FOREST, HABITAT OF P.p.ORNATUS

SPECIES	NO. OF TREES	NO.OF POINTS OF OCCURRENCE	RELATIVE FRE= QUENCY (F)	RELATIVE DENSITY (D)	IMPORTANCE VALUE(I.V.)	TOTAL COVER (m^2)
Tabernaemontana ventricosa	25	19	16,81	16,45	16,63	78,50
Nectaropetalum zuluense	22	11	9,73	14,47	12,10	50,00
Cassipourea gerrardii	15	14	12,39	9,87	11,13	26,75
Garcinia gerrardii	17	12	10,62	11,18	10,90	42,00
Rinorea angustifolia	19	10	8,85	12,50	10,68	58,50
Psychotria capense	9	7	6,19	5,92	6,06	14,25
Drypetes gerrardii	8	6	5,31	5,26	5,29	23,50
Bequaertiodendron natalense	7	6	5,31	4,60	4,95	21,00
Tricalysia capense	6	5	4,42	3,95	4,19	9,50
Rothmannia globosa	5	5	4,42	3,29	3,86	7,50
Ochna sp	3	3	2,65	1,97	2,31	5,00
Podocarpus latifolius	2	1	0,88	1,32	1,10	6,50
Cryptocarya myrtifolia	1	1	0,88	0,66	0,77	1,50
Millettia sutherlandii	1	1	0,88	0,66	0,77	5,00
Olea capensis	1	1	0,88	0,66	0,77	4,00
Erythrococca berberidea	1	1	0,88	0,66	0,77	1,50
Oxyanthus speciosus	1	1	0,88	0,66	0,77	4,00
Anastrabe integerrima	1	1	0,88	0,66	0,77	1,00
Oricia bachmanii	1	1	0,88	0,66	0,77	4,50
Fagara davyi	1	1	0,88	0,66	0,77	3,00
Protorhus longifolia	1	1	0,88	0,66	0,77	4,50
Canthium siliatum	1	1	0,88	0,66	0,77	2,00
Apodytes dimidiata	1	1	0,88	0,66	0,77	3,00
Canthium inerme	1	1	0,88	0,66	0,77	0,25
Eugenia sp.	1	1	0,88	0,66	0,77	1,50
Memecylon natalense	1	1	0,88	0,66	0,77	3,50
	152	113	99,9	100,02	99,86	382,25

TABLE 20

POINT-QUARTER ANALYSIS OF THE CANOPY LAYER IN COASTAL FOREST ON THE EASTERN SHORES OF LAKE ST.LUCIA (MKWAKWA), HABITAT OF P.p.TONGENSIS

SPECIES	NO. OF TREES	NO.OF POINTS OF OCCURRENCE	TOTAL BASAL AREA (cm^2)	RELATIVE FRE= QUENCY (F)	RELATIVE DENSITY(D)	RELATIVE DOMINANCE(Do)	IMPORTANC VALUE(I.V
Dialium schlechteri	48	26	397081,1	29,89	37,50	50,63	39,34
Hymenocardia ulmoides	30	15	121676,8	17,24	23,44	15,51	18,73
Manilkara discolor	14	11	126291,8	12,64	10,94	16,10	13,23
Strelitzia nicolai	13	13	17694,0	14,94	10,16	2,26	9,12
Mimusops obovata	6	5	49224,5	5,75	4,69	6,28	5,57
Albizia adianthifolia	6	6	25285,4	6,90	4,69	3,22	4,94
Linociera peglerae	4	4	22358,4	4,60	3,13	2,85	3,53
Ficus natalensis	3	3	20273,6	3,45	2,34	2,59	2,79
Ptaeroxylon obliquum	3	3	3445,6	3,45	2,34	0,44	2,08
Drypetes natalensis	1	1	935,3	1,15	0,78	0,12	0,68
	128	87	784266,6	100,01	100,01	100,01	100,01

TABLE 21

POINT-QUARTER ANALYSIS OF SUBCANOPY LAYER IN COASTAL FOREST ON THE EASTERN SHORES OF LAKE ST.LUCIA (MKWAKWA), HABITAT OF P.p.TONGENSIS

SPECIES	NO. OF TREES	NO. OF POINTS OF OCCURRENCE	RELATIVE DENSITY(D)	RELATIVE FREQUENCY(F)	IMPORTANCE VALUE(I.V.)	TOTAL COVER(m^2)
Drypetes natalensis	40	24	31,25	23,76	27,51	101,0
Manilkara discolor	20	15	15,63	14,85	15,24	29,5
Hymenocardia ulmoides	13	13	10,16	12,87	11,52	39,0
Cussonia chartaceae	12	12	9,38	11,88	10,63	9,0
Eugenia natalitia	20	15	15,63	14,85	15,24	55,0
Scolopia zeyheri	4	3	3,13	2,97	3,05	3,5
Peddiea africana	3	2	2,34	1,98	2,16	5,5
Ficus natalensis	2	2	1,56	1,98	1,77	7,0
Deinbollia oblongifolia	2	2	1,56	1,98	1,77	3,0
Psychotria capensis	2	2	1,56	1,98	1,77	4,0
Erythroxylum emarginatum	2	2	1,56	1,98	1,77	4,0
Olea capensis	2	2	1,56	1,98	1,77	2,0
Canthium inerme	1	1	0,78	0,99	0,89	3,0
Tarenna pavettoides	1	1	0,78	0,99	0,89	2,5
Linociera peglerae	1	1	0,78	0,99	0,89	1,0
Carissa sp.	1	1	0,78	0,99	0,89	1,0
Ptaeroxylon obliquum	1	1	0,78	0,99	0,89	5,0
	128	101	99,22	99,99	98,65	272,0

TABLE 22

A COMPARISON OF VEGETATION IN NGOYE FOREST AND LAKE ST.LUCIA COASTAL FOREST (POINT-QUARTER ANALYSIS)

VEGETATION PARAMETER	NGOYE FOREST	LAKE ST.LUCIA COASTAL FOREST
CANOPY		
Total point-to-plant distance (cm)	63171,0	72889,0
Average point-to-plant distance (cm)	415,6 ± 226,1	569,5 ± 324,2
Total basal area (cm^2)	1054992,7	784266,6
Average basal area (cm^2)	6940,7	6127,1
Trees/ha	579,0 (or 0,058/m^2)	308,4 (or 0,031/m^2)
Total cover (m^2)	5552,3	14960,6
Average cover (m^2)	51,4	116,9
Average height (m)	21,1 ± 4,0	13,2 ± 5,7
SUBCANOPY		
Total point-to-plant distance (cm)	43218,0	32981,0
Average distance (cm)	284,3 ± 158,3	257,7 ± 145,7
Plants/ha	1236,9 (or 0,124/m^2)	1506,3 (or 0,151/m^2)
Total cover (m^2)	936,6	783,7
Average cover (m^2)	6,2	6,1
Average height (m)	17,3 ± 2,3	—

TABLE 23

A COMPARISON OF VEGETATION OF THE OPEN WOODLAND OF *P.c.CEPAPI* AND *F.c.CONGICUS* (THIRD-NEAREST INDIVIDUAL ANALYSIS)

	NABOOMSPRUIT		OTJITAMBI, SWA/ NAMIBIA WOODLAND
	TERMITARIA THICKETS NEXT TO FLOODPLAIN	WOODLAND ON SANDVELD	
Density estimate: (plants/m^2) D1	0,044	0,045	0,05
D2	0,042	0,049	0,05
Average height of canopy (m)	13,50 ± 1,64	12,50 ± 3,28	6,69 ± 1,76
Total basal area (m^2)	13723,34	6968,35	16696,74
Average basal area (m^2)	137,23	69,68	177,63
Time to complete measurements (h)	3,0	4,0	2,5

TABLE 24

THIRD-NEAREST INDIVIDUAL ANALYSIS IN HABITAT OF F.c.CONGICUS

SPECIES	NO.OF TREES	NO.OF POINTS OF OCCURRENCE	TOTAL BASAL AREA	RELATIVE DENSITY(D)	RELATIVE FREQUENCY(F)	RELATIVE DOMINANCE(Do)	IMPORTANCE VALUE (I.V.)
Colophospermum mopane	35	26	10142,73	37,23	32,10	60,75	43,36
Acacia reficiens	20	18	2333,45	21,28	22,22	13,98	19,16
Combretum apiculatum	10	9	310,23	10,64	11,11	1,86	7,87
Lonchocarpus nelsii	5	5	1428,84	5,32	6,17	8,56	6,68
Combretum imberbe	4	4	1267,54	4,26	4,91	7,59	5,59
Ziziphus mucronata	6	5	312,98	6,38	6,17	1,87	4,81
Dichrostachys cinerea	5	5	44,58	5,32	6,17	0,27	3,92
Boscia albitrunca	2	2	653,45	2,13	2,47	3,91	2,84
Terminalia prunioides	2	2	94,44	2,13	2,47	0,57	1,72
Acacia mellifera	2	2	57,54	2,13	2,47	0,34	1,65
Commiphora sp	1	1	28,77	1,06	1,23	0,17	0,82
Croton subgratissimus	1	1	12,57	1,06	1,23	0,08	0,79
Mundulea sericea	1	1	9,62	1,06	1,23	0,06	0,78
	94	81	16696,74	100,00	99,95	99,99	99,98

TABLE 25

THIRD-NEAREST INDIVIDUAL ANALYSIS IN SPIROSTACHYS FLOODPLAIN STUDY AREA OF P.c.CEPAPI

	NO.OF TREES	NO.OF POINTS OF OCCURRENCE	TOTAL BASAL AREA (m^2)	RELATIVE FRE=QUENCY (F)	RELATIVE DENSITY(D)	RELATIVE DO=MINANCE(Do)	IMPORTANC VALUE(I.V.
Spirostachys africana	57	36	10353,03	50,0	57	75,44	60,81
Acacia tortilis	12	11	794,53	15,28	12	5,79	11,02
Acacia luederitzii	11	9	554,01	12,50	11	4,04	9,18
Boscia albitrunca	7	5	945,61	6,94	7	6,89	6,94
Acacia nigrescens	7	5	819,95	6,94	7	5,97	6,64
Euclea crispa	3	3	53,91	4,17	3	0,39	2,52
Securidaca longipedunculata	1	1	153,90	1,39	1	1,12	1,17
Maytenus heterophylla	1	1	28,77	1,39	1	0,21	0,87
Ziziphus mucronata	1	1	19,63	1,39	1	0,14	0,84
	100	72	13723,34	100,0	100	99,85	99,99

TABLE 26

THIRD-NEAREST INDIVIDUAL ANALYSIS IN BURKEA/TERMINALIA SANDVELD IN THE STUDY AREA OF P.c. CEPAPI

SPECIES	NO.OF TREES	NO.OF POINTS OF OCCURRENCE	TOTAL BASAL AREA (m^2)	RELATIVE FRE=QUENCY (F)	RELATIVE DENSITY(D)	RELATIVE DOMINANCE(Do)	IMPORTANCE VALUE (I.V.)
Dichrostachys cinerea	38	29	2416,89	35,37	38,0	34,68	36,02
Acacia tortilis	21	17	1025,54	20,73	21,0	14,72	18,82
Terminalia sericea	17	14	314,35	17,0	17,07	4,51	12,86
Acacia karroo	12	11	338,03	12,0	13,41	4,85	10,09
Burkea africana	1	1	1809,56	1,0	1,22	25,97	9,40
Acacia grandicornuta	7	6	228,11	7,0	7,32	3,27	5,86
Acacia luederitzii	1	1	452,39	1,0	1,22	6,49	2,90
Acacia nilotica	1	1	314,16	1,0	1,22	4,51	2,24
Peltophorum africanum	1	1	56,75	1,0	1,22	0,81	1,01
Rhus engleri	1	1	12,57	1,0	1,22	0,18	0,80
	100	82	6968,35	100,00	100,00	99,99	100,00

DENSITY POLE MEASUREMENTS (Table 27)

A significantly lower density (or higher visibility) estimate was obtained in the Ngoye forest than in coastal forest ($P < 0,001$). On Mosdene, the woodland with termitaria thickets adjacent to the flood=plain had a better visibility than forest at Lake St.Lucia (P 0,001) but only slightly better than at Ngoye ($P < 0,4$). The sandveld wood=land on Mosdene was also significantly less dense than coastal forest ($P < 0,001$) and the Ngoye forest ($P < 0,005$). When every section of the pole is tested separately for the Ngoye forest and the termitaria thickets, the latter area is less dense up to 120 cm, after which it is more dense up to 210 cm. Upwards of this, readings are either more dense in termitaria thickets or the difference is non-significant. The Mosdene sandveld woodland shows no significant difference from Ngoye up to 210 cm above the ground after which the woodland is consistently denser.

Creepers which occurred in the two forests, were more numerous in the coastal forest than in Ngoye (38,2 <u>cf</u>. 15,8 mean number of occurrences per point sampled; and 71,67 <u>cf</u>. 34,17 per cent frequency of occurrence in the divisions on the pole respectively). The distance from which the pole is visible, is significantly less in the coastal forest at Lake St.Lucia (18,10 m) than in the Ngoye forest (36,0 m)($P < 0,001$). But the pole is visible from much further in the termitaria thickets and woodland on sandveld at Naboomspruit (76,45 m and 84,40 m), a highly significant difference:

Ngoye <u>cf</u>. Mosdene floodplain ($P < 0,001$)
Ngoye <u>cf</u>. Mosdene sandveld ($P < 0,001$)
Coastal forest <u>cf</u>. Mosdene floodplain ($P < 0,001$)
Coastal forest <u>cf</u>. Mosdene sandveld ($P < 0,001$)

The visibility distance is shorter for the floodplain than for sandveld at Naboomspruit ($P < 0,5$)

The average canopy height (Table 22) in Ngoye forest is significantly higher than at Lake St.Lucia coastal forest ($P < 0,001$, $t = 4,62$, $df = 40$

TABLE 27

DENSITY POLE ESTIMATES (% COVER, SD) IN NGOYE FOREST, COASTAL FOREST AT LAKE ST.LUCIA, SANDVELD AND FLOODPLAIN AT NABOOMSPRUIT

DIVISIONS FROM GROUND UPWARDS	NGOYE FOREST	COASTAL FOREST AT LAKE ST.LUCIA	NABOOMSPRUIT	
			FLOODPLAIN TERMITARIA THICKETS	SANDVELD WOODLAND
1	24,8 ± 37,64	66,0 ± 37,48	11,80 ± 28,97	25,50 ± 32,96
2	24,10 35,20	56,50 38,59	11,50 30,61	20,0 30,04
3	23,35 34,92	47,0 35,68	10,0 29,20	16,75 28,76
4	23,68 31,08	52,0 36,76	11,35 26,01	25,0 33,76
5	13,50 25,08	50,50 35,36	22,0 35,89	28,50 32,33
6	12,25 22,45	56,50 36,75	25,75 38,30	31,0 34,63
7	12,05 22,42	58,50 31,54	24,0 36,33	34,30 38,58
8	14,05 25,19	49,00 30,62	18,0 31,05	34,25 38,09
9	12,80 23,51	57,50 38,39	31,05 29,41	30,50 32,20
10	10,30 22,48	67,00 30,93	17,0 32,78	36,50 35,88
11	11,55 23,09	67,50 34,74	22,0 40,34	39,50 40,84
12	13,35 26,77	75,0 35,59	18,75 35,01	45,25 43,57
POLE VISIBLE FROM (m)	36,00 10,87	18,10 5,53	76,45 28,64	84,40 33,83

However, the canopy height at Lake St.Lucia did not differ significantly from the tallest tree height at Mosdene either on the floodplain or on the sandveld. The latter two regions did not differ significantly either, but the trees at Otjitambi were significantly shorter than at Mosdene woodland.

A count of the trees with dbh > 15 cm in the 10,08 ha study area in the Ngoye forest totalled 609 trees of 34 different species, i.e. 60,4/ha (Table 28). The highest percentage of 19,9 was represented by *Drypetes gerrardii*, and of 18,9 by *Millettia sutherlandii*. In the coastal forest at Lake St.Lucia 208 individuals from 19 different plant species were counted, in 2,59 ha i.e. 80,3/ha. *Dialium schlechteri* at 35,10% and *Hymenocardia ulmoides* at 26,9% (Table 29) were the most frequently encountered. At Naboomspruit in 5,4 ha, 287 trees with dbh > 15 cm were counted i.e. 53,2/ha (Table 30). *Spirostachys africana* individually made up 45,3% of this count. Table 31 shows a count of trees in sandveld on Mosdene with 4,92 trees (dbh > 15 cm) per ha. Trees in the study area of *congicus* were counted in one daily range and species throughout the study area were listed (Viljoen, 1978)(Table 32).

The study area at Otjitambi can be divided into three different habitat types namely rocky outcrops, vegetation alongside the dry river courses and open savanna. Research during the present study was limited to the former two habitat types as this had been indicated as the preferred habitat of the striped squirrel. Plant species collected from these two habitats are listed in Viljoen (1978).

LIGHT INTENSITY MEASUREMENTS

Light intensity inside, as well as the percentage light penetrating the canopy was consistently lower in Ngoye forest than in coastal forest at Lake St.Lucia (Figure 11). In Ngoye forest the light intensity at 12h00 varied from 169 lx in May to 380 lx in January, whereas in the coastal forest on the eastern shores of Lake St.Lucia

TABLE 28

COUNT OF TREE SPECIES (dbh - 15 cm) IN STUDY AREA OF P.p.ORNATUS (10,08 ha) IN NGOYE FOREST

SPECIES	A	B	C	D	E	F	G	IV %
Drypetes gerrardii	1	22	16	28	16	38	121	19,87
Millettia sutherlandii	7	26	24	23	15	20	115	18,88
Garcinia gerrardii	3	9	2	15	5	18	52	8,54
Syzygium gerrardii	5	3	2	28	-	-	38	6,24
Olea capensis	2	7	3	11	1	-	24	3,94
Harpephyllum caffrum	6	9	4	3	1	-	23	3,78
Croton sylvaticus	3	6	1	8	-	1	19	3,12
Flagellaria guineense	2	3	2	7	2	2	18	2,96
Schefflera umbellifera	5	1	2	8	1	1	18	2,96
Podocarpus latifolius	1	3	2	9	0	2	17	2,79
Chrysophyllum viridifolium	-	3	-	7	3	3	16	2,63
Macaranga capensis	3	-	2	7	-	3	15	2,46
Trichilia dregeana	1	1	2	7	2	2	15	2,46
Cassipourea gummiflua	1	3	3	6	-	1	14	2,30
Cryptocarya myrtifolia	-	1	3	7	3	0	14	2,30
Fagara davyi	4	3	3	1	-	-	11	1,81
Combretum krausii	2	2	1	3	1	-	9	1,48
Phyllanthus discoideus	-	-	1	2	5	-	8	1,31
Protorhus longifolia	1	-	5	2	-	-	8	1,31
Albizia adianthifolia	-	3	2	2	-	-	7	1,15
Ficus bizanae	-	-	-	-	-	7	7	1,15
F.natalensis	-	2	1	2	-	1	6	0,99
Strychnos henningsii	1	-	1	-	1	3	6	0,99
Xymalos monospora	-	1	-	1	2	0	4	0,66
Cassipourea gerrardii	-	-	-	-	1	3	4	0,66
Mimusops obovata	-	-	-	1	2	-	3	0,49
Rauvolffia caffra	-	1	1	1	-	-	3	0,49
Teclea natalensis	-	-	2	-	-	1	3	0,49
Bequaertiodendron natalensis	-	-	-	-	1	2	3	0,49
Crytocarya myrtifolia	-				1	1	2	0,33
Calodendrum capense	-	1	-	-	-	-	1	0,16
Sapium ellipticum	-	1	-	-	-	-	1	0,16
Ochna sp.	-	-	-	-	1	-	1	0,16
Nuxia floribunda	-	-	-	-	1	2	3	0,49
							609	99,98

A - Bomvu's (West) (1,53 ha)
B - HcS$_1$ (South) (2,38 ha)
C - HcN$_1$ (North) (0,77 ha)
D - J's to river (3,63 ha)
E - Jocks (1,31 ha)
F - Meg's (0,47 ha)

TABLE 29

COUNT OF TREE SPECIES (dbh ≥ 15 cm) IN STUDY AREA OF *P.p.TONGENSIS* (2,59 ha) AT LAKE ST.LUCIA

	TOTAL NO. OF TREES	% OF TREES	AREA A *	AREA B	AREA C
Dialium schlechteri	73	35,10	23	11	39
Hymenocardia ulmoides	56	26,92	35	7	14
Strelitzia nicolai	18	8,65	11	3	4
Manilkara discolor	16	7,69	5	1	10
Albizia adianthifolia	14	6,73	10	1	3
Inhambanella henriquesii	6	2,88	4	2	0
Apodytes dimidiata	5	2,40	4	0	1
Ekebergia capensis	3	1,44	3	0	0
Olea woodiana	3	1,44	2	0	1
Ficus natalensis	2	0,96	2	0	0
Vepris lanceolata	2	0,96	2	0	0
Sapium ellipticum	2	0,96	1	1	0
Strychnos madagascariensis	2	0,96	0	0	1
Ozoroa obovata	1	0,48	1	0	0
Canthium inerme	1	0,48	1	0	0
Cussonia sphaerocephala	1	0,48	1	0	0
Eugenia natalitia	1	0,48	1	0	0
Gardenia *sp.*	1	0,48	0	0	1
Mimusops obovata	1	0,48	0	0	1
	208	99,90			

* A Resident study area (2,01 ha)
B 10 m on either side of path through study area (0,26 ha)
C 5 m on either side of path through habitat analysis area (0,32 ha)

TABLE 30

COUNT OF TREE SPECIES IN STUDY AREA OF P.c.CEPAPI (5,4 ha) AT NABOOMSPRUIT ADJACENT TO A FLOODPLAIN

	NO. OF TREES/ SHRUBS	PERCENTAGE OF TREES/ SHRUBS
Trees with dbh> 15 cm		
Spirostachys africana	130	45,30
Securidaca longipedunculata	52	18,12
Boscia albitrunca	45	15,68
Acacia tortilis	24	8,36
A. detinens	13	4,53
A. robusta	9	3,14
A. nigrescens	7	2,44
Dichrostachys cinerea	5	1,74
Combretum hereroense	2	0,70
Total	287	100,0
Trees with dbh< 15 cm		
Euclea crispa	70	49,30
Maytenus heterophylla	57	40,14
Diospyros lycioides	10	7,04
Rhus lancea	4	2,82
Ziziphus mucronata	1	0,70
	142	100,0

Trees with holes (possible nests) 29

TABLE 31

COUNT OF TREE SPECIES IN SANDVELD STUDY AREA OF P.c.CEPAPI (11,8 ha) AT NABOOMSPRUIT

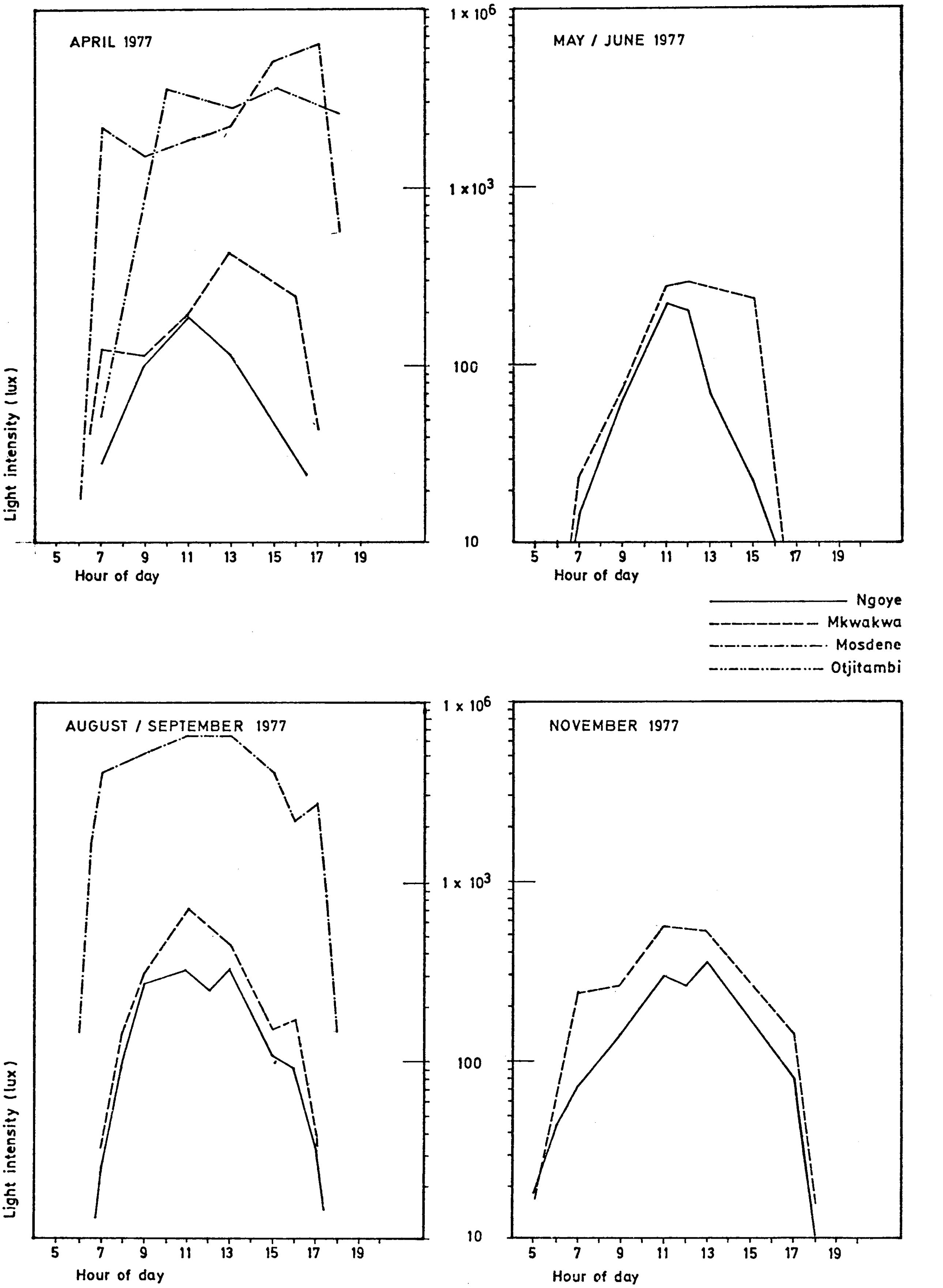
	NO. OF TREES/SCHRUBS	PERCENTAGE OF TREES/SHRUBS
Trees with dbh $>$ 15 cm		
Burkea africana	29	50,0
Melia azedarach	9	15,52
Acacia karroo	7	12,07
A.galpinii	5	8,62
Ziziphus mucronata	4	6,90
Peltophorum africanum	2	3,45
Acacia tortilis	2	3,45
	58 4,92/ha	100,00
Trees with dbh $<$ 15 cm		
Grewia sp.	77	28,10
Dichrostachys cinerea	29	10,58
Maytenus sp.	27	9,85
Rhus engleri	25	9,12
Acacia tortilis	21	7,66
A.karroo	19	6,93
Terminalia sericea	19	6,93
Diospyros lycioides	16	5,84
Acacia nilotica	15	5,47
Ziziphus mucronata	10	3,65
Peltophorum africanum	6	2,19
Burkea africana	5	1,82
Combretum apiculatum	2	0,73
A.galpinii	1	0,36
A.robusta	1	0,36
A.nigrescens	1	0,36
Total	274 23,2/ha	100,00

TABLE 32

COUNT OF TREE SPECIES IN ONE DAILY RANGE (0,4 ha) OF A GROUP OF F.CONGICUS

TREE SPECIES	SHRUB	SUBCANOPY	CANOPY	TOTAL
Acacia mellifera *var* detinens	8	4	-	12
A.reficiens	-	27	4	31
Boscia albitrunca	-	1	-	1
Colophospermum mopane	150	5	24	179
Combretum apiculatum	11	12	1	24
C.imberbe	-	-	2	2
Commiphora pyracanthoides	1	-	-	1
Croton gratissimus *var* subgratissimus	4	-	-	4
Dichrostachys cinerea	31	-	-	31
Grewia bicolor	87	-	-	87
G.flavescens	62	-	-	62
G.villosa	7	-	-	7
Lonchocarpus nelsii	8	10	6	24
Maytenus senegalensis	7	-	-	7
Mundulea sericea	2	-	-	2
Terminalia prunioides	17	2	-	19
Ziziphus mucronata	3	3	-	6
TOTAL	398	64	37	500

Figure 11. Light intensity measurements (lx) throughout the day in habitats of four tree squirrel species: *P.p. ornatus* (Ngoye forest), *P.p. tongensis* (Mkwakwa forest), *P.c. cepapi* (Mosdene), *Funisciurus c. congicus* (Otjitambi).


APRIL 1977
MAY / JUNE 1977
AUGUST / SEPTEMBER 1977
NOVEMBER 1977
1 x 10^6
1 x 10^3
100
10
Light intensity (lux)
Hour of day
5
7
9
11
13
15
17
19
Ngoye
Mkwakwa
Mosdene
Otjitambi

the readings varied from 275 to 437 lx, and at St.Lucia Estuary (less dense forest) up to 589 lx was recorded.

Results of t-tests for paired statistics for light intensity measure= ments in four different habitats (March/April):

Habitat	Level of significance (probabilities <)
Ngoye _vs_. Mkwakwa	0,05
Ngoye _vs_. _cepapi_ woodland	0,005
Ngoye _vs_. _congicus_ woodland	0,005
Mkwakwa _vs_. _cepapi_ woodland	0,025
Mkwakwa _vs_. _congicus_ woodland	0,025
Cepapi woodland _vs_. _congicus_ woodland	NS

Percentage light penetration and probability levels (for paired t-tests for a comparison between the forests of _ornatus_ and _tongensis_ at different times of the year:

Time of year	% light penetration		Level of significance
	Ngoye	Mkwakwa	
Nov. 77	54,4	61,2	0,05
Jan. 78	55,7	60,8	0,025
May/June 77	53,3	58,8	0,1
May 78	50,8	56,5	0,05
Aug 77	57,8	61,6	0,01

This difference does not reflect on the horisontal visibility as much as on the continuous high canopy cover in Ngoye _cf_. broken canopy at Lake St.Lucia. An estimate of the percentage canopy cover at 50 points in these two forests, was 80,94 ± 7,41 cover in Ngoye and 65,08 ± 4,29 in the St.Lucia coastal forest.

In the two savannas, the light measured in the shade and percentage light penetration was considerably higher than in the two forests. At Naboomspruit light intensity in the shade was 6 606 lx at 12h00 in September and 2 089 lx in April when it was 3 631 lx at Otjitambi. Statistical differences (paired t-tests) for the means of the different areas for March/April are given above. Inside the two forests, light remained low towards sunrise and sunset, whereas light in the open habitats was elevated relative to light intensity outside.

Distance at which three tree squirrel species (Paraxerus spp.) realise an observer:

Species	Mean realising distance (m)	S.D.	Range	Sample size
P.palliatus ornatus	13,49	7,62	4-50	61
P.p.tongensis	8,46	5,47	1-20	39
P.cepapi cepapi	24,93	21,28	6-100	40

Distance at which squirrels realised the presence of an observer in the two forests and in savanna reveal that visibility is low and plant density therefore high in tongensis habitat, and that the cepapi woodland has the greatest visibility. The significance of the mean distances were tested (t-test) between Ngoye forest and Mkwakwa forest and was found to be highly significant ($P < 0{,}001$).

PHENOLOGY

The phenology of forest tree species that could produce squirrel food in the habitat of P.palliatus (compiled from Coates-Palgrave, 1977) is summarised in Table 33. January to May is the main fruiting time when 55,5% of the 355 fruiting occurrences were noted; the peak occurs from March to April (both of these months showed 55,1% of the 78 tree species in fruit) with slightly lower values for January and May (44,9% in both instances). However, fruit is available throughout the year and even in October, the month with the lowest percentage of fruiting trees, 16,7% of the tree species were in fruit. Flowering reached a peak in the last four months of the year when 60,1% of the 268 flowering occurrences was recorded; and 59% of the 78 tree species flowered both in October and November, 48,7% in December and 34,6% in January.

Data collected from Ngoye forest during the present study are presented in Table 34 for tree species known to be, or probably serving as a sour of squirrel food. Fruiting mainly occurred from December to May with

SA NO OF TREE	FAMILY	SPECIES	J	F	M	A	M	J	J	A	S	O	N	D
18	Podocarpaceae	Podocarpus latifolius	fr	fr					cones-------|					fr
40	Ulmaceae	Celtis gomphophylla	-------------fr						fxxxxxxxxxxxxxxxxxf					fr
41		C.mildbraedii									fxxxxxf	fr----fr		
42		Trema orientalis	xxxxxxf (but also before and after) fr-----------------------------fr											f
43		Chaetacme aristata	fr---fr									fxxxxxxxxxxxxf		
57	Moraceae	Ficus natalensis	fr						fr------------------------------					
105	Annonaceae	Annona senegalensis	fr-----------fr									fxxxxxxxxxxxxf		
105,1		Artabotrys monteiroae									fr-----------------fr			
111	Trimeniaceae	Xymalos monospora	-------------------------fr					fxxxxxxxxxxxxxxxxxxxxxxxxf					fr------	
115	Lauraceae	Cryptocarya myrtifolia	fxxxxxf					fr-----------------fr						
116		C.woodii	fr-----------------------fr									fxxxxxxxxxxxxxf		
117		C.wyliei	f	fr----------fr										f
227	Papilionoideae	Millettia grandis	f					fr-----------------fr						
228		M.sutherlandii	f			fr-------------------------------fr								
229		Craibia zimmermanii			fr------------------------------------fr						fxxxxxxxxxxxxf			
247	Erythroxylaceae	Nectaropetalum zuluense	fr					fxxxxxf(sometimes to D)				fr------------		
249		Erythroxylum emarginatum	fr-----------------------fr								fxxxxxxxxxxxxxxxxxxxf			
250		E.pictum	xxxxxxxf fr-----------------fr									fxxxxxxxxx		
253	Rutaceae	Fagara capensis	f	fr-----------------fr										
254		F.davyi	f fr------------------------fr									fxxxxxxxxxxxxxx		
257		Oricia bachmanii				fr			fxxxxxxxxxxxxxxxxxxf					
261		Vepris undulata	xxxxxxxxxxxxxxf				fr----------fr							f
263		Teclea gerrardii	fr							fxxxxxxxxxxxxf				fr
264		T.natalensis	fr							fxxxxxf(or later)			fr-------	
296	Meliaceae	Turraea floribunda	f	fr-----------------------------fr								fxxxxxxxxxxxxxxx		
298		Ekebergia capensis	-------------------fr (or even to June)								fxxxxxxxxxxxf			fr
300		Trichilia dregeana	fr------------------------fr									fxxxxxf		
301		T.emetica	-------------fr							fxxxxxxxxxxxxf				fr
311	Euphorbiaceae	Phyllanthus discoideus	------fr									fxxxxxf		fr
313		Drypetes arguta			fr----------fr								fxxxxxxf	
314		D.gerrardii	-------------------fr								fxxxxxxxxxxxxf fr-------------------			
316		D.natalensis	-------------fr								fxxxxxf →			fr
317		Hymenocardia ulmoides	fr-----------------fr										fxxxxxxf	

TABLE 33 (continued)

SA NO OF TREE	FAMILY	SPECIES	J	F	M	A	M	J	J	A	S	O	N	D
318		Antidesma venosum	f		← fr---	-------	--fr →					f xxxx	xxxx	xxxx
330		Croton sylvaticus			fr---	fr						f xxxx	xxxx	xxf
332		Cavacoa aurea	------	fr								f xxxx	xxxx	xxf fr
332.1		Erythrococca berberidea	------	fr									f xxxx	f fr
335		Macaranga capensis	f		fr---	fr						f xxxx	xxxx	xxxx
336		Clutia abyssinica			f xxxx	fr--- xxxx	----- xf →	-----	-----	-----	--fr			
361	Anacardiaceae	Harpephyllum caffrum		f						fr				
364		Protorhus longifolia								f xxxx	xxxx	fr--- xxf	-----	--fr
380		Rhus chirindensis	------	fr									f xxxx fr---	xxf -----
424	Sapindaceae	Allophylus dregeanus			f		fr---	-----	-----	fr				
426		A. natalensis				f			fr					
429		Atalaya natalensis	f	fr---	-----	-----	fr						f xxxx	xxxx
430		Deinbollia oblongifolia				f xxxx	f		fr---	-----	-----	fr		
447	Rhamnaceae	Ziziphus mucronata	xxxxx	f	fr---	-----	-----	-----	-----	fr			f xxxx	xxxx
489	Violaceae	Rinorea angustifolia	fr									f xxxx	f	
491	Flacourtiaceae	Rawsonia lucida		fr							f xxxx	xxxx	xxf fr---	-----
529	Rhizophoraceae	Cassipourea congoensis	f fr---	-----	-----	-----	fr				f xxxx	xxxx	xxxx	xxxx
530		C. gummiflua	xxxx	xxxx	xxxx	xf fr---	fr							f
540	Combretaceae	Combretum krausii		fr---	-----	-----	-----	fr		f xxxx	xxxx	xxxx	xxf	
553.1	Myrtaceae	Eugenia capensis capensis	xxxx	xxxx	xxxx	xf fr---	-----	-----	f xxxx -----	xxxx -----	xxxx -----	xxxx -----	xxxx -----	xx fr

TABLE 33 (continued)

SA NO OF TREES	FAMILY	SPECIES	J	F	M	A	M	J	J	A	S	O	N	D
553.2		E.c.natalitia	---	---	---	---	---	---	--- fxx	--- xxx	--fr xxx	xxx	xxx	xxf
555	Myrtaceae	Syzygium cordatum	---	---	-fr					fxx	xxx	xxx	f/fr--	---
556		S.guineense gerrardii					fxx	xxx	xxx fr-	xxx ---	xxx ---	xxf → ---	---	--fr →
580	Sapotaceae	Chrysophyllum viridifolium	fxx	fr-- xxf	-fr									
582		Beguaertiodendron natalense	xxx	xxx	xxf						fr--	---	---	f fr
583		Mimusops caffra	xxx	xxx	xxf	fr--	---	---	---	---	fxx -fr	xxx	xxx	xxx
584		M.obovata	---	---	-fr					fxx	xxx	xxx	fr-- xxf	---
591		Inhambanella henriquesii								f		fr--	fr	
592		Manilkara discolor	---	---	-fr			fxx	xxx	xxx	xxf			fr
616	Oleaceae	Linociera peglerae	xxx ---	xxf ---	---	---	-fr			fxx	xxx	xxx	xxx fr--	xxx ---
618		Olea capensis	xxx	xxf → fr--	---	---	---	---	---	fxx ---	xxx -fr	xxx	xxx	xxx
620		O.woodiana			fr--	fr							f	
624	Loganiaceae	Strychnos decussata			fr--	---	---	---	---	---	-fr	fxx	xxx	xxf
625		S.henningsii	---	---	-fr			fxx	xxx	xxx	xxx	xxf		fr
626		S.madagascariensis		fr--	---	---	---	---	---	fxx ---	xxx ---	xxx ---	xxx -fr	xxf
629		S.spinosa	f		fr--	---	---	---	---	-fr		fxx	xxx	xxx
645	Apocynaceae	Tabernaemontana ventricosa				fr--	---	---	---	---	-fr	fxx	xxx	xxf
646		Voacanga thouarsii	xxx ---	xxf ---	---	---	---	---	---	fxx ---	xxx -fr	xxx	xxx	xxx fr
696	Rubiaceae	Oxyanthus speciosus	f		fr--	---	-fr						fxx	xxx
698		Tricalysia capensis		fr--	---	---	---	---	-fr			fxx	xxx	xxf
		T.sonderana	---	---	---	-fr					fxx	xxx	xxx	fr xxf
700.1		Kraussia floribunda	f			fr--	---	-fr					fxx	xxx
705.1		Canthium ciliatum		fr--	---	---	-fr					fxx	xxx	xxf
705.2		C.gueinzii	-xx	xxx	xxx	xxx	xxx	xxf	fr-	---	fxx ---	xxx -fr	xxx	xxx
708		C.inerme	---	---	-fr						fxx	xxx	xxf fr--	---
		TOTAL FRUITING 355	35	41	43	43	35	23	25	22	27	13	20	28
		FLOWERING 268	27	15	19	6	4	6	10	20	31	46	46	38
		PERCENTAGE FRUITING	9.86	11.55	12.11	12.11	9.86	6.48	7.04	6.20	7.61	3.66	5.63	7.89
		FLOWERING	10.07	5.60	7.09	2.24	1.49	2.24	3.73	7.46	11.57	17.16	17.16	14.18

PHENOLOGY OF 51 TREE SPECIES EITHER IDENTIFIED AS (Q) OR PROBABLY UTILISED AS FOOD OF THE RED SQUIRREL, P.P.ORNATUS (NOMENCLATURE FOLLOWING COATES-PALGRAVE, 1977)

TREE SPECIES		1976			1977						1978		
		JUNE	SEPT.	NOV	JAN	APR	JUNE	AUG	OCT	DEC	JAN	MAY	AUG
Bequaertiodendron natalense	Q								xxx* fr →				
Calodendrum capense	Q				xx fr						xx fr		
Canthium inerme	Q		f						f	fr	xx fr		
Canthium gueinzii	Q									fr	xx fr	fr	f
Cassipourea congoensis	Q								f	fr	xx fr	fr	fr
C.gummiflua	Q						xx fr						
Chrysophyllum viridifolium	Q				fr		xx fr			xx fr	xx fr		
Croton sylvaticus	Q	D	D							f	fr		
Cryptacarya myrtifolia	Q				fr						fr	fr	xx fr
Drypetes gerrardii	Q								f	fr			
Ekebergia capensis	Q					fr						fr	
Eugenia natalitia									f		fr		
Fagara davyi								D					
Ficus bizanae	Q				fr					xx fr	xx fr	fr	
F.natalensis		xx fr			fr	fr	xx fr	D		fr	xx fr	xx fr	D
Flagellaria guineensis	Q	fr/f			xx fr	xx fr				f	xxx fr		
Garcinia gerrardii	Q	xxx fr/f		f	fr	xx fr	xxx fr	f	f	fr	fr xx		f

TABLE 34 (continued)

TREE SPECIES	1976			1977						1978		
	JUNE	SEPT	NOV	JAN	APR	JUNE	AUG	OCT	DEC	JAN	MAY	AUG
Sapium ellipticum Ω				fr				fr		frxx		f
Solanum geniculatum Ω										frxx		
S.giganteum				frxx	frxx							
S.mauritianum Ω			frxx/f		f	frxx	fr/f		frxx		fr/f	
Strychnos henningsii								fr			fr	
Syzygium guineense gerrardii Ω			D		fr	frxxx	frxx	frx	frx	frx	frxx	
Tabernaemontana ventricosa	frxx		frx/f	f	frxx	frxx	fr		f	fr	frxx	f
Tarenna pavettoides	frxx		f		f	fr/f	f		f	fr	fr	
Teclea natalensis										frxx		
Trema orientalis						frxx				frxx	frxxx	
Trichilia dregeana Ω	fr				fr				f		frxx	
Urara camaroensis									frxx		f	

*fr - green fruit; frxx - full fruit; frxxx - fruit ± finished

TOTAL VALUES

	1976 JUNE	SEPT	NOV	1977 JAN	APR	JUNE	AUG	OCT	DEC	1978 JAN	MAY	AUG
Deciduous	3	1	1	0	0	0	4	1	1	0	1	1
Fruiting	10	4	6	14	15	18	9	6	15	26	20	5
Flowering	3	3	5	5	3	1	6	7	8	3	3	8

TABLE 34 (continued)

TREE SPECIES		1976 JUNE	SEPT.	NOV	1977 JAN	APR	JUNE	AUG	OCT	DEC	1978 JAN	MAY	AUG
Grewia sp.										f	f		
Halleria lucida							fr					f	
Harpephyllum caffrum	⊗		fr	$\overset{xx}{fr}$	f	fr	$\overset{xx}{fr}$	$\overset{xx}{fr}$	$\overset{xxx}{fr}$		fr/f	fr	fr
Macaranga capensis	⊗	fr			f	fr	$\overset{xx}{fr}$	D		D	f	$\overset{xx}{fr}$	
Millettia grandis						fr	$\overset{xx}{fr}$	fr					
M.sutherlandii		fr	f	f	f	fr	$\overset{xx}{fr}$			f	f	$\overset{xx}{fr}$	
Mimusops obovata			f		fr	fr		f	f		$\overset{xx}{fr}$	fr	f
Ochna natalitia								f	$\overset{xx}{fr}$				f
Olea capensis macrocarpa	⊗	$\overset{xx}{fr}$	$\overset{xx}{fr}$	fr		$\overset{x}{fr}$	fr	fr	fr	fr	$\overset{xx}{fr}$		
Oxyanthus speciosus	⊗	$\overset{xx}{fr}$	$\overset{xx}{fr}$	fr	fr/f	fr/f	$\overset{xx}{fr}$	$\overset{xx}{fr}$		f	$\overset{x}{fr}$	fr	fr
Phillanthus discoideus		D			fr					fr	$\overset{xx}{fr}$		
Podocarpus latifolius					fr		$\overset{xx}{fr}$					fr	
Protorhus longifolia		f	fr	$\overset{xx}{fr}$				$\overset{xx}{fr}$					$\overset{xx}{fr}$
Rauvolfia caffra	⊗	D					fr	fr/D		fr	$\overset{xx}{fr}$	D	f
Rawsonia lucida											$\overset{xx}{fr}$		
Rhoicissus tomentosa											$\overset{xx}{fr}$		
R.tridentata											$\overset{x}{fr}$	fr	
Rhus chirindensis										fr	$\overset{xx}{fr}$		
Rinorea angustifolia					fr			f	$\overset{x}{fr}$/f	$\overset{xxx}{fr}$			f
Salacia gerrardii										$\overset{x}{fr}$			

less fruiting from then until November. From April 1977 to May 1978 the following percentages of fruiting tree species (out of 109 fruiting occurrences) were recorded:

April 1977 13,8%, June 16,5%, August 8,3%, October 5,5%, December 13,8%, January 1978 23,9% and May 18,4%. The highest percentage of the 51 tree species were in fruit in January 1978 namely 51,0%. The 31 flowering occurrences were distributed as follows for the same period: April 1977 9,7%, June 3,2%, August 19,4%, October 22,6%, December 25,8%, January 9,7% and May 9,7%. The flowering therefore mainly occurred from August to December.

Phenological observations in the coastal forest areas of Cape St. Lucia, Cape Vidal and the Mkwakwa study area halfway between these two localities showed fruiting mainly from October to May and flowering from October to January (Tables 34 and 35). Trees at Cape Vidal were phenologically more advanced _cf._ those at Cape St. Lucia 30 km to the south. For the year from May 1977 to May 1978 the percentage of fruiting tree species (out of the 97 occurrences), was as follows:

May 1977 6,2%, September 11,3%, October 21,7%, December 15,5%, January 1978 27,8% and May 17,5%; and flowering for this period out of 41 occurrences was: May 1977 2,4%, September 9,8%, October 39,0%, December 12,2%, January 1978 22,0% and May 14,6%. There was a peak of 50,0% of the 54 tree species fruiting in January and a peak of flowering from October when 29,6% of the tree species were in flower.

In Ngoye forest, 47 tree species or shrubs not utilised as squirrel food were also monitored from September 1977 to August 1978. 79,3% of 29 flowering occurrences were recorded from October to May and 88,2% of the 42 fruiting occurrences from December to April/May.

TABLE 35

PHENOLOGY OF 54 TREE SPECIES EITHER IDENTIFIED AS (Q), OR PROBABLY UTILISED AS FOOD BY P.P.TONGENSIS IN COASTAL FOREST LAKE ST.LUCIA

TREE SPECIES		1976	1977					1978		
		OCT	JAN	MAY	SEPT	OCT	DEC	JAN	MAY	AUG
Allophylus natalensis									f	$\overset{\text{xxx}}{\text{fr}}$
Annona senegalensis								$\overset{\text{xx}}{\text{fr}}$		
Antidesma venosum						f	fr/f	fr	$\overset{\text{xx}}{\text{fr}}$/f	f
Apodytes dimidiata	Q	f		fr				fr/f	$\overset{\text{xx}}{\text{fr}}$	$\overset{\text{xxx}}{\text{fr}}$
Artabotrys monteiroae	Q			fr						
Canthium inerme						f		$\overset{\text{xx}}{\text{fr}}$		
Cassine transvaalensis	Q							$\overset{\text{xx}}{\text{fr}}$		f
Celtis africana					fr/f/D	fr	fr	fr	$\overset{\text{xxx}}{\text{fr}}$/D	f/D
Chaetacme aristata								fr		
Dialium schlechteri	Q	D	fr		D	D	f	$\overset{\text{xx}}{\text{fr}}$	$\overset{\text{xxx}}{\text{fr}}$	D
Diospyros inhacaensis						fr/f		fr	-	
D.natalensis	Q				f	fr/f	$\overset{\text{xxx}}{\text{fr}}$	$\overset{\text{xx}}{\text{fr}}$	$\overset{\text{xx}}{\text{fr}}$	
Dovyalis longispina	Q	fr			$\overset{\text{xx}}{\text{fr}}$	$\overset{\text{xx}}{\text{fr}}$			$\overset{\text{x}}{\text{fr}}$	f
Drypetes natalensis		fr/f	fr					$\overset{\text{xxx}}{\text{fr}}$		f
Ekebergia capensis	Q				fr/D	fr/f	$\overset{\text{xx}}{\text{fr}}$	$\overset{\text{xx}}{\text{fr}}$/f	f/D	f/D
Eugenia natalitia						f				
Fagara capensis								fr		

TABLE 35 (continued)

TREE SPECIES		1976 OCT	1977 JAN	MAY	SEPT	OCT	DEC	1978 JAN	MAY	AUG
Ficus capensis						fr				
F.natalensis					D	fr	fr	fr	xx fr	xx fr
F.vogelii					D					
Garcinia livingstonei	Q						xx fr			
Grewia occidentalis	Q	f	fr/f			fr/f	fr	xx fr/f	fr	
Halleria lucida										f
Inhambanella henriquesii	Q	fr	xx fr			f/D		xxx fr		
Kraussia floribunda				xx fr	xxx fr					
Landolphia kirkii	Q		fr		fr	fr/f	fr/f	fr	fr	
Linociera peglerae	Q			fr	xxx fr	f		f	xx fr	xxx fr
Macaranga capensis									f	
Manilkara discolor	Q					f	xx fr	fr		
Mimusops caffra		fr				xx fr	fr	f	f/D	fr/f/D
Ochna natalitia					f	f/fr				f

TABLE 35 (continued)

TREE SPECIES	1976 OCT	1977 JAN	MAY	SEPT	OCT	DEC	1978 JAN	MAY	AUG
O.woodiana				fr	fr/f	fr	xx fr		
Ozoroa obovata			xx fr					fr	xx fr
Pancovia golungensis						xx fr			
Parinari capensis incohata Ø			fr	xx fr	fr/f				
Ptaeroxylon obliquum					fr				
Rhoicissus tomentosa							xx fr		f
Rhus natalensis								xx fr	
Salacia leptoclada Ø							fr		
Sapium integerrimum Ø						fr	xx fr		
Scolopia zeyheri				fr	fr			f	
Scutia myrtina Ø					fr	fr		xx fr	
Sideroxylon inerme					fr				fr
Strychnos decussata							fr	xx fr	
S.madagascariensis Ø				fr	fr				

TABLE 35 (continued)

TREE SPECIES		1976 OCT	1977 JAN	MAY	SEPT	OCT	DEC	1978 JAN	MAY	AUG
S.spinosa								fr	xx fr	
Teclea natalensis						fr/f		f		f
Trema orientalis	⊗	fr	fr		fr/D	f	f	fr/f	xx fr	fr/f
Trichilia emetica	⊗			fr/f	f	fr/f		xxx fr		f
Vepris undulata	⊗							f	xx fr	
Ximenia caffra			fr			fr	xx fr			
Ziziphus mucronata	⊗	xxx fr				D	f	fr/f	xx fr	xxx fr
TOTAL VALUES										
Deciduous		1	0	0	6	3	0	0	3	3
Fruiting		6	7	6	11	21	15	27	17	9
Flowering		3	1	1	4	16	5	9	6	13

May.

When considering the fruiting and flowering times of the two savanna squirrels, these were found to be similar. Werger and Coetzee (In: Werger, 1978 p.354) discuss *Colophospermum mopane* woodland, which coincides mainly with the 5°C winter isotherm for mean daily temperature of the coldest month i.e. July (a common distribution habitat for *P.cepapi,* which is sometimes called the mopane squirrel). They state that woody species, in this habitat, flower mainly from October to February, with a peak in January, coinciding with the maximum precipitation; and that from March onwards, flowering decreases and the number of fruiting woody species increases until it reaches a peak in May. The herby undergrowth mainly flowers during the rainy season. Most of the undergrowth species are only physiologically active during the rainy season and die off when rainfall decreases in March and April. On the Mosdene study area at Naboomspruit phenology was recorded in March 1978 as follows: abundant fruit on *Acacia tortilis*, *A.karroo*, *A. robusta*, *Dichrostachys cinerea*, *Diospyros lycioides*, *Rhus engleri*, *Ziziphus mucronata* (still not completely ripe) *Terminalia sericea*, *Combretum apiculatum*, *Grewia flava,* *Maytenus polyacantha*, *Ochna pulchra* and *Melia azedarach* (exotic plant, green fruit). *Spirostachys africana* and *Euclea crispa* had just finished flowering. And in May 1979, after an extremely dry summer, *Spirostachys africana* was flowering whereas *Acacia tortilis*, *A.karroo*, *Burkea africana*, *Peltophorum africanum*, *Combretum apiculatum*, *Ziziphus mucronata* and *Melia azedarach* were in full fruit and *Acacia hebeclada*, *Terminalia sericea*, *Diospyros lycioides*, *Maytenus polyacantha* were terminating fruiting, whereas *Euclea crispa* was starting fruiting.

Data from Nylsvley, adjacent to Mosdene, from 10 tree species - *Burkea africana*, *Combretum zeyheri*, *Dombeya rotundifolia*, *Diplorhynchis condylocarpa*, *Lannea discolor*, *Grewia flavescens*, *Terminalia serica*, *Acacia tortilis,* *A.nilotica*, *A.karroo* - indicates new leaves in September - October which start to fall from April, flowering mainly from early September to late in December and fruit from December to

April (Huntley, pers.comm.)*. Many of the tree species in P.cepapi habitat also occur in that of F.congicus. Phenology of trees from the habitat of the latter squirrel species is summarised in Table 36 (from Coates-Palgrave, 1977) indicating fruiting mainly from January to May (64,2% of all the 232 fruiting occurrences) and in March 53,0% of the 66 tree species were fruiting. Flowering was prevalent from September to December which made 61,8 % of all the 217 flowering occurrences, with 59,1% of the 66 tree species flowering in this month. Only 10,6% of the 66 tree species fruited in the months with lowest fruiting, i.e. August and September and 4,6% flowered in the low months of April and May.

Thirty additional tree species from bush squirrel habitat (from Werger and Coetzee, 1977) are listed in Table 37. Of the 132 fruiting occurrences, 47% were recorded from March to June, and of the 30 tree species 56,7% were in fruit in May, followed by 53,3% both in April and June. Flowering reached a maximum from September to December when 59,9% of the flowering occurrences were recorded. Out of the 30 tree species, 70% were in flower in October, followed by 66,7% in November.

DISCUSSION

In this chapter the first aim was to establish whether differences exist between the habitats of the four squirrel species but the main emphasis was once again on comparing the two forests in KwaZulu. It is essential to include a study of habitat when comparing the results of different ecological studies (Flowerdew, 1976). Flowerdew states that in studies of mammal populations, a simple estimate of ground cover in terms of density of the vegetation is often all that is required and as an alternative measure, light penetration has been used.

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STUDY AREA AT OTJITAMBI AND FROM DESOUSA CORREIA, 1976

SA NO	SPECIES	J	F	M	A	M	J	J	A	S	O	N	D
102	Ximenia americana	---	fr							f	---	---	f fr
106	Hexalobus monopetalus	fr	---	---	fr						f	f	fr
122	Boscia albitrunca								f	---	f fr	---	fr
124	Boscia foetida		fr	---	fr				f	f			
137	Moringa ovalifolia	---	f			fr	---	---	---	---	---	f----- fr	
137.4	Montinia caryophyllacea		f	--- fr	f ---	---	---	---	fr	f or	f		
129	Cadaba aphylla								f	---	---	---	fr
150	Albizia anthelmintica						f	---	---	fr f	---	fr	
159	Acacia albida					f	---	---	---	fr f	fr		
160	Acacia ataxacantha	---	fr ---	---	--- f	fr							f
165	A.fleckii	--- fr	---	f ---	---	fr						f	f to Mrch
168	A.erioloba	fr	---	fr				f	f				fr
170	A.hebeclada	fr	---	fr				f	---	f	fr	---	fr
176	A.mellifera var. detinens	fr	---	---	fr					f	---	f	
177	A.montis-usti		fr	---	---	fr						f	f
179	A.nilotica	f		fr	---	---	---	---	---	f fr	---	---	
181	A.reficiens	f	f	fr	---	---	fr						
188	A.tortilis heteracantha	f		fr	---	---	fr					f-----	
198	Colophospermum mopane	---	---	f fr	---	---	fr				f	---	
190	Dichrostachys cinerea	f		fr	---	---	---	---	---	fr	f	---	
192.1	Elephantorriza suffroticosa	fr	fr								f	--- fr	f fr
208	Adenolobus garipensis	f	---	fr						f	--- fr	--- ---	---
215	Peltophorum africanum	- - -	--- fr	f ---	---	fr				f	---	---	
226	Mundulea sericea	f	fr	fr							f	---	
236.1	Pterocarpus antunesii	fr	---	---	---	---	fr					f	f
239	Lonchocarpus nelsii					fr	---	---	---	f fr	f		
267	Kirkia acuminata	fr→									f	f	
271	Commiphora anacardiifolia					fr						f	
272	C.angolensis		fr	fr							f	f	
274	C.crenato-serrata	fr ---	f									f	f fr
276	C.glaucescens		fr	fr→								f-----	
280	C.mollis		fr	---	fr					⟵	f	f	⟶

TABLE 36 (continued)

SA NO	SPECIES		J	F	M	A	M	J	J	A	S	O	N	D	
550	Terminalia prunioides		f fr	-----	-----	-----	-----	-----	fr			f	-----	-----	
569	Steganotaenia araliacea		fr ⟶							f	-----	f	fr	-----	
595	Euclea divinorum		f						f	-----	-----	fr -----	----- -----	fr f	
598	E. pseudebenus			fr	-----	-----	fr			f	f				
605	D. lycioides		fr	-----	-----	-----	fr				f	-----	-----	f	
606	Diospyros mespiliformis					fr						f	f	fr	
622	Salvadora persica		fr	fr				f	-----	-----	f fr	-----	-----	-----	
648	Pachypodium lealii								f	f			fr		
617	Olea africana		-----	f	fr	-----	-----	-----	fr			f	-----	-----	
674	Rhigozum brevispinosum		fr	-----	-----	-----	fr				f	-----	-----	fr f	
702	Vangueria infausta		fr	-----	-----	fr					f	f			
733	Tarchonanthus camphoratus					f	-----	f fr	-----	-----	fr				
973	Rhod. Cordia sinensis									f				fr	
	TOTAL NUMBER FRUITING		26	31	35	30	27	16	11	7	7	9	13	20	
		TOTAL													232
	($^n/232$) % OF ALL SEEDERS		11,21	13,36	15,09	12,93	11,64	6,90	4,74	3,02	3,02	3,88	5,60	8,62	
	($\frac{n}{66}$) % OF TREES		39,39	46,97	53,03	45,45	40,91	24,24	16,67	10.61	10,61	13,61	19,70	30,30	
	TOTAL NUMBER FLOWERING		25	16	9	3	3	5	7	15	27	35	39	33	
		TOTAL													217
	$^n/217$		11,52	7,37	4,15	1,38	1,38	2,30	3,23	6,91	12,44	16,13	17,97	15,21	
	$\frac{n}{66}$		37,88	24,24	13,64	4,55	4,55	7.58	10,61	22,73	40,91	53,03	59,09	50,0	

TABLE 37

PHENOLOGY OF 30 TREE SPECIES IN HABITAT OF P.C.CEPAPI (FROM COATES-PALGRAVE, 1977)

		J	F	M	A	M	J	J	A	S	O	N	
102	Ximenia americana	------fr								fxxxxxxxxxxxxxxxxx			
122	Boscia albitrunca								fxxxxxxxxxxxxf		fr---------		
126	Boscia mossambicensis				fxxxxxxxxxxxf		fr----------------fr						
162	Acacia caffra	-----------fr								fxxxxxxxxxxxf			
172	Acacia karroo	fr ⟶ xxxxxxf									fxxxxxxxxxx		
178	A.nigrescens	fr----------------------------fr							fxxxxxxxxxxxxxxxf				
179	A.nilotica	f		fr-------------------------------------fr						fxxxxxxxxxxxxxxxxx			
188	A.tortilis	f		fr---------------fr								fxxxxxx	
189	A.xanthophloea	fr⟶								fxxxxxxxxxf			
190	Dichrostachys cinerea	f		fr-------------------------------------fr							fxxxxxxxxxx		
197	Burkea africana		fr------------------------------fr							fxxxxxxxxxxf			
267	Kirkia acuminata	fr⟶									fxxxf		
303	Securidaca longipedunculata				fr----------------------fr				fxxxxxxf ⟶				
360	Sclerocarya caffra				fr----------fr					fxxxxxxxxxxf			
375	Ozoroa paniculosa	xxxxxxf		fr								fxxxxxx	
399	Maytenus heterophylla	fr	fxxxxxxxxxxxxxxxxxxxxxxf			fr---							
401.2	M.polyacantha		fxxxxxxxxxxxf			fr----------------fr							
458	Grewia bicolor	f		fr---------------fr							fxxxxxxxxxxx		
459	Grewia flava	xxxxxxxxxxxxf-----fr									f----------		
459.2	G.flavescens	xxxxxxxxxxxxf						fr---fr					
467	Adansonia digitata				fr----fr						fxxxxxxxxxx		
470	Dombeya kirkii			fxxxxxxxxxxxxxxxxxf	fr------------------fr								
471	D.rotundifolia							fxxxxxxxxxxxxxxxxxf			fr---------		
532	Combretum apiculatum	xxxxxxf fr---------------------fr								fxxxxxxxxxxxxxxxxxx			
539	C.imberbe	xxxxxxxxxxxxf	fr-----------------------fr ⟶									fxxxxxx	
550	Terminalia prunioides	f fr-----------------------------------fr									fxxxxxxxxxxx		
594	Euclea crispa		f		fr---						fxxxxxxxxxx		
601	Euclea undulata	xxxxxxxxxxxxxxxxxf			fr--fr								f
621	Salvadora angustifolia	------------fr				fxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxf						fr----	
657	Ehretia rigida	fr xxxxxxf							fxxxxxxxxxxxxxxxxxxxxxxxxx		fr---------		
	TOTAL NUMBER FRUITING	12	12	13	16	17	16	12	10	6	5	5	8
	TOTAL												132
	TOTAL NUMBER FLOWERING	12	11	7	5	4	5	2	6	13	21	20	16
	TOTAL												117
	PERCENTAGE FRUITING	9,1	9,1	9,9	12,1	12,9	12,1	9,1	7,6	4,6	3,8	3,8	6,1
	TOTAL												100
	PERCENTAGE FLOWERING	10,3	9,4	6,0	4,3	3,4	4,3	1,7	5,1	11,1	18,0	17,1	13,7
	TOTAL												100

When attempting habitat analyses, time is a limiting factor and must be weighedagainst the value of the analyses. Initially, Theron* (pers.comm.) suggested the use of the point-quarter method and after this method had already been implimented in the two forests, Theron pointed out that the third-nearest individual method would save time and would probably still give good comparative results. The point-quarter analyses were therefore first completed in the two forests, and the third-nearest individual method was used in the savanna habitats of cepapi and congicus. For comparative purposes this method wasthen also implimented in the Ngoye and Mkwakwa forest.

It transpired that the point-quarter analyses were not in vain as it yielded comparative data on canopy versus subcanopy layers of the two forests which the third-nearest individual method does not reveal. The canopy trees in Ngoye forest occurred at a greater, and the subcanopy trees at a lesser density than in Mkwakwa forest. This, together with the greater canopy height in Ngoye, results in the lower light intensity in Ngoye forest. A count of trees on the actual study areas also revealed a higher density for Mkwakwa than for Ngoye forest. However, the important difference in density between these two forests is evident from the vertical density profile analysis which portrays visibility and which showed that Mkwakwa forest has a much greater obstruction to visibility than Ngoye forest.

Density pole measurements indicated that the forests also have greater obstruction to visibility than open savanna and light intensity measurements showed that a much greater percentage of light penetrates the two open habitats. Analysis of variance of the point-to-plant distances of the third-nearest individual method as well as a count of the trees on the study area showed that the forests had a greater density than both of the open habitats (dbh $>$ 2,5 cm).

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Flowerdew (1976) also states that a description of the rock and soil formation is an essential factor in determining the vegetation cover. Soil analyses were completed only in the two forests where the greater moisture retention in Ngoye forest indicates a more moist habitat than in the coastal Mkwakwa forest. With the concomitant greater leaching in the latter habitat the vegetation type is of lower succession.

The second aim of this chapter was to investigate phenology of the fruit-bearing trees. There was a seasonal pattern in all four of the habitats with flowering from October to January in the forests and from September to December in savanna. The flowering peak was also slightly earlier (September) in the forests than in the savanna (December). Fruiting mainly occurred from December to May in Ngoye forest and from October to May in Mkwakwa forest with a peak in both these forests in January. Fruiting was retarded in the savanna and occurred from January to May for congicus with a peak in March and from March to June for cepapi with a peak in May.

The results of this and the previous two chapters are summarised in Table 38. The colour of the four species appears to be an adaptive balance between advertisement and crypticity, with the largest and darkest species, ornatus in the habitat with the lowest light intensity and the highest canopy cover. In the Ngoye forest there are large areas of climax forest, a lower subcanopy tree density and greater visibility than in the coastal forests, and ornatus probably has to move over a greater 'unproductive' volume to maintain its knowledge of the seasonal resources. The coastal forests are on more leached soil and at an earlier stage of plant succession. The light intensity is higher and consequently the colour of tongensis is a lighter shade and blends into the general background. The volume over which the smaller tongensis has to move is also not as great with the lower canopy cover. Cepapi and congicus inhabit open wood=

TABLE 38

SUMMARY OF DIFFERENCES BETWEEN HABITATS OF FOUR TREE SQUIRREL SPECIES

	PARAXERUS PALLIATUS ORNATUS	P.P.TONGENSIS	P.CEPAPI CEPAPI	FUNISCIURUS CONGICUS CONGICUS
ass (g)	366	206	223	112
olour	Red ventrum, face, legs. Almost black dorsum	Orange ventrum, face, legs. Dark brown speckled dorsum	White ventrum & cream face & legs Light brown speckled dorsum	White ventrum, face, legs Light brown dorsum & cream side-stripe
abitat	Evergreen moist forest 80,9% canopy cover	Coastal forest & thicket 65,1% canopy cover	Woodland	Savanna & woodland
ainfall range (mm)	1315 - 1868	628 - 1466	100 - 1024	100 - 400
emperature range (°C)	9,7 - 10,6 frost-free	7,9 - 11,5 frost-free	10,2 - 17,4 frost	14,3 - 27,4 frost
elative humidity at 08h00/ 4h00 (approximate data)	-	84/70	67/33	63/26
egetation density rees/m^2 (dbh-2,5cm)(third-earest individual method)	0,29	0,16	0,04	0,05
hade light intensity - 2h00, March (lux)	152,7	315,7	2089,0	3631,0
Vertical cover	16,3	58,6	19,2 -termitaria clumps 30,6 -woodland on sandveld	-
istance that squirrels ealise danger (m)	13,5 (4 - 50)	8,5 (1 - 20)	27,1 (4 - 100)	-
pproximate branch pathway idth (cm)	5 - 23 and more	2 - 20	1 to 20	0,4 to 14

areas than the two forest species. The use of the available space as evident from the area over which the species move and their degree of terrestriality will be investigated in the following chapter, and comparative aspects of energy within the habitats, and of adaptive communicatory patterns, in Chapters 6 to 9.

CHAPTER 5

USE OF SPACE

INTRODUCTION

Habitat which is influenced by climate and geology is the space at the disposal of any mammal. In tree squirrels, use of space not only involves area, but also volume. The quality of a particular part of the habitat and the individual's role in its community also affects the animal's use of space. In this chapter an attempt is made to approximate the area in use and the population densities of the squirrel species and to point out differences in available volume, and use of space as influenced by the already described habitats.

MATERIALS AND METHODS

COMPARISON OF THE TWO STUDY AREAS

Localities of the two study areas of P.palliatus are shown in Figures 2 and 3, and maps of these study areas in Figures 9 and 10 In Ngoye forest, the study area was larger than at Mkwakwa, for the following reasons:

(a) There are large open areas of climax forest (Figure 12) which are devoid of any food source;

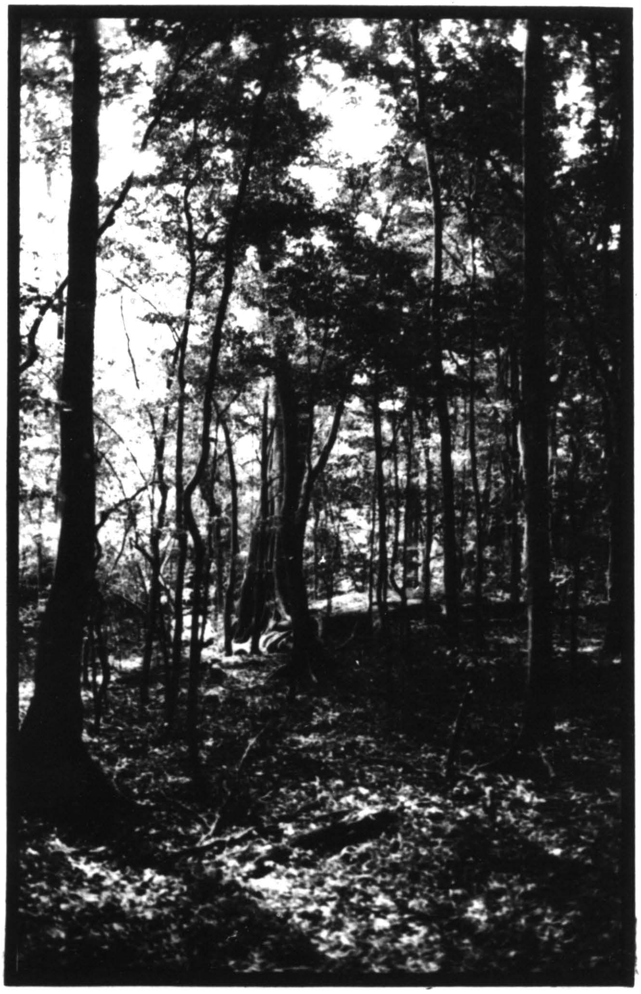
(b) Food sources and successful trapping sites are widely spaced;

(c) There was much overlap of movement of individuals e.g. at trap station 1 in Ngoye forest (Figure 9), 23 individuals were caught from January 1977 to May 1978. This represents a larger degree of movement when compared to e.g. cepapi where only the individuals of the nesting group, consisting of five on average, would be trapped for two years at one trapping station (Viljoen, 1975);

(d) The nests that had been located, were at least 200 m apart and as it is extremely difficult to locate a nest in the dense, high forest, they had to be included in the study area even though they were far apart.

Observations in Ngoye were mainly made by walking until a squirrel

Figure 12. Clearings in climax areas in Ngoye forest. The forest floor is clear of growth and covered in leaf litter.



was seen or heard, then stopping to observe it. It was difficult to obtain detailed information about any one group because of their wider movements and unstable nesting behaviour. At Mkwakwa, the area was smaller, and much denser (see Vegetation and also Figure 13). The Tonga squirrels were extremely difficult to observe and less vocal (see Communication) and as it is almost impossible to move silently in these forests, most observations had to be made by waiting where squirrels had been seen frequently and would probably move. Feeding stations at Mkwakwa were maintained during my absence, and therefore more detailed information about the one resident group of squirrels was obtained than in Ngoye.

OBSERVATIONS RECORDED

On sighting a squirrel, the following observations were recorded: moult, age, sex, mark, number of squirrels together, layer of vegetation occupied, vocalisation frequency and type, feeding behaviour, activity and time of day, as well as position on the study area map and subsequent movement when possible.

TRAPPING AND MARKING

36 "Have-a-heart" wire mesh live traps (410 x 50 x 50 mm) were placed on habitual pathways of the squirrels (Figure 14). The traps were not placed in a grid as is customary with terrestrial small mammals, as no captures would have been made if the traps had been placed on the ground and even if trees were chosen a fixed distance apart, trapping would have been much less effective. Before the branches used as pathways had been established, only two squirrels were caught in 550 trap-hours in Ngoye forest and one in 731 trap-hours in coastal forest. Trap-hours exclude traps sprung or overturned, or birds caught, and are the product of the number of traps and the number of hours trapped. Traps were prebaited for two days on arrival at the study sites with a mixture of Huesli*, peanutbutter, sunflower oil, honey, oats and condensed milk,

* Huesli - Manufactured by Honey Crunch (Pty) Ltd., Newlands, Johannesburg.

Figure 13. Dense growth within forests: Above - Ngoye forest, in the foreground secondary growth where mature trees have fallen thus permitting penetration of sunlight; and in the background mature forest with a closed canopy. Below - dense vegetation in coastal forest at Mkwakwa.

Figure 14. 'Have-a-heart' live trap placed on habitual squirrel pathway in dense coastal forest at Mkwakwa.

together with fresh fruit. Traps were subsequently set at sunrise and checked every three hours. Captured squirrels were sedated with ether, weighed, measured and marked with Nyanzol D fur-dye (Giles, 1971), tail was fur-clipped, and toes were clipped following Melchior and Iwen (1965) for permanent identification. No more than two toes were clipped on one individual. Freeze-branding (Hadow, 1972) was attempted as a permanent marking method but, although the results on captive squirrels were satisfactory, both with Frion 12 (Dichloridifluoromethane, under 5 Bar, -29,8°C boiling point) and with Frion 22 (Dichlorofluoromethane, under 9 Bar, -40,8°C) a wound resulted which took two weeks to heal. The Frion is applied for 8 to 10 s at 5 cm distance on a fur-clipped portion, and after three weeks, white hair appeared. Frion 22 is less successful as it escapes from the aerosol can at the higher pressure. Frion 12 is commercially available as "Dust-off" at photographic shops. It was considered inadvisable to subject wild squirrels to this treatment.

DENSITY ESTIMATES

These were made using the Petersen estimate (Lincoln index) and the Jolly-Seber model as described in Golley et al (1975). One period of marking is followed by one period of recapture and the ratio of marked to unmarked animals is used to calculate density. The Lincoln index requires the following assumptions:

1 The animals do not lose their marks;
2 the captures are correctly recorded as marked or not marked;
3 marking does not affect the probability of survival;
4 there is no gain or loss of members during sampling;
5 the population is randomly sampled so that every animal has the same probability of capture.

The estimated density:

$\hat{N} = Mn/m$,

where M = number of marked animals released from the first sample
n = number of animals in the second sample
m = number of marked animals in the second sample

The Jolly-Seber stochastic model sequentially estimates population size and requires, additional to the above assumptions, that there is no recruitment and immigration, but death and emigration affect marked and unmarked animals equally (instead of 4 above).

In this case

$$\hat{M} = n_i + \frac{n_i Z_i S_i}{m_i r_i}$$

$(i = 2, \ldots, k-1)$

where samples are taken on k occasions and the population size is estimated at time i, and where:

M_i = estimated number of marked animals in the population at time i;
Z_i = number marked before the ith sample which are not caught in the ith samples but are caught subsequently;
S_i = number released from the ith sample;
r = number of the S_i that are caught subsequently.

During a study on bush squirrels (Viljoen, 1975) the population size could be determined by establishing nest group size at sunset and sunrise Therefore, this was also envisaged for the study of the forest squirrels. However, in a forest it sometimes takes up to 14 days to locate a nest, as the squirrels can disappear in the dense vegetation within seconds. Further problems arose from the habits of these forest squirrels which do not always nest together and/or in the same nest on consecutive nights as do savanna squirrels. They are very wary in the proximity of the nest and when disturbed on one night, they would probably not use the nest the following night. Certain nests were never located even though the nesting tree must have been within less than 15 m. Estimates of squirrels along 1 km of road (to minimise noise disturbance) were also made by repeatedly walking this distance and counting squirrels either seen or heard vocalising or chewing on nuts.

HOME RANGE

Points of capture and resightings of individual squirrels were marked on a grid map of the study area. Where only two positions were available, the distance was measured between the two points. Where more than two positions were available, the area of the polygon was measured to determine home range.

As these forest squirrels could not be followed for any distance, telemetry was used to obtain a more reliable estimate of movement in the short time available. Six transmitters (148 MHz, AVM Instrument Company, Champaign, Illinois - LA12 Receiver (weight 1,4 kg) and SM1 transmitters with MP675T2 batteries (1,7 cm diameter and 0,5 cm height)) werefitted to a leather and vinyl harness (Figure 15). A belt as used on bush babies by Bearder* (pers.comm.) was slipped within seconds and squirrels had to be harnessed both around the neck (a, in Figure 15) and the chest (b) with a tight-fitting harness and an interconnecting section (c). The battery (g) and transmitter (h) were fixed to the leather harness (f), with dental acrylic, taking care to smooth the surfaces. Brass studs (d) were used to fix the harness sections together. The antenna (E - string of electric guitar) is inserted in the collar, between the leather and a brightly-coloured inner vinyl harness which is stuck onto the inside of the leather with Genkem*

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1 *Dr. S.K. Bearder, Zoological Society, Regent's Park, London NWI 4RY.

2*Genkem contact adhesive - General chemical corporation Ltd. Johannesburg adhesive. This bright colour facilitates finding of the harness in the event of it falling off. The smooth vinyl also protects the animal's body from the rough antenna.

RESULTS

Time was a limiting factor during this study and had to be divided between the two study areas. The number of observation hours and the periods of visit, selected to represent all seasons, are given in Table 39. In Ngoye forest 188,5 h more were spent than at Mkwakwa. The total of 845,5 h in Ngoye and 657 h at Mkwakwa represent only observation time, whilst trapping and habitat analyses occupied additional time. Initially, time spent in KwaZulu was unproductive. This was so in Maputoland as it took almost a year to find a study area where squirrels were reasonably tame but without the dense ground cover. Isoglossa sp., which totally obstructs visibility from the ground up to a height of 1 m. In Ngoye forest, many hours had to be spent travelling (approximately 4 h daily), as permission to remain in the forest was only obtained after 12 months. The forest squirrels are extremely difficult to trap due to: first the dense habitat which makes it difficult to observe their movements; secondly abundance of food and/ or different bait preference to that of savanna squirrels; and thirdly their arboreal habits (traps on the ground were totally ineffective). In contrast, bush squirrels could be captured exclusively on the ground (Viljoen, 1975) with traps baited only with carrots.

Trapping results are summarised in Table 40. In Ngoye 181 squirrels were caught during the period April 1976 to May 1978 in 15 394,2 trap-hours. This gives a trapping success rate of 1,18%. However, during April 1976 no squirrels were caught in 442 trap-hours and during June only 10 were caught in 1 148,5 trap-hours. Very few were caught until April 1977. But from June 1977 knowledge of the pathways resulted in more successful trapping with 161 squirrels caught in 8 570 trap-hours i.e. a success rate of 1,88%.

Figure 15. Radio-tagging harness cut open to release the squirrel: a. neck circle, b. chest circle, c. interconnecting section, d. brass studs, e. vinyl surface, f. leather surface, g. battery and h. transmitter, both the latter covered with dental acrilyc.

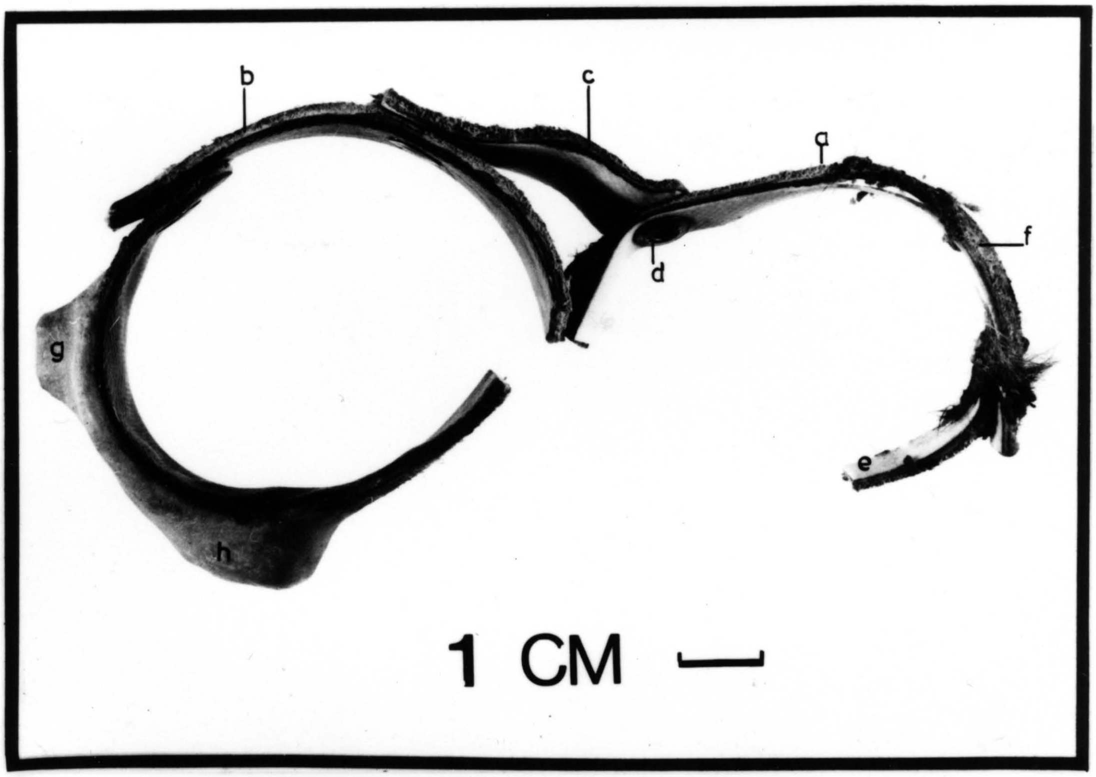

b
c
a
d
f
g
e
h
1 CM

TABLE 39

NUMBER OF OBSERVATION HOURS IN THE FIELD ON P.PALLIATUS FROM APRIL 1976 TO MAY 1978

MKWAKWA FOREST		NGOYE FOREST	
SPECIES P.p.TONGENSIS		SPECIES P.p.ORNATUS	
MONTH	NUMBER OF HOURS	MONTH	NUMBER OF HOURS
		April 1976	19
		June	95
October 1976	135	August	87
January 1977	69	January 1977	74
March	107	April	93
June	83	June	106
August	92	August	90
November	90	October	59
May 1978	81	December	80
		January 1978	85
		May	57
TOTAL	657	TOTAL	845

Total 1 502 hours in 273 days

TABLE 40

TRAPPING RESULTS FOR P.p.ORNATUS AND P.p.TONGENSIS FROM APRIL 1976 TO MAY 1978

	MONTH	TRAP-HOURS	NO. OF SQUIRRELS CAUGHT	
P.p.ornatus	April 1976	442	0	
	June	1148,5	10	
	November	550,0	2	
	January 1977	1892,0	5	
	April	2791,5	3	
	June	3151,0	22	
	August	1768,0	31	
	November 1977	1734,2	69	
	May 1978	1917	39	
	TOTAL	15394,2	181	1,18%
P.p.tongensis	April 1976	731	1	
	August	680	0	
	October	1179,5	26	
	January 1977	1714,0	8	
	March	1318,0	12	
	May	1961,5	9	
	August	2119,5	9	
	October	780	6	
	November	1757,5	18	
	May 1978	2074,5	14	
	TOTAL	14315,5	129	0,90%

For tongensis only one squirrel was caught in 731 trap-hours in April 1976 at Kosi Bay, where movement patterns were unknown. At Mkwakwa 102 squirrels were caught in 13 165,5 trap-hours i.e. a success rate of 0,77% from October 1976 to May 1978. These squirrels had been feeding on refuse at the camp of the Zulu game guards and it was relatively easy to establish their habitual pathways.

The much lower trapping rate for tongensis is possibly a result of the smaller study area (6,94 ha at Mkwakwa cf. 10,08 ha at Ngoye) but as is evident from the density estimates, probably also signifies a smaller population.

DENSITY ESTIMATES

Mark-recapture estimates:

Juvenile squirrels were excluded from each estimate to fulfill requirement 4, that no gain of members should occur during sampling. Only three estimates were made for the Ngoye forest, namely, in August and December of 1977, and May 1978, as too few squirrels had been caught before June 1977 to enable a reliable estimate. The Petersen estimate from recaptures gave a mean density of 43,5 squirrels in the 10,08 ha of Ngoye forest or 4,32 squirrels/ha (Tables 41 and 42). The mean estimate from resightings was 40,2 squirrels or 3,99 squirrels/ha for four visits (January included). In January 1978 squirrels were not trapped as they still showed fur dye clearly and the opportunity was taken to spend the short time available exclusively in observation. However, a resighting estimate of the ratio of marked to unmarked individuals in January also gave an estimate similar to previous estimates (44,2 squirrels, i.e. 4,38/ha). The Jolly-Seber sequential model necessitates a pre- and post-trapping period and was only calculated for December. This density estimate was 43,78 (4,34/ha) i.e. between the 48,64 and 37,14 for recapture and resighting estimates of December. The mean biomass estimate at a mean adult mass of 368,19 g (n = 104) was 1 590,98 g/ha. (Table 42).

TABLE 41

POPULATION STRUCTURE OF P.PALLIATUS IN KWAZULU

	MONTH	NUMBER OF SQUIRRELS CAUGHT		NUMBER OF NEW SQUIRRELS	
		♂	♀	♂	♀
P.P.ORNATUS	August 1977	18	9	10	5
	December	24	14	9	4
	May 1978	13	11	0	3
		45	34	19	12
P.P.TONGENSIS	January 1977	4	4	0	1
	March	5	7	0	0
	May	4	6	0	0
	September	6	6	4	0
		19	23	4	1

TABLE 42

PETERSEN RECAPTURE DENSITY ESTIMATES FOR P.P.ORNATUS ON 10,08 ha AND FOR P.P.TONGENSIS ON 6,94 ha (JUVENILES EXCLUDED AT EACH ESTIMATE)

	MONTH	NO.OF SQUIR= RELS CAUGHT	NO. OF NEW MARKS	RECAPTURE ESTIMATE	SQUIRRELS/ ha	BIOMASS g/ha
P.P.ORNATUS	August 1977	27	15	42,0	4,17	1535,35
	December	38	13	48,6	4,82	1774,68
	May 1978	24	3	39,7	3,94	1450,67
	Mean population size =		43,5±4,62		4,32	1590,58
P.P.TONGENSIS	January 1977	8	1	16,0	2,31	482,93
	March	12	0	17,0	2,45	512,20
	May	10	0	11,0	1,59	332,41
	September	12	4	13,5	1,95	407,67
	November	11	0	17,0	2,45	512,20
	Mean population size =		14,90±2,61		2,15±0,37	449,48

In the 6,94 ha of study area at Mkwakwa forest the Petersen estimate from recapture data of five occasions (January, March, May, September and November of 1977) indicates a mean of 14,9 squirrels (Table 42). The Jolly-Seber model for September 1977 estimates 14,4 squirrels. A problem arose on calculating density and biomass estimates from these figures as the area studied was 6,94 ha, but the area trapped was mainly 3,9 ha with an extremely dense, untrapped 600 m to the next trapping station, inclusion of which brings the area to 6,94 ha. Calculations of density was 3,80 squirrels/ha for 3,9 ha, but it must be kept in mind that this is probably an overestimate. Conversely, if calculated for 6,94 ha, the density would be under-estimated (see Table 42). Working with 3,8 squirrels/ha, the biomass estimate is 794,43g/ha (i.e. at 209,06 g mean adult mass, n = 60).

Juvenile recruitment into the populations was low. Indeed only two juvenile ornatus were caught (one in May 1978 and one in August 1977), and only eight juvenile tongensis (one in January, three in September and four in November of 1977). However, more juveniles were seen (Table 81, in Cahpter 10) and it seems possible that they are trap-shy at this age. Table 81 indicates two juvenile ornatus in Ngoye forest in June/August of 1977 and four in May 1978, and at Mkwakwa forest, four juvenile tongensis from October 1976 to March 1977 and 11 from August 1977 to May 1978. Biomass estimates can therefore be adjusted to a maximum of 1 659,8 g/ha in Ngoye forest (i.e. an average of three juveniles per breeding season at 231,8 ± 45,6 g (n = 6) thus totalling 695,7 g for the study area), and to 1 054,64 g/ha for Mkwakwa forest (i.e. at an average of 7,5 juveniles per breeding season at 135,3 g ± 19,8 (n = 13), thus totalling = 1 014,8 g for the study area).

In sandveld on Mosdene where an additional estimate of cepapi density was made from nest group observations during the present study, 2,3 squirrels numbered between 25 and 31 in 12 ha i.e. 2,08 to 2,58 squirrel ha. At a mean adult mass of 216 g (n = 60) this would indicate a biomass from 449,3 g to 557,3 g/ha. One male in this area was radio-tagged the possibility of losing a squirrel was greater in the dense vegetation. This cepapi was followed for 30 d over a range of 1,26 ha. (The squirrel subsequently dropped the harness and was caught a year later unharmed). The area of his range is larger than territory sizes derived for cepapi in termitaria-thicket habitat (Viljoen, 1975) of 0,23 ha ± 0,06 (n = 6). Population density in the latter area was also higher at 15 to 30 squirrels on 5,4 ha or a bio= mass of 600 to 1100 g/ha.

NESTING GROUPS AND BEHAVIOUR AT SELECTING A NOCTURNAL NEST

Five nests were observed at sunrise and sunset during the first two visits to Ngoye forest and four nests during subsequent visits. (Table 43). The average nest group size was 2,98 ± 1,39 (n = 50). With eleven nests on 10,08 ha this averages 32,78 squirrels on the study area. This estimate is lower than the estimates of the Petersen index, probably because all nests had not been located. The numbers of ornatus and tongensis seen together during the day (social group) are summarised in Table 44. The mean group size for ornatus was 2,09 (n = 173) and for tongensis 1,66 (n = 238) ($P < 0,001$).

At Mkwakwa, nest group structure was more accurately followed in the smaller study area. The average group size throughout the duration of the study was 3,1 ± 1,17 (n = 20). Four nest groups consisted of 14 squirrels as listed in Table 45. During November 1977 thirteen of the squirrels visited a feeding station which had been baited prior to the November visit. However, the whole area was defended by the adult female of the group which occupied the greater part of the study area (Group 1, in Table 45). The composition of this group throughout the months, consisted of this resident female with her successive litters and, frequently, an adult male. Two adult males were associated with her, one during October 1976 and the other from January 1977 to May 1978. The litters born to her during the period of the study were evicted once they became subadults: (1) Female, Toe 200, evicted especially by the adult male, Toe 7000, but also by the adult female, Toe 4000, in March 1977; subsequently Toe 200 was only seen towards the south of the area which she invaded for only

TABLE 43

NUMBERS OF P.P.ORNATUS NESTING TOGETHER IN NGOYE FOREST

	MONTH	NUMBER OF SQUIRRELS
Nest 1 (*Ficus natalensis*)	January 1977	5
	March	3
	June	2
	August	4
	December	3
	January 1978	4
	May	4
Nest 2 (*Podocarpus latifolius*)	November 1976	5
	January 1977	4
	April	2
	June	5
	August	4
	October	3
	January 1978	3
	May	6
Nest 3 (*Ficus bizanae*)	March 1977	2
	June	2
	August	2
	October	2
	December	2
	January 1978	1
	May	2
Nest 4 (*Drypetes gerrardii*)	June 1977	3
	December	3
	January 1978	1
	May	3

TABLE 44

NUMBER OF P.P.ORNATUS AND P.P.TONGENSIS SEEN TOGETHER

P.P.ORNATUS				P.P.TONGENSIS			
MONTH	MEAN GROUP SIZE	S.D.	SAMPLE SIZE	MONTH	MEAN GROUP SIZE	S.D.	SAMPLE SIZE
August 1976	2,38	1,07	21	October 1976	2,19	0,98	16
January 1977	2,08	0,86	25	January 1977	1,63	0,60	19
April 1977	2,93	4,88	29	March 1977	1,37	0,67	59
June 1977	2,36	0,96	33	June 1977	1,91	0,54	11
August 1977	1,88	1,27	16	August 1977	2,73	3,97	22
October 1977	2,27	0,90	11	November 1977	2,16	1,03	25
December 1977	2,06	0,87	18	May 1978	1,40	0,68	20
January 1978	1,60	0,65	25				
May 1978	1,83	0,98	35				
Mean	2,09	0,95	238	Mean	1,66	1,28	173

TABLE 45

NEST GROUP SIZE AND STRUCTURE OF P.P.TONGENSIS IN COASTAL FOREST AT LAKE ST.LUCIA (MKWAKWA)

	MONTH	ADULTS		SUBADULTS		JUVENILES	
		♂	♀	♂	♀	♂	♀
Nest 1	October 1976	T10	T4000				T200
	March 1977	T7000	T4000		T200		T20
	May	T7000	T4000		T20		
	August	T7000	T4000		1	(T1,T40) 2	
	November	T7000	T4000	(T1,T40) 2			1
	May 1978	T7000	T4000		1	1	
Nest 2	November 1977	1	T*1			1	1
	February 1977		T1	1	1	1	
	May 1978		T1		1	1	
Nest 3	June 1977	T900	T700				
	September		T700			1	
Nest 4	November 1977	T200	T200			1	
Nest 5	November 1977		T20			litter?	

*T = Toe

0,14 ha. The same border line had been defended the previous year by a subadult male.(2) Female, Toe 20, evicted in the spring and subsequently established a home range towards the western edge of the forest where she bore a litter in November. (3) Males, Toe 1, and Toe 40, disappeared between November and January when 3-5 months old.

The home range was stable for the resident adult female of Group 1. Such a situation also existed in the group occupying the home range to the north (Female, Toe 1, in Table 45). However, overlap of movements did occur, especially when a good food source was available not far away. During the study, intruding females were never seen in the core area of the home range, but males often strayed far afield. Chases at the feeding station indicated consistent dominance by the resident female over all age and sex classes except for the adult male which sometimes shared her nest.

Behaviour at nesting time is relevant if a density estimate is to be attempted from nest group numbers. The forest squirrel species often moved from one nesthole to another and at a subsequent visit, might not be found in the nest which they had frequented the previous visit. Groups often also broke up into two, and when a subadult was in the process of being evicted, it would often sleep alone. The group members frequently range separately during the day, departing in different directions at emergence from the nest. They might remain in vocal contact distance during foraging, and recongregate at nesting time. Forest squirrel species show evasive behaviour at nesting time: they sometimes sit motionless for up to 50 min 5 m from the nest before moving towards it, if all is clear, and then sit motionless right at the entrance for a while before entering. If there is some disturbance, such as an observer, they would often move off, sometimes even after dark and would frequently avoid sleeping in that nest for several ensuing nights. Squirrels sometimes urinate on branches at nesting time, and on approaching the nest they sniff around the entrance. One got the impression that they recognised who had been at the nest shortly beforehand, and would either relax and stay in the tree, or immediately leave after sniffing. At nesting time a female *tongensis* which would tolerate me at the feeding station, would give the alarm immediately on sighting me close to her nest. It also seemed as if females gave the alarm at nesting time more easily than did the males. It can be seen from these nesting behavioural patterns that an estimate of numbers from the numbers of forest squirrels nesting together, will not necessarily give a valid density estimate, and also that social groups seen during the day do not signify nesting group numbers.

A description of nests (P.cepapi included) is given in Table 46. P.p.ornatus nest at a much greater average height than tongensis and cepapi. This also points to the greater volume of space that they have to utilise.

VOCALISATION CLASH-POINTS

During the study it became clear that squirrels vocalised repeatedly from certain trees or clashpoints (Figures 9, 10, Table 47). In Ngoye forest 71,03% of trills and 70,86% of clicks (70,91% of all calls) were given at these clashpoints. In Mkwakwa 71,03% of all calls were given at clashpoints surrounding the residential area. The average distance between clashpoints in Ngoye was 432,9 m ± 131,78 (n = 12) i.e. double that found at Mkwakwa of 216,66 ± 48,16 (n = 6). This indicates a smaller home range for tongensis

Density estimates made whilst walking 1 km on roads or paths through the forests, revealed almost twice as many ornatus (22 to 30 individuals) than tongensis (15).

HOME RANGE

Movement patterns of ornatus and tongensis are summarised in Table 48. Males roamed over greater distances than females. There was considerable overlap of movement as can be seen from the number of individuals caught at one trapping station, e.g. in Ngoye forest at Station 1 (Figure 7) 23 individuals were caught during the period January 1977 to May 1978, at Station 2, 16 individuals, and at station 3, 11 individuals.

TABLE 46

NESTHOLES OF PARAXERUS SPP. IN THREE HABITATS

	HEIGHT (m)	DIMENSIONS (cm)	TREE SPECIES	HOLE FACING
PARAXERUS CEPAPI CEPAPI Open woodland habitat	2,2	7 x 5	Spirostachys africana	west
	1,0	3 x 10	S. africana	south-west
	6,0	4 x 5	Faurea saligna	south-east
	8,0	4 x 12	S. africana	south-west
	6,0	5 x 5	S. africana	skywards
	2,5	3 x 8	S. africana	north-east
	1,5	6 x 12	S. africana	east
	5,0	5 x 5	S. africana	east
	2,5	4 x 5	Burkea africana	south-east
	2,0	10 x 20	B. africana	east
	1,0	9 x 80	B. africana	west
	1,5	10 x 60	S. africana	south-west
	2,5	7 x 6	S. africana	south-west
	1,5	8 x 2,5	S. africana	east
	3,0	4 x 4	B. africana	south-east
P.PALLIATUS TONGENSIS Coastal and dune forests on the Moçambique plain	5,5	5 x 3	Hymenocardia ulmoides	north-east
	1,0	7,5x 10	H.ulmoides	east-south-east
	4,0	5 x 6	Dialium schlechteri	skywards
	5,0	8 x 8	Dialium schlechteri	east
	3,5	5 x 6	D. schlechteri	north-east
	2,5	3 x 8	F. natalensis	south-west
	0,5)	10 x 8)		skywards
	1,5)	5 x 5)	H. ulmoides	south-west
	1,75)	4 x 6)		south-west
	1,5	5 x 10	D.schlechteri	south-east
P.P.ORNATUS Ngoye forest, moist, evergreen, montane forest	7,0	10 x 20	Millettia sutherlandii	north-east
	3,0	6 x 12	Drypetes gerrardii	skywards
	10,0	5 x 6	Ficus natalensis	north-east
	8,0	3 x 3	M.sutherlandii	east
	12,0	5 x 15	M.sutherlandii	east
	2,0	3 x 25	Podocarpus latifolius	north-east
	10,0	6 x 15	F.natalensis	south-west
	12,0	inaccessible	F.natalensis	skywards
	4,0	7 x 13	D.gerrardii	south
	13,0	inaccessible	Syzygium gerrardii	north-east
	4,0	8 x 12	S. gerrardii	north

TABLE 47

VOCALISING FREQUENCY AT "CLASHPOINTS" IN NGOYE & MKWAKWA FORESTS

	MONTH	NUMBER OF CALLS :			
		TRILLS		CLICKS	
		At clash=points	Total	At clash=points	Total
P.P.ORNATUS (Ngoye Forest)	January 1977	2	3	68	81
	April	12	16	103	128
	June	18	19	46	50
	October	3	4	25	37
	December	1	4	28	59
	January 1978	5	6	41	63
	May	11	21	44	83
	TOTAL	52	73	355	501
P.P.TONGENSIS (Mkwakwa Forest)	November 1976	2	2	13	17
	March 1977	6	6	38	63
	September	0	1	7	7
	May	0	0	8	8
	November	4	4	27	37
	TOTAL	12	13	93	132

TABLE 48

HOME RANGE (ha) AND DISTANCE MOVED FOR *P.p.ORNATUS* AND *P.p.TONGENSIS* FROM JANUARY 1977 TO MAY 1978

	HOME AREA (ha)	MAXIMUM DISTANCE (m)	AVERAGE DISTANCE (m)
P.p.ORNATUS			
Males	3,18 ± 1,72 (12)	1 065,6	605,53 ± 187,06 (23)
Females	2,19 ± 0,93 (6)	699,3	463,64 ± 142,88 (13)
P.p.TONGENSIS			
Males	4,33 ± 1,34 (3)	1 142,8	587,9 ± 429,90 (4)
Females	0,73 ± 0,10 (3)	685,7	220,9 ± 228,50 (6)

squirrels could be followed in the time available. Although it was difficult to navigate the yagi antenna in the dense forest at Mkwakwa, the AVM system never gave any problems and on flat bushveld country the signal could be detected for 300 to 320 m, compared to 100 m or less in dense forest. However, with the relatively small home range of squirrels, and the fact that the movements could be predicted to a large extent from former knowledge of the individuals, a greater distance was unnecessary. The transmitter pack with harness weighed 12,3 ± 1,57 g (n = 6) and chest girth for ornatus was 13,26 ± 0,92 cm (n = 11) and for tongensis 11, 8 ± 0,88 cm (n = 7).

A brief recapitulation of what happened to radio-harnessed squirrels (Figures 9 and 10) follows:

Tongensis Toe 200 got suck in a hole and had to be sawed free. The harness-cum-transmitter was then redesigned so that the battery fitted under the one arm and the transmitter under the other. He was released and therefore had only been tracked for 4 days during which his body mass decreased by 2 4 g. However, even in this short period of tracking two new nests were disclosed. Toe 70 was tracked for 10 days and lost his harness but the radio was still working and thus found. He might have succumbed as he was never retrapped. Toe 700 was tracked for 6 days during which he lost 4 g in mass, then retrapped and the harness removed which had been extensively chewed. The chest circle of the harness had also been kicked over the head, and the squirrel was tripping over it.

Ornatus: Toe 20 was followed for 11 days, showed very little mass loss (6 g) when recaptured to remove the harness. Toe 1 showed greater mass loss (43 g), was tracked successfully also for 11 days showing much greater movement than expected in very short periods of time. On recapture the harness was removed which had chafed his neck but the squirrel was released after a day, and subsequently recaptured and also seen again. Toe 7 was found dead after 8 days. His harness had got stuck on a branch and some predator had caught him there.

There are definite hazards to putting a harness on such a small, very active, arboreal animal which has to manoeuvre through small holes and dense twigs. The harness also tends to chafe the neck, and if it does not fit very tightly around the chest, it is lost. In fact, the chance of loosing the squirrel and also of not obtaining natural data is great as it must be more conspicuous and less mobile. However, some information can be obtained in no other way in such a dense habitat where you cannot follow the squirrels at all as a result of crackling leaf litter and branches.

Telemetry demonstrated that the two forest squirrel species range over similar areas. However, one must keep in mind that ornatus ranges over a greater volume than tongensis. A maximum area of 5,64 ha was calculated for one of the radio-tagged Ngoye squirrels and the average for the three males was 4,16 ha. Average size of home range of 12 male ornatus measured by both radio-tracking and recapture and resightin data was 3,18 ± 1,72 ha and for 6 females it was 2,19 ± 0,93 ha. The distance between furthest points of capture or resighting (maximum distance) was 1 065 m for ornatus males, and 699,3 m for females. A maximum area of 4,55 ha was measured for a radio-tagged tongensis male and the average male home range was 4,17 ± 1,23 (n = 3). The average female tongensis home range was 0,73 ± 0,10 ha, (n = 3). The maximum distance between furthest points of capture for tongensis was 685,68 m for females and 1 142, 80 m for males. Average maximum distances are included in Table 48. The tongensis female of the main group had a core area of 0,26 ha and her neighbour had a core area of 0,15 ha. This core is the area that the pups utilise when still too small to accompany the adults. Six males and four females of tongensis were only caught on the boundary of the residential area and no distance or area calculations could be made for them.

DEGREE OF TERRESTRIALITY/ARBOREALITY

Ornatus was observed on the ground significantly more frequently than tongensis (Table 49). In 268 sightings of cepapi in March 1977, 36,9% were of squirrels on the ground, and in 211 sightings on congicus

TABLE 49

OBSERVATIONS OF P.P.ORNATUS AND P.P.TONGENSIS ON THE GROUND AND IN TREES

P.P.ORNATUS				P.P.TONGENSIS			
MONTH & YEAR	GROUND	TREE	% OF OBSERVATIONS ON THE GROUND	MONTH & YEAR	GROUND	TREE	% OF OBSERVATIONS ON THE GROUND
4/77	30	117	20,4	3/77	6	198	2,9
5/78	9	62	12,7	5/78	1	46	2,1
6/76	53	89	37,3	6/77	1	23	4,2
6/77	48	138	25,8	8/77	19	111	14,6
8/76	32	52	38,1	10/76	6	97	5,7
8/77	46	76	37,7	11/77	30	188	13,8
10/77	28	71	28,3	1/77	30	73	29,1
12/77	31	120	20,5				
1/77	13	80	14,0				
1/78	4	69	5,3				
TOTAL	294	874	33,6	TOTAL	93	736	12,6

in April 1978 39,3% were of squirrels on the ground. These figures are similar to those for ornatus. It therefore appears as if tongensis is the least terrestrial, but it is not clear whether this observation results from behavioural differences or from a difference in vegetation density which restricts vision in the forests of tongensis.

DISCUSSION

DEFINITIONS

Brown (1966) states that the small mammal cannot survive long as a wanderer - a 'home' is vital to its existence. The living space needed by any individual small mammal varies, from one species to another and can be classified in three ways: as home range, territory or vital space (Jewell, 1966). Home range has been described as the area used by the individual within a specific period of time, territory as that area defended intraspecifically and vital space is the whole space necessary for an animal to achieve its annual cycle (Saint Girons and Saint Girons, 1959). In the present study home range and territory are relevant. Territory is used as described by Brown and Orians (1970) to have essentially:

(a) a fixed area which may change over time
(b) acts of territorial defence by the possessor which evokes escape and avoidance in rivals so that
(c) the area becomes the exclusive area with respect to rivals.

Within the areas of the Paraxerus spp.and F.congicus, wehther it be territory or home range 'foci of activity' could be determined. These are areas which are used more frequently, small in size and scattered throughout the home range (Carpenter, 1940). Carpenter found that in forest animals fruit-bearing trees form these focal points whereas other trees form places for resting and night roosts.

But in the tree squirrels here considered, foci of activity existed in fruit-bearing trees both for the forest and the open habitat squirrel species. However, definitions are limited because we are attempting to state in static terms (e.g. hectares) the area of activity of a living mobile animal that may have its movements influenced by a great many factors in the physical and biological environment (Blair, 1951; In: Brown, 1966).

METHODS

Hayne (1949) summarises the methods for calculating territory sizes under three headings:

1 those using only the area enclosed by the points of capture
2 those adding to this area a boundary zone to compensate for the lack of traps in the boundary area and
3 those considering the greatest distance between points of capture to be the major axis of the home range area, whether they proceed farther and compute an area or leave that to the reader. (Stickel, 1954, In: Brown, 1966) - range lengths may be used without conversion to areas)

Methods 1 and 3 were used in the present study. Lines connecting the outside points of capture of an animal will form a polygon, and this area is termed 'minimum home range' (Mohr, 1947) - home range is thus stated in a conservative manner, as known to be of at least a certain size. But an arbitrary system of trap setting could only rarely be expected to coincide exactly with the home ranges of resident animals. The maximum distance between points of capture is felt to be the most important clue to the home range since it represents the maximum distance moved by the animal within the period of investi= gation and to the certain knowledge of the investigator (Brown, 1966). One must look at the data obtained, in the light of the methods employed. In the present study, trapping was not on the conventional small mammal grid and was adapted to obtain the maximum amount of relevant data in the short time available.

Taylor <u>et al</u> (1971) found the mathematical expression of home range as used by Calhoun and Casby (1958) inapplicalbe for S.carolinensis, not only because of their non-random methods used to collect the data, but also because such expression requires the assumption that ranges tend to be circular. But the shapes of squirrel ranges were related to the shapes of areas of suitable woodland habitat.

Brown (1966) mentions that statistical calculation tends to sacrifice for the biologist the majority of the information gained in the field. It may be based on the assumption known, or later proved, to be invalid (Blair, 1951, In: Brown, 1966). Statistical significance may demonstrate methodological rather than biological regularities (Brant, 1962). Once again we are stating in static terms t area of activity of an animal.

SOCIAL SYSTEM, POPULATION DYNAMICS, BIOMASS AND HOME RANGE OR TERRITORY SIZES

Geist (1974) states that territoriality is permitted to evolve where diversity and productivity of plant matter is relatively great and continuous such as to fulfill the living requirements of the species on a small area; and that dispersed and diffused food of low density per unit area will lead to a selection against food competition by overt aggression, as will highly localised food sources at high density. Thus overt aggression will be selected for as a means of intraspecific competition where it will resort in a significant return in food in short supply, compared to the cost of defending it. A parallel can be found in the southern Africa tree squirrels where dispersed food sources in the Ngoye forest result in a system of overlapping home ranges with little agression for ornatus, although nest trees were defended by lactating females. Energy available within a given area is limited in Ngoye forest and the squirrels cannot maintain locally dense populations but require a large home range. In the other forest species, tongensis, defence of area was executed by adult females, but it is difficult in the dense habitat to know whether this is concomitant with dispersed food supplies, However, evidence from density and biomass estimates indicate that Mkwakwa does have a lower carrying capacity than Ngoye and is, in terms of tree squirrel requirements, less satisfying.

In contrast, cepapi (Viljoen, 1975) and probably also congicus (Viljoen, 1978) maintain territories in their open habitats where food resources are clumped and localised, but are scattered throughout the territory and are used on a seasonal basis. The only temperate tree squirrel that maintains a territory, is T.hudsonicus (Smith, 1968) Table 50. This squirrel has to defend a huge food cache, also a localised food supply, at low density.

Whether the southern African tree squirrel species maintain home ranges or territories, they all make use of calls as spacing mechanisms (see Chapter 9). Smith (1968) also describes spacing calls for the territorial T.hudsonicus which defends large caches of nuts (up to 16 000 per cache, Rusch and Reeder, 1978). And Emmons (1975) mentions the possibility that tropical rainforest squirrels might be using high intensity alarm calls in spacing context. For forest primates Devore (1963) also concludes that the different groups are kept apart not so much by overt aggression and fighting as by the daily routine of a monkey group in its own range, by rigid social boundaries of organised groups in many monkey species and in some species by loud vocalisations. The P.palliatus forest squirrels exhibit a vocal spacing system both for ornatus which have widely overlapping home ranges, and for tongensis in which females defend an area.

The pronouned family group social system of the southern African tree squirrel species indicates possible kin selection, as does the increased calling when young are present. Collins (1975) states that a theory of group selection does not preclude individual handicaps, even well-developed handicaps. But a condition of homeostasis emerges, in which the disadvantage to individual survival by adhering to the handicap, is counterbalanced by the reproductive advantage deriving from it, i.e. a critical disability system - of survival value to a reproductive breeding group but probably of negative survival value in individual selective terms.

TABLE 50

SOCIAL SYSTEM OF TREE SQUIRRELS

SPECIES AND HABITAT	SOCIAL SYSTEM	REFERENCE
Sciurus carolinensis (Mixed hardwood forest)	Completely overlapping home ranges; social tolerance; social groups 2,58 ± 0,4	Thompson, 1978
S.niger (Upland pine and hardwood forest)	Monogamous No large food cache	Allen, 1942
S.aberti (Ponderosa pine forest)	Loose system and widely overlapping home ranges Adults solitary	Farentinos, 1974
S.granatensis (Seasonal rainforest)	Solitary except in breeding season	Heaney and Thorington, 1978
Tamiasciurus hudsonicus and *T.douglasii* (Lodgepole pine forest)	Territorial individuals Adults solitary	Smith, 1968
Paraxerus palliatus ornatus (Sub-tropical evergreen forest)	Widely overlapping home ranges Social group family	Present study
P.p.tongensis (Sub-tropical coastal forest)	Overlapping ranges, but breeding territorial Social group family	Present study
P.cepapi cepapi (Savanna and woodland)	Territorial groups Social group family	Viljoen, 1975
Funisciurus congicus congicus (Savanna, woodland)	Territorial groups? Social group family	Viljoen, 1978
LOWLAND EVERGREEN FOREST *F.isabella*	NON-TERRITORIAL Solitary or small groups	Emmons, 1978
F.anerythrus	Tolerate physical contact, sometimes up to four together	Emmons, 1978
F.lemniscatus	Solitary and small groups	Emmons, 1978
F.pyrrhopus	Solitary	Emmons, 1978
Protoxerus stangeri	Solitary, strong avoidance and aggression towards conspecifics	Emmons, 1978
Epixerus ebii	Solitary, but tolerance of conspecifics	Emmons, 1978
Heliosciurus rufobrachium	Solitary and pairs	Emmons, 1978
Aethosciurus poensis	Solitary or pairs, a "contact" species	Emmons, 1978
Myosciurus pumilio	Solitary	Emmons, 1978

Exclusion of subadult squirrels from the group system when the winter approaches (March to May) was observed for both tongensis and cepapi and in captivity offspring of all four the species were driven out of the breeding group at a certain level of intolerance determined hormonally and/or by number pressure. It is therefore very probable that population regulation in the southern African tree squirrels is maintained through social intolerance. Population numbers are regulated by density dependant mortality through intra=specific intolerance in S.carolinensis (Thompson, 1978) and in T.hud=sonicus (Rusch and Reeder, 1978; Smith, 1968).

Rusch and Reeder found that within monotypic habitats, territories were of a similar size - with the smallest in white spruce, the best habitat, and regulation of squirrel densities was at levels which preclude critical food shortage. S.carolinensis (Barkalow and Shorten, 1973) and T.hudsonicus (Smith, 1968) also showed a sensitive (anticipatory in the latter species) breeding response to environmental conditions. It is doubtful whether the breeding response in palliatus and cepapi is anticipatory, but under poor veld conditions, breeding is reduced (see Chapter 10), and in captivity cepapi can breed through=out the year (Viljoen, 1975). Food is likely to be the limiting fac=tor for granivores in contrast with croppers which are predator-limited (Harrison et al, 1960; Odum et al, 1962). It seems probable that both intraspecific strife and food, limit the numbers of southern African tree squirrels.

Tentatively one might speculate that ornatus has a lower breeding rate (see Chapter 10) as well as a lower turnover rate. This would tie in with the greater body mass of this species. Geist (1974) states that large species of ungulates have a low turnover rate and non-damaging intraspecific fighting. Difference in weight can also account for differences in home range sizes (McNab, 1963; Harestad and Bunnell, 1979) as large species must derive more energy to supply their requirements. This is, however, modified by the trophic status and density and productivity of the resource base (Harestad and Bunnell, 1979). In tropical rainforest tree squirrels, home ranges were found to be as large or larger than the largest of those of temperate squirrels by Emmons (1975).

As far as weight-related differences between tree squirrel species, as summarised in Table 51, are concerned, habitat appears to have an overriding influence so that some of the smaller species, such as ornatus, and tongensis, occupy larger areas than the larger S.granatensis and S.aureogaster. However, the larger S.carolinensis and S. niger do have larger home ranges than the smaller species, but there is much variation in estimates of home range figures from different habitats and different authors. Social systems may influence the size of the home range, for instance, T.hudsonicus and P.cepapi which are both territorial species (the former temperate and the latter subtropical), which defend small and localised food resources, move over smaller areas than tongensis, even though the mass of these three species is of the same order. Thus it is almost impossible to draw any conclusions from a comparison of tree squirrel home range and biomass figures. However, it does seem consistent that females have smaller home ranges than males. This is closely related to reproductive behaviour where oestrus is usually signalled olfactorily (cepapi is an exception) and males have to roam over considerable areas to establish contact. Females remain localised and rear their offspring on familiar terrain.

There are also large variations in estimates of biomass and population density, e.g. from 507 to 2 438 g is reported per ha for Tamiasciurus spp. (Table 51). These figures will undoubtedly vary seasonally and with habitat quality. The estimates of 1111 g/ha for cepapi and 1100 g/ha for congicus are maximum numbers (just after the breeding season in March) for the particular habitats. The estimate for ornatus of 1 660 g/ha is probably representative for the forest as a whole (the study area included clearings as well as dense regenerated forest with secondary growth) and were consistent over the year. This indicates a low turnover rate for ornatus. It is difficult to generise about the tongensis estimate gross g/ha)

TABLE 51

USE OF SPACE BY TREE SQUIRREL SPECIES

SPECIES AND HABITAT	MASS (g)	RANGE OF MOVEMENT (ha)	REFERENCE	POPULATION DENSITY (no./ha) AND REFERENCE WHERE ADDITIONAL	BIOMASS (g/ha)
Sciurus carolinensis (Mixed hardwood forest)	500	♂20 ♀5 - 15	Robinson & Cowan, 1953	5 (MacKinnon, 1978)	2 500
		♂ 0,53 ♀ 0,4	Doebel & McGinnes, 1974	2 to 3	1 000 to 1 500
		0,40 to 1,2	Flyger, 1960		
		♂ 1,7 to 4,1	Thompson, 1978	0,07 to 0,12	
		♀ 1,2 to 2,0			
		0,95 (n=99)	Harestad & Bunnel, 1979		
S.niger (upland pine & hardwood forest)	907	♂ 7,56 (n=20) ♀ 3,55 (n=17) Yearlings 15,20	Adams, 1976	0,07 to 0,12 (Allen, 1942)	63,5 to 108,8
S.aberti (Ponderosa pine forests)	624	♂18,21 ♀9,26	Farentinos, 1979	-	
S.granatensis (seasonal rain forest)	440-464	♂ 1,49 (n=2) ♀ 0,64 (n=4)	Heaney and Thorington, 1978	2,5 to 5	1 125 - 2 250
S.aureogaster (dense tropical forest)	425	♂ 2,3 (n=18) ♀ 0,9 (n=9)	Brown and McGuire, 1975)	2,47	1 050
Tamiasciurus hudsonicus & *T.douglasii* (Lodgepole pine forest)	254	1,10(n=40)	Hearney and Thorington, 1978	5,5 to 9,6 (Kemp & Keith, 1970)	1 397 to 2 438
		0,24 to 0,66	Rusch and Reeder, 1978		
	196	1,66 to 3,81	Mohr, 1965		507 to 611 (Mohr, 1965)
Paraxerus palliatus ornatus (Moist subtropical forest)	368	♂ 3,18(n=12) ♀ 2,19(n=6)	Present study	4,32 to 4,62	1 660 maximum
P.p.tongensis (Subtropical coastal forest & thickets)	209	♂ 4,33(n=3) ♀ 0,73(n=3)	Present study	3,80	1 055 maximum
P.c.cepapi (Woodland and savanna)	223	0,31 to 1,26	Viljoen, 1975	2,99 to 4,98	449 to 1 111
Funisciurus c.congicus (Woodland and savanna)	112	0,50 to 0,56	Viljoen, 1978	10,00	1 100 maximum

g/ha) as the Maputoland forests vary considerably in quality when subjective assessments are made. However, *tongensis* within the Mkwakwa forest occurred at a lower density and biomass than *ornatus* in Ngoye forest. Certainly, at all the localities in the *tongensis* distribution area that were visited, this species appeared to be less common, but one must keep in mind that they are also the more cryptic and shy species.

In summary, it is evident from results in this chapter that the two forest species move over larger areas than the savanna species (see also Addendum, Viljoen, 1978). And even though the home range figures for *ornatus* and *tongensis* are similar, the greater mass of *ornatus* and the higher canopy height of the Ngoye forest, indicate that the former should have a larger home range both in area and in volume.

The social systems of the species are also adaptive to the niche that they occupy: *ornatus* has a great overlap of movement although the females are comparatively stationary. In *tongensis* overlap of movement was visible for the adult males but adult females tended to remain localised, and defend an area around their nest trees. In the savanna, the social systems of *cepapi* and *congicus* show greater group cohesion, evident also from a greater degree of allogrooming in these two species (Chapter 8) which indicates that they are "contact" species. This cohesive group system is possibly an adaptation for crossing large open areas (safety in numbers). Also, from the point of view of the extreme temperatures that they have to face in winter, the cohesive group can huddle together at night for extra warmth. The groups of these species defend territories which are smaller than the ranges of the forest species.

One fact requiring additional mention, is that *congicus* is the only species to build dreys. This could be as a result of paucity of nest holes in certain areas of their distribution. They also have a peculiar knock-kneed manner of moving about, almost like a Karate practiser does, to maintain balance. They move sideways at an incredible speed, thus being able to rapidly avoid danger in their open habitat.

The questions to arise next are whether there is also a difference in the energy partitioning, both within the habitats (distribution and amount of kJ)of resources and within the squirrels (metabolic rate, feeding efficiency and activity levels). In the next three chapters, food utilisation, energy metabolism and activity will therefore be investigated.

CHAPTER 6

FOOD UTILISATION

INTRODUCTION

Food utilisation, which is an important aspect of niche characterisation and habitat requirements, was studied with regard to relative feeding efficiency, food choice and chemical analyses of the food value of wild fruits. The bush squirrel, P.c.cepapi was included in this part of the study to obtain a comparison between the spectrum of habitats, from open bushveld to evergreen forest.

MATERIALS AND METHODS

Food selected by squirrels in the field was noted during the course of the study for P.palliatus and for F.c.congicus (Viljoen, 1978). Observations on food selection by P.c.cepapi have already been published (Viljoen, 1977c). The amount of time (seconds) spent feeding by four individuals of the three different squirrel species, was recorded for 10 of each of 23 different species of undamaged fruit collected in the forests of KwaZulu and stored in a refrigerator. Feeding time on flesh (exo- and mesocarp) and seed (endocarp and -sperm) were noted separately. In an attempt at establishing possible preferences for different classes of fruits, arbitrary divisions were made between fleshed and non-fleshy fruits (flesh mass more than 70% and less than 70% of total mass, respectively), and between small, medium and large seeds (less than 0,5 g; 0,5 to 1,5 g; and more than 1,5 g respectively).

Lengths of stomachs, small intestines, caeca and large intestines were taken in the fresh state to obtain an estimate of frugivory/insectivory of the different squirrels.

Proximate analyses (moisture, ash, fibre, protein, fat and carbohydrate values of the mesocarp and endosperm, i.e. peeled flesh and dehusked seed) were made by the Council for Scientific and Industrial Research, of the above 23, and 42 additional species of fruit to obtain infor= mation on the energy available to the squirrels in the different habitats.

RESULTS

FEEDING OBSERVATIONS

Field records of food of *ornatus* and *tongensis* are listed in Tables 52 and 53 respectively. Both feed on large (*Garcinia gerrardii* for *ornatus* and *G.livingstonei* for *tongensis*) and small fruits (*Macaranga capensis* for *ornatus* and *Trema orientalis* for *tongensis*). But in captivity both these squirrels prefer the fruits that have a large endosperm such as *Harpephyllum caffrum* and *Garcinia spp*. They search for ripe fruits (observed e.g. on *Solanum mauritianum* and *Flagellaria guineensis* by *ornatus* and *Trema orientalis* by *tongensis*, but when nothing much else is available they do take green fruits (e.g. green *Harpephyllum caffrum* was opened by *ornatus* in June of 1977 and part of the endosperm removed through the germination pore, and similarly *Drypetes gerrardii* in January of 1977).

METHOD OF FEEDING

Squirrels characteristically take a food item to a comfortable perch, mostly a branch, but sometimes a large rock, if food had been picked up off the ground. They are wasteful feeders and bits of skin, fruit, husk and even endosperm are scattered around. One can detect a feeding squirrel by the sound of dropping food and gnawing of the seed-coat for more than 30 m. Signs of digging and scuffling on the ground is only sometimes obvious. They often chase one another to obtain food rather than pick their own. If disturbed whilst feeding, they will carry the food with them to a new perch.

Close observation reveals that they gnaw by holding the top incisors steady, pressing the nut against them, and moving the lower incisors rapidly whereupon the actual incision is made. Usually the germination pore is opened (Figure 16), but *ornatus* sometimes halves a nut such as that of *Olea woodiana*, or *H.caffrum* from a heap of baboon dung. *Sapium integerrimum* nuts have three seed-houses, and are opened at the three pores by *cepapi* and *tongensis* but *ornatus* with the obviously superior gnawing ability just severs off one of the three hard seed houses in six minutes and then extracts the two other seeds from the middle in two minutes.

TABLE 52

FEEDING RECORDS OF P.P.ORNATUS FROM APRIL 1976 TO MAY 1978 IN NGOYE FOREST

PLANT PART UTILISED	SPECIES	MONTH & YEAR
Mesocarp & endosperm	Trichilia dregeana	6/76; 5/78
	Solanum mauritianum	6/76; 1/78
	S.geniculatum	1/78
	S.giganteum	1/78
	Oxyanthus speciousus	6/76
	Harpephyllum caffrum	11/76; 10/77
	Flagellaria guineense	4/77
	Ficus polita	11/77; 12/77
	Ekebergia capensis	1/78
Endosperm	Garcinia gerrardii	4/76; 4/77; 8/77; 2/78; 5/78
	Harpephyllum caffrum	11/76
	Cassipourea gummiflua	1/77
	C.congoensis	1/77
	Syzygium guineense gerrardii	4/77
	Macaranga capensis	6/77
	Protorhus longifolia	8/77
	Drypetes gerrardii	11/77
	Croton sylvaticus	1/78
	Sapium ellipticum	1/78
	Olea capensis	2/78
	Calodendrum capense	1/78
	Rauvolffia caffra	1/78
	Phyllanthus discoideus	1/78
	Teclea natalensis	1/78
	Rinorea angustifolia	1/77
	Strophanthus speciousus	6/76; 5/78
	Dalbergia armata	6/76
Leaf	Tree orchid	1/78

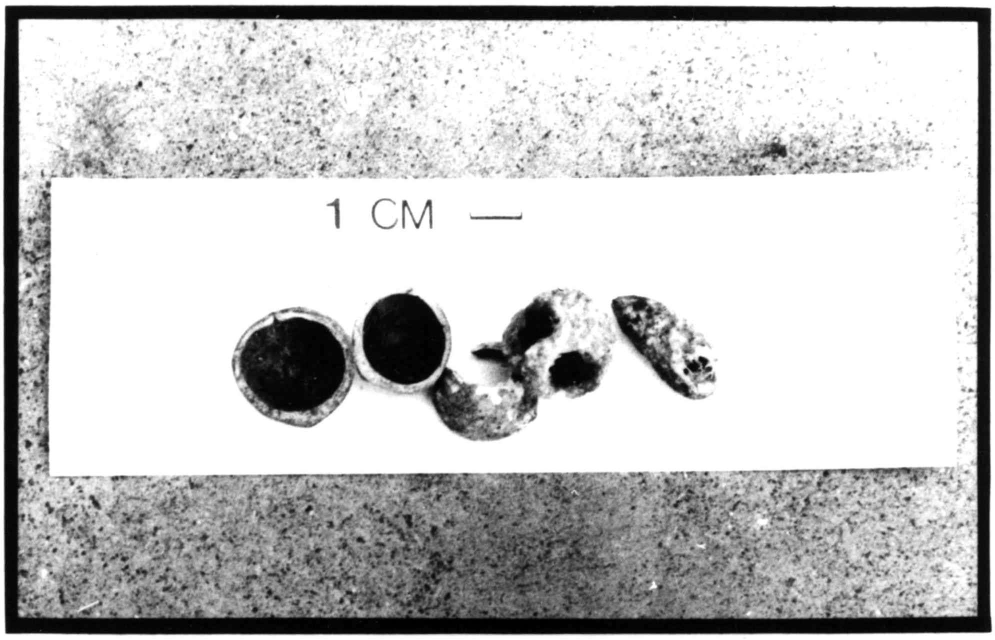
TABLE 53

FEEDING RECORDS FOR P.P.TONGENSIS IN MAPUTOLAND

PLANT PART UTILISED	SPECIES	MONTH AND YEAR	REFERENCE*
Mesocarp	Strychnos spinosa		I.F.G.
	S.madagascariensis		I.F.G.
	S innocua		I.F.G.
	Monanthotaxis caffra		I.F.G.
	Balanites maughamii		I.F.G.
	Vitex sp.		I.F.G.
	Uvaria caffra		I.F.G.
	Diospyros natalensis		p.s.
	Landolphia kirkii		p.s.
Mesocarp and endosperm	Garcinia livingstonei	1/75	R.T.
	Ziziphus mucronata	11/75; 8/76	p.s.
	Ximenia caffra		I.F.G.
	Scutia myrtina	6/76	p.s.
	Ficus petersii	8/76	p.s.
	Inhambanella henriquesii	1/77	p.s.
	Apodytes dimidiata	5/77	p.s.
	Salacia kraussii	2/78	p.s.
	Artabotrys monteiroae	6/77	p.s.
	Trema orientalis	4/76	R.T. & F.J.
	Parinari capensis incohata		p.s.
	Manilkara discolor		p.s.
Endosperm	Sapium integerrimum	2/78	p.s.
	Dialium schlechteri	1/77; 4/77; 5/78	p.s.
	Grewia occidentalis	6/76	p.s.
	Croton gratissimus	11/75	p.s.
Leaf growth points	Isoglossa sp.	11/75	p.s.
	Celtis africana	11/75	p.s.
Roots	Tree fern		p.s.
Lichen			p.s.

*I.F.G.	I.F. Garland
R.T.	R Taylor
F.J.	F. Joubert
p.s.	Present study

Figure 16. Aspects of the use of food by _P.p. ornatus_: Above - opening of hard seeds, cut open horisontally and opened at the germination pore; Below - _Garcinia gerrardii_ seedling 'planted' against the trunk of a mature forest tree.


1 CM

Surplus seeds are scatter-hoarded after removing exo- and mesocarp. Only large seeds are hoarded e.g. *Drypetes gerrardii*, *Syzygium guineense gerrardii*, *Garcinia gerrardii*, *Harpephyllum caffrum* and *Trichilia dregeana*, by *ornatus*; and *Ziziphus mucronata*, and *Inhambanella henriquesii* by *tongensis*. Preferred hoarding sites are against a trunk (Figure 16) or rock, or in a hole in a tree, and sometimes wedged between two branches, but no large food stores are made. Squirrels are omnivorous and have been recorded on occasion to take fledgelings (not encountered in the present study and probably a very rare occurrence). However, a glossy starling once mobbed a Ngoye squirrel and a black-crowned tinker barbet, a Tonga squirrel, indicating some danger to birds associated with squirrels. Hand-reared squirrels will eat raw liver and biltong, but in the wild, they mainly feed on the flesh and kernels of fruits, as well as on invertebrates which must form a greater part of their diet than can be detected merely by observing feeding in the field. Captive squirrels display hunting behaviour, following ants and chasing and reaching up for moths and winged termites. They often scratch underneath bark to extract insects and also obtain larvae from parasitised seeds (e.g. larvae in *Millettia sutherlandii* and *Protorhus longifolia* by *ornatus*). Of 556 seeds of *P.longifolia*, only 12,4% were not parasitised, but captive *tongensis* fed on the seed and the parasitic larvae. Skin of the fruit and husk of the kernel are discarded by all the squirrel species and the forest squirrels frequently also discard the flesh.

They move widely through the home range even though they might have enough food in one tree. This is probably not only for social reasons but also to familiarise themselves with the ripeness of various food items throughout their home range. At certain times they feed almost exclusively on a single species e.g. *ornatus* feeding on *S.mauritianum* in June of 1976 and on *G.gerrardii* in April 1977.

Food supply is to a large extent seasonal (see Chapter 3), causing both savanna and forest squirrels to be opportunistic feeders. Bush squirrels e.g. take nectar, chew on aloe leaves, lick pollen and eat green shoots and new leaves (Viljoen, 1977c). Although squirrels drink much water in captivity, they are sometimes far from surface water in the field, but do take water from holes in trees.

Divergent tastes and feeding abilities of the different squirrel species made it impossible to use certain fruits and seeds in the comparison of feeding rates. *Cepapi* was unable to open the hard outer coat of the tennis ball sized *Landolphia kirkii* or *Strychnos madagascariensis* (sometimes they did so after a few days of intermittent gnawing). Once the outer coat had been cracked for them, they did feed on the fruit, but not on the very hard seeds; *tongensis* could open the *S.madagascariensis* seedcoat in 2 to 15 min., and that of *Landolphia kirkii* in a slightly longer time; *ornatus* chews a pick-up hole in the outer coat of *Strychnos spp*. in a few minutes, then carries this heavy fruit to a perch where they open it (in ± 20 min.) - enough to extract the seeds which are closely surrounded by the flesh. Both *tongensis* and *ornatus* feed on the fruit and part of the seed but never finish or bury these seeds, indicating that they are not very palatable.

Garcinia gerrardii and *G.livingstonei*: *Cepapi* only sniffs at, or peels and then drops the nuts of the non-fleshy *G.gerrardii*; they take the flesh of the more fleshy *G.livingstonei* but drop the nut. In contrast to this, both *tongensis* and *ornatus* immediately rush to either of the *Garcinia* spp., which they pick up and peel and they feed on some of the flesh of *G.livingstonei*; they only peel the non-fleshy *G.gerrardii*, and either feed on the nuts or bury them. Of 13 *G.livingstonei*, *tongensis* dropped eight nuts, buried two and finished two in an average of 540 s.; of 10 *G.livingstonei*, *ornatus* dropped no nuts, buried six and finished four in an average of 315 s. The following example of behaviour of captive *ornatus* when *G.gerrardii* nuts are presented to them, show how sought-after these nuts are:

"29/9/1977: Female 1 picks the G.gerrardii fruit up, runs around for 13 min., trying to get away from two companions who persistently follow her. As soon as she attempts to bury it, the proximity of the other two causes her to dig it up again; the male twice tries to take it from her and he murmurs quite a few times whilst chasing her, she grunts; she buries it again and the second female immediately digs it up, peels it, and runs around with the one nut (the other nut dropped in the peeling) for seven minutes, then buries it". Within the first hour of presenting them with a Garcinia seed, ornatus buries and reburies it, trying to avoid group mates who follow and immediately dig it up. Sometimes they feed on it shortly before reburying. Activity levels rise when G.gerrardii nuts are presented to them, and they obviously need distance to bury them away from feeding mates. In the field an ornatus fed for 16 min. on one, even so only getting through $^3/4$ of the nut. On two other occasions Ngoye squirrels fed for 11 min. and 12 min., also not finishing the nuts. G.gerrardii nuts remain well-preserved for months and the seedfall of March 1977 was still in excellent condition in January 1978. Figure 16 shows a G.gerrardii seedling which had probably been "planted" next to the tree trunk of a mature forest tree by ornatus.

To establish how well these nuts could last and how soon they germinate, 230 seeds were planted on 20/6/78. By December, 13 could be transplante another 7 in January 1979, 11 in February, 13 in March and 12 in April. Another 38 seeds showed signs of germination by July 1979. Therefore, a total of 104 seeds germinated by July 1979, i.e. 45,2%. Half of the seeds had husks when planted and the other half were dehusked as peeled by ornatus: 37,6% of the husked seeds germinated, whilst 62,4% of the dehusked seeds germinated indicating that ornatus might actually be contributing to successful germination of the nuts. (118 Seeds rotted of which 88,2% were husked and 11,8% dehusked). Three different shapes of these seeds occur, round, flat on one side and triangular, according to the number of seeds per fruit (one, two or three). The single and round seeds which were slightly larger than the other two classes, had a 58% germination, whereas the two- and three-class seeds had 35% and 37% germination rates respectively.

Exotic acorns elicit similar response as that to G.gerrardii i.e. peeling the exocarp, sometimes feeding shortly, then burying, chasing and trying to steal from one another. They all feed extremely slowly on Garcinia seeds and acorns, also on the red aril of Trichilia spp. where they often ignore the nut.

A seed preferred by cepapi and congicus but ignored by ornatus and tongensis, is that of Colophospermum mopane. Mouthwiping which always follows when a squirrel has been feeding on a nut which it does not particularly like, always resulted in the two forest squirrels when confronted by C.mopane. Cepapi feeds on these seeds in 223,1 ± 52,9 s (n = 15) and congicus in 290,5 ± 97,7 s. (n = 22). A further discrimination by ornatus is against small seeds. In cages they showed little interest in seeds of Apodytes dimidiata, Allophylus natalensis, Rinorea angustifolia, Phyllanthus discoideus, Croton sylvaticus, Cassipourea gummiflua, Trema orientalis and Rhus chirindensis, even though they do take some of these in the field. None of the squirrels were interested in nuts of Hyphaene ventricosa (extremely hard), Phoenix reclinata (taken, but not finished) or Xeromphis sp. (very aromatic); Pancovia golungensis nuts are also dropped by ornatus after only a taste or feeding halfway (90 - 135 s.) and they then clean their throats; tongensis finishes these nuts in 217,5 s (n = 4). Another Tonga forest fruit buried by tongensis in the field but which elicits mouthwiping and is merely dropped by ornatus is I.henriquesii. Parinari curatellifolia was only tested on tongensis and cepapi; tongensis feeds on the fruit only when ripe, and takes from 20 to 65 min. to open the nut and cepapi only feeds on the ripe fruit. Seeds of Erythrina sp. are not taken by any of the squirrels. Bark feeding (number of observations in parenthesis) was recorded for tongensis as follows: October (4), November (2), August (2), May (2), April (1), January (1). Some of the fruit species have a deterrent effect on squirrels such as stickyness (Chrysophyllum viridifolium) or an adverse chemical compound (Teclea natalensis, which is very aromatic). Both these fruits induce a considerable amount of mouthwiping and the fruit is soon dropped, which is to the advantage of the seeds which are then dispersed mostly unharmed and with a better chance of escaping insect and further squirrel predation away from the parent tree. Seeds that hold some deterrent too, or at least are handled with indifference by bush squirrels, were G.gerrardii, Diospyros natalensis, Trichilia emetica, T.dregeana, Syzygium guineense gerrardii and Linociera peglerae. Seeds of Diospyros lycioides, D.natalensis and Mimusops spp. were tasted after the fruit had been eaten but soon discarded, followed by squawking sounds and an obvious dry throat.

LENGTHS OF PARTS OF INTESTINAL TRACTS

There were significant differences between the lengths of small and large intestines and caeca of the squirrel species studied (Table 54). But stomach lengths are extremely variable and were only significant between cepapi and ornatus . Cepapi has a longer large intestine and shorter small intestine than tongensis which has a similar mean adult mass. Table 55 shows that the southern African tree squirrel species have comparatively short small intestines and caeca.

FEEDING EFFICIENCY

Mass of fruits varied from 0,07 g for Ozoroa obovata to 25,46 g for G.gerrardii and seeds varied in mass from 0,09 g for Grewia occidentalis to 10,25 g for G.gerrardii. To obtain an idea of seed size from the different habitats, measurements for seed size were taken from Coates-Palgrave (1978) (13,0 mm ± 10,98, n = 13 for cepapi; 17,58 ± 10,69, n = 24 for tongensis; and 20,77 ± 8,06, n = 14 for ornatus) and these together with measurements from the present study are presented in Tables 56, 57 and 58. The measurements for seeds from bushveld do not include grass seeds on which cepapi does, however, also feed. All the fruits tested were indigenous except Solanum mauritianum which occurs extensively in KwaZulu and is taken by P.palliatus; and Melia azedarach which is found in bush squirrel habitat.

There are great differences in texture, taste, hardness of husk, and searching time which result in no correlation between seed size and the time spent feeding. Examples of two fruits of the same mass (0,3 g)

TABLE 54

INTESTINAL TRACT MEASUREMENTS OF THREE *PARAXERUS* SPP. (MEANS AND LEVELS OF PROBABILITY OF T-TESTS FOR TWO MEANS)

	C*	T	C	N	T	N
Stomach	39	39	39	46	39	46
	NS		<0,1		<0,2	
Small intestine	952	1294	958	2684	1294	2684
	<0,001		<0,001		<0,001	
Large intestine	296	205	296	283	205	283
	<0,001		<0,001		<0,001	
Caecum	50	46	50	68	46	68
	<0,1		<0,001		<0,001	

*C = *Paraxerus cepapi*
T = *P.palliatus tongensis*
N = *P.p.ornatus*

TABLE 55

RELATIVE SMALL INTESTINE AND CAECAL LENGTHS, CALCULATED FOR 100 mm OF LARGE INTESTINE IN NINE SPECIES OF TREE SQUIRRELS (FIRST SEVEN FROM RAHM, 1972)

SPECIES	SMALL INTESTINE	CAECUM
Protoxerus stangeri	1103	360
Heliosciurus rufobrachium	1246	331
Funisciurus carruthersi	771	176
F.pyrrhopus	2036	286
Paraxerus alexandri	2067	433
P.boehmi emini	2571	439
F.anerythrus	2821	359
Paraxerus c.cepapi	350	18
P.palliatus tongensis	631	24
P.p.ornatus	948	22

TABLE 56

MEASUREMENTS OF FRUITS FROM HABITATS OF THREE TREE SQUIRREL SPECIES (FROM COATES-PALGRAVE, 1977)

HABITAT	TREE SPECIES	FRUIT MEASUREMENTS (mm)	
Bushveld	Spirostachys africana	10	
	Ozoroa paniculosa	7 - 10	
	Boscia rehmanniana	10	
	Acacia tortilis	5 - 9	
	Ziziphus mucronata	15	
	Diospyros lycioides	20	
	Euclea undulata	4 - 6	
	Maytenus senegalensis	2 - 6	
	Mayrua cafra	45	
	Grewia flavescens	8 - 14	
	Ehretia rigida	5 - 7	$\bar{x}$ = 13,04±10,98
Coastal forest KwaZulu	Trema orientalis	4 - 6	
	Inhambanella henriquesii	20 - 30	
	Manilkara discolor	12	
	Mimusops obovata	30	
	Grewia occidentalis	25	
	Linociera peglerae	25	
	Cassine aethiopica	10 - 20	
	Sideroxylon inerme	12	
	Diospyros natalensis	12	
	D.inhacaensis	15	
	Ficus natalensis	10	
	Croton gratissimus	10	
	Garcinia livingstonei	25	
	Trichilia emetica	25 - 30	
	Parinari curatellifolia	50	
	Olea woodiana	10	
	Pancovia golungensis	25	
	Sapium integerrimum	17	
	Scutia myrtina	8	
	Annona senegalensis	40	
	Ziziphus mucronata	15	
	Ozoroa obovata	7 - 10	
	Dialium schlechteri	25	
	Drypetes natalensis	23	$\bar{x}$ = 17,58±10,69
Ngoye Forest	Olea capensis	20	
	Solanum mauritianum	25	
	Trichilia dregeana	30	
	Garcinia gerrardii	30	
	Harpephyllum caffrum	25	
	Syzygium guineense gerrardii	30	
	Podocarpus latifolius	15	
	Teclea natalensis	10	
	Drypetes gerrardii	10	
	Beguaertiodendron natalensis	20	
	Ficus bizanae	25	
	Cryptocarya myrtifolia	12	
	Chrysophyllum viridifolium	30	
	Rauvolfia caffra	30	$\bar{x}$ = 20,77±8,06

TABLE 57

FEEDING RATES OF P.P.ORNATUS, P.P.TONGENSIS AND P.C.CEPAPI ON SEEDS FROM KWAZULU FOREST TREE SPECIES (FEEDING TIME OF LARGER SQUIRREL SPECIES AS A PERCENTAGE OF THAT OF THE SMALLER)

NO. OF SEEDS PER FRUIT	TREE SPECIES	MASS (g)	MEASURE= MENTS(mm)	TONGENSIS VS CEPAPI	ORNATUS VS TONGENSIS	ORNATUS VS⊛ CEPAPI
	Teclea natalensis	1,12	19,2x12,0	20,7	87,3	18,0
	Melia azedarach	0,37	9,7x 7,3	38,6	50,5	19,5
(3)	Sapium integerrimum	0,90	19,0x16,0	15,9	129,2	20,6
(5)	Chrysophyllum viridifolium	0,45	15,9x11,2	23,9	124,4	29,8
	Diospyros natalensis*	0,19	9,9x 5,4	62,3	54,5*	33,8*
	Harpephyllum caffrum	1,10	22,2x10,6	48,4	72,1	34,9
	Canthium inerme	0,12	7,0x 3,4	65,6	69,6	45,6
	Ozoroa obovata	0,16	6,0x 4,3	64,2	71,4	45,9
	Apodytes dimidiata	0,11	8,2x 6,4	107,4	43,7	46,9
	Ziziphus mucronata	1,16	12,5x12,5	87,1	60,4	52,6
	Mimusops obovata	0,26	12,6x 6,2	64,7	83,0	53,9
(3)	Grewia occidentalis	0,09	6,2x 3,5	129,3	46,3	59,9
	Syzygium guineense gerrardii*	1,09	12,0x11,0	64,3	95,7	61,6
	Cassine aethiopica	1,76	16,4x13,8	52,5	125,6	65,8
(5)	Trichilia dregeana	1,38	24,0x11,3	118,3	67,1	79,3
	Dialium schlechteri	0,09	15,9x10,9	162,6	56,2	91,3
	Sideroxylon inerme	0,14	6,1x5,8	59,8	158,4	94,7
	Linociera peglerae*	1,48	17,8x12,7	*	28,4	*
	Garcinia livingstonei*					
	Garcinia gerrardii*	10,15	29,6x27,3			
	Colophospermum mopane*	0,77	28,1x18,9	101,8	*	*
	Rhus englerae	0,03	3,0x3,0	49,8	*	*
	Olea capensis	0,87	15,5x13,9	29,3	81,5	23,9
	Phyllanthus discoideus				126,0	

* Refused to feed by one of the species

⊛ Arranged for most efficient feeding of ornatus

TABLE 58

FEEDING RATES OF P.P.ORNATUS, P.P.TONGENSIS AND P.C.CEPAPI ON FRUITS FROM FOREST TREE SPECIES (FEEDING TIME OF THE LARGER SQUIRREL SPECIES AS A PERCENTAGE OF THAT OF THE SMALLER)

TREE SPECIES	MASS (g)	MEASURE=MENTS (mm)	TONGENSIS VS CEPAPI	ORNATUS VS TONGENSIS	ORNATUS VS CEPAPI
Grewia occidentalis	0,65	11,8x11,6	41,0	38,8	15,9
Cassine aethiopica	4,45	23,9x23,6	64,9	54,0	35,0
Ziziphus mucronata	2,01	18,0x18,0	75,7	56,1	42,4
Syzygium guineense gerrardii	3,15	17,8x17,7	102,6	44,8	45,9
Solanum mauritianum	0,99	13,3x11,6	94,0	50,4	47,3
Diospyros natalensis	0,37	10,6x 8,3	61,6	93,8	57,8
Linociera peglerae	2,35	21,8x18,6	109,1	59,2	64,6
Sideroxylon inerme	0,45	9,8x 9,7	67,5	96,5	65,1
Apodytes dimidiata	0,30	10,9x 7,3	90,7	75,0	68,0
Harpephyllum caffrum	2,70	24,0x16,0	94,8	75,0	71,1
Melia azedarah	0,36	12,7x12,3	78,6	102,7	80,8
Ekebergia capensis	1,44	19,7x16,2	87,8	100,0	87,8
Sapium integerrimum	6,03	24,0x22,0	100,8	113,6	114,4
Dialium schlechteri	0,22	21,1x14,6		50,6	
Trichilia emetica	0,58	20,1x12,6		90,7	
Trichilia dregeana	0,31	20,4x13,0		62,3	
Canthium inerme	0,51	10,1x 6,1	81,6		
Colophospermum mopane	0,75	Only skin	267,9		
Mimusops obovata	1,32	15,0x12,0	62,5	102,8	64,2
Ozoroa obovata	0,07	6,5x4,4			

but with different squirrel feeding rates, are *Apodytes dimidiata*, which takes *ornatus* 50,8 s , *tongensis* 67,2 s and *cepapi* 75,3 s , and *Trichilia emetica* which takes *ornatus* 126,0 s , *tongensis* 220,0 s , and *cepapi* 255,0 s. On the small seeds, *cepapi* is relatively more efficient than on the large seeds, sometimes even feeding in a shorter time than *tongensis* and nearly as quick as *ornatus*. Similarly, *tongensis* is sometimes more efficient than *ornatus* on the small seeds. However, on the medium- and large-sized seeds *ornatus* is much more efficient than *cepapi*; and *tongensis* and *ornatus* are more efficient on large seeds than on fruits when compared to *cepapi*.

In Tables 57, 58 and 59 comparative feeding time of the larger species was calculated as a percentage of that of the smaller squirrel species. Therefore, the closer to 100% the figure, the more equal are the two squirrel species being compared in feeding rate, and the lower the percentage, the more efficient is the larger squirrel species. Generall the larger *ornatus* feeds at a quicker rate than *tongensis* and both these forest squirrel species feed more efficiently than *cepapi*, even though *tongensis* does not differ significantly in size from *cepapi*

Cepapi appears to be adapted to handling small seeds and flesh of fruits whereas *ornatus* and *tongensis* mainly concentrate on kernels. When feeding efficiency on ten species of small and on 11 species of medium and large-sized seeds are compared, *ornatus* and *tongensis* are both more efficient than *cepapi*. *Ornatus* and *tongensis* feed in 41,4% and 59,5% of the time respectively that *cepapi* does on medium and large seeds as opposed to 69,2% and 78,6% of the time respectively on the small seeds. *Ornatus* and *tongensis* show similar efficiency on the small seeds with *ornatus* feeding in 100,3% of the time that *tongensis* does, but *ornatus* is more efficient on the larger seeds at 66,7% of the feeding time of *tongensis*. Fleshy and non-fleshy fruits are not utilise noticeably differently by the different species: for ten species wit fleshy fruits, *tongensis* feeds in 75% of the time that *cepapi* takes,

TABLE 59

FEEDING RATES OF FRUIT AND SEED TOTAL FOR P.P.ORNATUS, P.P.TONGENSIS AND P.c.CEPAPI (FEEDING TIME OF THE LARGER SQUIRREL SPECIES AS A PERCENTAGE OF THAT OF THE SMALLER)

TREE SPECIES	MASS (g)	TONGENSIS VS CEPAPI	ORNATUS VS TONGENSIS	ORNATUS VS CEPAPI
Canthium inerme	0,64	37,8	49,1	18,5
Sapium integerrimum	6,03	30,4	98,8	30,1
Melia azedarach	0,73	46,2	69,8	32,2
Grewia occidentalis	0,95	37,3	127,7	47,7
Apodytes dimidiata	0,41	100,0	58,3	58,3
Cassine aethiopica	6,20	96,8	47,4	45,9
Sideroxylon inerme	0,59	80,7	90,0	72,6
Allophylus natalensis	0,29	74,6	133,1	99,3
Colophospermum mopane		111,0		

ornatus in 54% of this time, whilst *ornatus* feeds in 74% of the time taken by *tongensis* on fleshy fruit. In seven species with non-fleshy fruit, *tongensis* and *ornatus* feed in 68% and 54% respectively of the time that *cepapi* takes, and *ornatus* in 81% of the time taken by *tongensi* *Ornatus* is apparently not much more efficient on non-fleshy than on fles fruits, relative to *tongensis*, but the latter is slightly more efficient than *cepapi* on non-fleshy compared to fleshy fruits.

FOOD ANALYSES

Analyses of fruits and seeds from 17 and 10 plant species respectively from the savanna habitat (CSIR data, Table 60) are compared to fruits and seeds from 33 and 35 plant species respectively from forest habitat (data from present study and from CSIR, Tables 61 and 62). These data indicate a higher energy content for both fruits and endosperm from forest plant species. The fat content is noticeably higher in fruits and endosperm from the forest species but the protein content of endosperm from the savanna species is higher than in those from the forest. Differences between values for *tongensis* and *ornatus* habitats do not appear significant apart from the higher carbohydrate value for *ornatus* seeds.

DISCUSSION

Squirrels depend on food resources that fluctuate seasonally both in temperate and tropical regions. In deciduous forests of temperate regions there is a peak in supply of fungi, seeds, bulbs of herbaceous plants and invertebrate populations in spring and early summer, whereas mast (fruits of beeches, oaks etc) is abundant in late September and October (Yahner and Svendsen, 1978). Winter is the crucial time of food scarcity. In tropical regions of Africa (Emmons, 1975; Rahm, 1970) insects are at a maximum in October and a minimum in February. In the bushveld of subtropical southern Africa, habitat of the bush squirrel, the main seeding-time is from January to May, and in northern Zululand, where two subspecies of the East African red squirrel, *P.palliatus* occur, the bulk of fruits are available from December to August with peaks mainly in January but also in June. The prime time for insects to emerge in South Africa, is from January to March (De Villiers,

TABLE 60

PROXIMATE ANALYSIS OF FRUITS AND SEEDS FROM TREE SPECIES IN HABITAT OF P.CEPAPI

	g/100 g DRY WEIGHT					kJ/100 g
	ASH	PROTEIN	FAT	FIBRE	COH	ENERGY
Fruits						
Combretum apiculatum	5,25	11,76	1,4	33,2	48,4	1064
Diospyros lycioides	4,3	3,9	0,6	16,3	74,9	1347
D. mespiliformis	4,2	3,6	1,3	9,3	81,7	1482
E. polyandra	4,0	3,2	1,1	10,6	81,2	1460
V. infausta	3,8	3,7	0,4	13,2	78,9	1405
Z. mucronata	7,2	13,0	0,8	15,8	63,3	1312
Grewia flava	4,2	9,0	1,5	15,6	69,7	1379
G. flavescens	3,1	4,7	0,2	52,6	39,5	746
G. occidentalis	2,9	4,3	1,6	25,4	65,8	1238
G. retinervis	3,4	5,3	0,3	17,1	74,0	1344
G. villosa	6,7	10,9	0,7	6,3	75,4	1476
Sclerocarya caffra	2,8	4,0	1,0	5,8	86,5	1558
Carissa bispinosa	3,9	4,0	6,3	7,3	78,6	1626
Ehretia rigida	9,0	12,0	2,2	4,7	72,1	1496
Citrullus vulgaris	18,8	7,2	1,0	19,6	53,4	1056
Coccinia adoensis	5,6	18,1	4,5	15,3	56,5	1423
Artabotrys brachypetalus	4,3	3,1	4,5	29,6	58,8	1239
Kernels						
Artabotrys brachypetalus	1,7	7,6	10,5	54,7	25,5	953
Sclerocarya caffra	4,4	32,1	59,3	2,5	1,7	2809
Citrullus vulgaris	0,2	16,7	16,6	54,4	12,1	1111
Lonchocarpus capassa	5,0	53,3	3,6	15,4	22,7	1413
Acacia albida	4,2	26,5	2,4	7,3	59,7	1539
A.ataxacantha (green)	4,8	29,1	8,4	7,1	50,5	1655
(dry)	4,8	26,5	11,3	8,6	48,8	1692
A. giraffae	5,0	23,9	4,2	16,5	50,3	1405
A. karroo	6,1	20,9	3,5	12,1	57,5	1449
A. sieberiana	4,6	20,8	3,1	15,2	56,4	1414
Flower						
A. sieberiana	4,7	11,1	1,5	36,7	45,9	1014
Gum						
A. benthamii	2,4	1,1	1,4	0,9	94,2	1654

TABLE 61

PROXIMATE ANALYSES OF FRUITS AND SEEDS OF FOREST TREE SPECIES (g/100 g) ON A MOISTURE-FREE BASIS IN ORDER OF ENERGY CONTENT

SPECIES	ASH		FIBRE		PROTEIN		FAT		CARBOHYDRATES		ENERGY	
	1*	2*	1	2	1	2	1	2	1	2	1	2
Parinari curatellifolia (b)	6,0	1,4	3,1	4,5	8,8	17,2	13,4	65,4	68,6	11,5	1808	2936
Allophylus natalensis (b)		2.8		3,5		21,8		65,1		6,4		2935
Cryptocarya myrtifolia (b)		2,4		2,6		9,3		60,6		25,2		2869
Cassipourea gummiflua (b)		3,4		9,5		18,0		52,2		17,0		2561
Manilkara discolor (b)		3,3		5,9		12,3		41,6		36,7		2398
Trichilia emetica (b)	3,5	2,9	10.4	21,5	8,5	17,7	46,9	50,2	31,0	8,0	2436	2329
Harpephyllum caffrum (b)	7,2	4,8	13,6	18,4	5,6	15,1	1,6	38,2	72,0	23,7	1364	2096
Sapium integerrimum (a)(b)	3,5	3,0	4,0	20.8	7,5	18,6	0,4	38,7	84,4	18,9	1560	2094
Ziziphus mucronata (a)(b)	5,2	3,5	4.0	13,2	6,5	32,5	1,9	31,7	82,6	18,9	1569	2061
Mimusops obovata (a)(b)	4,1	2,0	4.8	9,8	4,4	10,6	2,7	23,7	84,0	52,8	1588	1985
Trema orientalis (b)	9,9	8,5	6,9	30,9	15.0	17,1	47,6	42,5	20,6	0,8	2397	1907
Rinorea angustifolia (b)		2,9		9,8		19,7		19,2		48,8		1875
Podocarpus latifolius (b)		2,8		2,0		7,5		10,8		77,0		1828
Garcinia gerrardii (b)		2,3		3,4		5,8		10,9		77,6		1814
Protorhus longifolia (b)		6,0		3,1		8,8		13,4		68,6		1808
Garcinia livingstonei (a)(b)	2,5	2,3	4.4	4,6	5,0	5,8	1,9	9,8	86.3	77,6	1602	1770
Teclea natalensis (a)(b)	4,0	2,6	1,7	4,4	10,1	11,7	3,4	9,6	73,8	72,0	1537	1769
Apodytes dimidiata (b)	8,3	4,2	7,4	25,1	12,0	6,1	35,5	23,5	36,8	41,0	2162	1681
Vepris lanceolata (a)(b)	9,6	4,8	10.4	30,2	10,4	13,8	16,1	28,3	53,6	23,1	1684	1676
Linociera peglerae (a)(b)	3,0	2,5	20,8	1,8	4,6	4,3	2,3	1,0	69,4	90,3	1319	1627
Pancovia golungensis (b)	3,3	2,6	5,4	1,9	6,2	9,3	0,4	0,6	84,9	85,7	1545	1615
Syzygium cordatum (b)	5,4	2.3	6,2	4,6	4,5	6,7	1,2	0,7	82,7	85,9	1510	1582
Syzygium guineense gerrardii (a)(b)	1,6	1,7	6,7	6,7	3,6	3,6	2,9	1,9	85,2	86,4	1602	1582
Oxyanthus speciosus (a)(b)	4,2	2,8	29,6	31,8	5,2	14,4	1,9	22,8	59,3	28,4	1156	1579
Drypetes gerrardii (b)		4,5		3,2		11,0		0,9		80,5		1570
Olea woodiana (b)		5,4		8,4		12,0		5,2		69,2		1560
Strychnos innocua	4,5	5,7	15,3	26,9	3,8	3,1	30,4	18,9	39,9	45,5	1883	1531
Chrysophyllum viridifolium (a)(b)	2,7	2,5	4,6	37,3	6,6	13,8	8,5	22.5	77,8	24,0	1738	1487
Dovyalis longispina (b)	3,2	4,0	4,0	21,2	4,8	13,5	0,8	4,9	87,2	56,3	1576	1359
Sideroxylon inerme (a)(b)	10,3	1,9	5,3	36,9	10,0	10,4	11,1	14,7	63,4	35,8	1653	1333
Diospyros natalensis (a)(b)	4,6	1,7	27,8	31,2	3,9	3,9	1,4	4,4	62,3	58,8	1166	1218
Croton sylvaticus (b)		9,0		25,5		17,6		1,2		46,7		1125
Phyllanthus discoideus (b)		1,5		52,4		6,9		6,8		32,5		918
Grewia occidentalis (b)	2,9	4,8	25,4	51,9	4.3	8,1	1,6	5,3	65,8	29,8	1238	835
Ekebergia capensis (a)(b)	6,3	2,9	9,9	2,0	22,1	18,7	8,7	27,2	53,1	49,1	1592	826
Macaranga capensis (b)		4,3		59,3		8,9		6,0		21,1		731
Mean (n=35)		3,48 ±1,79		17,39 ±16,13		11,91 ± 6,22		21,68 ±19,59		45,32 ±26,75		1772,4 ± 536,9

TABLE 62

AVERAGE VALUES FOR PROTEIN, LIPID, CARBOHYDRATE (g/100 g DRY WEIGHT) AND ENERGY (kJ/100 g DRY WEIGHT) OF MESOCARP AND ENDOSPERM FROM HABITATS OF THREE TREE SQUIRREL SPECIES

	BUSHVELD P.c.CEPAPI	COASTAL FOREST P.P.TONGENSIS	NGOYE FOREST P.P.ORNATUS
(a) Fruits: Sample size	17	32	8
Protein	7,16	6,75	5,06
Lipid	1,73	9,80	2,33
Carbohydrate	68,14	67,13	74,0
Energy	1332	1599	1419
(b) Endosperm: Sample size	10	12	9
Protein	25,74	13,68	10,87
Lipid	12,29	29,58	23,39
Carbohydrate	38,52	36,76	53,27
Energy	1544	1989	1961

pers.comm.[*]) even though the social insects such as the Termitidae are available as food throughout the year.

Tree squirrels are omnivorous and opportunistic to a large extent. They are fortunate in being small-bodied and can feed on highly digestible forage (fruits, seeds, flowers, sprouting shoots) which are only available in small bits, are dispersed and relatively rare (Geist, 1974). They take invertebrate material in varying amounts depending on their habitat and the season of the year. Nevertheless, there are subtle differences which lead to niche separation. Emmons (1975) found that body size seems to operate in partitioning fruits among nine sympatric species of Gabonese rainforest squirrels along a spectrum of size and hardness; and MacKinnon (1977) also working on nine squirrel species but in a Malayan tropical forest, found divergence facilitated by differential use of forest strata associated with differences in locomotor adaptations, different dietary specialisations, different activity times, and different foraging patterns resulting from major difference in body size and also in differences in social organisation and spatial distribution. Among temperate woodland squirrels sympatry can occur where two species show dietary differences (*Tamiasciurus hudsonicus* and *T.douglassii*; Smith 1970) or despite close similarity in diet, where species show different spatial use of the habitat (*S.carolinensis* and *S.niger*; Smith and Follmer, 1972). MacKinnon (1978) found that the competing red and grey squirrels in Great Britain had similar dietary preferences (seeds and hard food mast) and t they also had a similar social organisation and spatial distribution with overlapping individual home ranges. But because of a higher intrinsic rate of increase, the grey is ousting the red squirrel in most of its natural habitat. Weigl (1978) found niche differentiation resulting from a divergence in the food and nesting requirements of flying squirrels, *Glaucomys volans* and *G.sabrinus*, that are also of slightly different size.

The three squirrel species studied in KwaZulu and the Transvaal show decided preferences for seeds of different texture, hardness and size despite the similar mass of *cepapi* and *tongensis*. *Ornatus* is the larger and also the more efficient feeder on the hard and large kernels. Differential feeding efficiency revealed that *cepapi* is a relatively faster feeder on the smaller seeds and fruits. Smith (1975) states that the feeding rate of the seed predator increases linearly with seed size if one assumes that the main time-consuming activity is finding the seed or extracting it from the fruit or seed-coats for large predators; if chewing seeds were the main time-consuming activity, then feeding rates would not be proportional to seed size and the graphical arguments would not apply; if the predation rates are proportional to seed size, then the percent of the day needed for feeding increases at a geometric rate with decreasing seed size. Both from field records and observation on captive squirrels it is clear that the three *Paraxerus* *spp*. differentially utilise mesocarp and endosperm. *P.p.ornatus* prefers larger seeds such as *G.gerrardii*, but if these are unavailable, they feed on small fruits and seeds such as *Flagellaria guineense*, *Macaranga capensis* and *Cassipourea gummiflua*. That they do not prefer these small fruits is apparent from captive squirrels which ignore these. It is slightly more difficult to determine the natural preference of *tongensis* but they do take the same foods as *ornatus* in a captive situation, even though the fruits and seeds available to them in their natural habitat are smaller than in *ornatus* habitat. *Cepapi* has a different choice of foods in its natural habitat with smaller seeds available and a preference for smaller seeds is also evident from observations on captive squirrels. This has resulted in an inability to handle, or aversion to, some of the forest fruits e.g. *Strychnos madagascariensis* and *Landolphia kirkii* and even *H.caffrum* which takes *cepapi* 24 min. to open *cf*. eight minutes for *ornatus*. *Cepapi* also takes food not taken by *ornatus* such as grass seeds, herb leaves, nectar, pollen and leaf growth tips.

A squirrel has to feed on an item that does not cost it more energy than it gains. Golley (1961) found seeds to have the highest caloric value of five different plant parts when comparing 57 species. From analyses of fruits and seeds it is also clear that a large kernel is th best item to feed on as far as energy yield is concerned, e.g. Garcinia gerrardii with 1 814 kJ/100 g (moisture-free) yields 184,12 kJ for one average-sized seed (10,2 g); whereas Grewia occidentalis with 835 kJ/100 g, (moisture-free) yields 0,75 kJ per seed (0,09 g). Therefore, to obtain as much energy as from one G.gerrardii, 245,5 Grewia seeds will have to be consumed. A predator will gain more by discriminating among the seeds of species with small seeds than species with larger seeds and much more by distinguishing between the two species, than by discriminating between the seeds of large-seeded species (Smith, 1975). Thus, it is also more advantageous for ornatus to feed on larger seeds. However, it will probably not pay cepapi to feed on ornatus-type fruits as they take too long to open the hard ecto- and endocarp. They also do not have the physical ability to move through the large volume of forest as ornatus does to detect ripe fruits.

It is generally so that the smaller the seeds of a plant the more seeds it produces and vice versa. Species whose seedlings become establishe in shade also have heavier seeds (and less) than those whose germinatio occurs in full light, and species that grow in more advanced stages in a sere have heavier seeds than those that grow in the earlier successional stages (Baker, 1972 & Smythe, 1970). Harper, Lovell and Moore (1970) also state that species occupying early phases in succession (colonising species) have a high reproductive effort, usually in the form of a large number of seeds and a correspondingly high intrinsic rate of natural increase (r spp.); species in stable habitats in later phases of succession have less seeds that are heavier (K species). Therefore seed numbers and seed size represent alternative strategies in dispersion of reproductive resources. Both these instances are related to heavier seeds having a larger provision of food reserves for the seedling enabling it to establish its leaf system quickly. It is relatively easy for a cepapi in its habitat of 'colonising' species to remain in one small clump of trees and shrubs (30 x 5 m, i.e. 150 m^2) for a whole day and obtain sufficient food (unpublished observation). This is also true for the striped squirrel F. c. congicus

(Viljoen, 1978). In contrast, the large ornatus moves over ± 5 ha per day (see Chapter 5) probably not only in search of food, but also to 'test' trees about to fruit in this habitat where food resources are not clumped but spread over a wider area.

Squirrels are well-documented as dispersal agents (Baker, 1972; Ridley, 1930; Smith, 1975). Tropical (Emmons, 1975) and subtropical squirrels of the genus Paraxerus and Funisciurus, scatter-hoard. By hoarding, squirrels thus remove the seed from the parent tree where maximum insect infestation takes place. Squirrels of the genus Paraxerus peel the fruit before doing so, thus enabling better gemination and less rot, and "plant" it against a tree or rock. The larger forest squirrels will be more efficient in carrying the heavy and large forest fruits and conversely it would not pay them to trade only in small seeds of open savanna. Multiple-seeded fruits such as those of Chrysophyllum viridifolium and Grewia occidentalis have an advantage as all the seeds are not killed and some are dispersed to still give rise to seedlings.

Smith (1975) lists five general patterns with which seed predators can interact with seeds. He found that T.hudsonicus chooses trees with large numbers of seeds per lodgepole pine cone but also affecting the choice are various traits that make cones difficult to remove from trees. But this species has co-evolved closely with conifers and hoards up to 16 000 cones in one cache (Rusch and Reeder, 1978). The sub-tropical squirrels tend to be omnivorous, scatter-hoard, and take whichever species is available but are deterred by hardness of husk and texture of fruits of certain species, utilising Smith's methods 1, 3 and 4.

The method of opening fruit also differs between the four species, indicating differing jaw strength. Whereas cepapi and tongensis open hard seeds at the germination pore, ornatus can easily cut through the endocarp and frequently does so. Feeding and dispersal of the very large Strychnos and Landolphia spp. by the palliatus squirrels are probably similar to that described for Sciurus granatensis of

Scheelia sp. (Smith, 1975) which also has an impermeable exocarp and a fleshy mesocarp within, which surrounds hard seeds; this mesocarp has the same caloric value as the seed, and functions to supply nutrition to the animals at the time that the seeds are scatter-hoarded The mesocarp of *Strychnos* and *Landolphia* is also a prized food for *P.palliatus* and has a high kJ value, but the seed is not fed on extensively partly because it is too hard. The mesocarp sticks tightly to the endosperm which is thus distributed.

A brief mention of *G.gerrardii* is also warranted as *ornatus* seems to be the sole dispersal agent for the fruit in Ngoye forest. It is a non-fleshy fruit with the endosperm almost completely filling the fruit. Fruits contain one, two or three seeds. Janzen (1969) states that as the number of species of dispersal agents for a plant species decreases, this co-evolution of plant and dispersal agent may become very close, e.g. co-evolution of *Sciurus spp*. in America and acorns. A similar relationship exists between *ornatus* and *G.gerrardii*.

Bark-feeding has been recorded for various squirrel species (*Sciurus aberti*, Farentinos, 1979; *S.carolinensis*, Taylor *et al*, 1971,, *S.aureogaster*, Brown and McGuire, 1975 and *S.granatensis*, Heaney and Thorington, 1978). This is often correlated with a lack of natural foods. However, it is not clear to what extent *Paraxerus* were feeding on inner bark, or merely picking at bark to extract insects. To *F.c.congicus* bark is important in the diet and they display extensive bark-stripping at any time in cages.

From measurements of different portions of intestinal tracts, it does seem as if the *Paraxerus* species are unusually insectivorous particular so for *cepapi*. Rahm (1972) set a standard for large intestine length, calculated the relative lengths of small intestines and caeca of seven species of tree squirrels. He concluded that the more frugivorous *Funisciurus carruthersi*, *Protoxerus stangeri* and *Heliosciurus rufobrach* have relatively longer caeca and small intestines. The more insectivorous *Paraxerus boehmi emini* and *Funisciurus anerythrus* have relativel short small intestines and caeca. When the South African squirrels

squirrels of the genus *Paraxerus* are compared with these tropical squirrel species they appear to be much more insectivorous (Table 55) with *cepapi* the most insectivorous. They have extremely long large intestines and short small intestines and caeca. Although caecal measurements are slightly unreliable, the difference is surprising.

CHAPTER 7

ENERGY METABOLISM

INTRODUCTION

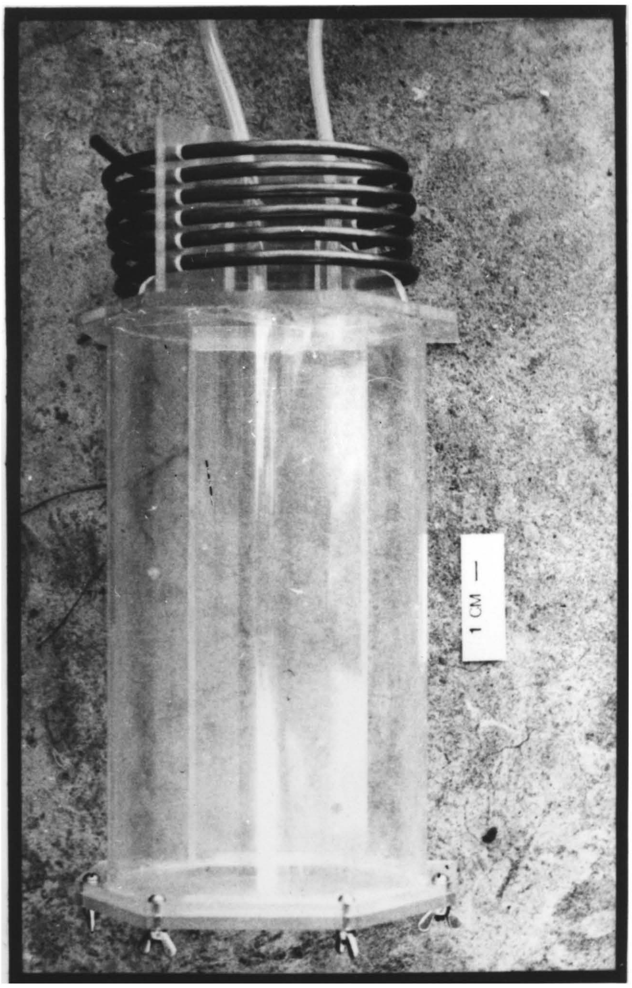
Metabolic rate of an animal can indicate adaptation to xeric or mesic conditions whilst thermal conductance values which are simultaneously derived, indicate thermal adaptation to habitat. This chapter investigates energy metabolism and body temperature of the four squirrel species on a comparative basis at various ambient temperature to obtain an indication of niche separation with regard to climatic conditions.

MATERIALS AND METHODS

A Beckman Model E2 paramagnetic oxygen analyser was used to measure oxygen consumption (VO_2) of four adults of the four squirrel species by determining the concentration of O_2 in the in- and outflowing gases, in a small volume respirometer, through which dry ambient air was passed at 600 mℓ/min. The experiments were carried out in July soon after the winter solstice, when daylight length is reasonably constant. Minimum and maximum temperatures averaged 8,0°C and 20,7°C respectively during the experiment, whereas the mean July minimum and maximum temperatures for Pretoria, where the experiments were done, over 26 years average 0,8°C and 18,6°C respectively (Weather Bureau, Pretoria).

The perspex metabolic chamber is illustrated in Figure 17. A copper coil (2 820 mm long) entered at the lower end of the chamber beneath a perspex base plate on which the squirrel crouched. The copper coil served to bring inflowing air to the desired temperature. The chamber was placed in a temperature-controlled water bath where water was continuously stirred. Low temperatures (12 and 18°C) were maintained by means of crushed ice and a cooling pump. Holes in the opposite end of the base plate permitted air to move to the upper part of the chamber and to flow out at the top on the same side as the inflow. The base plate fitted into a slit to prevent the squirrel from moving it. A copper/constantan thermo-couple inserted in a perspex tube to protect it, measured temperature in the chamber. Silica

Figure 17. Above - metabolic chamber used to determine oxygen consumption: perspex tube, copper coil to adjust temperatures of ambient air, plastic inlet and outlet tubes. Below - Funisciurus c. congicus with tail characteristically curled over the back and head.



1 CM

gell beneath the base-plate, dried air inside the chamber. In addition, air filtered through two silica gell driers before entering the chamber and two after leaving it, to dry air entering the chamber and the oxygen analyser respectively.

Hart (1971) states that considering the species, seasonal and geographic differences that occur in energy metabolism, it is important to conduct comparisons betwen different species during the same season and that animals should have the same thermal history. Therefore the experimental squirrels had all been in outdoor cages under the same conditions. They were each tested at six different experimental ambien temperatures. Individuals were acclimated for one and a half to two hours at ambient temperatures 12, 18, 25 and 30°C but only for one hour at 34°C and above, to reduce possible heat stress. Oxygen consumption was measured at each temperature every three minutes for 15 to 30 min depending on the variability of the reading. Only the highest readings within 30 units of the maximum were noted, thus representing the minimum movement and oxygen consumption. Each individual was tested only once per day and then rested for two days before retesting at a different temperature. Squirrels were caught in wire mesh traps, immediately transferred to a dark bag, weighed and transferred to the darkened metabolic chamber. All measurements were made in daytime as these are strictly diurnal species. Body temperatures were measured rectally immediately after the metabolic measurements had been completed by means of a copper-constantan thermo-couple inserted for 3 cm in the rectum, and each individual was then reweighed.

RESULTS

Oxygen consumption as a measure of resting metabolic rate (RMR): Grodzinsky and Wunder (1975) define RMR as the metabolic rate of the animal at rest under a prescribed set of environmental circumstances. However, as explained by Hart (1971) no objective method for excluding activity periods based on simultaneous measurement of both activity and metabolism has generally been applied; therefore, the term 'resting' instead of 'minimal' metabolism has been used for animals in the thermoneutral range in which gross activity has been excluded.

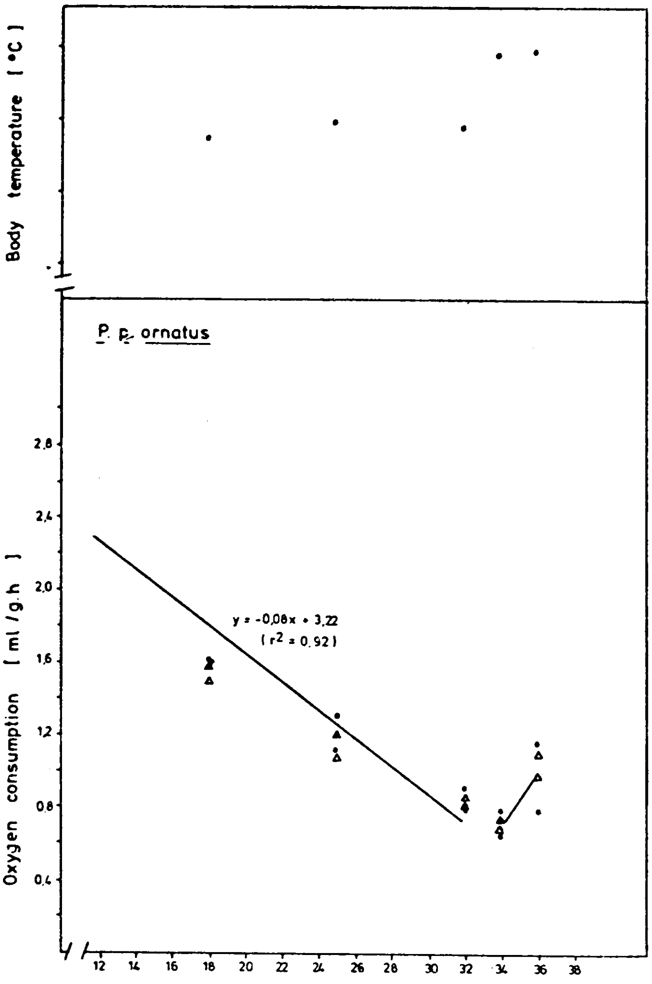
Thus RMR here also represents minimum measured VO_2 which occurs in the thermoneutral zone at ±34°C in all four squirrel species (Table 63). The thermoneutral zone lies slightly below 34°C for tongensis, at 34°C for cepapi and ornatus, and from 34 to 36°C for congicus (t-tests for significant difference between VO_2 at 32,34 and 36°C were made to determine this zone). A linear regression fit of oxygen consumption (mℓ O_2/g.h) as a function of ambient temperature (°C) was calculated for each species (Figure 18). The increment of VO_2 after 34°C ambient temperature is steeper in the mesic than in the xeric squirrels. Increment in VO_2 below the lower critical temperature was at a higher rate in congicus than in the three squirrels of the genus Paraxerus, indicating a lower thermal conductance in the latter group. RMR for congicus was 0,85 mℓ/g.h, the same as for tongensis which is twice as heavy. In cepapi and ornatus the RMR was of the same order namely 0,65 mℓ/g.h and 0,71 mℓ/g.h respectively. However, both in the mesic and xeric pairs, the smaller squirrels of the two (tongensis and congicus respectively) had the higher RMR.

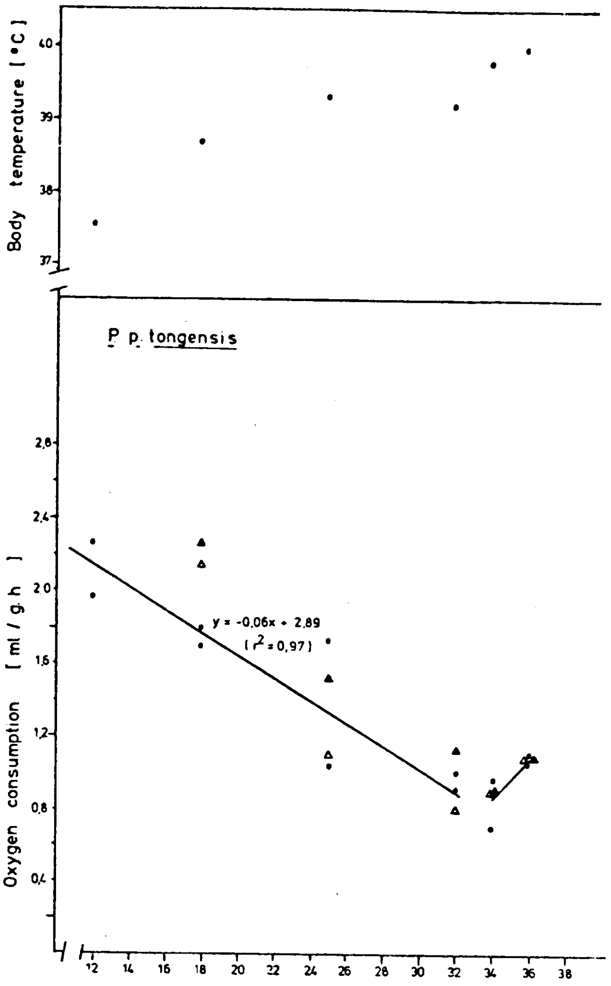
Thermal conductance (TC): TC is the relationship between metabolism and body temperature. Above the lower critical temperature (L_c), TC increases with constant body temperature (Hart, 1971) because of evaporative cooling. If the animal's body loses heat according to Newton's law (i.e. heat loss is proportional to excess temperature) the thermal conductance remains constant at temperatures below L_c. TC can be regarded as being at a minimum at the lower end of the thermoneutral zone and was here calculated at 32°C using Hart's (1971) equation:

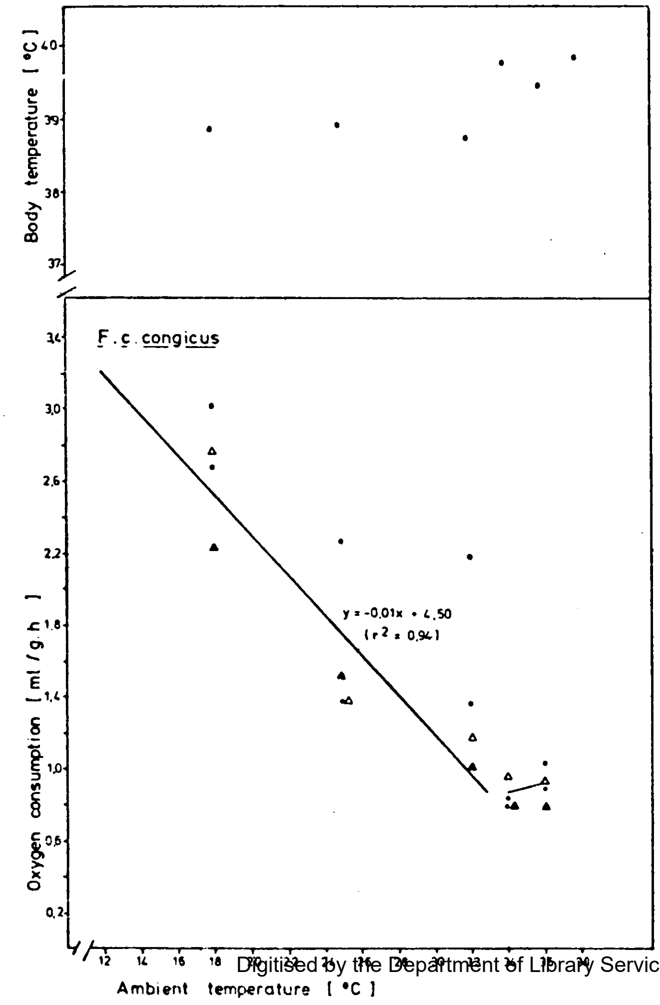
$$TC = M/_{T_b - T_a}$$

with T_b = body temperature and T_a = ambient temperature in °C, M = mass in g. Cepapi had the lowest conductance of 0,10 mℓ/g.h °C and congicus the highest at 0,21 mℓ/g.h °C with the two mesic animals having intermediate values (Table 63).

Figure 18. Oxygen consumption (ml VO_2/g.h) and rectal body temperature (°C) of four southern African tree squirrel species at different ambient temperatures.


Body temperature [°C]
P. p. ornatus
Oxygen consumption [ml / g.h]
y = -0,08x + 3,22
(r² = 0,92)
2,8
2,4
2,0
1,6
1,2
0,8
0,4
12 14 16 18 20 22 24 26 28 30 32 34 36 38


Body temperature [°C]
40
39
38
37
P. p. tongensis
Oxygen consumption [ml / g.h]
y = -0,06x + 2,89
(r² = 0,97)
2,8
2,4
2,0
1,6
1,2
0,8
0,4
12 14 16 18 20 22 24 26 28 30 32 34 36 38


Body temperature [°C]
40
39
38
37
F. c. congicus
Oxygen consumption [ml / g.h]
y = -0,01x + 4,50
(r² = 0,94)
3,4
3,0
2,6
2,2
1,8
1,4
1,0
0,6
0,2
12 14 16 18
Ambient temperature [°C]

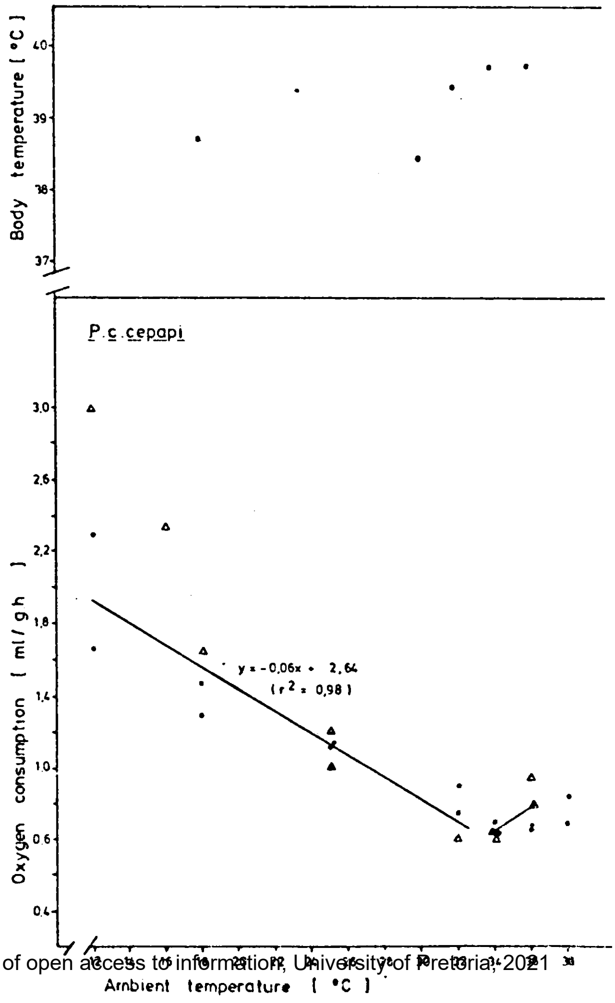

Body temperature [°C]
40
39
38
37
P. c. cepapi
Oxygen consumption [ml / g h]
y = -0,06x + 2,64
(r² = 0,98)
3,0
2,6
2,2
1,8
1,4
1,0
0,6
0,4
Ambient temperature [°C]

TABLE 63

ENERGY METABOLISM (mℓ O_2/g.h.) OF FOUR TREE SQUIRREL SPECIES AT AMBIENT TEMPERATURES RANGING FROM 12°C TO 38°C (n = 4 FOR EACH VALUE)

SPECIES	TEMPETATURE RANGE (°C) (n = 4)						
	12°	18°	25°	32°	34°	36°	38°
Funisciurus c.congicus	3,22	2,65	1,42	1,18	0,85	0,91	1,04
Paraxerus c.cepapi	1,98	1,46	1,11	0,74	0,65	0,77	0,76
P.palliatus tongensis	2,12	1,88	1,22	0,96	0,87	1,08	-*
P.p.ornatus	2,48	1,57	1,17	0,86	0,72	1,00	-*

*Not tested as they already showed severe heat stress at 36°C

Insulation is the reciprocal of TC, and among smaller mammals there is a clear correlation between fur thickness (and insulation) and the size of the animal (Schmidt-Nielsen, 1975).

BODY TEMPERATURE

The body temperatures of the four squirrel species were similar (Table 64). In the two open habitat species, temperatures did not ris as sharply after 34°C. Body temperature of congicus increased sharply above an ambient temperature of 32°C and little or no salivation occurred up to 36°C ambient temperature, although one individual did salivate slightly at 38°C. Pronounced salivation spread over the face with the paws occurred in the two mesic squirrels at 36°C ambient temperature, and therefore they were not subjected to higher temperatures.

NEST-BUILDING

The two savanna species are diligent nest-builders and will carry any suitable piece of paper, wool or leaves into nests in captivity. However, the forest species could not be induced with any nesting material (cotton wool, grass, shredded material and peat moss) to nest-build. Nesting material had to be placed in the nests for them, and only after more than a year did they commence nest-building of their own accord with leaves of shrubs placed in their cages and with bark shredded from branches. But nest-building was often seen in the forest species in the field e.g. a tongensis female Toe 200, on 19/3/77 picks leaves (± 10 cm long) 13 times within 20 min and carries them into the hole; and an ornatus female picks a bunch of leaves (± 3,5 cm) 25 times in 30 min, each time bringing a bunch of about five leaves, thus totalling about 125 leaves. Holes are also lined with grass and/or the inner fibres of the bark which are gnawed off the inside of the nest. This gnawing was heard only in May both in Ngoye and at Mkwakwa, possibly indicating a seasonal trend for better insulation in winter. F.c.congicus is the only of these squirrel species to build dreys (Viljoen, 1978).

TABLE 64

BODY TEMPERATURES OF FOUR TREE SQUIRREL SPECIES AT AMBIENT TEMPERATURES FROM 12°C TO 38°C

	AMBIENT TEMPERATURE RANGE						
	12°	18°	25°	32°	34°	36°	38°
Funsiciurus congicus congicus	39,0	38,9	38,9	38,7	39,8	39,4	39,8
Paraxerus cepapi cepapi	39,3	38,7	-*1	38,4	39,5	39,8	39,7
Paraxerus palliatus tongensis	37,6	38,7	39,3	39,2	39,9	40,1	-*2
P.p.ornatus	-*1	38,7	39,0	38,9	39,9	39,9	-*2

*1 Thermo-couple broke

*2 *Paraxerus palliatus tongensis*, and *P.p.ornatus* not measured at 38°C as they already showed severe heat stress at 36°C

DISCUSSION

BODY TEMPERATURE IN RELATION TO HABITAT

Body temperatures of desert rodents are lower than those of mesic and boreal species and therefore apart from a lower RMR, lower T_b also appears to be a related adaptation to hot dry conditions (Hart 1971). From a series of species it can be deducted that body temperature regulation in rodents is independant of air temperature (Ta) to varying degrees from less than 0°C, to above 30°C and that body temperature increases in the range in which only small differences exist in the gradient between T_b and the equality line (where $T_a \neq T_b$) (Hart, 1971). Body temperatures of the four squirrel species, were of the same order but in the two xeric species it increased less when ambient temperature exceded 34°C indicating a better adaptation to extreme heat. Body temperatures for all these four species are lower than those of Abert's and Kaibab's squirrels (<u>Sciurus aberti</u> and <u>S.a.kaibabensis</u>) (Patton, Radcliff and Rodgers, 1976 and Golightly and Ohmart, 1978), red squirrels, <u>Tamiasciurus hudsonicus</u> (Morrison, 1962 In: Hart, 1971) and flying squirrels <u>Glaucomys volans</u> (Neumann, 1967 In: Hart, 1971). All of the latter species occur in the Nearctic region and can withstand very low ambient temperatures e.g. <u>T.hudsonicus</u>, a diurnal non-hibernator of the subarctic region, which is active on the surface at temperatures down to -32°C; this species has a RMR of 1,5 mℓ/g.h.°C, (measured in winter) and a thermal conductance of 0,085 mℓ/g.h.°C., i.e. a higher RMR and a lower TC with critical temperature at 20°C also lower (Irving <u>et al</u>, 1955) than squirrels of similar mass in the present study.

Observed VO_2 in relation to weight-expected metabolism and habitat: VO_2 increases linearly over a range corresponding to about four magnitudes of body mass in approximate relationship with the solid line representing the Brody-Proctor equation, $VO_2 = 3,8\ W^{0,73}$ mℓ/h for the entire animal, or $VO_2 = 3,8\ W^{-0,27}$ mℓ/g.h (Hart, 1971). Schmidt-Nielsen (1975) calculated a slightly different slope of 0,75, thus finding $VO_2 = 3,8\ W^{0,75}$ mℓ/h for the whole animal, or $VO_2 = 3,8\ W^{-0,25}$ mℓ/g.h . This latter equation for the whole animal was used in Table 65 as a standard reference. There are, however, rather large variations associated apparently with variation in activity

TABLE 65

ASPECTS OF ENERGY METABOLISM IN FOUR SPECIES OF TREE SQUIRRELS (M = METABOLIC RATE, RMR = RESTING METABOLIC RATE)

SPECIES AND HABITAT	AVERAGE ADULT MASS (g)	BRODY-PROCTOR EXPECTED RMR ($m\ell\ O_2/g.h.$)	OBSERVED RMR IN JULY AT 34°C ($m\ell\ O_2/g.h.$	% THAT OBSERVED M IS LOWER THAN EXPECTED M	THERMAL CONDUCTANCE AT 32°C	BODY TEMPERATURE	
						34°C	32°C
Funisciurus c congicus (arid, open savanna)	112,3(n=20)	1,17	0,85	26	0,21	39,7	38,7
Paraxerus c.cepapi (open, woodland)	223,6(n=69)	0,98	0,65	34	0,10	39,5	38,4
P.palliatus tongensis (mesic to xeric, subtropical forest)	206,0(n=48)	1,00	0,87	13	0,134	39,9	39,2
P.p ornatus (moist evergreen subtropical forest)	366,6(n=98)	0,87	0,72	18	0,124	39,9	38,9

in the chamber, and species differences. Species differences result in generally higher levels among the mesic rodents than those given by the standard curve. Hot climate, and desert species have a reduced RMR relative to the Brody-Proctor equation, averaging around 10% below the line, and non-desert species average around 10% above the line. All four species in the present study had RMR values below the expected (calculated from $VO_2 = 3{,}8\ W^{0{,}75}$ mℓ/h indicating their adaptation generally to a warm climate. However, the two xeric species, *cepapi* and *congicus* were further below the expected Brody-Proctor values for their weight (35% and 26% below the expected respectively) than were the two mesic species (Table 65).

It seems that *cepapi* is especially well-adapted to conserve energy, therefore the low observed RMR and the equally low TC. In an environment where resources are seasonally abundant and also clumped to a large extent, it would be essential for them to maintain energy with as little food as possible. *Cepapi* with the lowest TC and VO_2 35% below the expected Brody-Proctor value, and *tongensis* with higher TC and VO_2 only 12% below the expected value, have a similar body mass. By means of the low TC, *cepapi* can obtain the same metabolic energy as *tongensis* with less food because it loses energy at a slower rate. There probably is less energy (see Chapter 6) in the food supply of *cepapi* which is also territorial thereby suggesting limited and clumped resources (Viljoen, 1975). It probably thermo-regulates by pulmonary evaporative cooling.

The species which has evolved in the hottest and most arid conditions, *congicus*, is the smallest and has the highest TC (0,21 mℓ/g.h. °C). This combination will allow it to get rid of heat easily, having a greater surface area in relation to body volume and a sparse hair cover. Furthermore, this species has evolved distinct thermoregulatory behaviour patterns such as the carrying of the tail over the back (Greek, Sciouros = shade barrier) thus throwing a patch of shade over the head and presenting the white ventral surface to the sun's rays (Figure 17) (Viljoen, 1978). This habit is similar to that of the ground squirrel, *Xerus inauris* (Marsh, Louw and Berry, 1978) which also occurs in hot, open regions and has been shown to be effective by Golightly and Ohmart (1978) who found that Abert's squirrels (*Sciurus aberti*) have a much higher reflectance from the white ventral surface of the tail than from the grey dorsal body pelage.

All four species are relatively inactive at the hottest time of the day (unpublished observations) thus reducing possible overheating. Golightly and Ohmart (1978) found that in temperature-monitored *T.hudsonicus*, T_b decreased considerably when the animal was motionless after a bout of activity. It was the two mesic squirrel species from the forested habitats that experienced heat stress at a lower ambient temperature (and of these two, *ornatus* noticeably more so): in captivity on warm days, they would lie flat with limbs spread out laterally on the cement or branches, frequently after urinating on the surface. They also showed heat stress in the metabolic chamber when T_a exceeded 32°C and spread saliva over the facial region. This pronounced salivation is described as an emergency regulation for a limited period to reduce the gradient between T_b and T_a and it also occurs in the Spermophilous group of squirrels (Hart, 1971). The three *Paraxerus* sp. all have sudoriferous glands on the foot-soles (Chapter 8) and probably sweat to cool by means of evaporation (*Funisciurus* not investigated).

The two xeric species inhabit areas with a wider temperature range (down to -7°C in certain areas), whereas the mesic species live in an essentially frost-free region where rapid temperature changes are further buffered by the forest. The xeric species have adapted by commencing activity later and returning to the nest earlier than mesic species (Chapter 7). On cold mornings they bask for prolonged periods in their open habitats (Viljoen, 1977a). Golightly and Ohmart (1978) found that such basking does substantially raise T_b in temperature-monitored Abert's squirrels. Furthermore, the two xeric species have a closely-knit group structure and nest huddled together (contact species) (Viljoen, 1975 and 1978). Huddling in flying squirrels *Glaucomys*, reduced thermo-regulatory energy by 33%

(Neuman, 1967 In: Hart, 1971). In the coldest months the population of *cepapi* (Viljoen, 1975) was still at a maximum and group size averaged five. On the other hand the forest squirrels have a less cohesive group system and often nest singly (Chapter 5). The xeric species when in captivity also show more diligent nesting behaviour than the mesic species. A nest of cotton can reduce VO_2 by an amount equivalent to raising the air temperature by about 15°C in *Spermophilus tereticaudus* (Hudson, 1964).

The fur of the two mesic species appears thicker and especially that of *ornatus* is very dense, with longer tail and body hair, whereas *congicus* has the shortest and the least dense fur. When comparing the two mesic species, the smaller of the two has a higher RMR but this value is only 12% below the expected, whereas that of *ornatus* is 18% below the expected. The smaller of the two also has a slightly higher TC than *ornatus* which frequents a slightly cooler environment.

CHAPTER 8

ACTIVITY

INTRODUCTION

Initial observations revealed that the activity levels of the two forest species are higher than those of the two species from open woodland. This part of the study was not carried out in depth but rather aimed at detecting and quantifying, if possible, the most obvious interspecific differences. Therefore, although weather variables such as temperature, wind, rainfall and light intensity do influence activity of tree squirrels (Hicks, 1949; Bahnak and Kramm, 1977; Golightly and Ohmart, 1978; and Pauls, 1978) these were not taken into consideration as this would have considerably broadened the scope of the study. Furthermore, daily activity patterns were not investigated. The investigation was aimed only at the parameters that superficially showed interspecific differences, such as movement, grooming, tailflicking, murmuring and time spent motionless. Grooming, tailflicking and murmuring frequencies would indicate behavioural adaptations to niche, whereas movement and motionless duration would additionally indicate conservativeness in energy expenditure, which might be related to metabolic rates and distribution of food resources.

MATERIALS AND METHODS

Observations on general activity throughout the day (divided into two-hourly periods) were made both in the field and in captivity. Field observations were made throughout the year on *ornatus* and *tongensis*, and on *congicus* in April of 1978 (Viljoen, 1978). The three *Paraxerus* spp. were monitored in captivity but *congicus* specimens were obtained too late to be included. Field observations on wild squirrels included the number seen and heard, as well as times of leaving and re-entering nests at the start and end of the activity period. In captivity, the following parameters were recorded on two males and two females of each species: number of times that the squirrel moves and the distance of each movement (m); duration of feeding time (s); duration motionless (s); frequency of auto- and allogrooming; frequency of contact murmuring and tailflicking (see Communication).

The squirrels were caged out of doors and were tame but could not be handled. Five minutes were allowed to accustom the squirrels to my presence before commencing observations. Recordings were then made non-stop for 15 min on one individual, recording all the parameters on a note sheet. Thereafter the other individual in the same cage was observed for 15 min. To exclude observer fatigue, no more than an hour was spent at one observation session. Observations on the three species, through the hours of one day, were completed during a fortnight on cloudless days to preclude influences of daylength and climatic variations respectively. These recording sessions were made at different times of the year inbetween the visits to the study areas in KwaZulu.

Analysis of variance were carried out on the results from both wild and captive squirrels to ascertain whether any interspecific difference existed. This analysis for the field data was employed to test the number of squirrels heard and noticed of the two KwaZulu species during all hours of the day for the months January, March, June, August and November of 1977, and May of 1978. For observations in captivity two different analyses of variance were carried out, the one testing the seven activity parameters for all hours of the day between the three _Paraxerus_ spp. for the months February, April, July and October of 1977 and July 1978; and the second testing for only five parameters (tailflicking and murmuring excluded) between _tongensis_ and _ornatus_ through all hours of the day for the months February, April, July and October of 1977, August, October and December of 1976 and July of 1978. This latter test included data from 1976 when _cepapi_ had not yet been included. Only five parameters had at that stage been monitored.

RESULTS

COMMENCEMENT AND TERMINATION OF ACTIVITY

Times of leaving the nest in the morning and returning to it in the later afternoon are summarised in Table 66 for wild *ornatus* and *tongensis*. Both species usually left the nest shortly after sunrise and returned some time before sunset (Table 66b), apparently influenced by light intensity. However, low temperatures, rain and wind also delayed nest leaving and hastened return to it. These variables have a considerable influence and therefore times of leaving and re-entering nests were not tested between the different species. *Congicus* and *cepapi* leave later and return earlier than the *palliatus* sp. This is also evident from Table 67 where the former two species were still in the nests for the first monitored hour and is related to their lower activity levels, and greater degree of energy conservation.

FIELD OBSERVATIONS

During 731 h in Ngoye forest, 1 446 *ornatus* were either seen or heard, i.e. 1,98 squirrels per h. In Mkwakwa forest in 660 h, 674 *tongensis* were noted i.e. 1,02/h. The numbers of squirrels vocalising were 1 249 or 1,71/h for *ornatus* and 259 or 0,39/h for *tongensis*. Therefore, 86,4% of the *ornatus* that were noted, vocalised and only 38,4% of the *tongensis*. Both the numbers heard and the numbers noted indicate a higher level of activity for *ornatus* than for *tongensis*.

The analysis of variance for the field data indicated differences for the hours of the day:

T1, $P<0,01$; T2, $P<0,01$; T3, $P<0,05$; T4, NS; T5, NS; T6, $P<0,05$; T7, $P<0,05$. (T1 = 05h00 - 07h00; T2 = 07h00 - 09h00; T3 = 09h00 - 11h00 T4 = 11h00 - 13h00; T5 = 13h00 - 15h00; T6 = 15h00 - 17h00; T7 = 17h00 - 19h00).

The overall conclusion is that significantly more *ornatus* were encountered during a day than *tongensis*. This might not necessarily indicate only a difference in activity, but also points to a difference in behaviour as *tongensis* is a more cryptic, shy and less vocal species.

TIMES OF LEAVING AND RE-ENTERING NESTS IN THE FIELD BY P.P.ORNATUS AND P.P.TONGENSIS
(MEAN AND S.D., SAMPLE SIZE IN PARENTHESIS)

P.P.ORNATUS			P.P.TONGENSIS		
MONTH	LEAVE	ENTER	MONTH	LEAVE	ENTER
January	(15)0547 ± 0.22	(16)1838 ± 0.17	February	(3)0548 ±0.06	(2)1828
April	(3)0641 ± 0.08	(16)1703 ± 0.20	March	(3)0555 ±0.13	(3)1716 ± 0.27
May	(9)0642 ± 0.08	(14)1704 ± 0.10	May	(14)0649 ±0.12	(15)1708 ± 0.08
June	(13)0747 ± 0.27	(22)1619 ± 0.17	June	(3)0710 ±0	(1)1630
August	(21)0641 ± 0.17	(25)1659 ± 0.17	August	(9)0652 ±0.28	(13)1653 ± 0.32
Oct/Nov	(11)0603 ± 0.16	(16)1729 ± 0.16	Oct/Nov	(21)0540 ±0.27	(13)1743 ± C.19
Dec	(13)0528 ± 0.08	(14)1810 ± 0.23			

TABLE 66b

TIME OF SUNRISE AND SUNSET AND DAY LENGTH THROUGHOUT THE YEAR (AT THE MIDDLE OF EACH MONTH) IN FOUR DIFFERENT SQUIRREL SPECIES' HABITATS

MONTH	NGOYE FOREST 28°50'S, 31°42'E			LAKE ST.LUCIA, 28°30'S,32°30'E			NABOOMSPRUIT, 24°34'S, 28°47'E			OTJITAMBI, 20°15'S, 15°15'E		
	SUNRISE	SUNSET	DAY LENGTH	SUNRISE	SUNSET	DAY LENGTH	SUNRISE	SUNSET	DAY LENGTH	SUNRISE	SUNSET	DAY LENGT
January	0508	1856	13.80 (hrs)	0505	1853	13.80 (hrs)	0528	1900	13.53 (hrs)	0433	1746	13.22 (hr
February	0534	1840	13.10	0531	1837	13.10	0551	1848	12.95	0452	1737	12.75
March	0552	1812	12.33	0549	1809	12.33	0605	1823	12.30	0502	1717	12.25
April	0610	1736	11.43	0607	1733	11.43	0620	1751	11.52	0511	1649	11.63
May	0628	1710	10.70	0625	1707	10.70	0634	1729	10.92	0521	1631	11.17
June	0643	1702	10.32	0640	1659	10.32	0647	1723	10.60	0532	1628	10.93
July	0645	1712	10.45	0642	1709	10.45	0650	1732	10.70	0535	1637	11.03
August	0625	1729	11.07	0622	1726	11.07	0630	1746	11.27	0523	1647	11.40
September	0553	1745	11.87	0550	1742	11.87	0603	1759	11.93	0456	1655	11.98
October	0516	1801	12.75	0513	1758	12.75	0532	1811	12.65	0429	1702	12.55
November	0451	1824	13.55	0448	1821	13.55	0511	1829	13.30	0413	1716	13.05
December	0449	1847	13.97	0446	1844	13.97	0511	1851	13.68	0415	1735	13.33

TABLE 67

ACTIVITY RECORDED IN APRIL: ON CONGICUS (IN THE FIELD), CEPAPI, TONGENSIS AND ORNATUS (IN CAPTIVITY)

ACTIVITY PARAMETER / 15 min

TIME OF DAY	DISTANCE MOVED (m)				NO. OF TIMES MOVED				FEEDING (sec)				MOTIONLESS (sec)			
	F *1	C	T	N	F	C	T	N	F	C	T	N	F	C	T	N
0700	-*2	-*2	80	48.5	-	-	26.5	15.8	-	-	150	255	-	-	53	68
0700 - 0900	41.7	10.3	85.0	91.4	11.8	6.3	32.9	25.5	210	86	153	86	87	608	45	75
0900 - 1300	25.2	14.2	62.7	111.6	7.7	6.8	24.6	30.7	159	90	141	83	43	414	156	300
1300 - 1600	17.6	16.5	39.3	131.5	6.3	8.1	18.9	35.8	223	288	80	108	176	355	403	123
1600 - 1900	11.1	24.8	40.6	148.0	2.3	11.4	16.5	37.3	327	60	90	83	47	229	394	135
$\bar{x}$	23.9	16.5	61.5	106.2	7.1	8.2	23.9	29.1	230	131	123	123	88	402	210	140

*1 F = F.c.congicus
C = P.c.cepapi
T = P.p.tongensis
N = P.p.ornatus

*2 Not yet out of nest

The lesser difference at T4 and T5 could be related to a lull in activity which is obvious in *ornatus* but not so obvious in the cryptic *tongensis*, and similarly the increased difference ($P < 0,05$) at T6 and T7 could be related to renewed activity of *ornatus* making them once again more obvious.

During 69 h spent in *cepapi* habitat at Naboomspruit, 156 squirrels were noted (2,26/h) of which only 34,6% vocalised (0,78/h). The large numbers of *cepapi* noted is indicative of the greater visibility (see Habitat Analyses). However, they are not as vocal as *ornatus* (see Communication).

During 29 h in *congicus* habitat, 53 squirrels were noted (1,83/h) of which 62,3% vocalised (1,14/h). Visibility is also good in *congicus* habitat (see Habitat Analyses), but they appear to be more vocal than *cepapi*. Although sample size and time spent in *congicus* habitat are insufficient for statistical comparisons, these tendencies were confirmed from observations on captive squirrels.

CAPTIVITY OBSERVATIONS

A comparison between the recorded activity parameters of the three *Paraxerus* spp. in captivity and that of *congicus* in the field (Table 67) shows that *cepapi* and *congicus* are less active that the two forest species. The only data available for *congicus* is from the field, and as this species is extremely tame, one could approach to within 2 m of them in some instances. Consequently, more complete field data were recorded for this species, which are here compared with the data from captive *Paraxerus* spp.

Results from the analysis of variance for captive squirrels between the three *Paraxerus* spp. indicate that the distance that the three species moved as well as the time spent motionless differed significantly with *ornatus* the most active and *cepapi* the least active ($P < 0,01$). This result was expected and is also evident from Tables 67 and 69. Feeding times did not differ significantly, and Tables 67 and 69 also show that of the two savanna species, *congicus* takes longest to

TABLE 68

ACTIVITY IN CAPTIVITY OF THREE TREE SQUIRREL SPECIES THROUGHOUT ONE DAY

	DISTANCE (m)			NO. OF TIMES MOVED			FEEDING (s)			MOTIONLESS (s)		
	*C	T	N	C	T	N	C	T	N	C	T	N
February 1977	464	3106	3436	250	1088	1074	3180	6660	2820	23520	14310	16560
April 1977	551	2934	5472	261	1121	1485	2850	5760	4980	23440	11040	8220
July 1977	522	2670	3583	263	910	1141	3480	2550	3660	28020	18030	11280
July 1978	508	1921	4914	317	877	1635	5280	2610	4980	20610	9510	7740
October 1977	632	4882	5998	423	1650	1926	4515	3935	4770	41475	6660	14220
Mean	535,4	3102,6	4680,6	302,8	1129,2	1452,2	3861,0	4303,0	4242,0	27413,0	11910,0	11604,0
S.D.	62,5	1092,9	1136,9	72,1	310,1	353,2	1009,0	1854,3	965,5	8296,5	4395,8	3804,4

*C = P.cepapi cepapi
T = P.palliatus tongensis
N = P.p.ornatus

TABLE 69

ACTIVITY IN CAPTIVITY OF TWO TREE SQUIRREL SPECIES THROUGHOUT ONE DAY

	DISTANCE (m)		NO. OF TIMES MOVED		FEEDING (s)		MOTIONLESS (s)	
	*T	N	T	N	T	N	T	N
February 1977	3106	3436	1088	1074	6660	2820	14310	16560
April 1977	2934	5472	1121	1485	5760	4980	11040	8220
July 1977	2670	3583	910	1141	2550	3660	18030	11280
August 1976	2637	3510	847	804	7770	5460	16980	12150
October 1976	4321	4350	1231	1001	5468	4950	11880	15660
December 1976	3495	4963	948	1247	5730	3750	15050	13880
October 1977	4882	5998	1650	1926	3935	4770	6660	14220
July 1978	1921	4914	877	1635	2610	4980	9510	7740
Mean	3245,8	4528,3	1084,0	1289,1	5060,4	4421,3	12932,5	12463,8
S.D.	961,4	966,9	264,9	368,8	1873,8	902,3	3863,7	3249,4

*T = P.palliatus tongensis
N = P.p.ornatus

feed and *cepapi* takes about the same time as *ornatus* and *tongensis*. This is probably related to a lower efficiency of feeding in the savanna species (see also Food Utilisation). Tables 68 and 69 show that *tongensis* probably also spends more time feeding than *ornatus* does even though it is only half the mass. This also indicates that *tongensis* is a less efficient feeder than *ornatus*. As far as grooming is concerned, there was a significant difference in allogrooming ($P < 0{,}01$) but not in autogrooming frequency between the three species. This was also anticipated and the magnitude of the difference is reflected in Table 70 with the 'contact' species *cepapi* doing by far the most allogrooming. Both the frequencies of tailflicking and murmuring also differed significantly between the three species ($P < 0{,}01$). Table 71 shows that *cepapi* seldom tailflicks and that *tongensis* and *ornatus* frequently do so, and murmuring is also a slightly depressed behaviour in *cepapi*. The frequency of murmuring was the only parameter which differed seasonally and this is no doubt related to the increased murmuring of males during the breeding period.

The second analysis of variance tested only between *tongensis* and *ornatus* and therefore shows that differences found above were mainly between *cepapi* and the two forest species and not between the latter two species. There was a significant difference ($P < 0{,}01$) between the distances moved with *ornatus* the more active, but no significant difference between the times spent motionless. This last result was not indicated by the first analysis of variance and was probably obscured by the fact that three species were compared there. Table 69 also indicates that *tongensis* is only slightly less active than *ornatus*.

Feeding time did not differ significantly and this indicates *tongensis* as being a less efficient feeder. There was no significant difference between allogrooming of these two species as can also be seen from Table 70. Therefore the difference in allogrooming indicated by the first analysis of variance was also between *cepapi* and the two forest species. There was a significant difference between grooming in the different months. The comparison of grooming data (Table 70) shows that *tongensis* and *ornatus* spend less time allogrooming (10,6% and

TABLE 70

GROOMING (AUTO- AND ALLO-) FREQUENCY OF THREE SPECIES OF TREE SQUIRRELS IN CAPTIVITY THROUGHOUT THE DAY

	AUTOGROOMING			ALLOGROOMING		
	C	T	N	C	T	N
February 1977	203	210	172	112	13	30
April 1977	78	121	168	44	14	24
July 1977	157	167	147	44	13	14
July 1978	111	105	131	22	27	14
October 1977	132	193	112	65	41	6
August 1976	-	96	135	-	5	41
October 1976	-	105	85	-	7	12
December 1976	-	113	141	-	12	8
Monthly Mean	116,2	138,8	136,4	57,4	16,5	18,6
S.D.	74,1	44,6	28,5	34,1	11,9	12,1

12% respectively of grooming frequency) than *cepapi*, (33% of grooming) but that they spend slightly more time autogrooming. From field observations it appeared that *congicus* also allogrooms more frequently (34% of grooming frequency, n = 38) than the two forest squirrel species. The two open habitat species appear to have a closer group cohesion or contact.

DISCUSSION

The purpose of this part of the study was to determine interspecific differences in activity levels where possible. Differences are evident from the results, indicating that the two species from open habitats are less active. *Cepapi* is the least active of the three species of *Paraxerus*, moving about less and spending longer motionless. The difference in movement between *cepapi* and *congicus* probably reflects the artificiality of the caged situation, as *cepapi* is recorded as having similar number of moves but moving a shorter distance. This is inconceivable as *cepapi* probably moves over a similar or slightly larger area then *congicus*. Metabolic rate of *cepapi* (Chapter 6) also indicates that it is particularly well-adapted to conserve energy, correlating with the low activity level. *Congicus*, also in a habitat where efficient heat loss is essential, similarly has a low level of activity.

Tongensis and *ornatus* occur in the less exacting, habitats as far as moisture and temperatures are concerned and have higher levels of activity. *Ornatus* was the most active, moved the furthest, and the most frequently, and spent the least time motionless. *Tongensis* is only slightly less active than *ornatus* and spends a similar amount of time motionless but moves less. The forested habitat no doubt requires a greater degree of movement with food resources which are widely scattered and it is therefore more time-consuming to locate and/or assess the degree of ripeness of fruit.

The time spent feeding, does not necessarily reflect activity but does indicate that *tongensis* and *ornatus* need less time to feed than do *cepapi* and *congicus*. The former two species are the more efficient feeders which is also confirmed by observations on food utilisation (Chapter 5). *Congicus* is the least efficient feeder.

CHAPTER 9

COMMUNICATION

INTRODUCTION

Tree squirrels communicate extensively by visual, auditory and olfactory signals. At low levels of excitation, they often use only visual signals such as tail pilo-erection and tailflicks, footstomping and eye-narrowing, or head-bobs. At a slightly higher level, auditory signals are introduced and given at an increasing rate and higher intensity with increasing excitement. Other visual signals are included when the vocalisation is at a high level, e.g. ears are wagged and other body movements, such as forelimb or anterior body jerks, and turning around or moving up and down, are introduced. An additional visual signal is present in the slight movement of the huge and extremely visible scro= tal sac during the murmur of the male. Olfactory signals are less noticeable but are distributed by mouthwiping, urination and anal-dragging.

It soon became clear that within the different habitats the relevant tree squirrel species differed both in the quality and quantity of the patterns of communicatory behaviour. This chapter describes and quantifies where possible, these differences and further indicates the niche separation between the species.

MATERIALS AND METHODS

OBSERVATIONS

During field work, different calls were recorded throughout the day (divided into two-hourly periods) for ornatus and tongensis. Behavioural context was described on a casette recorder or note-book whenever possible. Observations on visual and olfactory signals were described from squirrels in the field and in captivity and inter= preted wherever possible. The frequency of tailflicking throughout the day was recorded in captivity.

SOUND RECORDINGS

Sounds were recorded at 19 cm/s on Uher 4200 and 4400 tape recorders, with a directional Sennheiser microphone (MKH 804) in a windshield. The microphone was hand-held due to the dense vegetation. Most of the recordings were made in the field, but soft calls such as murmurs and growls, were recorded in cages and traps respectively. Pup vocalisa= tions were all recorded in captivity during post-natal growth measure= ments. Additional recordings in the field were made on a National Panasonic casette-recorder to obtain data on tempo, duration and sequence of calls. Frequency of daily calling was also noted during field work. Playbacks were made only in the two forests, usually in the early mornings for periods of 5 to 10 min at a time, followed by an equal time break and a repetition of the playback if no reaction was recorded after the first playback. Reaction within the 30 min following the second playback was noted.

One hundred and ninety sections (selected to be representative of the different calls) were analysed in wide band on two different spectro= graphs i.e. a Kay Electric sound spectrograph, type 6061-A. Due to breakage and unobtainable spare parts, the analyses were completed on a Voice Identification VII Series.

The calls of cepapi have been described in detail in Viljoen (1977a) to which frequent reference is made and additional notes on this species are included here. Vocalisations of congicus have been described (Viljoen, 1978) but have not been extensively recorded. Spectrograms of the soundsof both these species are included for comparative purposes.

The different calls are used overlappingly in different contexts, and therefore a dual classification system for the calls is necessary i.e. according to the

(i) physical structure and auditory impression of the calls and
(ii) behavioural context.

The calls are first described according to the former classification and then according to the behavioural context, and the function and significance of the call in a particular habitat are discussed.

Incidental auditory communication is made by chewing of hard objects, and rapid scratching during autogrooming. Interspecific signals are also mentioned.

TERMINOLOGY (from Davis, 1964; and Bondesen and Davis, 1966)

Figure	Sound which produces a single, complete and distinct impression
Formant	A resonance pattern within a spectrum in which the amplitude reaches a peak. (The frequencies within this pattern are called formant frequencies). A formant is frequently described or named by its peak frequency but the width of the base may also be of interest.
Fundamental tone	The component of lowest frequency in a complex tone
Harmonic	A component of a complex tone having a frequency which is an integral multiple of the fundamental (f_1 = first harmonic)
Motif	A group of sound units or figures that has a special rhythmic or melodic character. Phrases are always motifs but motifs are not always phrases
Note	A tone of a single, definite pitch and definite duration
Overtone	A component of a complex tone having a frequency higher than the fundamental
Pattern	Arrangement of a group of sound units in time
Period	A group of phrases forming a cycle. This terminates with more finality than a phrase.
Phrase	A part of a composition terminated by some form of cadence. A phrase may consist of one or more motifs or figures.
Pitch	The subjective interpretation of frequency, but partly dependent upon the intensity of the sound

Resonance bands	Resonance cavity acts as a filter and condenser which stores energy and then discharges it in a rearranged pattern, resulting in resonance bands
Section	A division of a phrase consisting of coherent units
Segment	A part of a figure
Tone	A sound sensation having pitch (a) Simple tone: A Sound sensation characterised by a single frequency (b) Complex tone: A sound sensation characterised by more than one frequency
Trill	A rapid series of evenly spaced and similar syllables (Brand, 1976)
Voiced sound	A sound wave generated by an oscillator in a voice-box (Unvoiced sounds such as hisses and clicks, whispers and whistles, do not vibrate the vocal cords)
White noise	All frequencies are represented

HISTOLOGICAL SECTIONS OF SKIN

Histological sections were made of sections of the oral angle and footsoles of the three Paraxerus spp. to investigate glandular presence. Skin was fixed in Formal-acetic-acid, paraffin-embedded, sectioned at 15 μm, and stained with Picro-Ponceau.

RESULTS

VISUAL SIGNALS

Visual signals are present in the following:

Tail pilo-erection and tail flicks. The tail which is carried with hair flat in the two open habitat species but thick in the forest animals, is fluffed out at slight alertness. In the two forest species, the tail is flicked frequently during the course of the day (Table 71) at a rate of 9,19 flicks per 10 s (±2,42, n = 27) in tongensis. However, in the two open habitat species the tail is seldom flicked out of alarm context. Even the forest species increase the rate of tail-flicking when alerted e.g. a subadult ornatus female descends from a tree, unaware of me, tailflicks, 6,6,7 & 6 times, turns, descends, and moves towards the west away from me. After a while she returns,

TABLE 71

DAILY FREQUENCY OF MURMURING AND TAILFLICKING FOR THREE PARAXERUS SPP. IN CAPTIVITY

MONTH	P.C.CEPAPI			P.P.TONGENSIS			P.P.ORNATUS		
	MURMUR		TF	MURMUR		TF	MURMUR		TF
	♂	♀		♂	♀		♂	♀	
February 1977	775	34	19	0	13	2352	0	590	349
April 1977	45	0	43	0	0	1961	0	598	334
May 1978	8	0	48	0	0	1332	1	66	456
July 1977	1059	0	14	127	0	1615	187	624	306
July 1978	275	0	10	174	0	1098	128	56	515
July 1978	792	0	127	700	0	901	281	0	
October 1977	1926	0	48	550	29	2114	128	50	1228

ascends the tree again, moves through it, tailflicking 5,4,&3 times, then notices me whereupon the tail flicks 21 and 14 times and she moves off completely. When the animal clicks, it flicks its tail in unison with the clicks although sometimes only with every second click. Tailflicks are only given sporadically during the trill.

Tailflicking is very obvious during mobbing behaviour, when the tail is flicked high over the head. Sporadic tailflicking throughout the day in the forest species, is probably to advertise their presence - a flicking tail is often the first indication one has of the presence of a squirrel. In the open habitat of cepapi, this continuous flicking could be detrimental as it is easily detectable by predators. It is probably not necessary to advertise their presence in such open habitat, as they can see another moving individual from at least 70 m.

Tail hairs have conspicuous bars in the four squirrel species (Figure 19). In juveniles of P.palliatus the tail is less conspicuous with only two black bars until after the first moult. The bars are not normally visible from the dorsal tail surface but when the tail is flicked high or seen from directly behind the squirrel, the bars stand out vividly.

EAR-WAGGING AND OTHER BODY MOVEMENTS

Ear-wagging was present in the three species of the genus Paraxerus but was not noticed in F.congicus possibly because of limited observations. The ear is pulled back sharply with each click, sometimes only every few clicks, and during rattles, it is flicked back with the first pulse and thereafter vibrated to the end of the rattle. Other body movements accompanying violent clicks and rattles is a limb or body movement e.g. an adult male tongensis sees me at 2 m, stops, tail pilo-erects and tail-flicks 6,5&6 times with intervals. Simultaneously he lifts his one paw and forelimb with the same frequency as the tail flicks. This is the paw that is not carrying the weight of the body. He moves a few metres and repeats the flicking and limb movement, reacting to my slightest movement such as winking an eye. When the squirrel clicks at high intensity the mouth opens wide and with

Figure 19. Visual signalling aids of tree squirrels, illustrated here for *P.p. tongensis:* Above - Pilo-erected tail displaying six black bands; Below - Prominent scrotum (note also the pigmented footsoles which are unpigmented in *P.c. cepapi*).

each pulse the whole body jerks forwards and backwards, making the squirrel much more obvious. During some clicks, 'revvs' or trills in the P.palliatus squirrels, the squirrel will occasionally turn around or move up and down from branch to branch and to and fro on one branch thus "enhancing" his presence. This was not seen in cepapi which becomes conspicuous in its open surroundings merely by flicking the tail. However, a more subtle signal only seen in cepapi is a quick head-bob, repeated a few times on first realising that danger threatens. It is the same movement that the squirrel makes on attempting a long leap, but at a quicker rate. This might give the squirrel a clearer vision of the object causing alarm, by eliminating parallax, but could also advertise the individual's own presence to any other squirrel in the vicinity.

Scrotal movement was seen only in cepapi i.e. whilst the squirrel murmurs, the scrotum vibrates with the pulses. The scrotum is conspicuous in an adult male squirrel in the breeding season (Figure 19), and probably also serves a communicatory purpose in the forest species.

Another very subtle but significant means of communication is a narrowing of the eye which is surrounded by a lighter ring. This ring is white in cepapi and congicus but only a lighter hue of the orange or red than surrounding dorsal fur in the two forest squirrel species. Eye-narrowing in a dominant cepapi causes the submissive squirrel to flee, whereupon he is chased.

Foot-stomping is seldom seen but occurred four times (three males) in tongensis and was possibly missed in the other two Paraxerus spp. The hindfeet are moved quickly up and down. This occurred in situations where the squirrel was wary, as when suddenly becoming aware of my presence.

During auto-grooming when scratching itself, a squirrel makes a drumming sound with the hindfoot. This sound as well as the movement can serve as communicatory signals. Such scratching is often done as displacement behaviour in agnostic situations.

OLFACTORY SIGNALS play an important part in squirrel behaviour. Al=though it does not seem to be prominent, this is more a result of the crypticity of the behaviour patterns and our own inability to perceive the signals than of a lack of, or insignificant role of olfactory signals. In the three squirrels of the genus Paraxerus, olfactory signals were obvious in mouthwiping (spittle and/or glandular secretions distributed), urination and analdragging, and all these activities together with a continuous sniffing were very evident in some captive situations. Tree squirrels that have been caged for some time, leave a pungent odour, especially on the nestboxes and branches. The odour of the striped squirrel, F.c.congicus, is completely dif=ferent from that of the other three species. P.p.ornatus can also be distinguished from the other two Paraxerus spp.

MOUTHWIPING

This was often just an action following feeding to clean the lips, but was also frequently seen whilst grooming, such as mouthwiping on a branch inbetween selfgrooming or on another squirrel's back whilst allogrooming. It is a wiping of the lower lip and cheecks as well as the split upper lips up to the nose tip, including the inner lip sur=faces. A modified form of mouthwipe was seen in cepapi (Viljoen, 1975) where a squirrel would wipe its mouth a few times consecutively. In such instances, the squirrel seemed to eat merely to stimulate it to mouthwipe: inbetween the mouthwipes, it would pick up a piece of strong-smelling food (often carrots) and nibble slightly or merely smell it, and sometimes the mouthwipe would be executed after merely grooming and smelling their own hands preceding the wipe, which was inter=spersed with a continual tasting action. The nose is raised in the air resembling flehmen and with outstretched hands, as in a trance, the squirrel would move to the customary place to mouthwipe. This trance-wipe was seen at any time and not necessarily in response to strangers, and therefore constituted a routine marking of the territory. It was never seen in the two subspecies of *P.palliatus* in this ritualised form, but mouthwiping did occur with and without contact with food. Another indication that scent is strong in the oral region, is the naso-nasal greeting sniff directed towards the oral angle.

Histological sectioning of skin in the oral region, revealed well-developed sebaceous and salivary glands but no sudoriferous glands. Sudoriferous glands were, however, present on the foot-soles of the three *Paraxerus* spp. (*Funisciurus* specimens were not available).

URINATION

Urine excretion is controlled and the squirrels can leave small drops whenever they need to. Collected squirrels always had full bladders, also suggesting a 'saving-up' of urine. *P.palliatus* individuals often urinated on hard surfaces in cages and in the field they were seen to do so on branches. One *tongensis* urinated over my head whilst clicki and tailflicking at me. They have a typical braced hindleg stance when urinating which could also visually convey information to other squirrels. Characteristically they smelt the object before and after urinating on it. An additional role of urine is that of cooling the squirrel, seen only in *ornatus* on very hot days in Pretoria, when it would urinate on the cement or branch and then immediately lie down in it. This would also enhance its own smell.

ANAL-DRAGGING

Two small glands are situated on either side of the female anus, and the male has extremely well-developed bulbo-urethral glands. It is possible that these glands play a role in the depositing of scent, as typical anal-dragging is often seen to leave a wet smear on surfaces.

Selfgrooming plays an important part in the distribution of the squirrel's smell over its whole body, especially the face-tail-face grooming sequence which can distribute scent from facial glands and spittle to the tail and from anal secretions to the face. Defaecation is merely incidental and pellets are dropped at any and all times. However, one aspect of defaecation in P.palliatus which deserves mention is the fact that it is apparently not deposited in the nest during the night. Squirrels caught early in the morning, leave many more pellets under the trap than during the rest of the day.

Sniffing is very often seen. Especially ornatus at nesting time sniffs all the way down to the nest, then waits some distance from the entrance before retiring. If slightly uncertain, it will use another nest. Bush squirrels however, use the same nest for prolonged periods, but in their open habitat they could probably detect a strange presence very easily, especially as they do not move far from the nest tree during the day.

AUDITORY SIGNALS

Description of physical characteristics, sequence of calls, behavioural context and/or function of the calls of the four species:

1 Murmur - a short distance/contact-seeking call. Lengths of pulses are given in Table 72. A murmur consists of a small group of inverted U-shaped pulses with low frequency reach and amplitude (Figures 20a to k). The pulses can be subdivided into three parts:

(i) a prepulse with (Figures 20b,c,d and j) or without harmonic structure (Figure 20a,e,f,h and i) and frequency reach usually below 4 kHz coupled to the

(ii) main inverted U-shaped pulse - the fundamental frequency of this pulse is often the highest frequency displayed(Figure 20c and d) and this frequency usually descends slightly within the group of pulses;

(iii) a straight vertical, short post-pulse sometimes reaching up to and over 8 kHz (Figures 20f and i). This post-pulse was once heard alone as nasal sniffs in tongensis pup (Figure 20g). Species, age and sex differences are evident in number of pulses per group, pulse length and frequency reach. In congicus (only a juvenile recorded) a higher frequency is reached and the post-pulse is harmonically structured (Figure 20a). In cepapi the pre-pulse is clear and the male call has many rapid pulses whereas the adult female only emits a short group

TABLE 72

CHARACTERISTICS OF MURMURS AND GROWLS OF SOUTHERN AFRICAN TREE SQUIRREL SPECIES (SAMPLE SIZE IN PARENTHESIS)

SPECIES AND CALL TYPE	PRE-PULSE AND MAIN PULSE (ms)	INTER-PULSE INTERVAL (ms)	DOMINANT FREQUENCY (kHz)
MURMURS			
F.c.congicus juvenile	82,55 (12)	98,41 (10)	2,5
P.c.cepapi	83,88 (49)	32,76 (37)	1 - 1,5
P.p.tongensis juvenile	95,42 (51)	65,55 (41)	2,2 - 2,8
adult	126,91 (25)	73,20 (18)	1,5 - 2,8
P.p.ornatus	157,36 (25)	75,67 (21)	0,9 - 1,2
GROWL/GRUNT			
P.c.cepapi	78,10 (20)	22,18 (19)	1,5 & 3,5
P.p.tongensis	99,94 (30)	202,54 (21)	a 0,5to 1,5 b 2,7to 5
P.p.ornatus	138,84 (30)	105,16 (27)	a 0,5to 1 b 2 to 6

of pulses and at a slower rate (Figure 20d). (No juvenile cepapi recorded.) The pre-pulse (sometimes preceded by one pulse) in the cepapi female is frequency modulated and has a higher frequency than that of the male. In the two species of palliatus the murmur is of higher amplitude. In tongensis the U-shaped pulses are clear (Figure 20e and f) and slightly shorter than in ornatus. In ornatus, the pulses sound fuller and deeper than in any of the other species. The adult male pulse is more clear than in the female and has a higher fundamental frequency (Figure 20e). Juveniles of both these subspecies have clear pulses and in ornatus the first harmonic is present. (Emmons, 1975, Type 2 - contact seeking calls, C).

BEHAVIOURAL CONTEXT AND FUNCTION

Murmurs are given in various situations but mostly seem to be stimulated by the desire to contact another individual whether aggressively or amicably. Murmurs were heard in the following situations:

(a) Nesting - close to nesting time the forest species murmur more often and in captive squirrels it is the adult females that call at this time. Juveniles respond immediately to this call by advancing towards the caller e.g. an adult ornatus female approache the nest, murmurs, two subadult squirrels which had been sitting overhead in the sun, immediately descend to the nest; and a tongensis female approaches the nest, murmurs when reaching the tree adjacent to the nest tree, whereupon a juvenile immediately answers and follows her for a grooming bout. Murmurs can also be heard inside the nesthole for a few seconds after the group has entered.

(b) Juvenile - adult female contact - Apart from being given as a contacting call at nesting time, this call is also given during the day by adult females and their pups. This call develops before pups leave the nest (Chapter 10). The handrearlings often call thus when the handler-parent talks, or later when it notices the handler and wishes to make contact. The female *cepapi* which never otherwise gives this call, assembles her pups thus around the time that they leave the nest, on day 19.

(c) Mating call of the male - adult males of the three *Paraxerus* species give this call in mating context with increasing frequency as the mating season draws closer (Table 71). The call is very often given in and around August and disappears from the male repertoire from January - this cycle closely follows the cycle of male scrotal size of the bush squirrel and is probably androgen controlled. In cages the male usually accompanies this call with a short chase of the female, and an attempted mount, whereupon the female grunts/growls a few times and tries to evade him. The call possibly serves to bring the female into oestrus, and the female presence stimulates the male to emit the call. In the field a murmuring *P.palliatus* male following a female is often seen; when he catches up with the female, she turns around, they give a naso-nasal sniff, the male allogrooms and tries to investigate the female's anal region. Upon this the female moves off again. This is repeated a few times, during which they are oblivious of an intruder's presence.

Captive *cepapi* males often give this call sporadically and on the day that the female is in oestrus and calls extensively (Viljoen, 1977d) the many males that are attracted, continuously murmur.

(d) Spacing context - A dominant squirrel gives this call spontaneously, or on seeing another squirrel, presumably to seek contact and asses the 'intruder'. In captive squirrels it is answered from cage to cage by squirrels of the same species (males of *cepapi* and females of *ornatus* or *tongensis*). Examples:

(i) An adult *ornatus* clicks, after 15 min it descends from the tree, hesitating at each step. When it reaches the ground, it quickly scats up the tree again, and after some time hesitantly approaches another adult male, which also approaches. They sniff naso-nasally, both murmuring alternatively. Both turn and move in different directions and the first individual recommences clicking.

(ii) An adult female *crnatus* accompanied by her pup (± 6 weeks old) defends a fruiting *Drypetes gerrardii* (10/12/77). Her pup murmurs and she moves towards it with loud murmurs, allogrooms it. Then another squirrel, an adult male, murmurs towards the north-east and the female immediately moves towards it. After 2 min she commences clicking which lasts for 12 min, whilst moving in a 20 m half-circle around the *Drypetes*. The previous day I watched her for 15 min clicking towards all sides of the tree where her pup was: first moving 30 m towards the east, then 30 m to the west, it then saw me and proceeded into the rattle, the ears rattle in synchrony i.e. are flicked back and forth, then vibrated. Then she moves again towards the east, returns, clicks another 10 min, then murmurs and is immediately answered by her pup as they move towards one another. The female twice stopped her clicking to 'listen' to 'answers' from 60 m off.

(iii) Dominant *tongensis* in cages were often seen to chase submissive squirrels whilst emitting this murmur (both males and females).

(iv) At a food source, (peanuts strewn on a seed-table) or for a prized food article (acorns in cages or a big nut in the field), a dominant squirrel will also chase a submissive individual who flees with occasional grunt/growls if the pursuer makes contact.

2 *Female receptive sound* - The only female receptive sound, heard during oestrus of *cepapi*, was a high-pitched, short pulse with harmonic structure. In Figure 20k it is followed by two soft grunts/ growls. The female gives this call whilst the male is mounting her.

3 *Growls and hisses* - a short distance aggressive call. These are sounds with a wide frequency span from 0-8 kHz. (Figure 20m - o). Amplitude and major energy concentration and pitch varies slightly in different pulses. There is some semblance of harmonics although these are not always readily distinguishable. The pitch is low with

major energy at less than 500 Hz and a lesser energy band from 3-4 kHz (P.pallaitus Figure 20n and o) or 4 to 5 kHz (cepapi - Figure 20m

Duration is variable but the sounds are given both on in- and ex=halations, the former yielding shorter pulses (Figure 20m). It is difficult to distinguish between the different species (congicus was not recorded).

At a slightly lower level of excitation, a hissing sound is some=times heard interspersing the growls and given at the same rate, but when the squirrel is not voicing the sound. These are short pulses from 3 to 6 kHz in Figure 20 where the first pulse has a growl below 1 kHz.

BEHAVIOURAL CONTEXT AND FUNCTION

These calls are given when the squirrel is in danger.

(a) Squirrels in traps growl when the trapper approaches - at a lower level of fright they only hiss;

(b) A squirrel, disturbed in its nestbox will grow, ready to lunge and bite the intruder;

(c) During intra-specific chases (as a result of mating or in a food-envy context) the chased individual gives short grunts or growls.

Function: This call inhibits or attempts to inhibit contact - a war=ning call. (Emmons, 1978, classifies growls as defensive calls, Type 4, termed D).

4 Chewing noises - short distance attractant

Squirrels chewing on hard fruits or nuts can be heard from at least 40 m and this noise attracts other squirrels in the immediate vicinity. These are short pulses which reach up to 6 kHz in ornatus. (Figure 20ℓ)(not recorded for the other squirrels).

5 Continuum of sounds - in rising alertness scale, used in alarm as well as in spacing context. The significance of this series of calls in the forest species and savanna is discussed separately as they differ markedly in certain aspects of this sequence of sounds (Tables 73 and 74).

(a) P.palliatus: At a low level of alertness, the sharp pulses (clicks) are given as straight, vertical lines (Figures 21a and 22a) and as alertness increases, two vertical lines (a couplet), are emitted in close succession, the second one now gradually dominating, and the first pulse disappearing (Figure 22b&c). The amplitude is then higher and the second line shows harmonic structure and eventually widens to an inverted-V with clear harmonics (Figures 21b&c, 22d,e&i) and reaches up to and over 8 kHz, whilst the first pulse is dropped, or only present as a faint pre-pulse up to 4 kHz. These 'chucks' are given at varying intensity and frequency reach. Fundamentals and harmonics vary with tempo and amplitude, being slightly higher at a higher tempo. As excitement and tempo steadily increase, more white noise infiltrates these pulses (noisy pulses) at a slightly higher frequency level than that of the harmonic with the major frequency (Figures 21d and 22g).

Ornatus noisy pulses have a distinct frequency band from 1 to 4 or 5 kHz, concentrated at 2 and especially 5 kHz (Figures 21d and f) becoming higher with rising excitement in sharp chucks (Figure 21c). In tongensis the frequency is often interrupted from 3 to 4 kHz (Figure 22i and j) and energy is concentrated at the lower end of the white noise (Figure 22g). Ornatus has a lower fundamental than tongensis (1,8 to 2 kHz cf. 2 to 2,1 kHz) (Table 73) and more harmonics are present with a very clear and accentuated fundamental frequency.

TABLE 73

DURATION (ms) OF PULSES, INTERPULSE INTERVALS AND TOTAL NOISE LENGTH OF ALERTNESS CALLS OF P.p.ORNATUS (*1) AND P.p.TONGENSIS (*2) (SAMPLE SIZE IN PARENTHESIS)

	PULSE (PRE-PULSE & MAIN PULSE)(ms)	TOTAL NOISE (WHEN PRESENT)(ms)	INTER-PULSE INTERVAL (ms)	DOMINANT FREQUENCY (kHz)	FUNDAMENTAL FREQUENCY (kHz)
Soft clicks *1	31,24 (6)		281,16 (3)	0,5	
*2	34,21 (34)		281,71 (28)	0,5 to 1	
Noisy chucks *1	83,72 (41)	269,29 (39)	307,56 (35)	2,6 & 4,8	1,6 to 2
*2	90,05 (12)	229,46 (17)	269,05 (24)	3 & 4 to 6	2,1 to 2,6
Sharp chucks 1	95,75 (33)	322,16 (5)	363,87 (28)	1,8 to 2,5, & 3,2 to 4,2	1,5 to 1,8
2	56,93 (62)	105,44 (6)	291,39 (54)	2,3 to 3, & 4,5 to 6	2 to 2,5
Double chucks 1	63,26 (55)	401,63 (9	403,2 (26)	2 to 5	1,1 to 2
2		413,93 (1)	1069,97 (1)	2,5 to 5	1
Rattles 1	47,17 (53)		69,12 (47)	1,2 & 2,8	1,2 to 1,5
2	70,29 (15)		21,48 (12)	1,5 & 2,4	1,5 to 2,3
Revvs 1	46,07 (77)		98,48 (66)	3,5	1,2
2	not recorded				
Deep, full trill 1	42,50 (113)		84,04 (93)	1 & 3 to 4	1 to 1,3
2	41,31 (125)		82,08 (123)	1 to 2,5 & 4 to 4,8	1,5 to 2,1
High trill 1	48,03 (72)		86,22 (72)	1,2 to 2	1 to 1,3
2	39,75 (67)		96,30 (63)	1 to 2	1,5

TABLE 74

CHARACTERISTICS OF ALERTNESS CALLS OF *F.C.CONGICUS* AND *P.C.CEPAPI* (SAMPLE SIZE IN PARENTHESIS)

SPECIES AND CALL TYPE	PULSE LENGTH (ms)	INTER-PULSE INTERVAL (ms)	DOMINANT FREQUENCY (kHz)	FUNDAMENTAL FREQUENCY (kHz)
F.c.congicus Chirps	38,35 to 102,00	92,16	2 to 3,5 (chirp) 4,5 initially	4 to 5 down to 1,8 to 2,1
P.c.cepapi				
High intensity rattle: adult	40,22 (87)	49,67 (66)	2,5 and 3,7	2,5
juvenile	54,67 (7)	54,67 (6)	4,5 to 5,5	4,5 to 5,5
Harsh clicks	51,98 (20)	46,35 (23)	2 to 5,5 (noise)	2 to 3,5
Soft clicks	13,04 (3)	570,13 (2)	2	2

The main difference between ornatus and tongensis clicks or chucks is that the former have three clear harmonics whereas that of the latter mostly only show two. To the ear, the clicks have an occasional deep sound (spectrographically represented by the pre-pulse Figure 21i), synchronised with two higher frequencies. The middle frequency is the one present in the rattle, whereas the high frequency is only sometimes present. One squirrel can thus be thought to be two individuals calling almost in unison.

When given at a still faster rate and higher excitement level, the pulses graduate into higher amplitude couplets, triplets and eventually rattles of 4 to 13 pulses (Figures 21g and j; 22i). The pulses then sometimes proceed to a trill (Figures 21k-m; and 22ℓ to o) i.e. a continuous series of pulses, sometimes deep and full (Figures 21 and 22) but often reverting to a high sustaining trill (Figures 21m and 22o). This trill probably saves the squirrel a considerable amount of energy cf. clicks or chucks: it has a lower amplitude and involves less tail=flicking and bodily movement. To compensate for this loss of communicative distance, the call is at intervals interspersed by 'revvs' (Figure 21g, h&i) that have a suppressed fundamental (moves down from 2,1 to 1,5 kHz in ornatus), a higher amplitude and more white noise than the trill. These 'revvs' are always given whilst the squirrel turns around to face a different direction and serves the purpose of once again making the animal audible over a considerable distance for the length of the call, albeit at intervals. The 'revvs' can initiate this continuum of sounds and are sometimes followed by chucks before the squirrel recommences the trill. During these chucks the squirrel can hear any 'answers' possibly given by other individuals. The pulses are sometimes regular, sounding high, but at length might be modulated down the middle (Figure 21ℓ and 22m). A base sound is often included in chuck and trill pulses, and is caused by the occasional pre-pulse (Figures 21i and 22m&n). The trill is usually terminated abruptly by a few sharp chucks. In ornatus the trill has the fundamental around 1 kHz and in tongensis slightly higher at 1,2 kHz. Ornatus once again has three clear harmonics whereas tongensis has two harmonics with an almost continuous energy band from 1 to 3 kHz, a partial "wipe-out" between 2 and 4 kHz, and the pulses are more slender.

The deep barks which often initiate this continuum of calls have not been recorded as they are usually unexpectedly heard whilst one is unprepared to record. However, to the ear, they have a frequency similar to the 'revvs'. These alarm barks are often interspersed or followed by slow clicks or chucks (5/10 s) and/or revvs.

(b) P.c.cepapi: The calls of this species have been described in detail by Viljoen (1977a). The main difference from the calls of palliatus is that the fundamental and harmonics are higher in cepapi and the pulses have a high frequency reach (Table 74). The trill is never heard in cepapi but replaced by a series of very noisy rattles (Figure 23g to j). The clicks in cepapi do not attain the same intensity as those of palliatus. But the single line clicks (Figure 23m) are followed by noisy clicks or chucks (Figure 23ℓ) and then by rattles (Figure 23k). Only the initial pulses of the cepapi rattle are wide, thereafter becoming slender and almost unrecognisably sandwiched inbetween noise. Fundamentals are initially extremely high with the pre-pulse slightly lower. The pulse splits after a while and starts showing high frequency reach and noise (Figure 23g). Pitch of the initial rattle pulses are usually descending. The series ends with harsh triplets (Figure 23k and ℓ). There is a similarity between the cepapi pulses of Figure 23g and the ornatus trill of Figure 21m, the latter, however, at a much lower frequency.

(c) F.c.congicus (Viljoen, 1978): These bird-like calls differ markedly to the human ear and must be separated from those of the Paraxerus group. The pulses are sharply pointed (Figure 23a to f), so sharp that often only the descending and ascending sides of the inverted-V's are seen with the fundamental very high. These pulses reach ≥ 8 kHz. The major energy of the alertness series is high at 3 kHz and the pulses are emitted in very rapid succession. As the call proceeds, descending, the pulses are given at a slightly slower rate and only the right hand side of the inverted-V is displayed on the spectrograms. In the juveniles the initial fundamental is at 5,5 kHz (Figure 23a). A chirp series of pulses usually follows at a slightly lower level of alertness (Figure 23b) with the frequency of the fundamentals now at 3 kHz. Still lower on the alertness scale, Figure 23c to e, represents mild alarm.

The above-described continua of sounds on a rising scale of alertness clicks to rattle (P.cepapi) or to trills (P.palliatus), clicks and chirps (F.congicus) is given with a rising level of excitation, be it in alertness/alarm or a spacing context e.g.

(a) at ground predators clicks, chucks and rattles are given during mobbing behaviour. In tongensis there are three slightly different reactions to an observer:

(i) the squirrel freezes, peers, then moves off; or it just quickly moves off (n = 22)
(ii) a few clicks and/or tailflicks, then moves off (n = 8)
(iii) clicks for some time, often more than one squirrel present, plus mobbing behaviour (n = 6)

Tongensis reacts to lesser disturbance but is less inclined to mob an observer than ornatus who habitually reverses to some distance, from where it calls. If it is calling at an observer who then moves slightly, the squirrel increases the tempo and pitch; but if one suddenly approaches, they stop calling. A typical example is the following: an adult female *tongensis* is clicking, then sees me, stops calling, tailflicks 12,12,8,10,10,8 times, now moving, 8,8,10, selfgrooms, then moves away. When sudden close danger is felt, the squirrel gives a deep bark whilst descending into denser vegetation.

Mobbing clicks of *ornatus* are given at ground predators, human, slender mongoose, snakes (also in trees). At a certain distance they vocalise at a human observer, often when you are motionless, e.g. 22/4/76: a feeding *ornatus* notices my presence, motionless, it stops feeding and commences vocalising with head down on tree trunk, tail flicking overhead. If you are motionless and they come across you, they back away or if they had been on the ground, they ascend into a tree and then, sometimes after freezing a short while, start vocalising. When you approach them and they notice you first, they wait until you have passed for a safe distance, approximately 15 m, and then commence vocalising usually by clicks. If you surprise *ornatus* suddenly, it will give the high intensity alarm bark sometimes quickly repeated, which it also gives on sighting raptors. This bark is of a low frequency and allelomimetic for squirrels up to 35 m apart. In the same context, the open habitat squirrels give a high-pitched whistle, also allelomimetic (Viljoen, 1977a and 1978). If the stimulus remains in the close vicinity as in the case of a human, then one of the squirrels will probably proceed into the series of clicks, double clicks and rattles and if the threshold for the trill series is low, it will proceed into the trill. When squirrels are in the process of mobbing one, they stop at sudden movements or coughs from the suspected subject, but at subtle movements, such as just slightly shifting your weight, they intensify their vocal effort, move around, ears and tail flicking furiously and the whole body jerking. Whilst the source of danger is close, the squirrel does *not* proceed into the trill. Therefore the trill is probably not a call of intense alarm (as found by Emmons, 1978). It is more likely that there is at a certain time of the year a low threshold for trilling and this is why it is also heard in alarm context when the source of danger is further.

It has more value in spacing context.

(b) Spacing or testing for presence of other squirrels, or advertising own presence:

(i) At nesting time <u>ornatus</u> frequently calls e.g. 2/10/77 at 17h15 an adult male fast-clicks whilst moving to and fro, up and down and then into the top of the nest tree and descends whilst smelling the branches up to the nest, where he sits motionless, after tail-flicking for some time - at 17h40 he enters the nest. Meanwhile a second squirrel clicks exactly as described for the first individual and also descends to the nest. During daytime, clicks are also given in this 'testing'/advertising context, without necessarily making contact with another individual, but sometimes merely causes squirrels to move into different directions (see also example under Murmur).

13/5/78: <u>Podocarpus falcatus</u> nest: At 16h15 vocalisation from stream to the south; 16h40 individual from nesthole to the ground, inspects a trap; 16h50 into the hole but out immediately again; 16h55 up into the canopy, clicks for 30 s then off to the west.

16/5/1978: <u>Ficus natalensis</u> nest: At 16h30 clicks towards south where they call every night; 16h32 an excited series of barks and clicks; 16h43 adult male jumps up back of the tree and sits motionless 3 m high and enters hole at 16h48; (16h45 barks 100 m towards the north at the <u>Drypetes gerrardii</u> nest); 17h00 bark from behind my back, i.e. to the east; answered immediately from the nest tree and a reply again from behind me; 17h02 clicks 200 m to the south, as on other evenings; 17h05 another squirrel jumps up into the tree from the west and at the same time the unmarked adult female comes the habitual SSE route, jumps onto the tree, sniffs the branch route to the nesthole; as she gets to within 2 m from the nest, the pup bounces out of a fold in the roots of the fig with a single murmur pulse (contact sound) and the female sniffs her and moves past. The juvenile immediately follows her into the nest. Juvenile squeaks audible from inside the nest for 30 s. At 17h10 individual pushes head out of the hole again, barks three times and sits motionless thus for 8 min. All finally in at 17h18.

5/2/78 ornatus individual clicks 40 m to the south of the nest tree, fast clicks 10 m from the tree and at 17h30 the three that habitually nest in this tree congregate from different directions, allogroom and enter the nesthole at 19h19.

(ii) In tongensis the clicking was seen during territorial behaviour; 20/11/77: At 12h00 two adult females are clicking, one behind Inhambanella, another 30 m to the north. When very close to one another at the 'border', number 2 is very nervous, moves quickly, suddenly turns around and reverses, moves, forages, selfgrooms, moves, turns around. Four chases then follow between the two, first towards the Inhambanella, then immediately reversed, the females also reversing roles. Number 2 is seen to murmur but both the squirrels could have been murmuring alternately. Such chasing between these two individuals was subsequently seen on three occasions. In cages, adult females also murmur in this context. Therefore both clicking and murmuring are associated with spacing.

(iii) The trill is used in spacing context: in tongensis (25/3/77) at 06h35 the sub-adult female of the group which has been relentlessly chased by the adult male of the group, calls in a Dialium schlechteri tree more or less in the middle of the territory, fast clicks, proceeding into the trill for a total time of 40 min and then moves 20 m towards the south. At 07h20 the adult male has moved into the Dialium and commences a similar series of vocalisation, calling in all directions for 15 min.

(c) Either contact or spacing context:
The trill or rattle was on two occasions given after dark, both times when an adult female tongensis was highly alert because of having pups in the nest. It could be that she was calling the young who could have strayed, or else she was merely trying to warn other squirrels off (a tongensis female with pups is intolerant of other individuals of the same species and nests alone with her litter). On another occasion a stray tongensis pup, already out of the nest, i.e. more than 21 days old, gave a short series of trills and thus immediately attracted its mother.

Function: The clicks very often have the effect of attracting other individuals of the same species. During mobbing behaviour this adds numbers to the mobbing group, and in other instances it has the function of 'testing' for presence of strangers. The trill series mainly advertises the presence of a squirrel and is often given repeatedly from fixed trees and answered from other fixed trees. The raptor alarm bark causes other squirrels to repeat the call and flee. Juveniles, if present, flee unhesitatingly with no sound. (Emmons, 1978 - Types 6,7&8 - Alarm, A and Aℓ calls).

Possible differentiation between ornatus and tongensis with regard to vocal intensity and rates of pulse utterance was investigated, and results are included at this point together with data from cepapi, as the alertness continuum of sounds featured prominently in the results.

The most noticeable difference between vocal communication of ornatus and tongensis was that ornatus called much more frequently (1 249 in 731 h) than tongensis (259 calls in 660 h) (Table 75). In both species, clicks were more often given

TABLE 75

FREQUENCY OF VOCALISATION PER HOUR OF P.P.ORNATUS(*1) AND P.P.TONGENSIS(*2) FROM OCTOBER 1976 TO MAY 1978

MONTH	CLICKS		TRILL		MURMUR		GRUNT		BARK	
	*1	*2	1	2	1	2	1	2	1	2
October 1976-1977	1,25	0,2	0,25	0,04	0,05	0,01	0	0	0,17	0
January 1977	1,43	0,43	0,12	0,00	0,07	0,01	0,03	0	0,14	0
March - April 1977	2,43	0,55	0,24	0,06	0,02	0,03	0,01	0,04	0,19	0
June 1977	1,22	0,17	0,39	0	0,13	0	0,05	0	0,14	0
August 1977	0,92	0,21	0,22	0,03	0,11	0,05	0,0	0	0,10	0
November - December 1977	1,14	0,67	0,11	0,06	0,11	0,67	0,04	0,06	0,05	0
January 1978	1,67	-	0,53	-	0,07	-	0	-	0,05	-
May 1978	1,47	0,20	0,38	0,03	0,02	0	0	0	0,17	0
Average	1,44	0,34	0,24	0,04	0,08	0,02	0,02	0,01	0,12	0
Total no.	929	225	151	26	48	16	12	9	80	0

than trills and both of these calls more often than murmurs or barks (Table 75). There was no significant difference between the duration of the clicks and trills (Table 76). In cepapi in 69 h, 46,3% of the calls were clicks, therefore almost as many as the rattles, and calls did not last as long as in ornatus and tongensis. (Clicks lasted 3,8 min ± 2,7, n = 5, and rattles lasted 2,0 min ± 1,4, n = 8).

The rate of pulses/10 s were counted for the two forest squirrels: Ornatus clicks at a high level of excitement were given at a rate of 21,71/10 sec (n = 512) and at a low level of excitement at a rate of 13,48/10 s (n = 102). Slow clicks just after the alarm barks, are given at 5/10 s and the fastest rate was 42/10 s immediately prior to the trill. Double clicks were given at a rate of 15,02/10 s (giving 30,04 pulses)(n = 258) and triple clicks at 6,71/10 s (giving 20,13 pulses/10 s)(n = 17). Rattles of seven pulses each were given at a rate of 6,43/10 s giving 42 pulses/10 s. The trill is sustained at 46,23 pulses/10 s. (n = 37).

In tongensis the rate of clicks at a high level of excitement was 25,13/10 s (n = 271) and at a lower level at a rate of 13,13/10 s (n = 87) ranging from 0 to 30 per 10 s.

Cepapi clicks are given at 32 to 34 per 10 s (33,50 ± 1,98, n = 12) for 12 min then down to 14/10 s for 3 min. These rates were not tested statistically as it is impossible to obtain samples of the rates at exactly the same level of excitation and therefore at a strictly comparable rate. Lengths of pulses, pre-pulses, interpulse intervals and also the dominant frequencies of calls as taken from spectrographs are summarised in Tables 72 to 74, for the four species but were similarly not investigated statistically.

TABLE 76

DURATION OF CALLS (MIN) OF *P.P.ORNATUS* AND *P.P.TONGENSIS* FROM JUNE 1976 TO MAY 1978

CALL TYPE	*P.P. ORNATUS*			*P.P.TONGENSIS*		
	MEAN DURATION ± SD	n	TOTAL TIME	MEAN DURATION ± SD	n	TOTAL TIME
Clicks	12,86 ± 13,23	132	1697,5	11,32 ± 7,32	37	419,0
Trills	18,04 ± 17,65	38	685,5	22,44 ± 15,25	9	202

The intensity of the calls of the two forest squirrels can subjectively be judged, from the distance at which the calls were audible:

tongensis:	clicks 74 m ± 28,39 (n=5) (up to 105 m).
ornatus:	clicks 222,5 m ± 28,72 (n=4) (up to 260 m) trill 140 m (n=2)

In the open woodland of cepapi, the rattles were audible up to 150m.

This audibility distance of calls that function in a spacing context, points to a larger home range for ornatus than for the other two species. Amplitude of calls were measured with a dB - meter whenever possible. Although such measurements are influenced by reflection of sound from obstructing vegetation, a rough comparison can nevertheless be drawn between amplitude of tongensis calls and those of ornatus. In tongensis, soft clicks registered 51 dB at 3 m, 50-59 dB at 4,5m (n=3), and 45-49 dB at 10m. However, the first few sharp clicks were louder, i.e. they registered 60 dB at 4,5m. The trill was considerably softer and registered less than 40 dB at 6m. In ornatus the soft clicks registered 46-52 dB at 6m, 50 dB at 16m, and 40-43 dB at 28m, whereas the sharp initiating clicks registered 52 dB at 18m and 55 dB at 11m. The ornatus trill was once again softer, at 40-50 dB at 25m and the revv slightly louder than the trill at 48-50 dB at 20m. Soft clicks of cepapi did not register at 18m, but no other data for this species could be gathered.

6 High intensity alarm calls - isolation calls - of nestlings:
Both these calls have a high amplitude and frequency reach and commen and terminate abruptly. The dominant frequencies vary slightly in the different squirrels (Table 77, Figure 24). The barks are a rapid series of loud, sharp inverted U-shaped pulses. Ornatus has the lowest fundamental frequency (Figure 24i and j) followed by tongensis (Figure 24g), cepapi (Figure 24d and e) and congicus (Figure 24a). Ornatus has more harmonics to the pulses.

The squeaks (Figure 24h) are possibly not alarm calls, but food-eliciting sounds. These calls were only recorded for the three Paraxerus squirrels and were always given when I approached the cage hand-rearlings who were 'enticing' me to feed them. The frequency and amplitude is modulated. The harmonics are horisontal, convex or sometimes sharply skew to either side.

Behavioural context

(i) These calls are given when pups are removed from the nest to weigh and measure them and are probably related to the temperature drop, or strong light intensity, as the call ceases when the squirrel is returned to the nest or makes contact with another nestling.

(ii) In January 1977 this piping call of a very young ornatus was heard 9 m up in a tree. The call was given in short bursts lasting from 50 to 80 s, interspersed with 30 to 60 s intervals. Each time the burst would start high with rapid barks of 36,8 ± 3,3 pulses (n = 18) per 10 s which diminished to 14,0 ± 10,05 (n = 7) pulses per 10 s whilst descending in pitch. At the end of each burst, there were from 5 to 11 double pulses, the second one with higher pitch. This call lasted for 33 min until I left to fetch the tape recorder. Presumably this was exactly what the mother had been waiting for to carry the pup off to safety.

TABLE 77

CHARACTERISTICS OF ISOLATION BARKS AND SQUEAKS OF JUVENILE TREE SQUIRREL SPECIES (SAMPLE SIZE IN PARENTHESIS)

SPECIES AND CALL TYPE	PULSE LENGTH (ms)	INTER-PULSE INTERVAL (ms)	DOMINANT FREQUENCY (kHz)	FUNDAMENTAL FREQUENCY (kHz)
F.c.congicus				
Barks	75,76 (10	145,27 (10)	2 - 3,5	1,2 to 2 and possibly higher
P.c.cepapi				
Barks	100,25 (30)	259,23 (25)	2,5 to 5	1,8 to 4,5
Squeaks	68,77 (31)	102,29 (25)	3,5 to 4,5	1,8 to 4,4
P.p.tongensis				
Barks	106,55 (24)	195,58 (24)	3,5 to 4,6	1,5 to 1,8
Squeaks	86,85 (43)	137,22 (36)	1 to 4 and 3,5 to 5,5	1 to 2
P.p.ornatus				
Barks	63,86 (26)	161,59 (23)	3	1 to 1,2
Squeaks	58,69 (12)	179,16 (8)	1 to 4	0,8 to 1,8

(iii) In *tongensis* it was once heard at nesting time and soon after, the mother carried the pup away from the nest probably because of my presence, towards another nest.

(iv) Both *cepapi* and *congicus* show similar behaviour. A lactating *congicus* female released next to her nest tree, gave a sharp chirp, answered by chirps of a pup from the nest, which immediately caused the female to go to the nest. In bush squirrels, both the male and the female remain within the vicinity of the nest and are extremely vocal when the pups are small - a male once charged me as I attempted to weigh the barking pups, and it was impossible to remove pups from cages when the mother was still free as she would attack without hesitation.

Function: These calls have the effect of bringing the female to the rescue and to carry the pup to safety by the belly skin.

7 Ticking sounds (short distance contact, unrecorded): Nestlings of *congicus*, *tongensis*, *ornatus* and *cepapi* gave this soft noise (Emmons, 1978, Type 12a). It is probably a contact-seeking noise towards the female.

8 Teeth grinding was heard at close quarters in *cepapi* as a warning - it is not entirely clear whether the sound is made by the incisors or molars (Emmons, 1978, reports incisor tooth-chatters).

9 Interspecific communication: Squirrels were often alerted by sounds coming from other species: Hadedah or dove wing noise can cause a quick bark or flight. Puffback shrikes, tinker barbet and starling were seen to mob squirrels. Duiker alarm snorts alert squirrels, and if the squirrel is calling at the time, it immediately stops and 'listens'. Monkeys cause passive fleeing, with the squirrels just moving away, but a sharp monkey alarm bark can cause a squirrel to freeze. Wind noise and consequent sudden branch movements alert squirrels and during strong wind, they are less easily seen. Weavers make a sharp 'chick' when discovering a food source and this

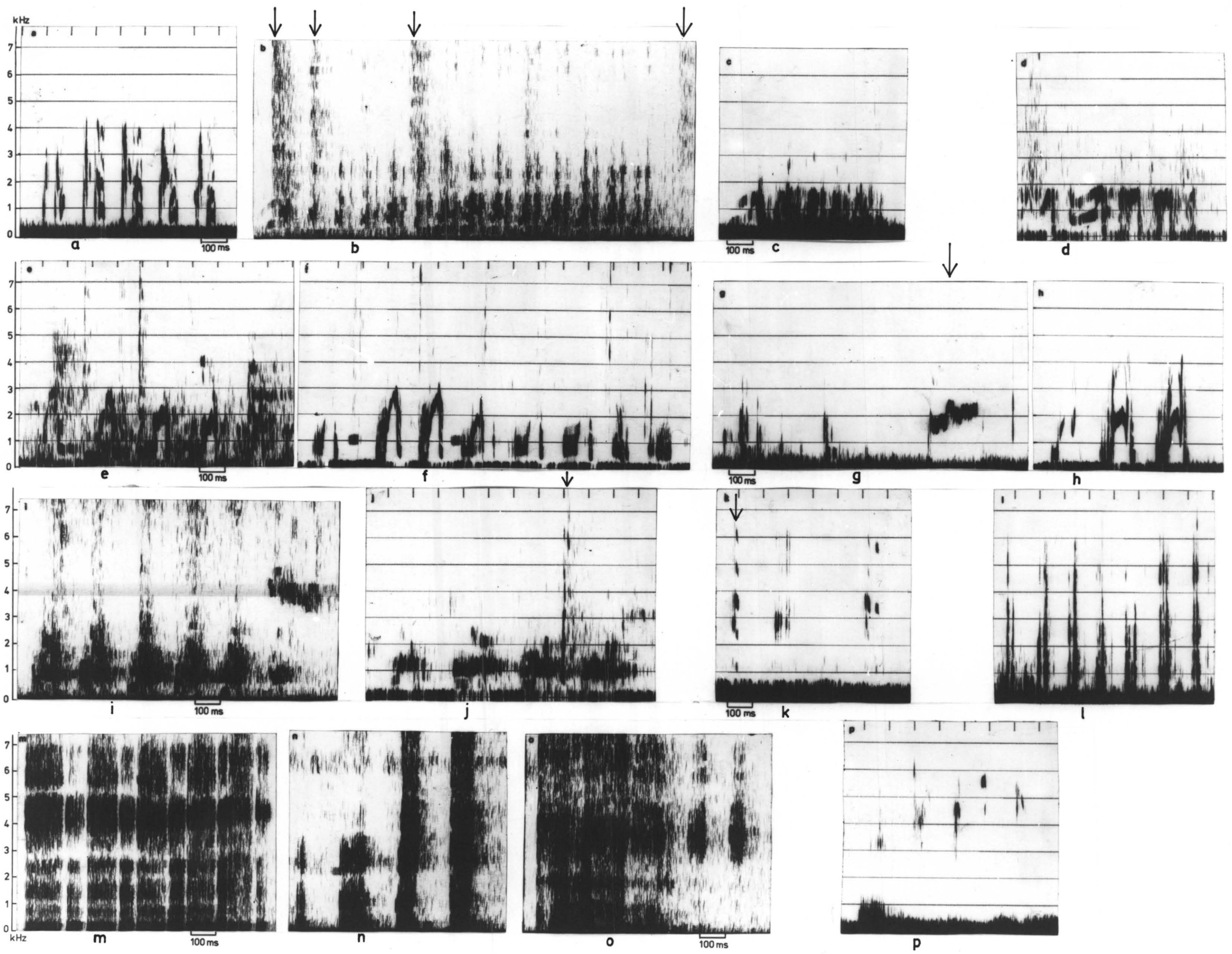
Figure 20. Sound spectrograms of murmurs (a - f, & h - j), grunts/growls (m - o), and closely related sounds of *Paraxerus p. ornatus*, *P.p. tongensis*, *P.c. cepapi* and *Funisciurus c. congicus*.: a. *congicus*, male, 3-weeks-old; b & c *cepapi*, adult male; d. *cepapi*, adult female; e. *tongensis*, adult male; f. *tongensis*, pup; g. *tongensis*, pup, nasal sniff plus an unusual 'cheww'-sound; h. *ornatus*, pup; i. *ornatus*, adult female; j. *ornatus*, adult male; k. *cepapi*, adult female, receptive sound during oestrus; l. *ornatus*, chewing on acorn; m. *cepapi* adult male; n. *tongensis*, adult male; o. *ornatus*, adult female; p. *tongensis*, growl/grunt, followed by hisses.

Figure 21. Sound spectrograms of clicks/chucks, double and triple clicks, rattle, and trills of *P.p. ornatus* (alertness series): a&b soft clicks; c. fast, sharp clicks/chucks; d. noisy clicks/chucks; e. triple click/chuck; f. fast clicks/chucks after a 'revv', arrow indicates base sound; j. triple click/chuck and rattle prior to 'trill'; k. 'revv' within a trill; l. deep, 'full' trill; m. high-pitched trill.

Figure 22. Sound spectrograms of clicks/chucks, double clicks and trill of *P.p. tongensis*. (alertness series): a. soft, nasal clicks; b. soft clicks, double sound audible; c. sharp loud clicks/chucks; d&e sharp clicks, slightly higher-pitched than in c; f. fast, sharp clicks/chucks; g&h noisy clicks/chucks; i, j&k fast clicks and double clicks/chucks, in j, just prior to the trill; l-n deep, 'full' trill, arrow indicated base sound; o. high-pitched trill.

Figure 23. Sound spectrograms of chirp series of *F.c. congicus* (a - e), and clicks and rattles of *P.c. cepapi* (g - m), (alertness series). Also, the call of the woodland kingfisher, *Halcyon senegalensis* (f). a. high intensity alarm (almost a wistle) of 3-week-old *congicus*; b - e. chirps slightly lower progressively (b to e) on the alertness scale; g, i&j *cepapi* adult female in oestrus, rattles; h. *cepapi* adult male alarm/alertness rattles; k&l. *cepapi* adult female concluding harsh barks after rattles; m. *cepapi* adult male soft clicks.

Figure 24. Sound spectrograms of high intensity alarm calls, isolation calls, of nestlings of *P.p. ornatus*, *P.p. tongensis*, *P.c. cepapi* and *F.c. congicus*: a&b. *congicus* one-week-old; c-f *cepapi*, sharp barks; g. *tongensis*, sharp barks; h. *tongensis*, frequency-modulated squeaks; i. *ornatus*, barks-squeaks; j. *ornatus*, sharp barks.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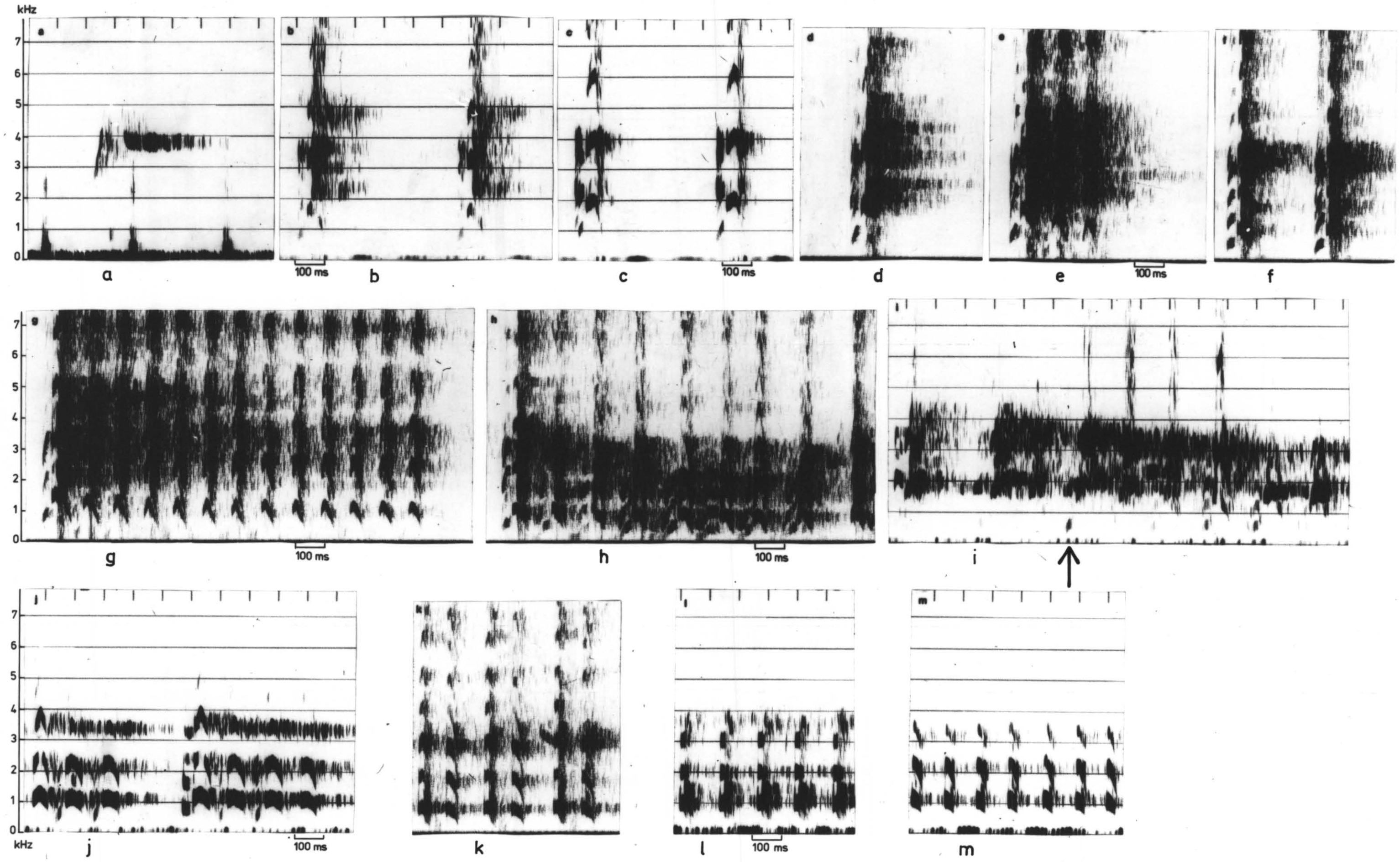
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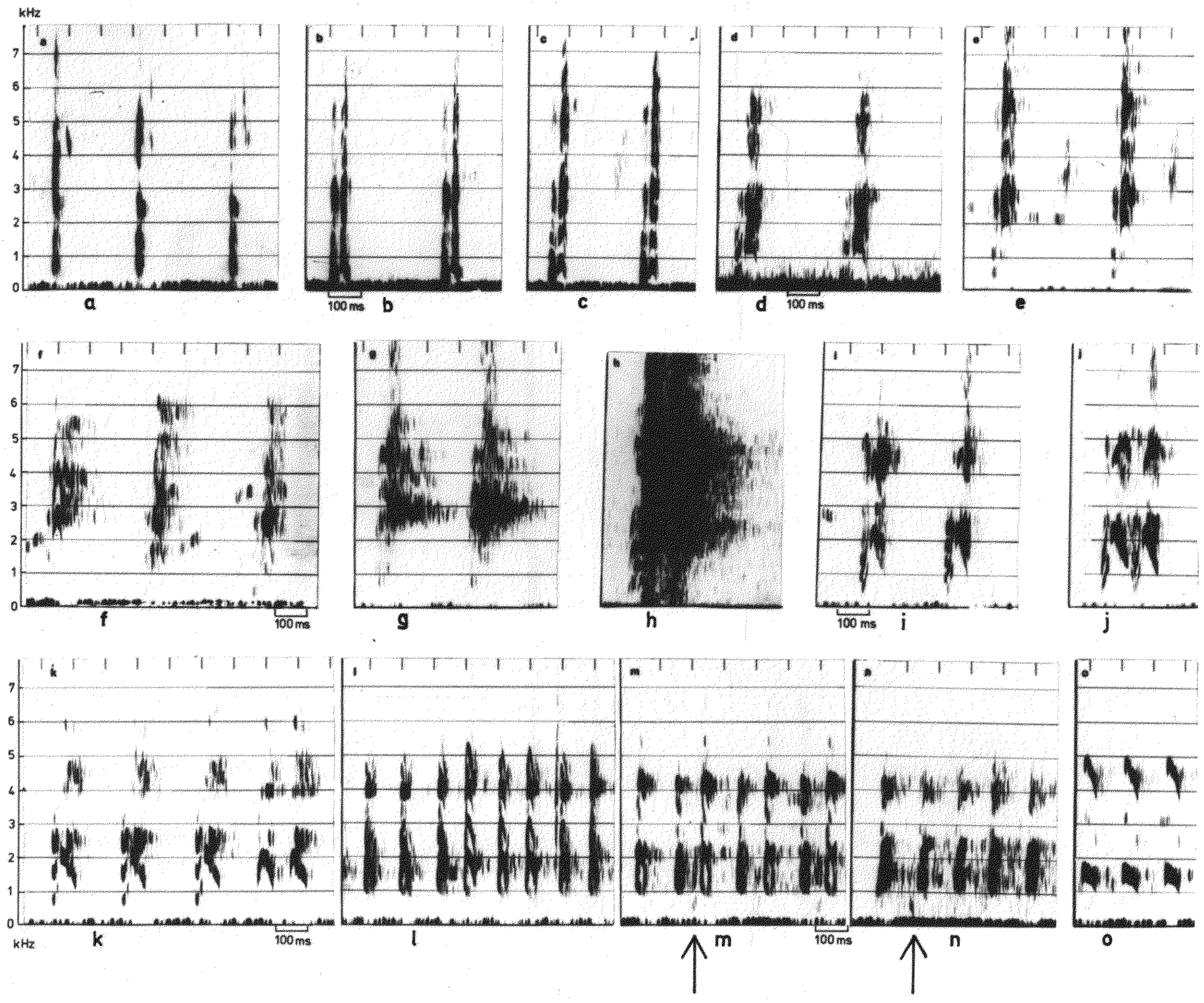
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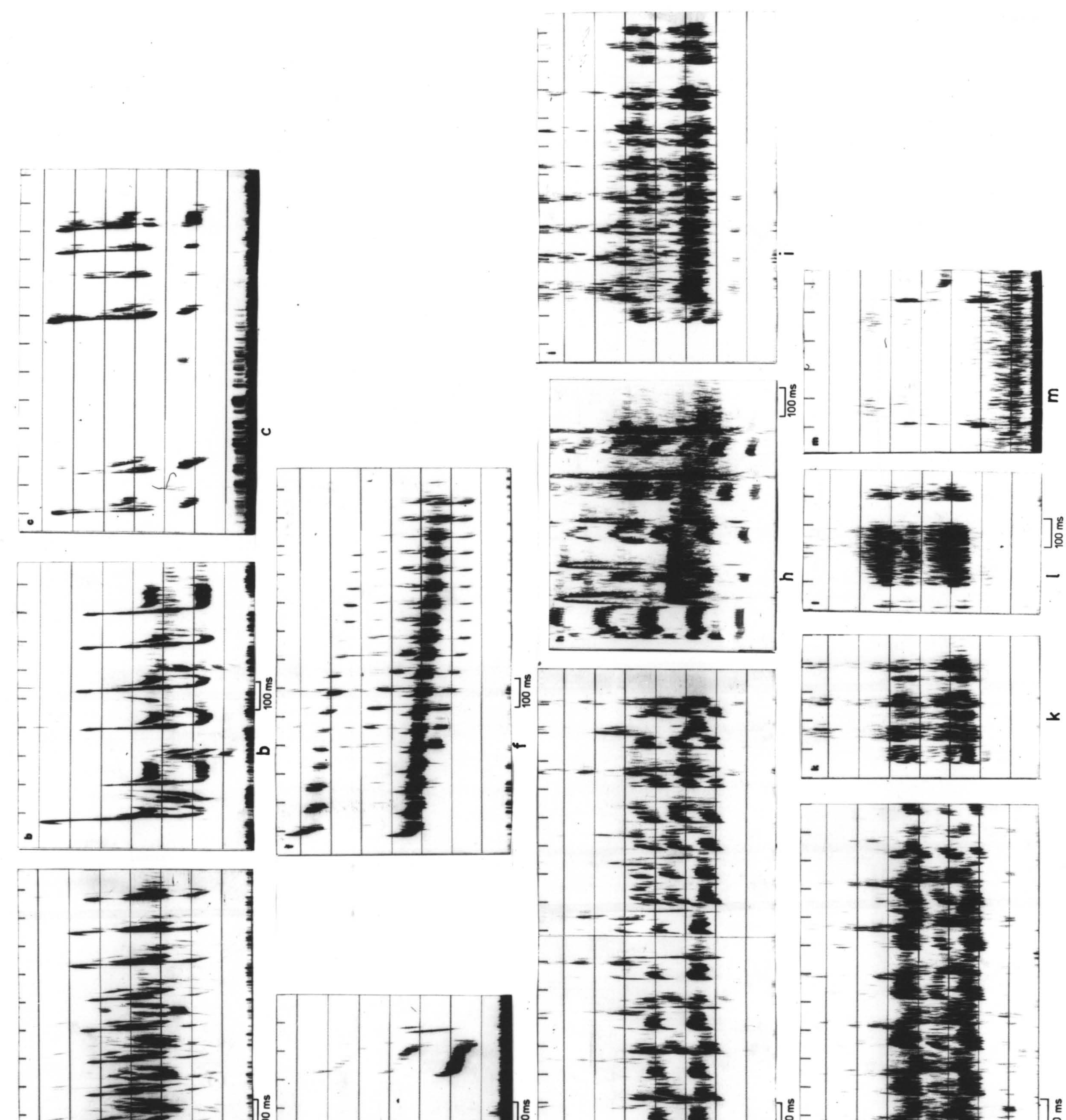
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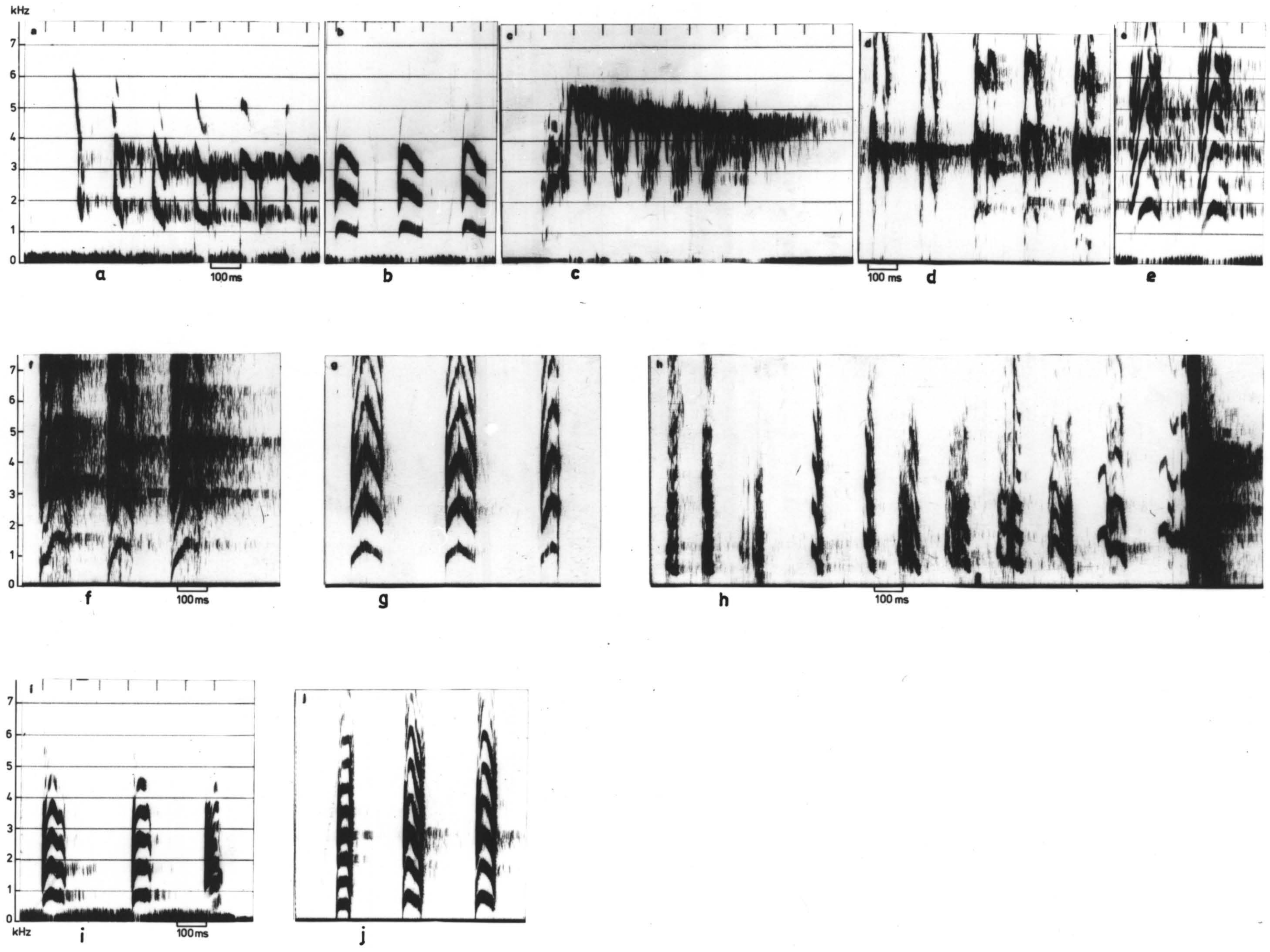
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attracts tongensis in the vicinity.

Reaction of the two forest squirrels, ornatus and tongensis to playbacks of clicks and trills:
The number of playbacks of the different calls is insufficient to predict reaction from the squirrels. Squirrel reaction was influenced by sex, age and distance from the playbacks, which further complicates any conclusions with regard to reaction. The small size of the squirrels in the dense vegetation also hindered observation of subtle reactions such as momentary attention, or avoidance. However, some of the playbacks did attract squirrels, some caused flight or immobility, whilst yet others evoked answers, usually within 5 min of the playbacks.

Ornatus: Reaction to playbacks of clicks and rattles, was usually similar clicking from around 10 m (i.e. mobbing towards me), and "testing" clicks from 20 to 150 m with a duration of the latter calls from 1 min to 90 min (Table 78). It seemed as if adult females vocalised for longer periods. There were three instances where calls were not included in the reaction: the first instance around midday (when threshold for calling was higher than in the early morning); secondly, an adult male merely passed the area rapidly, 20 m from me, and thirdly, two individuals (male and female) which were mating. During mating, squirrels are usually oblivious of any surrounding disturbance (Viljoen 1977a). Reactions to 7 playbacks of trills were recorded as follows: at close quarters, avoidance and no calling in three instances; at a distance of 40 to 100 m, replies were given as clicks in three instances and as a prolonged trill with calling in all directions, in one instance.

A few examples of reactions gives a better appreciation of the context of calling:

TABLE 78

REACTION TO PLAYBACKS OF CLICKS OF *P.P.ORNATUS* (REACTION WITHIN 30 MIN)

PLAYBACK NO.	REACTION BY	DISTANCE (m)	DURATION (min)
Clicks 1	Adult	10	2
2	2	10	3
3	1	20	5
4	1	30	5
5	1	20	3
6	1	30	90
7	1	50	1
	plus 1	150	5
8	Adult	40	30
	plus 1	60	5
9	1	40	1
10	Adult	160	20
11	1	40	1
12	1	40	3

1 18/6/76 two individuals are mobbing me, I record them and replay the recording, whereupon they "furiously" increase their rate and intensity of clicking.

2 7/9/77 Replay a tape of clicks 350 m from where it was recorded 30 min previously; clicks commence in 'reply' 20 m off.

3 10/12/77 At 08h20 an adult male ascends tree to feeding perch where he eats a seed of Drypetes gerrardii, tailflicks 10 times, as he lands on the perch. He descends again and I replay tape of clicks, double clicks and trill. He carries on feeding, but after a while jumps onto the perch again, 'listens', starts to feed, makes intention movements to descend, but decides to the contrary eventually, and moves off to the east with tail flicking. Ten minutes later, clicking for two minutes from that direction. Then I replay again, but no further reaction.

4 10/12/77 Adult male and female with juvenile at 09h00 move off and when they are 20 m off, I replay clicks, no reaction.

5 1/2/78 Play tape of June 1976 (clicks, rattles by adult female) for 10 min at 07h20 (amplified to 60 dB at 7 m). After 5 min an adult male passes quickly 20 m to the east. At 07h43 clicking for one minute 50 m to the north. Play another 5 min during which this individual again calls shortly. At 08h00 replay for 5 min and when I stop, a squirrel is calling 150 m to the north which lasts for 5 min. At 08h15 replay and at 08h20 one clicks and rattles 40 m to the north. An adult female moves into sight, clicks for 30 min (selfgrooming and scratching inbetween). Then another squirrel 'answers' her, 60 m off.

Tongensis: Fewer playbacks were made, but reactions were similar. A few examples are again listed:

1 25/8/76 Replay clicks - an adult female storms up with tail flicking

2 3/11/76 An adult female trills, I record her and 15 min later, another adult female trills 50 m from the first. I replay no 1 whereupon no 2 approaches, sees me, then commences harsh mobbing clicks.

3 2/4/77 Replay clicks to an adult male, whilst he is still clicking, he approaches rapidly and at the same time, another squirrel clicks above me. Replay these clicks one hour later, which is "answered" within 5 min and again 5 min later.

4 13/11/77 At 07h35 replay clicks just after subadult male crossed overhead. Although he should still be within hearing distance, he gives no reaction. At 08h10 an adult female (out of her territory) passes overhead, I replay clicks, and she visibly accellerates towards her own area. No vocal reaction from her, but 10 min later soft clicks 15 m off from two directions opposite to the one in which the female had disappeared.

5 8/2/78 Playback with amplifier, of clicks and trill at 07h15 for 10 min, no visible or audible reaction; at 08h10 replay again and at 08h40 trill comes from 60 m away, for 10 min.

From these reactions, it becomes clear that clicks are not merely used in mobbing context, but are replied to and also attract other squirrels to investigate. Sometimes, clicks cause movement away from the sound source, when an individual is in strange territory. They are used in the sense of 'I am here' or 'Where are you', or testing for presence. Trills seem to cause squirrels to approach if it is replayed in their area, but if replayed at some distance they reply.

DISCUSSION

The communicatory signals used by the South African tree squirrel species are summarised in Table 80. Aspects of the communicatory systems that are adaptive to the niche that each of these species occupies are the following:

(i) The tail of the forest species is fluffed and more obvious than in the savanna species where crypticity is important and where the tail hair is consequently held flat. Conversely, in the forests it is necessary to be more obvious to maintain some degree of intraspecific visual contact. As an extension of this

TABLE 79

BEHAVIOURAL CATEGORIES OF CALLS IN TREE SQUIRREL SPECIES

SPECIES	CONTEXT :		
	CONTACT-SEEKING	ALERTNESS	DEFENSIVE
Sciurus carolinensis (Horwich, 1972)	Muk-muk; buzzing	Kuks to quaas	Growl
S.aberti (Farentinos, 1974)	Juvenile sounds Mewing courtship notes	Chucks Barks	Growl
S.niger (Zelley, 1979)(Moore, 1957)	Whine & short grunting notes	Chatter barks Breathy barks	Groan
Tamiasciurus hudsonicus & *T.douglasii* (Smith, 1968 & 1978; Layne, 1954)	Buzz	Chirps Rattles, screech	Growl
Paraxerus cepapi (Viljoen, 1975)	Murmur	Clicks, rattle, whistle	Growl
P.palliatus ornatus & *P.p.tongensis* (present study)	Murmur	Clicks, barks, trills	Growl
S.vulgaris (Eibl-Eibesfeldt, 1951)	Muk-muk		Threat

TABLE 80

SUMMARY OF COMMUNICATORY SIGNALS AND HIERARCHY OF ALERTNESS SIGNALS OF TREE SQUIRRELS, PARAXERUS SPP.

Hierarchy of alertness signals

1 Pilo-erection of tail
2 +Tail flicking
3 +Foot-stomping (occasionally)
4 +Clicks together with ear and body movements
5 Pulses at increased rate and intensity and in *P.palliatus* lower amplitude trill is inserted and caller moves to face different directions
6 Raptor alarm - whistle, savanna and woodland species) allelomimetic
deep bark, forest species)

Additional signals

1 Auditory - gnawing, hindleg-drumming, tooth-grinding
murmur indicates contact-seeking and appeasement
growl, a defensive call
2 Visual - scrotum and chest vibrations, head bobbing, eye-narrowing
3 Olfactory - urination, anal dragging and mouth wiping (flehmen)

visual contact the species of the most dense habitat, *tongensis*, flicks the tail continuously. Although tailflicking is also more frequent in *ornatus*, the other forest species, it is not nearly as frequent as in *tongensis*. This is possibly related to the greater visibility distance in Ngoye forest.

(ii) With regard to vocalisations, the fundamental and dominant frequencies are lowered in the two forest species. This would enable bett penetration of the denser habitat. The call of extreme alarm is th also clearly adaptive to dense habitat in *ornatus* and *tongensis* which give a low-pitched bark in contrast to the savanna species which emit high-pitched whistles which are difficult to locate. Flight behaviour of the two pairs of squirrels deserves mention here, as the forest species with the locatable sound can immediately disappear into dense vegetation, whereas the savanna species have to seek for a hole to be ultimately safe, and these holes are not numerous.

(iii) The calls of the forest species are also more protracted and louder than those of the two savanna species. This is possibly to overcome the high background noise, but also because they are used extensively in a spacing context in the dense habitat. In the open habitat the species can see one another from a great distance, and they also have exclusively recognised group territories which possibly result in lesser calling of shorter duration. The fact that *ornatus* is more vocal than *tongensis*, is probably related to the density of habitat and to body size. *Tongensis* should have a larger body size to be able to emit calls at a greater amplitude to penetrate the denser vegetation. Yet, they are almost half the size of *ornatus* and range through a smaller volume of vegetation. It is therefore, conceivable that they resort more to visual and possibly olfactory communication, as the energy necessitated for frequent calling would in all probability be wasteful.

(iv) The contact murmur is given more often in the forest species by both sexes, whereas in the savanna cepapi, it is given by the male only in the breeding season, and very rarely by the female, only when she is rearing a litter to maintain contact with them. In the dense forest habitat where the visibility is low, this murmur serves the purpose of maintaining contact between group mates, whereas in the savanna, contact can once again be maintained visually.

A further aspect of the contact murmur is evident in mating context. Males of all three of the Paraxerus spp. murmur frequently in and prior to the breeding season. Therefore, it seems as if this call is given by the females of the forest species to maintain the group contact, throughout the year, whereas the males which roam extensively and are not as tightly knitted into the groups, murmur only in a breeding context.

(v) A striking difference between the forest species and cepapi, lies in communication of oestrus, vocally by the female cepapi which thus attracts males from adjoining territories and compels them to join in the mating chase even though they would be trespassing on foreign terrain, under normal circumstances, in this territorial species (Viljoen, 1977d). In contrast, the communication of oestrus in the forest species is olfactorily, and thus ties in with the continuous vegetation, overlapping ranges and greater degree of movement, especially of the males, which then detect an oestrous female by wandering greater distances over areas which are not territorially restrictive.

The cepapi and congicus whistles which are allelomimetic, are a clear 'warning' to conspecifics and from the species' social structure are especially effective to the kin, thus constituting nepotism. The low-pitched bark of the forest squirrels similarly fits into this warning, allelomimetic category. Sherman (1977) discussing the evolution of alarm calls in Belding's ground squirrels, found that nepotism is the most likel function of this ground squirrel's alarm call, this result implicates kin selection in a behaviour that, because it may involve risk to the alarm caller's phenotype, appears to be altruistic. He concludes that warning of kin might be a common function of sciurid alarm calls. Owings and Virginia (1978) working on California ground squirrels similarly described allelomimetic whistles to raptors which were less than 15 m high. They state that this calling suggests some adaptive advantage of keeping conspecifics informed about the location and behaviour of predators and could add to the inclusive fitness for the caller.

Emmons (1978) found little altruism involved in the alarm calling behaviour of the tropical African squirrels. She states that they do not call when the danger is great and only make themselves evident when no immediate risk is apparent. The subtropical *P.palliatus* and *F.congicus* do call in extreme danger, but do not make themselves evident. Although Searing (1977) reports to the contrary for *T.hudsonicus*, Smith (1978) found for that species that on hearing a chirp, increased alertness resulted, answering chirps and occasional escapes occurred, the function being to warn conspecifics and to annoy predators. This is also true for the allelomimetic *Paraxerus* and *F.congicus* calls, but in this case the conspecifics are very probably kin.

The intergeneric variation between the calls of *cepapi* and *congicus* (which occur in the same type of habitat and are sympatric in certain areas), is probably related to body size, with *congicus*, the smaller by 100 g, having higher-pitched calls. Morton (1977) also states that there is a direct relationship between low frequency sounds and the size of the animal, and Brand (1976) in *Eutamias* spp. found that there is a consistent interspecific variation in structure and temporal arrangement of chirps and that most of this variation correlates with body size. The structure of *cepapi* calls is more closely related to that of the other members of the genus although pitch, temporal patterning and frequency reach differ. Body size could also explain differences between *cepapi* and *ornatus*. However, *cepapi* and *tongensis* are of similar body size and the distinguishing factor between their calls, is probably habitat, with the open habitat animal displaying higher frequencies and the forest animal lower frequencies which would better penetrate the dense and humid vegetation.

Marler (1955) mentions that the features of a call which make it difficult to localise, are pure tonal structure, with few or no harmonics, gradual onset and ending, single repetition at long intervals and high frequencies. This was not so for the *ornatus* and *tongensis* trills. The *cepapi* whistle also consists of very rapidly emitted high frequency pulses with harmonic structure, sharp onset and ending and is difficult to locate. However, the latter whistle (unrecorded) must be similar in structure to the call of the woodland kingfisher (Figure 23f) which *cepapi* sometimes confuses with the whistle. Therefore the pulses of the whistle are probably emitted with such extreme rapidity that they form a "pure tonal structure" with "gradual onset and ending".

In forests, aspects of timing, location and physical structure of a vocalisation can all affect the distance over which a sound is audible, so that:

1. sounds with wavelengths shorter than objects in the sound path will be reflected
2. lower frequency sounds are absorbed less rapidly by humid air than higher ones
3. a frequency window exists near 2 kHz. (Waser and Waser, 1977).

The temperate tree squirrels are all forest-dwellers and although the nine tropical squirrels described by Emmons (1978) occur in different vegetation layers, they are also all incorporated in a forest habitat. However, the present study also describes two species of squirrels which inhabit open savanna. But generally tree squirrel calls have to penetrate vegetation and carry over some distance (usually at least for 100 m - i.e. for the open habitat *congicus*. The slow movement of squirrels compared to birds also makes locatable sounds important (Smith, 1978).

The alarm calls described for sciurids in the literature (Table 79) all have a wide frequency range with harmonic structure and are emitted in short, staccato units which result in sharp shifts in frequency and amplitude. These sounds are well-suited to carry information about position - more so than those of passerine birds which have a dominant frequency above 5 kHz (Smith, 1978). The rattle call of T.hudsonicus is described by Smith in Figure 3 as such a locatable sound. This call bears a close resemblance to the trill of ornatus (Figure 21m). However, I found these trills difficult to locate cf. clicks. Emmons (1978) found similar trills of F.pyrrhopus and E.ebii (her Figures 6c and 7a) difficult to locate and she suggests that the rapidity of the pulse utterance makes them hard to locate. However, the pulses of the above-mentioned T.hudsonicus rattle are emitted at the same or faster rate than those of the ornatus trill, and it is possible that the trill functions as an energy-saving device. Possibly also there is some variation in the sound propagation in the subtropical Ngoye and tropical forests on the one hand, and T.hudsonicus lodgepole pine forest on the other hand. The KwaZulu forests with many layers of vegetation should reflect more sound back than the lodgepole pine forests.

Smith equates the function of these rattle calls to spacing or defence of an area which purpose it also serves for ornatus, and it follows that these calls should be locatable. In T.hudsonicus the call only lasts from 1 to 5 min, whereas in tongensis and ornatus it can be sustained for 40 min and is rarely shorter than 10 min. The ornatus trill is interspersed with 'revvs' (Figure 21g) and clicks (Figure 21d to f) which have a frequency reach similar to the rattle of T.hudsonicus and which are easier to locate. This wide frequency span of the 'revvs' and extreme length of the call, could be the characteristics which make this call locatable. The length of the call also enables it to be heard above the high background noise present in the KwaZulu forests.

The low dominant frequency of the ornatus and tongensis trill calls is no doubt also an adaptation for maximum propagation through the cluttered environment. Bird species in closed habitats also have lower frequency songs than those of more open areas (Chappuis, 1971). Emmons (1978) found that the most notable difference between American and African species of tree squirrels is that the latter have a lower dominant frequency (e.g. 1,9 and 1,3 kHz for A.poensis and F.pyrrhopus - Emmons, 1978, but 4 kHz for S.carolinensis - Horwich, 1972).

Emmons (1978) grouped sciurid calls into six behavioural categories (C-contact, I-isolation, S-distress, D-defensive, A and Aℓ-alarm; and nestling ticking). The behavioural categories that she describes are indeed, widespread in the taxon, if not universal. Her table 13 illustrates a remarkable conservatism in both structure of the sound and in the contexts in which they are found. This conservatism results from the similarity of selection pressures and can clearly be seen in growls which are alike in many squirrel species (S.vulgaris - Eibl-Eibesfeldt, 1951; S.carolinensis - Horwich, 1972; S.niger - Zelley, 1971; S.aberti - Farentinos, 1974; Tamiasciurus hudsonicus and T.douglasii - Smith, 1968 and 1978). Growls are defensive calls and communicate inter=specifically. Conservatism of structure is also evident in the nestling isolation calls (S.vulgaris - Eibl-Eibesfeldt, 1951 and Shorten, 1954; S.carolinensis - Shorten, 1954; Barkalow and Shorten, 1973; Horwich, 1972; S.niger - Horwich 1972; Moore, 1957; S.aberti - Farentinos, 1974; T.hudsonicus - Layne, 1954),which are high intensity alarm calls and necessitate immediate reaction. The squirrels in the present study promptly reacted to nestling distress calls of any of the other species. Nearly all infant vocalisations are high frequency and pure tone-like sounds that would attract the adult. In nestlings old enough to see when the parent approaches with food, the calls rise in pitch and rate of utterance (an increasingly appeasing signal according to Morton, 1977).

Morton states that natural selection has resulted in structural conver=gence of many animal sounds used in a 'hostile and friendly' context. Harsh low frequency sounds are used for hostile reaction, and higher frequency, more pure tone-like sounds,when frightened, appeasing or approaching in a friendly manner. Intraspecifically, this moti=

vational-structural rule is often valid when short distance communication is involved. But long-distance signalling sounds are often moulded rather by the environment favouring selection pressures for certain physical properties that increase propagation. This is evident from the rattle and trill calls of the *Paraxerus* spp. and *F.congicus*. The calls of the four South African squirrel species fit the classification of Emmons (1978) to an extent. Her C-calls are the murmurs of the present study - she calls them contact-seeking calls and divides them into three types (*Protoxerus/Epixerus*, *Heliosciurus/Aethosciurus* and *Funisciurus*). However, the situation promises to be more complex as the double structure of the pulse on which she separates the *Aethosciurus* call is not necessarily a species characteristic as seen from the following example: the *Protoxerus* C-call (Figure 2a) resembles the murmur of a *cepapi* male (Figure 20b), and the *Aethosciurus* C-call (Figure 2b) resembles that of a *cepapi* female (Figure 20d). Therefore, care should be taken in summarily comparing species without consideration of sex and age differences within one species. The close-contact call, or murmur, is also present in *S.aberti* (Farentinos, 1974) described during mating, and regarded as a re-occurrence of a juvenile sound that may function to appease the oestrous female (this is well-known in birds). It has also been described for *S.vulgaris* (Eibl-Eibesfeldt, 1951), *S.carolinensis* (Horwich, 1972) and *T.hudsonicus* and *T.douglasii* (Smith, 1978).

The structual groupings of Emmons are complex in certain respects and tend to ignore the graded continuum of the calls, e.g. she distinguishes between snarls and growls but they seem merely to be on a graded series. Thus, it is possible that what she terms snarls are what are in the present study termed growls (described by her for hole-nesters), Her division of A (low intensity alarm) and Aℓ (high intensity alarm) calls also seems an artificial one as these are graded along a continuum. She was not able to determine the precise significance of the graded calls (long and short barks, chucks and warbles) but states that chucks are used in mobbing, and warbles often preceded 'high intensity calling'. She speculates that spacing might be included in the function of the latter Aℓ calls. This is possibly close to the truth, as in the Paraxerus spp. and F.c.congicus these calls which function in alarm, also function as spacing mechanism. This spacing function is also true for T.hudsonicus (Smith, 1978), S.aberti (Farentinos, 1974) and for eastern chipmunks, Eutamias sp. (Yahner, 1978)

In the last chapter, aspects of the communicatory systems as well as the other investigated facets, that are adaptive to the respective niche of the four tree squirrel species, will be discussed and summarised.

CHAPTER 10

REPRODUCTION AND EARLY POST-NATAL DEVELOPMENT

INTRODUCTION

Reproduction of a species forms an integral part of its biology. When planning this part of the study, great differences were not predicted between the four southern African tree squirrel species. However, difference from temperate squirrel species were very probable as already indicated from a previous study on P.cepapi (Viljoen, 1975) which revealed that it produces much smaller litters following a longer gestation period than temperate tree squireel species. Emmons (1975) reported similar findings for tropical squirrel species. This section of the study extends the investigation of the subtropical squirrel species to ornatus, tongensis and congicus.

MATERIALS AND METHODS

FIELD DATA

Lactating and pregnant females, presence of juvenile squirrels, and scrotal lengths of adult males (length of scrotal sac, accurate only to within 10 mm) were recorded from trapped squirrels in the field. In captivity births as well as the male murmuring vocalisation which varies seasonally with the breeding period, were recorded.

Collected specimens: Seven specimens of ornatus (3♂♂ and 4♀♀) and ten specimens of tongensis (5♂♂ and 5♀♀) were collected in the field.

(a) Females: Uterine horn length and ovarian mass were determined after fixing in Formal-acetic-acid. Ovaria were routinely paraffin-embedded, stained with Mallory and sectioned at 5 µm. In each ovary the number of large follicles (type 6, 7 and 8 of Peters, 1969) and corpora lutea were counted, the largest vesicula: follicle and corpora lutea were measured according to Mossman and Duke (1973) in the place of section. The measurement is an average of the greatest diameter and the least taken at right angles to the greatest, and extended from base to base of the follicular epithelium or luteal capsule, therefore excluding the thecal layer of the follicle and fibrous capsule of the corpus luteum.

(b) Males: Testes were fixed in Bouin's fluid, mass-measured, paraffin-embedded, stained with Delafield's haematoxylin and eosin and sectioned at 8 μm. The seminiferous tubule diameters of 10 round tubules in each testis were measured between the ex= ternal margins, with an ocular micrometer.

Problems were encountered for both Ngoye forest and Maputoland to obtain permission for collecting squirrels and the numbers here obtained were the absolute maximum permitted. No shooting was allowed in Ngoye forest and it was extremely time-consuming to trap when pathways were unknown. For obvious reasons squirrels could not be trapped for collecting in the study area where pathways were known.

Breeding in captivity and early post-natal development: Standard body measurements were taken and developmental stages recorded during early post-natal development of five litters of congicus, one litter of cepapi (information published in Viljoen, 1977a was added for comparative purposes); three litters of tongensis and five litters of ornatus.

Squirrels were kept in outdoor cages varying in size from 7,5 m^3 to 32 m^3. They were fed daily on chopped fresh fruit, fruit juice with multivitamin syrup, Epol mice cubes (*1) and a mixture of peanutbutter, wheatgerm, ProNutro (*2), honey, oats and sunflower oil and seeds, as

*1 Epol - Manufactured by Epol (Pty) Ltd., 37 Quinn St., Newtown, Johannesburg, 2001. Mice cube $^1/2$" size, Code 470074. Contains: Protein 18%; Fat 2,5%; Fibre 6,0%; Ca 1,4%; P 0,7%.

*2 ProNutro - Manufactured by Hind Bros and Co., Ltd., 166 Hendrik Ver= woerd Drive, Randburg, 2194. Contains: Maize, processed soya beans, non-fat milk solids, peanuts, sugar, wheat germ, food yeast, lysine, methionine, minerals, reduced micronised iron, vitamins. Percentage food values: Protein 22,0%; Fat 5,9%; Carbohydrates 59,1%; Minerals 5,4%; Fibre 2,3%; Linoleic Acid 3,6%; Energy/100 g : 1 630 kJ.

well as acorns. Each cage with two to five nestboxes, contained an adult pair except in two of the cages with ornatus which each contained three adults, one with two males and a female, the other with two females and a male.

GROWTH CURVES

Growth curves for mass, total length, tail length, ear, and hindfoot (c.u.), measurements were calculated. Modified exponential ($y_t = a\,(1 - br^t)$); logistic ($y_t = \dfrac{a}{1 + br^t}$) and Gompertz ($y_t = a\,(e^{-b})^{r^t}$) curves were computer-calculated for each of the 20 sets of measurements and the best fit was selected from the largest F-value. (a = final or adult measurement;

b = potential increment in measurement from $t = 0$;

r = rate of growth over the total period of growth;

t = time in days)

RESULTS

Field data and collected specimens:

(a) Females: Records of lactating and pregnant females, and births, are summarised in Table 81. In Ngoye forest, births of ornatus occurred from early August to March with the latest lactation recorded in May of 1978. Not all the adult females bred during the breeding season. Tongensis showed a similar incidence of births i.e. a quiescent period from April to August. Examples of breeding condition of two adult females throughout the year, is as follows:

Tongensis (Toe 1) Oct. 76 - lactating, Jan 77 - pregnant, March 77-pregnant, May 77 - no milk, not pregnant, Aug 77 - lactating. (Other adult females in the study area did not reproduce quite as frequently as this female which was dominant at the feeding station and possibly in the "best" part of the study area).

Ornatus (Toe 9000): Jan 77 - lactating, June - no milk, non-pregnant, Dec 77 - pregnant, May 78 - no milk, non-pregnant. (This was the pattern for most of the Ngoye females with a single litter produced during the breeding season).

TABLE 81

BREEDING RECORDS, (PRESENCE OF PREGNANT AND LACTATING ♀♀ , AND 3-TO-6-WEEK OLD JUVENILES) OF P.P.ORNATUS AND P.P.TONGENSIS IN THE FIELD

P.P.ORNATUS:			P.P.TONGENSIS		
PREGNANT	LACTATING	JUVENILES	PREGNANT	LACTATING	JUVENILES
Dec 77 - 2	Apr 76 - 1	Nov 76 - 1	Nov 76 - 2	Oct 76 - 4	Oct 76 - 1
	Jan 77 - 2	June 77 - 1	Jan 77 - 1	Aug 77 - 1	Jan 77 - 2
	Apr 77 - 1	Aug 77 - 1	March 77 - 1	Nov 77 - 1	March 77 - 1
	Aug 77 - 1	May 78 - 4	Aug 77 - 3		Aug 77 - 3
	Dec 77 - 1		Oct 77 - 2		Nov 77 - 5
	May 78 - 1				Feb 78 - 1
					May 78 - 2

Dissected females: No seasonal pattern can of course be detected in the small sample available (Table 82). However, the <u>tongensis</u> female collected in June showed no recent implantation scars and had large vesicular follicles possibly in preparation for the breeding season, whereas the one from October had embryos and the one from November had recent implantation scars. Ovaries from all three of the females contained corpora lutea: in the June female they were similar in size to those of the pregnant female, and those of the other female were much larger. In the two late-spring squirrels smaller accessory corpora lutea were also present.

The two <u>ornatus</u> females of April had no vesicular follicles although they still showed small degenerating corpora lutea, whereas the two from August and September had many vesicular follicles. However, one of these latter females had no corpus luteum even though she did have implantation scars. Possibly she had bred the previous season but not yet in the 1977 summer.

(b) Males: Scrotal measurements of adults do not indicate any seasonal trend (Table 83). However, captive <u>tongensis</u> males did show diminished scrotal size from December to March (not measured but very obvious). Variation does also occur in individual males from the field (Table 84).

Small sample size of dissected males once again precludes deduction of seasonality from testes tubule diameter or testes mass, or even differences between the two subspecies (Table 85). The only difference noticeable is that between subadult and adult squirrels.

An additional indication of male season can be inferred from the male murmuring vocalisation which males give with rising frequency in the breeding season (Table 71, Chapter 8).

TABLE 82

ANALYSIS OF FEMALE P.PALLIATUS REPRODUCTIVE TRACTS

			EYE LENS MASS (mg) ($\bar{x}$)	($\bar{x}$) HORN LENGTHS & WIDTH (mm)	OVARY MASS(mg) ($\bar{x}$)	RECENT I.S., EMBRIOS & FAT CONDITION OF UTERINE HORNS	NO.VESICULAR FOLLICLES, R/L*	DIAMETER OF LARGEST VESICULAR FOLLICLE (mm) R/L	DIAMETER OF CORPORA LUTEA (mm) R/L
P.p.tongensis									
Ad	T2	4.11.75	12,7	28,4 x 4,9	12,3	M^1			
	T4/6	4.6.77	16,1	31,7 x 4,2	8,9	M	20/18	,6150/,5330	,750/,9100
	TS4	20.10.77	20,5	33,0 x 9,7	7,6	2 embrios, one each horn, M	12/16	,4662/4671	,726/- ,448/,745
	TS6	2.11.76	19,0	28,7 x 4,7	10,5	2 embrios, one each horn, N^2	10/3	,5157/,5751	,946/,959 ,505/
Sad	T4	26.4.76	14,4	18,4 x 3,6	11,2	N to M	19/14	,4199/,4590	-
P.p.ornatus									
Ad	N1	22.4.76	21,8	22,9 x 3,2	7,0	N	0/0	-	,2916/-
	N4	23.4.76	21,4	20,2 x 4,0	9,4	2IS, one each horn, N	0/0	-	,1782/-
	N5	4.8.77	21,4	26,1 x 3,7	13,7	3IS, one left, two right horn, M	26/11	,4212/,4590	-
	N7	19.9.77	25,4	29,1 x 4,3	42,0	2IS, one each horn, N	5/7	,4226/,3965	,785/,862 1,025/,809

*R = right ovary
L = left ovary

M^1 = medium amount of fat
N^2 = no fat

TABLE 83

MEAN SCROTAL MEASUREMENTS (mm) AND MASS (g) OF ADULT MALE SQUIRRELS P.P.ORNATUS AND P.P.TONGENSIS FROM THE FIELD

	P.P.ORNATUS				P.P.TONGENSIS			
	SAMPLE SIZE	SCROTUM	Pp-ps *	MASS	SAMPLE SIZE	SCROTUM	Pp-ps	MASS
June 1976	4	41,5	42,1	359,8	-	-	-	-
November 1976	-	-	-	-	6	38,9	46,7	206,7
January 1977	3	43,9	46,6	359,6	3	36,7	37,8	202,3
March 1977	-	-	-	-	3	41,2	49,1	201,8
June 1977	9	47,7	54,8	354,8	4	42,1	46,8	203,8
August 1977	12	45,9	52,1	358,2	1	37,7	44,1	177,5
December 1977	20	45,4	53,4	340,5	3	42,3	47,5	207,6
May 1978	17	48,0	53,9	379,0	3	35,2	41,4	193,8

*Pp-ps = Measurement from posterior tip of the scrotum to the posterior base of the penis

TABLE 84

SCROTAL MEASUREMENTS OF INDIVIDUAL ADULT P.P.TONGENSIS IN THE FIELD

	OCT 76	JAN 77	MARCH	MAY	NOV
Male 1	42,20	46,40	43,25	42,95	44,75
2	33,45	20,85	38,60	40,20	42,20
3	41,50	42,90	-	41,95	-
4	42,45	-	41,70	43,40	-
Mean & S.D.	38,86 ±3,72	36,72 ±13,85	41,18 ±2,37	42,13 ±1,42	42,3 ±2,40

TABLE 85

ANALYSIS OF MALE P.PALLIATUS BREEDING CONDITION

			EYE LENS MASS (g)	Pp - ps (mm)	TESTES MASS (g)	TESTES TUBULE DIAMETER (µm)
P.p.tongensis						
Ad	T3	26.4.76	0,0178	53,1	2,0988	233,8
	TS3(T9)	20.10.77	0,0180	46,6	1,9628	205,1
	TS7	5.11.76	0,0174	47,4	2,5977	204,0
Sad	T1	25.10.75	0,0129	23,8	0,0790	66,6
	T5	26.4.76	0,0104	24,9	0,0600	
P.p.ornatus						
Ad	N6	19.9.77	0,0179	53,5	2,9200	205,7
Sad	N2	22.4.76	0,0147	23,1	0,0800	
	N3	22.4.76	0,0151	27,8	0,0868	63,3

BREEDING IN CAPTIVITY

From 2/12/77 to 2/3/79, all litters were born during the southern warm and rainy season. The earliest birth occurred on 26/8/78 and the latest on 2/3/79, by which time the testes of almost all the adult male had diminished considerably in size and they were probably infertile.

Breeding occurred only when the squirrels had adapted to captivity. The tamest squirrels bred first, and as a corollary the less wild woodland species congicus and cepapi bred before the forest species. No litter losses occurred in the former two species. F.congicus commenced breeding five months after capture producing 5 litters, three by the one pair and two by the other pair, within six months (mean litter size of 2,0 ± 0, n = 8, always ♂♀). P.cepapi could produce six litters in one year, each time conceiving at the post-partum oestru (Viljoen, 1977d). These two species, when disturbed in the wild, immediately flee to a hole in a tree, and in captivity they seek refuge in their nests where they feel secure. This is in contrast to the fores squirrel species whose natural flight reaction carries them into dense vegetation in their natural environment and never into holes in trees. Consequently tongensis and ornatus took longer to settle down in captivity, the former only breeding after 21 months and the latter after 26 months.

Only after thick plastic sheets had been fitted to both sides of certain parts of their cages, could they successfully seek seclusion behind this plastic. Only when the observer sat motionless would they emerge from this refuge. It was also difficult to satisfy the nesting requirements of the forest squirrels. Nests had to have a concealed entrance made by hanging sacking or plastic material over the whole nest, or by placing a small nestbox within a larger one and adding a plastic pipe as an entrance tunnel. Their nests had to be attached very securely as they would not tolerate the slightest movement of nests, in such cases preferring to sleep outside on top of the nest.

P.p.tongensis litters were spaced throughout the year as follows: August - 1, September - 1, October - 2, December - 4, January - 2, February - 1; and *P.p.ornatus* litters: August - 1, October - 2, November - 2, January - 3, February - 1. Mean litter size of *tongensis* in captivity was 1,69 ± 0,48 (n = 13, 9♀♀ : 7♂♂) and of *ornatus* it was 1,60 ± 0,52 (n = 10, 6♀♀: 10♂♂) (Table 86). In the field, observed litter size of nestlings was lower, with a mean of 1,38 ± 0,52 (n = 8) and 1,50 ± 0,55 (n = 6) for *tongensis* and *ornatus* respectively.

Four *tongensis* pups and a single *ornatus* pup died soon after birth as a result of the mother's protective behaviour. She often carries the pups following birth, and if no safe alternative nest is available to deposit them in, she continues carrying them and eventually penetrates the delicate skin on the stomach. After some time, she either drop the pup or starts chewing it. The adult male was one of the main factors indirectly causing death of the pups in *tongensis*: for 24 h after birth the female is almost continuously with her pups in the nest; then she starts to chase the male violently in an attempt to evict him from the vicinity. If the male is left in the cage, she will either kill him, or the pups. A precaution taken after the first litter losses, was to remove the male a day or two before parturition. He could then only be returned when the pups had been weaned and removed, for he would either relentlessly chase the pups (which would then be strange to him), or the adult female would still be very aggressive towards him. In the wild, *tongensis* females move away from the male at parturition or a day later, to one of the many nests in their forested habitat. On the other hand this strategy is not possible in open woodland where nests are at a distinct premium. *Ornatus* shows less intra-specific aggression and except for one occasion where the male had to be removed, the pups were reared within the group, but alternative nests still had to be available to the female to move away with her young.

As a result of this stress situation in the forest squirrels, very few of their pups could be observed and handled immediately after birth.

TABLE 86

LITTER ARRIVAL IN CAPTIVITY FOR THREE TREE SQUIRREL SPECIES

P.P. TONGENSIS		P.P.ORNATUS		F.C.CONGICUS	
LITTER SIZE	DATE	LITTER SIZE	DATE	LITTER SIZE	DATE
2	13.10.77				
2	2.12.77	2	26.8.78	2	1.11.78
2	11.1.78	2	19.11.78	2	18.11.78
1	24.2.78	2	31.10.78	2	1.1.79
1	23.10.78	2	15.1.79	2	17.1.79
2	11.12.78	1	27.1.79	2	2.3.79
		1	19.1.79		
2	Aug 79	1	Oct 79	2	Sept 79
2	Oct 79	2	Dec 79	2	Oct 79
2	Dec 79	1	Feb 80	2	Dec 79

Therefore, one litter of *tongensis* and one *ornatus* pup, were hand-reared with success to obtain data on the early stages of development. In the forest squirrels another factor reducing adaptability to captivity was their lack of nest-building behaviour. They could not be induced to take any nesting material (cotton wool, shredded material, grass or strips of paper) into their nests which had to be lined for them with cardboard, grass and material. Eventually they started to use leaves of live shrubs and trees placed in their cages.

The hand-reared squirrels were fed on Lactogen (*3) diluted 1:7 with water after Mallinson (1975), and administered through a tiny bottle teat. They were fed every two hours for the first 14 days, after which an interval of five hours was allowed at night. After day 16 when the whole body was furred except around the genitalia, the Ngoyé pup maintained heat well. On day 18 it was given 32,5 ml in 24 h, on day 28, 52 ml and on day 40,86 to 100 ml milk. A few drops of liquid paraffin were added to the diet every day to prevent constipation, which nevertheless was a problem. The pups had to be stimulated to defaecate and urinate by massaging around the anus, and penis or vulva with wet cotton wool or a finger. This problem was overcome in the Ngoye pup by allowing it from day 12 to drink additionally from a lactating cat whose kittens were one week old (Figure 25) and stimulating the squirrel whilst it was drinking. This cat-suckling also prevented the squirrel from becoming bloated from wind, taken in with the bottle-feed. Egg as well as an occasional vitamin drop were added to the milk from day 40. Before the cat's milk had been brought into the diet, the pup had to be given glycerine enemas on three occasions - a very smooth glass pipet was inserted into the anus and the contents blown out into the gut. The squirrel pups were kept warm under a reading lamp, and a hot-water bottle was placed underneath the nest-box.

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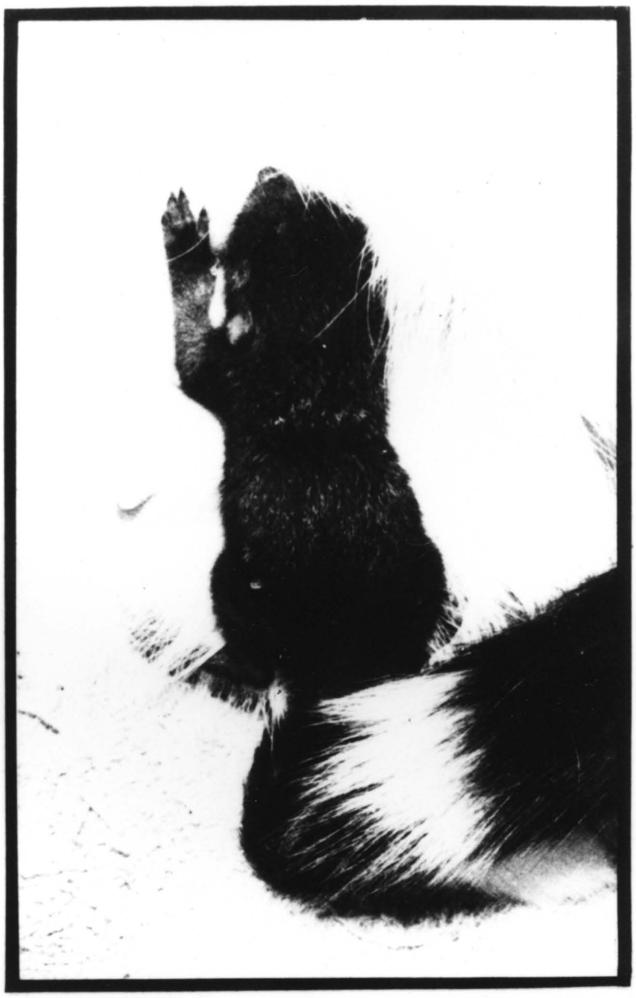
*3 Lactogen - Manufactured by Nestlé's South Africa, Nestlé House, 192 Hendrik Verwoerd Drive, Randburg, 2194. Contains: Fat 24% Carbohydrates 52,4%; Protein 16,1%; Salts (including ash 3,6%) 4,3%; moisture 3,0%; Energy/100 g of powder 2 050 kJ.

Figure 25. Hand-reared *P.p. ornatus* pups: Above - suckling from a lactating cat, 14 days post-partum; Below - drinking from a stiff tube, 52 days post-partum.



LITTER SIZE AND GESTATION PERIOD

Litter size varied from 1,6 in the two subspecies of *palliatus* to 2,0 in *congicus* and *cepapi* (Table 87). Exact dates of mating were not obtained for *congicus* and *tongensis* as they do not attract the observer's attention by oestrous vocalisation as does *cepapi* (Viljoen, 1977d). In *congicus* the intervals between two successive litters were 60 days in three instances: in *tongensis* the intervals were 84 and 89 days and in *ornatus* with a gestation period of 59 days (n = 1), it varied: 61, 66, 68 and 76 days. This interval in *cepapi* has already been established as 61 days and with a post-partum oestrus five days after parturition gives a gestation period of 56,5 days (Viljoen, 1977d). It is probable that gestation length in the other three squirrels is also close to this period as the females were certainly not in oestrus during the first three or four days post-partum The prolonged period recorded for *tongensis* is possibly artificial as the female and male had been separated for 15 days after parturition in the one instance, which would reduce the interval from 84 days to at least 69.

EARLY DEVELOPMENT

Early post-natal development of the four squirrels is summarised in Tables 88 and 89, and Figure 26. Comparative data from one Ethiopean, one Oriental and four Holarctic tree squirrel species are included in Table 88. Table 89 gives the percentage of adult dimensions reached at different ages. The largest squirrel, *ornatus* (average adult mass = 366,6 g n = 98) is the most altricial and is born at only 3,8% of adult mass. The smallest squirrel, *congicus* (average adult mass = 112,3 g n = 20) also develops slowly initially, but is born at eight percent of adult mass and soon catches up with *cepapi* which is the most precocial. Young of both of the latter species leave the nest on the same day post-partum. A comparison between development of *cepapi* and *tongensis*, which do not differ much in mass (223,6 g n = 69; and 206,0 g n = 48; average adult mass respectively), shows that the former woodland squirrel develops at a faster rate initially but that they also leave the nest at the same age. Both these species weigh six percent of adult mass at birth.

TABLE 87

ASPECTS RELATING TO LITTER MASS OF TEN TREE SQUIRREL SPECIES (ARRANGED IN ORDER OF LITTER MASS)

SPECIES AND REGION	MASS OF PUP AT BIRTH(g)	MEAN LITTER SIZE	MEAN TOTAL LITTER MASS (g)	MEAN ADULT MASS (g)	MEAN LITTER MASS AS % OF MEAN ADULT MASS	REFERENCES
Tropical (Ethiopean and Oriental)						
Aethosciurus poensis	9,91	1,3	12,9	100,0	12,88	Emmons, 1975
Funisciurus c.congicus	9,0	2,0	18,0	112,3	16,03	Present study
Funambulus pannanti	6,5	2,91	18,9	112,4	16,83	Purohit *et al*, 1966
P.palliatus tongensis	13,0	1,69	22,23	206,0	10,79	Present study
P.c.cepapi	11,88	2,0	23,76	223,6	10,63	Present study
P.palliatus ornatus	14,0	1,60	23,94	366,6	6,53	Present study
Palearctic and Nearctic						
Tamiasciurus hudsonicus	6,7	4,13	27,7	188,8	14,66	(Layne, 1954 (Kemp&Keith, 1965
Sciurus vulgaris	7,8	4,0	31,2	362,5	8,61	(Shorten, 1954 (Ognev, 1940
S.carolinensis	15,1	2,98	45,0	560,0	8,04	Shorten, 1951
S.niger	15,5	2,88	44,6	770,8	5,79	Allen, 1942

TABLE 88

EARLY POST-NATAL DEVELOPMENT OF ELEVEN TREE SQUIRREL SPECIES (DAY 0 = DAY AFTER BIRTH)

SPECIES AND REGION	DEVELOPMENT (DAYS)											
	EARS OPEN	EYES OPEN	INCISORS ERUPT		MOULT		URINATE & DE=FAECATE ON OWN (HAND-REARED)	FIRST SOLIDS	WEANING	OUT OF NEST AT WILL	GESTA=TION PERIOD	INTERBIRTH INTERVAL (CAPTIVITY)
			LOWER	UPPER	COMMENCES	TERMINATES						
Sub-tropical* (Ethiopean)												
F.c.congicus (present study)	6	16-20	9	16-20	84		26	28	20-50	18	±52	60
P.c.cepapi (Viljoen, 1977 and present study)	0	7- 9	0	6	41	110-120		18-29	35-42	18-22	56,5	61
P.p.tongensis (present study)	4	10	0	6	54-60	120-137	22	28	39-45	18-23	±65	84-89
P.p.ornatus (present study)	10	12-14	12	21	66-90	141-160	39	57	48-57	27-48	59	61-76
Tropical (Ethiopean)												
Aethosciurus poensis (Emmons, 1975)	0	10	0							18		
Tropical (Oriental)												
Funambulus pennanti (Purohit *et al*, 1966)	21	14							21-42		40-42	
Nearctic												
Sciurus carolinensis (Horwitch, 1972)	23-27	28-30	19-21	31-42				43-51		54-58	44	
S.niger (Allen, 1942)		40-44						47	70	47	45	
Tamiasciurus hudsonicus (Layne, 1954)	18	26-29	21	42				38-41		35	40	
Palearctic												
Sciurus vulgaris (Eibl-Eibesfeldt, 1951)		31	23	41				43-45		45	32-40	

*Sub-tropical in present study, but the species also occur in tropical Africa

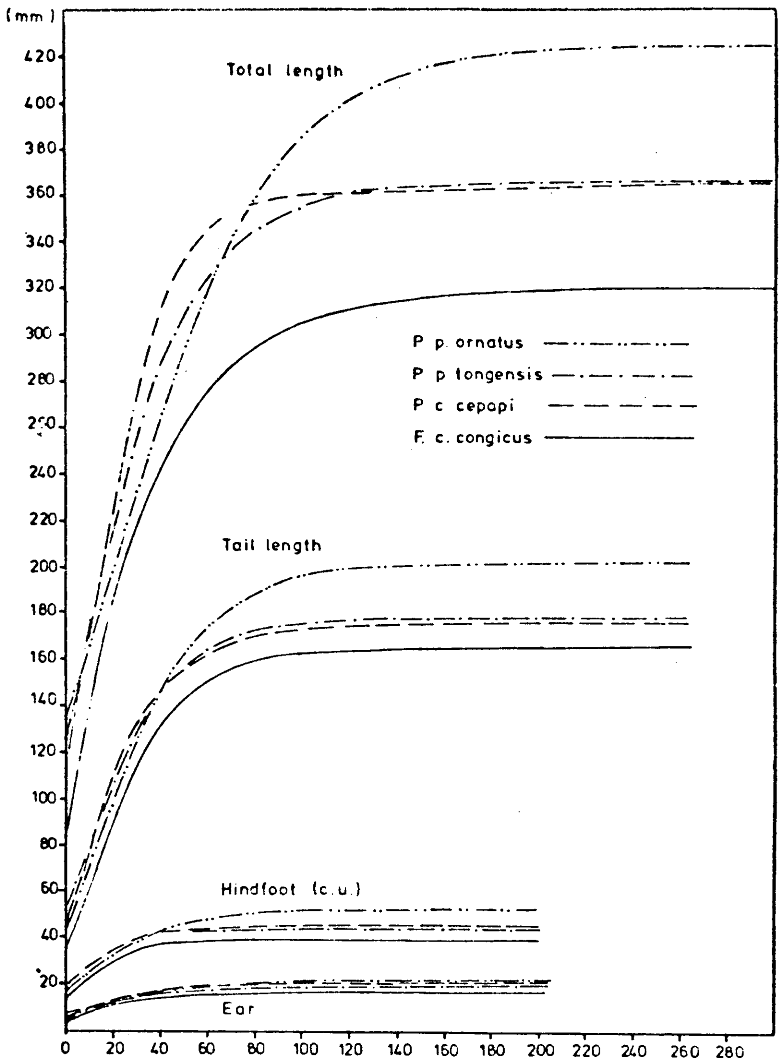
TABLE 89

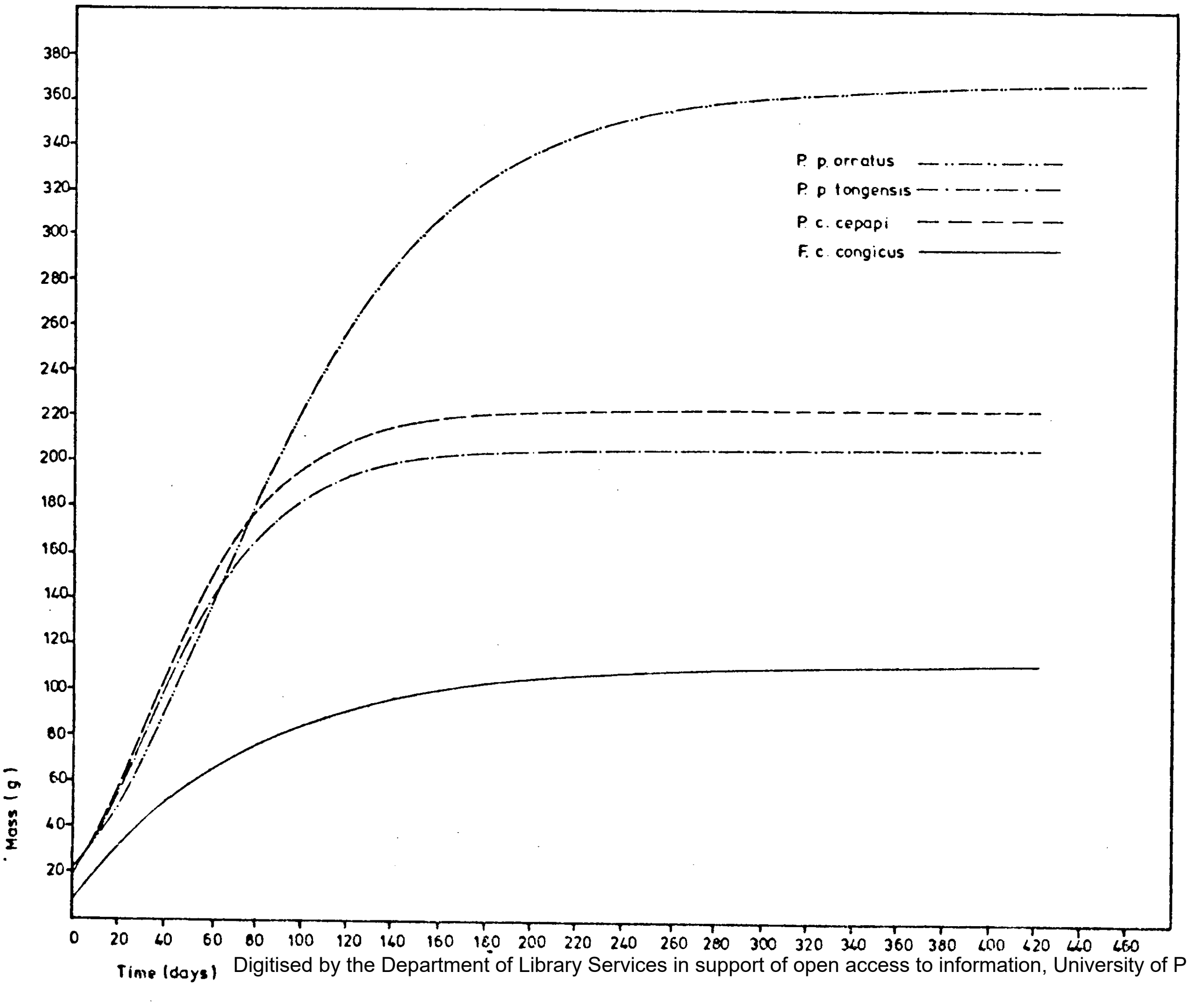
PERCENTAGE OF ADULT DIMENSIONS REACHED AT DIFFERENT AGES IN FOUR SOUTHERN AFRICAN TREE SQUIRREL SPECIES

DIMENSIONS AND SPECIES (LENGTH IN mm, MASS IN g)		DEVELOPMENT (DAYS)				
		0	19	30	50	100
HINDFOOT (c.u.)	F.c.c. *1	32,7	70,6	83,6	94,1	100,0
	P.c.c. *2	38,0	73,0	87,0	94,7	98,7
	P.p.t. *3	43,2	72,7	86,4	95,5	102,4
	P.p.o. *4	36,7	50,2	61,8	77,2	99,0
EAR	F.c.c.	30,2	72,6	84,7	96,8	99,0
	P.c.c.	33,0	64,0	84,0	87,9	105,5
	P.p.t.	30,9	61,7	72,0	87,5	100,0
	P.p.o.	29,1	48,5	58,2	77,6	99,0
TAIL	F.c.c.	25,6	50,0	68,2	82,3	95,1
	P.c.c.	24,0	60,0	79,0	96,3	99,4
	P.p.t.	27,7	53,4	67,9	83,7	100,0
	P.p.o.	24,8	35,7	48,6	66,4	92,7
TOTAL LENGTH	F.c.c.	30,7	54,8	68,3	81,5	92,2
	P.c.c.	33,1	65,6	79,5	92,2	99,9
	P.p.t.	33,0	60,5	71,5	85,2	99,4
	P.p.o.	35,8	58,6	70,8	79,8	91,7
MASS	F.c.c.	8,0	27,9	34,9	55,2	83,9
	P.c.c.	6,0	23,0	42,0	65,5	93,8
	P.p.t.	6,3	28,2	41,8	58,3	92,2
	P.p.o.	3,8	24,6	32,7	42,0	62,7

*1 F.c.c. = Funisciurus congicus congicus
*2 P.c.c. = Paraxerus cepapi cepapi
*3 P.p.t. = P.palliatus tongensis
*4 P.p.o. = P.p.ornatus

Figure 26. Post-natal development of four southern African tree squirrel species: Above - increment in head-body, tail, ear and hindfoot (c.u.) lengths (mm).


(mm)
420
400
380
360
340
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
Total length
Tail length
Hindfoot (c.u.)
Ear
P. p. ornatus
P. p. tongensis
P. c. cepapi
F. c. congicus


Mass (g)
380
360
340
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
340
360
380
400
420
440
460
Time (days)
P. p. ornatus
P. p. tongensis
P. c. cepapi
F. c. congicus

All four species are covered with fine hair on the head, back, dorsal surfaces of the paws and the tail at birth. Hair on the ventrum only develops after a few days, at first only on the anterior part, and later also around the genitalia. In the three squirrels of the genus Paraxerus the scrotum is not furred until the males become sexually mature, but in Funisciurus the scrotum becomes furred between day 19 and 25. Hindfoot and ear measurements were the first to reach adult dimensions, followed by tail, total length and lastly mass (Table 89).

GROWTH CURVES

Tables 90 and 91 give the coefficient of determination, best selected curve, growth rates and their 95% confidence intervals, for each of the 20 sets of measurements. To determine whether the growth rates of the four species differed for each of the five sets of measurements, the best average curve for each set was determined by calculating the mean F-value and using the curve with the highest mean F-value. For mass and hindfoot length, the best curve was the Gompertz, and for the total length, tail and ear measurements, the selected curve was the modified exponential. If the growth rate value of a species for a particular measurement fell within the 95% confidence intervals of the growth rates of the other three species, there was not a significant difference in th growth rates. In no case was any significant difference present (Table 91) but ornatus, the largest species which also takes the longest time to reach adulthood, had the fastest growth rate throughout. With more data, this difference might prove significant. The measurements for ornatus commence at a lower percentage than those of the other species in some instances (e.g. ear length) but have to grow to a greater adult length. Mass measurements averaged the highest growth rates of the five measurements (0,9758) and this dimension also took the longest to reach the end-reading. Growth rate of total length average (0,9728) and was followed by that of tail length (0,9661), ear (0,9645) and hindfoot (0,9436).

TABLE 90

GROWTH CURVES FOR THE 20 SETS OF MEASUREMENTS FOR FOUR TREE SQUIRREL SPECIES

MEASUREMENT	SPECIES	GROWTH CURVE	COEFFICIENT OF DETERMINATION (R^2)	ADULT DIMENSION REACHED (DAY)
Mass (g)	P.p.ornatus	$y_t = 366.6 \left[e^{-2.8408}\right] 0.9825^t$	0.8690	600
	P.p.tongensis	$y_t = 206.0 \left[e^{-2.3814}\right] 0.9701^t$	0.9515	400
	P.c.cepapi	$y_t = 223.6 \left(e^{-2.4505}\right) 0.9706^t$	0.9757	300
	F.c.congicus	$y_t = 112.39 \left[1-(0.9328)(0.9867)^t\right]$	0.9723	400
Total length (mm)	P.p.ornatus	$y_t = {}^{423.47}/\ 1+(2.0230)(0.97)^t$	0.8269	400
	P.p.tongensis	$y_t = 363.83 \left[e^{-1.0555}\right] 0.9630^t$	0.9608	300
	P.c.cepapi	$y_t = {}^{360.92}/\ 1+ (2.0361)(0.9391)^t$	0.9527	200
	F.c.congicus	$y_t = 319.15 \left[1-(0.7219)(0.9726)^t\right]$	0.9721	320
Tail length (mm)	P.p.ornatus	$y_t = 201.87 \left[e^{-1.4335}\right] 0.9630^t$	0.7984	300
	P.p.tongensis	$y_t = 176.83 \left[e^{-1.1941}\right] 0.9553$	0.9277	250
	P.c.cepapi	$y_t = 174.62 \left[1-(0.8344)(0.9597)^t\right]$	0.9524	250
	F.c.congicus	$y_t = 164.14 \left[e^{-1.4763}\right] 0.9528^t$	0.9775	200
Hindfoot (c.u.)(mm)	P.p.ornatus	$y_t = 51.81 \left[e^{-1.0891}\right] 0.9604^t$	0.8876	180
	P.p.tongensis	$y_t = 44.0 \left[e^{-0.8452}\right] 0.9375^t$	0.9327	150
	P.c.cepapi	$y_t = 45.45 \left[1-(0.6148)(0.9584)^t\right]$	0.9269	200
	F.c.congicus	$y_t = {}^{38.27}/1+(1.9252)(0.9105)^t$	0.9692	125
Ear (mm)	P.p.ornatus	$y_t = 20.63 \left[1-(0.6875)(0.9678)^t\right]$	0.8028	250
	P.p.tongensis	$y_t = 19.44 \left[1-(0.6021)(0.9708)^t\right]$	0.8112	300
	P.c.cepapi	$y_t = 20.25 \left(e^{-1.1588}\right) 0.9497$	0.9027	200
	F.c.congicus	$y_t = 16.58 \left[1-(0.7642)(0.9578)^t\right]$	0.9154	150

TABLE 91

BEST AVERAGE CURVE FOR 5 DIFFERENT SETS OF MEASUREMENTS, GROWTH RATES FOR THE CURVES AND 95% CONFIDENCE INTERVALS FOR THE GROWTH RATES

MEASUREMENT	BEST AVERAGE CURVE	SPECIES*	GROWTH RATE	95% CONFIDENCE INTERVALS
Mass	Gompertz	1	0.9825	0.9149 - 0.9966
		2	0.9701	0.9244 - 0.9885
		3	0.9706	0.9398 - 0.9859
		4	0.9799	0.9799 - 0.9799
Total length	Modified exponential	1	0.9805	0.9062 - 0.9962
		2	0.9708	0.9268 - 0.9886
		3	0.9674	0.8621 - 0.9930
		4	0.9726	0.9122 - 0.9918
Tail length	Modified exponential	1	0.9706	0.9064 - 0.9912
		2	0.9651	0.9191 - 0.9853
		3	0.9597	0.9189 - 0.9804
		4	0.9688	0.9170 - 0.9864
Hindfoot (c.u.)	Gompertz	1	0.9604	0.8900 - 0.9864
		2	0.9375	0.8639 - 0.9725
		3	0.9482	0.8890 - 0.9767
		4	0.9280	0.8519 - 0.9665
Ear	Modified exponential	1	0.9678	0.8419 - 0.9941
		2	0.9708	0.8977 - 0.9921
		3	0.9614	0.9253 - 0.9805
		4	0.9578	0.8944 - 0.9838

* 1 = *P.p.ornatus*
2 = *P.p.tongensis*
3 = *P.c.cepapi*
4 = *P.c.congicus*

DISCUSSION

The samll litter size of all four species is accompanied by a more precocial state of development at birth than in Nearctic and Palearctic squirrel species (Table 88), and independence at almost half the age. Emmons (1975) found a similarly small litter size and greater individual mass at birth for tree squirrels in Gabon in a rain forest; moreover in other tropical and subtropical regions, litter size also lies between one and 2,8 for 29 species of tree squirrels (Hill, 1942; Banerji, 1955, 1957; Harrison, 1955; Asdell, 1964; Purohit, Kametkar and Prakash, 1966; Seth and Prasad, 1969; Rahm, 1970; Brown and McGuire, 1975; and Kingdon, 1974). This is in marked contrast to litte size of Holarctic tree squirrels where litter size varies from 3,1 to 5,0 in nine different species (Ognev, 1940; Allen, 1942; Sollberger, 1943; Brown and Yeager, 1945; Robinson and Cowan, 1954; Shorten, 1954; Asdell, 1964; Keith, 1965; Smith, 1968; Millar, 1970b; Dolbeer, 1973; Nixon and McClain, 1975; Ferron and Prescott, 1977).

Gestation period is longer and litter size smaller for tropical and sub-tropical squirrel species than for Holarctic tree squirrels (Table 88), but if the development stages are calculated from the date of conception, development is on a par between the two regions. Therefore, the critical period for tropical squirrels is evidently the period spent as a nestling. A shorter nestling period is to the advantage both of the pup in defence against nest predators, and of the female in shortening the period of lactation and consequent heavy metabolic demands. If the litter was larger or had to spend 20 days longer in the nest, as do the Holarctic tree squirrels, the stress of maternal care could be too much for the female to raise any of the litter. On the study area of <u>cepapi</u> none of the adult females produced more than one litter in the season 1972/73, and almost all of these young had to be evicted from the groups by adults at the time of food scarcity. Therefore, the carrying capacity of the habitat of these squirrels can probably not sustain a greater recruitment. Nutrition plays a prominent role in sciurid breeding in both the tropics and in the northern cold climates, females conceiving and young being born when food supply is at a maximum (Viljoen, 1980). Limited food resources, and high preda=tion have been suggested as a reason for smaller litter size of tropi=cal birds (Lack, 1968; Skutch, 1949), and squirrels (Emmons, 1975). No predation was recorded for yellow-footed bush squirrels, cepapi which had an extremely high survival rate for nine months (Viljoen, 1977a). It is possible, therefore, that predation does not play as big a role in the present situation, as does food limitation and stress on the adult female.

When food is plentiful, they can conceive at a post-partum oestrus and thus produce more young in certain seasons. None of the Holarctic squirrel species have been reported as showing a post-partum oestrus, but it has been found in another tropical squirrel, Exilisciurus exilis (Conaway, 1968).

Environmental variables have a strong effect on reproduction of temperat zone squirrels where winter is a highly inclement period. However, it does also seem that in tropical (Emmons, 1975) and sub-tropical squirrels (Viljoen, 1975), breeding is seasonally related to the environment.

No single environmental variable exerts complete control over repro=ductive ability - variations in light regime are accompanied by climatic and nutritional variations. Averill (1964) found that ovulation onset in ewes in New Zealand will remain constant but that immediate climatic and nutritional factors will affect the onset of behavioural oestrus. Nutrition, inclement weather, rainfall and photoperiod are inter=related variables that have all been mentioned as affecting sciurid breeding seasons. Little experimental work has been done and when discussing these factors separately, one must keep in mind that they do not stand in isolation. An example of the complexity of environ=mental influence on some breeding patterns, is evident from studies on Paraxerus cepapi cepapi, at Naboomspruit (Viljoen, 1975). Rainfall commences in September, and soon after, the first females come into oestrus. This is at a time when flowers are abundant and there is a green flush of vegetation, with or slightly after the spring equinox. Male scrota show a sharp increase in size in June just before the winter solstice when temperatures are at their lowest and rainfall is at a minimum. This is the end of the period of food abundance. Scrotal shrinkage is apparent in late December and January during the rainy season, when maximum temperatures are at their highest and just after day length has started to decrease. The number of vesicular follicles per ovary are low from April to August (1,3 ± 1,6 in May, n = 6) and are much higher from September to December (22,8 ± 3,3 in September, n = 3). Corpora atretica show a reverse trend. Therefore, in South Africa, the seasonal availability of food has probably influenced evolution of breeding periods in tree squirrels, but this influence is not easily separated from rainfall and day length.

Nutritional influence on sciurid breeding has been well-documented (Allen, 1942; Baker, 1944; Layne, 1954; Shorten, 1951; Brown and Yeager, 1945; McKeever, 1963; Reddi and Prasad, 1968; Smith, 1968; Seth and Prasad, 1969; Kemp and Keith, 1970; Lampio, 1967; Millar, 1970b; Rahm, 1970; Brown and McGuire, 1975; Emmons, 1975; Nixon and McClain, 1975; Nixon, McClain and Donohoe, 1975; Thompson, 1977; and Yahner and Svendsen, 1978). Grey squirrels, Sciurus carolinensis failed to breed in Ohio in 1966 as a result of failure of the seed crop (Nixon et al, 1975). In the American red squirrel Tamiasciurus hudsonicus, mean dates of breeding varied up to a month between years (Kemp and Keith, 1970) and although weather might not be directly linked to this variation, summer conditions and flowering of the white spruce cone crops are definitely linked - high temperatures and low precipitation during the summer of bud differentiation is associated with increased cone production (Lester, 1967). The information necessary to predict the amount of conifer seed energy that will be available for nourishing a litter (pollination success) is present long before the litter is conceived since conifer cone buds can be distinguished from vegetative buds at least a year before cones mature (Smith, 1968). Smith also mentions another aspect of nutrition. He found that the variation in breeding time and litter size of squirrels can best be explained by the individual's ability to bring food to its young, one factor being the age and experience of the parent. From studies, both on fox squirrels, Sciuris niger (Brown and Yeager, 1945; Allen, 1942) and on grey squirrels (Shorten, 1951) it became clear that where food is always abundant such as in farmlands, litter size was larger and breeding more successful than in mixed hardwood or woodland. Another aspect of good nutrition is precocial breeding of females at only 75 to 85 percent of adult somatic growth (Nixon and McClain, 1975) and for adult breeders, a higher level of nutrition in summer cf. winter breeders results in a higher fecundity in female grey squirrels during spring and summer than in winter (this is substantiated by Shorten, 1951; and Smith, 1968).

In the East African red squirrel P.palliatus in northern Zululand anoestrus occurs soon after the June fruiting peak when day length starts to increase and the young are also weaned at the best time of the year after January. However, in captivity this species bred up to three times in a season and bush squirrels showed the potential to breed throughout the year confirming observations made by Purohit, Kametkar and Prakash (1966) on the northern palm squirrel, Funambulus pennanti, Kingdon (1974) on the Ochre bush squirrel, Paraxerus ochraceus, and by Mallinson (1975) on the Sierra Leone striped squirrel, Funisciurus pyrrhopus. Mallinson held his squirrels captive in England where there is a very marked seasonality of environmental variables. In all these instances, nutrition was the single constant factor affecting reproduction. Emmons (1975) working in Gabon found that in the African squirrel Funisciurus lemniscatus and F.isabella, the months of breeding inactivity, February to June, coincided with the minimum insect ingestion and concluded that food in the tropics may be as limiting as in temperat regions. Rahm (1970) describes a similar situation in Funisciurus anerythrus in Zaïre and found that breeding activity could be different in the same squirrel in different habitats and that seasonal food supply and food habits may influence breeding. In Botswana Smithers (1972) found pregnant bush squirrels in all months except May and September but with a distinct peak in November and December. This species bred seasonally further south at Naboomspruit, with pregnant females collected in February and from August to November (Viljoen, 1975). Further=

more birth on the study area at Naboomspruit occurred within a one-week period in November both in 1972 and 1973, with three additional litters in the first quarter of 1973 (Viljoen, 1977a). Body weights indicated that less food was available in 1974 than in 1973 (Viljoen, 1975) and the sporadic litters in 1973 could have been related to greater food availability as could the continuous breeding in captivi= ty. Viljoen (1977d) draws the conclusion that if nutrition does play a role, breeding synchronisation could enable the greatest number of young within a small group to attain adult age. There is an extremely high survival rate e.g. of 15 juveniles born in November 1973, all were still present in May 1974 and by July only two had disappeared from the study area. Juveniles are weaned when food supplies are at a maximum. From July to September of both 1973 and 1974 the total numbers of squirrels on the study area decreased from 28 to 15 in 1973 and from 30 to 19 in 1974 (Viljoen 1975). At this time of the year food was at a distinct premium.

Delany (1972) also found the tree squirrel species F.anerythrus and P.boehmi to display breeding seasons affected by nutrition. Kingdon (1974) referring to the literature, recorded births only between August and March, in 10 species of Ugandan tree squirrels, and throughout the year in two other species, one of which was captive and therefore had a constant food supply. Another instance of possible nutritional influence on breeding is from Malaysia where flying squirrel have a super-annual breeding rhythm (Muul and Lim, 1974). This might be related to poor nutrition during certain years.

To conclude, it does seem that sciurid breeding is closely geared to seasonal fluctuation in the food supply with young being born at the best nutritional time of the year. The actual reason for this nutritional influence, could be related to a high level of adreno-cortico activity which blocks oestrus (Nixon et al, 1975) or to facilitation of energy conservation during periods of food shortage by control mechanisms leading to inhibition of LH-secretion (Walker and Frawley, 1977).

INCLEMENT WEATHER

Inclement weather, and to a large extent very low temperatures, modifies the onset of breeding in temperate region sciurids (Shorten, 1951; Kirkpatrick, 1955; Smith, 1968; Kemp and Keith, 1970; Millar, 1970a; Millar, 1970b; Dolbeer, 1973; Pudney, 1976; Knopf and Balph, 1977; Michener, 1977; Rusch and Reeder, 1978; Yahner and Svendsèn, 1978). Deanesly and Parkes (1933) and Rowlands (1938) mention spring and summer breeding both in grey squirrels and red squirrels, *Sciurus vulgaris* in Great Britain.

Examples of climatic influence in reproduction of temperate tree squirrels: Dolbeer (1973) found that red squirrels bred a month later in 1970 than in 1971 and related this to a difference in spring weather (40 percent less snow in 1971 than in 1970 in April and May) Smith (1968) and Millar (1970a) noted a similar relationship between breeding chronology in this animal in British Columbia, and spring weather conditions affecting the numbers of litters, timing of breeding and the number of reproductive peaks in males.

Temperature effect on sciurid breeding is clearly seen in the hibernating ground squirrels which depend on spring temperatures to determine their date of emergence within limits (Michener, 1977; Knopf and Balph, 1977). Arousal is probably under endogenous control here and as in *Citellus lateralis* and *C.beldingi* (McKeever, 1963), highly synchronised breeding immediately after arousal usually occurs to enable births during the period of food availability. Photoperiod cannot influence them in their underground burrows.

Timing of breeding seasons in temperate squirrels seem to be under endogenous control with the spring temperatures having a modifying effect, either delaying or completely disrupting breeding.

Rainfall is mentioned only in connection with African squirrel species but weather has a direct effect on food supply and as such it is probably once again nutrition that actually influences the breeding. In the Sudan in semi-desert and dry woodland, Happold (1966) found rodent breeding in the first half of the dry season from October to December (peak in October) but no breeding in the hot/dry months of the second half of the dry period (rains from July to September). He says that many African rodents breed during the end of the rainy season and the first few months afterwards regardless of when the rainy season occurs. He reports Prakash (1960) as finding a similar situation in the Rajasthan desert in India in three species of rodents. Certainly Rahm (1970) found Muridae to have a reproductive peak at the end of the wet season but the two species of squirrel examined by him had a peak of embryos at the end of the dry season and the start of rains (August). Jewell and Oates (1969) in Biafra concluded that Prosimian births peak during the second half of the dry season and the start of the wet (October), but small rodent births peak at the end of the rain. In Malawi maximum rodent breeding activity occurs during the wet season/early dry season except in the montane forms where breeding commences in October and the end of the dry season (Hanney, 1965). In S.W.A./Namibia, the western striped squirrel <u>Funisciurus congicus congicus</u>, bred in October and March in 1977/78 (Viljoen, 1978) coinciding with the length of the rainy season. In the genus <u>Paraxerus</u>, breeding is also correlated with the months of rain from September to April in South Africa.

As stated by Sadleir (1969), there is therefore no constant relationshi between breeding and the timing of rainfall and consequent good nutritional conditions in Africa. However, in different species the pattern might be constant and additional information on niche occupation and behaviour of the various species could indicate the environemntal factors exerting the main influence. What in our estimation seem good conditions, might not prove to be so for the individual species.

PHOTOPERIOD

Latitudinal differences in breeding were mentioned by Robinson and Cowan (1954); Shorten (1951); Sadleir (1969); Reddi and Prasad (1968); Michener (1977); Ferron and Prescott (1977); and Thompson (1977), and additional indirect evidence for photoperiodic influence is evident from Kirkpatrick (1955), Seth and Prasad (1969), Millar (1972), Nixon and McClain (1975) and Knopf and Balph (1977).

Sciurid reproduction in tropical regions can be continuous e.g. in the Mexican red-bellied squirrel, Sciurus aureogaster in Florida, where Brown and McGuire (1977) found juveniles and subadults at all seasons but with a peak in May/June and a trough in November/December. Competition for food, and population density limited the numbers. However, in India the five-striped palm squirrel Funambulus pennanti was a seasonal breeder from January to the end of July with regression of male testes from August to September, and quiescence during October and November, but the palm squirrel F.palmarum, 16 degrees closer to the equator, was spermatogenically active throughout the year (Reddi and Prasad, 1968). The conclusion is made that it is unlikely that food limits reproduction here because of the wide range of items taken, and therefore that the difference in breeding patterns is the result of latitudinal differences in temperature and day length. However, the same wide range of food items is probably available to most squirrels but variation in seasonal availability of different items certainly must play a role. Indeed, Seth and Prasad (1969) also working on F.pennanti, found seasonal diet changes with insects available from February to October (the breeding season) and seeds from October to February. But they also state that paucity of food could not be a factor controlling the reproductive cycle and once again do not give attention to variation in availability of different items of diet. Reddi and Prasad (1968) stress that the decrease in testes size of F.pennanti commenced at the time that day length started to decrease but that recrudescence commenced when day length was yet at a decrease, therefore there was probably an internal rhythm to initiate the onset of reproductive activity. On the female, Seth and Prasad found recrudescence of ovaries commencing in December synchronised with a 12-minute increase in day length.

Conversely, photoperiod has been connected with redevelopment of testes in grey squirrels. Kirkpatrick (1955) found males showing testicular degeneration twice as numerous in summer and autumn than in winter and spring and a redevelopment only in the autumn when some environmental factor might prime the testes. Pudney (1977) reported male recrudes= cence in the months preceding spring mating concluding that endogenous hypohyseal mechanisms probably control the male's sexual regression but recrudescence is dependant on environemntal factors for initiation. The seasonal breeding will be regulated by the female's oestrous cycle as certain males are capable of breeding all year round although individual males do not remain fecund (also found by Allan= son, 1932; Shorten, 1951). Observations on the Paraxerus spp. indicate that fluctuating sexual cycles of males could possibly be determined by photoperiod but other environmental variables also fluc= tuate seasonally with photoperiod.

Another aspect of latitudinal influence is the general but not consis= tent trend for larger litters with increased latitute (Sadleir, 1969). Millar (1970b) from studies on the American red squirrel found other variables more important, and the potential litter size varied in response to environmental conditions at conception as there was corre= lation between larger litters and late breeding. However, his work was limited to study areas in temperate regions. Tropical and sub= tropical squirrel species (Emmons 1975; Viljoen 1977a) do have smaller litter size and a longer gestation compared to temperate region squir= rels. Emmons concludes that it is possible that the combination of a long breeding season and a small litter size enables some tropical rodents to spread the nutritional demands of breeding over a larger portion of the year than is possible in temperate climates.

CHAPTER 11

CONCLUSION

To conclude this dissertation, the investigated parameters will be summarised in this chapter in the context of differing habitats as summarised in Table 38.

With regard to the use of space, the three squirrel species in the habitats with higher visibility (ornatus, cepapi and congicus) were seen on the ground 30% of the time, whereas tongensis in the most dense habitat was only seen on the ground for 12% of the time. It is difficult to speculate whether this difference reflects the greater visibility to the observer or whether it signifies a greater degree of terrestriality.

The area utilised by the two forest species is larger than that of the savanna species. When considering only the smallest species, congicus from savanna, this difference could result from a difference in body size. Larger mammals usually do have larger home ranges (McNab, 1963). But distribution of food resources, energy metabolism and social system probably play a significant role, as is evident in the smaller area (a group territory) used by the savanna cepapi, which has the same mass as tongensis. Food resources of cepapi are localised and clumped and the energy per 100 g dry weight available in the food is less than in the forest fruits and kernels. Cepapi does sometimes remain in an area of just more than 150 m^2 for a whole day, feeding in one small clump of bushes, and its territorial system obviates the necessity for energy wasted through continuous spacing behaviour. On the other hand, cepapi probably conserves more energy by having a recognised territory than it loses by not being able to move freely to investigate different areas and by having to evict strangers.

In the Ngoye forest, food resources are dispersed and ornatus has to range over a vast 'unproductive' volume of forest to obtain its food and to ascertain the ripeness of the different fruit crops. Consequently the home ranges of the species are large and overlapping and body size is larger. *Ornatus* often calls to indicate its whereabouts intraspecifically, thus spacing themselves. Although the estimates for home range of *tongensis* males are similar to those for *ornatus* males, sample size for *tongensis* was small and indications are that area in use is smaller than for *ornatus*; *tongensis* calls are given at a lower dB strength and therefore are audible at a shorter distance; and *tongensis* females have considerably smaller ranges than *ornatus* females. Furthermore, *tongensis* does use a smaller volume in the coasta forest with the lower canopy.

When comparing *cepapi* and *congicus* habitat all indications are that *congicus* requires a slightly denser vegetation type than *cepapi*. The latter is found both on the plains and hills and the former never on the open plains. *Cepapi* has twice the mass of *congicus* although it does not measure much longer, and covers large distances between patches of vegetation and between trees, on the ground, whereas *congicus* at 100 g is able to and prefers to move from twig to twig and branch to branch, even though they do spend a substantial amount of their time on the ground when feeding. They are also in the habit of jumping considerable distances between branches which *cepapi* prefers not to do. The rocky outcrops might also have a different microclimate and even a small degree of additional heat in winter could be critical to such a small animal. On the other hand they seem to be better adapted to extremes of heat than *cepapi*.

The density and biomass estimates obtained are for the four specific study areas. In the Ngoye forest this study area included climax forest (unproductive in terms of squirrel food) and areas of secondary growth and is probably representative for the forest as a whole, as is the case for the *tongensis* study area at Mkwakwa. But the figures obtained for *tongensis* can probably not be extrapolated to other *tongensis* forests without a comparison of vegetation as the habitat suitable for *tongensis* is extremely variable in quality. The estimates for *cepapi* and *congicus* are for good quality habitat: for *cepapi* on termitaria thicket clumps bordering a floodplain and for *congicus* on the edge of a dry river course. Consequently these estimates for the savanna species are an absolute maximum for the areas of study. In sandveld on Mosdene, the density of cepapi was much lower and home range size slightly larger, and on the farm Otjitambi where congicus was studied, the squirrels confine themselves to the denser vegetation clumps with uninhabited areas inbetween (Schlettwein, pers.comm)* Both in Ngoye and in Mkwakwa forests the density remained relatively stable throughout the seasons and it is probable that ornatus and tongensis which also has a lower litter size than the savanna species, have a lower turnover rate. The density and biomass of ornatus is higher than that of the other species, and Ngoye forest probably has a higher carrying capacity for tree squirrels. Energy/g dry weight of forest fruits is also higher than for fruits from savanna. The lower density and biomass of tongensis signifies a lower carrying capacity for this forest which is also lower in plant succession. Density and biomass in the savanna is also lower than in Ngoye and is at the absolute maximum estimate close to 1 000 g/ha. The cepapi numbers present on 5 ha (Viljoen, 1975) also indicate a greater degree of fluctuation (from 30 after the breeding season, reduced to about 15 in September just prior to the following breeding period). Therefore it appears as if populations of cepapi and probably congicus too, suffer greater fluctuations in numbers, a more rapid turnover rate, and the habitat has a lower carrying capacity. These large fluctuations also indicate a habitat where the food supply also fluctuates, thus resulting in low numbers in poor periods and high numbers when the food supply is sufficient. The two savanna species also have slightly larger litters which enables populations to increase more rapidly when food supply is good to ensure that enough squirrels are produced to recolonise the vacant areas - a surplus production, which is disposed of by the social system where subadults are frequently expelled from the territory by adults.

A study of food utilisation reveals that the two forest species are more adept at handling and feeding on medium to large kernels than cepapi. Ornatus is more efficient than tongensis and also has the large kernels and fruits in its habitat. Cepapi, in contrast deals with the small seeds more efficiently. These results correlate with the fruit size as found in the respective habitats.

With regard to activity and energy metabolism it is clear that the forest species are more active than the savanna species where energy from the environment is less forthcoming and more fluctuating and where temperatures and aridity demand energy conservation. The high activity levels of the forest species is necessary for the squirrels to remain informed with regard to ripeness of the dispersed food supply.

That all four species studied, occur in hot regions, is also reflected in the oxygen consumption which is lower than the Brody-Proctor expected values. VO_2 of the two mesic species are close to the expected Brody-Proctor values, indicating that they are probably adapted to a cooler (but not extreme) moist environment where it is not always possible to bask because of the dense vegetation. The smaller forest species, tongensis, has a higher metabolic rate and with its slightly higher conductance this will allow it to offload excess heat more easily than ornatus which occurs in the cooler of the two habitats. The much lower metabolic rate than expected in the two xeric species indicates a better adaptation to hot, arid regions. F.congicus has a higher conductance and has to cope with an environ= ment where there is often very little shade and where efficient heat loss is a prerequisite; here the tail aids in thermo-regulatory behaviour. Cepapi has the lowest TC but it has a more protected microclimate than congicus. Furthermore, cepapi probably has to be extremely conservative with regard to its energy resources, in a habitat that has a clumped and fluctuating food supply. To enable cepapi and congicus to survive the extreme cold (below zero) they have a close group structure and invariably nest huddled together. They can also bask for prolonged periods in their relatively open habitat.

The fact that only congicus builds dreys, is an intergeneric difference. Other species of Funisciurus also build dreys, and whereas cepapi could possibly do well with dreys, they have not evolved the ability.

It is possible that in *Paraxerus*, the forest species formthe original stock. Both *cepapi* and *congicus* occur in areas where nestholes are at a premium. Certainly *cepapi* is a more avid nest-builder than the other two members of its genus here studied. Alternatively, it could be that *cepapi* is exposed to fire in its habitat more frequently than *congicus*, and therefore finds a greater degree of safety in holes in trees.

The alarm and flight behaviour of the forest and savanna species differ relative to the habitat. The forest species give a low-pitched bark and then disappear into the dense vegetation. The savanna species either freeze and try to conceal themselves behind a tree trunk or branch (*congicus* has a singular knock-kneed movement which would facilitate rapid dodging) or they will rush for a hole if available either in a tree or even in the ground. In cages, the forest species rarely went into the nest during the day, whereas *cepapi* and *congicus* spent long periods in the nests by day. The savanna species' call of extreme alarm is a high-pitched whistle, difficult to locate in the open habitat where they are more exposed. The low pitch of the forest alarm call is easier to locate, but can better penetrate the dense vegetation.

Body colour and tail carriage are also adaptive to habitat. The dark *ornatus* occurs in the forest with the lowest light intensity, the orange *tongensis* in the forest with inbetween light intensity and *cepapi* and *congicus* which are light-coloured in the open habitat with a high light intensity. The tail of the forest species is held fluffed and is flicked more frequently. It is conceivable that this is related to visibility as *tongensis* in the habitat with most obstruction to visibility tailflicks continuously, whereas *cepapi* and *congicus* rarely do so. In the latter two species the tail is only fluffed and flicked in alertness situations, i.e. either alarm or intraspecific situations. But much of the intraspecific communication in the savanna is visual and tailflicks are not always necessary and would merely make the squirrel more vulnerable to predators. Tailbars on the tail hair make the tails conspicuous during pilo-erection. Cepapi has other delicate short distance visual signals such as head-bobbing and eye-narrowing.

With regard to auditory communication cepapi calls less frequently than ornatus does. This is possibly due to the fact that cepapi has a territorial system with exclusively recognised areas and there is probably less necessity for calling than in ornatus where the home ranges are overlapping and the squirrels space continuously whilst taking turns at feeding sights. Once again cepapi also relies on visual communciation and can see 'strangers' at a distance of approximately 60 m. These arguments probably also hold true for congicus. The reduced calling frequency of tongensis is possibly related to the fact that sounds are propagated less well through the dense vegetation and the energy put into calling could just be wasted energy. Furthermore, female tongensis do defend 'territories' around a set of nest trees against other females and the same situation might hold true as for the territorial cepapi.

Group cohesion towards nesting time is maintained by the contact murmur of forest females. Once again the savanna species with the greater range of visibility rely on visual contact and the females only give this contact call when pups are very young, and the males do so in the mating context only.

One further aspect of communication is that related to oestrus, which is communicated vocally by the cepapi female on the morning of the day that she is on heat (Viljoen, 1977d). She thus compels males to join in the mating chase although they may be trespassing in the terrain of an incumbant territorial male. In the forests, oestrus is communicated olfactorily. Males detect this signal by roaming over large distances in the 'continuous' vegetation.

It is perhaps appropriate to mention Ngoye forest in a slightly broader context and more detail as this forest is unique with regard to the link it forms with the tropical forests of central and eastern Africa. In addition to the large tropical element shown in floristic composition and physiognomy, the forest's scientific novelty is emphasised by a large endemic flora and fauna (Huntley, 1964). Animal species commonly occurring in Ngoye forest, but which are very rare or absent elsewhere in South Africa are the following: Ngoye centipede, *Cormocephalus granulosus*, forest green butterfly, *Euryphera achlyus*, green barbet, *Buccanodon olivaceum*, bronze-naped pigeon, *Turturoena delegorguei*, Natal thrush, *Turdus fischeri*, and the Ngoye red squirrel, *P.p.ornatus* and the following plant species: *Alchornea hirtella* var. *glabrata*, *Pseudobersama mossambicensis*, *Cavacoa aurea*, *Celtis mildbraedii*, *Carissa wyliei*, *Asplenium saundersonii*, *Boluseilla maudiae*, *Corymborkis welwitshcii*, *Encepahlarctos woodii*, *Loranthus woodii*, *Nectaropetalum zuluense*, *Olyra latifolia*, *Stictocardia laxiflora* var. *woodii*.

Although the forest is clearly unique with regard to the species that it harbours, the present project on the Ngoye squirrel is the first long-term study to be undertaken in the forest. The proximity of the University of KwaZulu presents the Zulu people with an opportunity to learn at first hand about ecology and natural history and to undertake further studies in the forest.

Mammalian species occurring in the forest have been listed by Huntley (1964). However, it is doubtful whether the tree hyrax (*Dendrohyrax arboreus*) does occur there, and grey duiker, (*Sylvicapra grimmia*) and reedbuck (*Redunca arundinum*) are probably extinct. On the other hand, the banded mongoose (*Mungos mungo*) can be added to Huntley's list.

Exploitation of indigenous timber by Europeans was discontinued around 1924. However, the forest timber is exploited by natives from the surrounding Reserve No. IX to an alarming extent. Huge piles of felled saplings can be found and axe-chopping can be heard daily. Stumps of saplings are present everywhere throughout the forest. Another factor detrimental to the plants is the grazing of far too many cattle on the grass slopes outside the forest. Huntley (1964) states that during the last fifty years Aristida junciformis has replaced Themeda triandra as the dominant species of the Ngoye range grasslands. In addition, the local inhabitants burn the grasses every year without fail and thus curb the spread of forest. There is a resultant absence of forest margin seral communities. The Ngoye forest is also indispensable as a water catchment area for the Umlalazi and Umhlatuzi Rivers to the south and the north of the forest.

Any management programme should avoid causing unnecessary friction with the inhabitants of the native reserve. Huntley suggests that grazing and cutting of thatch grass should be permitted at a nominal cost, that forest guards should be increased and that fire breaks should be established as well as a burning programme. In any event, the erection of a small study centre and the appointment of a trained scientific officer to manage and plan the conservation of the forest, are priorities.

Ngoye is a beautiful forest and with only a handful of people having seen it, it is little wonder that few people are concerned about its future. Huntley's recommendations, made almost 20 years ago, have still not been implemented. Therefore, it would probably be to the advantage of both the forest and the KwaZulu people, if the forest could be made more accessible to people, be it as a tourist attraction and/or as a study area.

MOULT

Materials and Methods

Moult of eight P.p.ornatus and five P.p.tongensis in captivity was followed from June 1976 to September 1978. In the field, moult was recorded for all trapped squirrels and also for any observed squirrels. Information about juvenile moult commencement and progression was provided by two Tonga squirrels and one Ngoye squirrel reared in captivity.

Results

Moult Progression (Fig. 27)

Moult commences on the head and forepaws and follows on the hindpaws, where the outer digits and the distal joints of middle digits moult first. Then moult moves up the forelimb, more rapidly on the anterior and inner side. At the same time the hindfoot moults. The head moult joins the forelimb moult which moves as a saddle posteriorwards. This saddle reaches the rump by the time the hindfoot has moulted. As this saddle reaches the tail, portions of the hindlimbs still have to moult. The tail can commence moult before this saddle quite reaches it. Tail moult in P.p.ornatus typically commenced both on the proximal and the distal third, leaving the middle third with dark hair until last.

Captive squirrels (Table 92)

P.p.tongensis: From June to August 1976 when squirrels were first caged hindlimbs, hips and parts of the midbody showed some moult. In October, a new moult commenced on noses, fore- and hindpaws. In December this had progressed to forelimbs and shoulders and was also visible on hips and hindlimbs. Tails moulted during January. No squirrels were in moul from February to July of 1977. During August and September of 1977, moult recommenced, simultaneously on digits of both fore- and hindpaws, moving to fore- and hindlimbs respectively. By December and January, the tails were in moult, which was completed at the end of January. Dye that had been applied to squirrels in May 1977 showed that moult stopped on the hips and only recommenced in September 1977.

However, there was some moult on the body during winter, e.g. one female, dyed early in April, moulted from April to May 1976 as follows: by the 13th of April, digits of fore- and hindpaws had moulted, and a moult-line ran posterior to the shoulders, whilst the ventrum and dorsum displayed patchy moult. On the 6th May the moult line was posterior to the middle and by 27th May there were only a few black patches left on the hindlimb and on the middle of the hindpaw, and two small dye patches on the forelimb. On 12th August a few patches of dye were still left on the ventrum, and the rump and the tail were in moult.

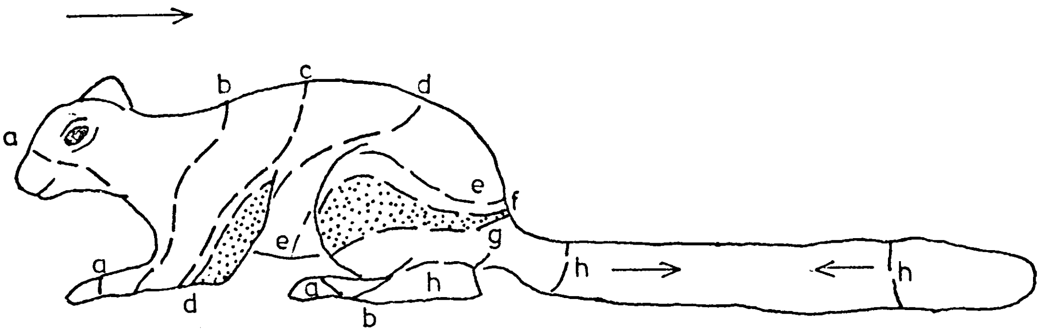
P.p.ornatus: Moult commenced in August 1976 on fore- and hindpaws and progressed to the fore- and hindlimbs and midbody by December. Tails moulted from December 1976 to February 1977 and moult then recommenced

TABLE 92

MOULT IN CAPTIVITY OF P.P.ORNATUS AND P.P.TONGENSIS FROM AUGUST 1976 TO MAY 1978

MONTH:	HEAD	HANDS/ FEET	ARMS/ SHOULDERS	HINDLEGS/ HIPS	MIDBODY	TAIL	NO MOULT
P.P.ORNATUS							
August 76/Sept 77	1	8	5				1
Oct 76/77/78	3	2		2	6		2
Dec 76/77		3	4	3	4	2	
Jan 77/February 78			2	12	2	11	
March 77/78				3		1	3
April/May 77							8
June 78/July 77/76		7	7		1		4
	4	20	18	20	13	13	18
P.P.TONGENSIS							
August 76/77/78				5	3	1	
September 77/78	3	1			1		
October 76/77/78		2	4	2	1		
December 76/77		2	3	4	2	2	
January 78/February 77				2	1	4	5
March 78	2	2	2				3
May 77/78	1			1	1		5
July 78							6
	6	7	9	14	9	7	19

Figure 27. Moult progression (arrows indicate direction of the moult) on *P. palliatus*: a to h indicate sequencial waves of moult. Shadowed sections are the last to moult.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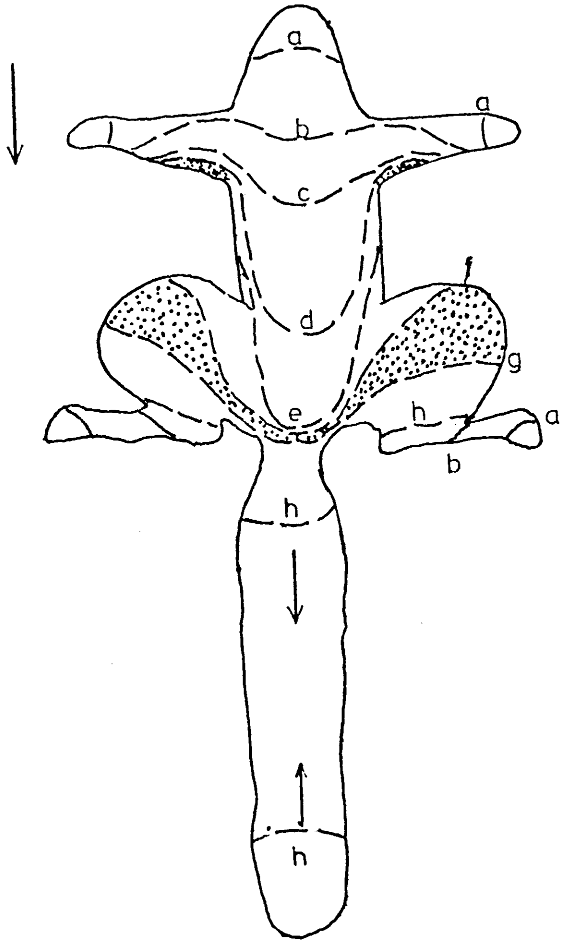
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in September 1977 and lasted until the end of January 1978. No moult was apparent from April to September of 1977, and from February in 1978. However, this might be a superficial observation, for one male was redyed just before the last part of the rump was to moult in February 1978. The anterior body then recommenced moulting (nose, forelimbs, hindpaws and shoulders) up to the middle. Moult in this individual ceased from August to October, when moult recommenced on the head. The last portion of the dyed hindlimb was only refurred by March 1979. Therefore, there is some moult in winter but this is difficult to observed on an undyed animal. Three squirrels in a par=ticularly sunny cage completed their tail moult (the end of the moult) by 3/2/77, whereas in the coolest and darkest cage the squirrels' mid=bodies were still moulting and the tails were just at the start of the moult. In a cage with intermediate light intensity, the hindbody was in moult and the tails had already started moulting. Moult progression of an adult male is shown in Figure 29.

Moult on squirrels in the field (Tables 93 & 94)

P.p.ornatus: If the juvenile/subadult squirrels are excluded, moult commences in October/November on the nose and forepaws (Table 93). Squirrels are in full moult in December, and terminate the moult in January. A few individuals showed a patchy moult over the nose, head and midbody during the period May to July, but from April to September, there was mostly no visible moult. However, the observations on cap=tive squirrels indicate that a degree of moult does take place in winter, but that it is not very obvious. In April there was a black sheen to the pelts, and this created the impression (if one did not look closely) that the squirrels had been dyed black. This blackness was the result of long black guard hairs. From June of 1977 and May of 1978, the tails turned darker and the hindbody was also more red from the hips backward. Noses and digits of the fore- and hindpaws were in moult from June to August. In the field, 90,3% of the adult squirrels showed no moult from May to August, and 87,2% from April to August. In June only 17% of the squirrels showed any moult, whereas 100% showed moult in October, 97% in December and 80% and 90% in January of 1977 and 1978 respectively.

P.p.tongensis: Moult progression (Table 94) was similar to that describe above for P.p.ornatus, commencing on the head and digits of the fore- and hindpaws in October, moving backwards to the fore- and hindlimbs and midbody in November and January, and tails moulting from January to May. Squirrels without moult (73,7%) were mainly recorded from the period March to August.

Juvenile moult: Moult on the P.p.ornatus pup commenced on day 65 with an orange flush of new hair on the ventrum. By day 68 the ventral orange fur also covered the proximal third of the tail and was emerging on the back through the black fur. On day 76 moult occurred on the head, hands and feet, and by day 82 the anterior portion of the body was completely moulted and the ventral surface of the tail was also covered with new red fur, but the body fur was still emerging. By day 105 the

TABLE 93

MOULT OF P.P.ORNATUS IN THE FIELD FROM APRIL 1976 TO MAY 1978

MONTH	TOTAL NO OF SQUIRRELS	HEAD		FEET		SHOULDERS		HIPS		MIDBODY		TAIL		NO MOULT	
		AD	SAD J*	AD	SAD J	AD	SAD J	AD	SAD J	AD	SAD J	AD	SAD J	AD	SAD J
Apr'76	4						1		1					2	
Apr'77	3													3	
May'78	30		2	2	2	2	1	1	1			1	1	18	1
Jun'76	12		2		2									6	4
Jun'77	16			1		1			2				1	13	
Aug'77	31													28	3
Oct'77	6	1				1	1	4							
Nov'76	2	1	1												2
Dec'77	37		1	5	1	8	2	7	5	11	1	4	5	2	
Jan'77	5											4	1		
Jan'78	10							4		4	1	1			
TOTAL	156	2	6	8	5	12	5	16	9	15	2	10	8	72	10

*Ad = Adult
Sad = Subadult
J = Juvenile

TABLE 94

MOULT OF P.P.TONGENSIS IN THE FIELD FROM OCTOBER 1975 TO MAY 1978

MONTH	TOTAL NUMBER OF SQUIRRELS	HEAD		FEET		ARMS/SHOULDERS		HINDLEGS/HIPS		MIDBODY		TAIL		NO MOULT	
		AD	SAD J	AD	SAD J	AD	SAD J	AD	SAD J	AD	SAD J	AD	SAD J	AD	SAD J
Oct '75	2					1		1	1		1				
Oct '76	21	7	1	1					1	2	2			4	
Oct '77	6	3		4	1	4			1				1		
Nov '77	8	3	4	1	1	4	2	4	1	3	2		3		
Jan '77	8	1	1			4	2	2	1	1	1	3		1	
March '77	10			1			1	2	3			2		4	
Apr '76	3	1		1					1				1		1
May '77	10	1		2						3		1		5	
May '78	14	1	2			1					3	6	1	3	4
June '76	2		1						1						
Aug '76	2	1												1	
Aug '77	8	1	3	3	3	1		1		3	1			1	
TOTAL	94	19	12	13	5	15	5	10	10	12	10	12	6	19	5

moult saddle of the body fur was just anterior to the hindlegs and the tail had started to moult on the dorsal surface. Juvenile moult of tails was from the middle to the extremities, i.e. in opposite direction to that of adult squirrels. By day 116 the moult saddle was still visible and by day 131 the tail had completely moulted, and only the hindlimbs still had to moult. At this stage a second moult commenced on the nose.

A single *P.p.ornatus* pup, born in December of 1976 in Ngoye forest, moulted anterior to the hips on 16th June and by 21st August the tail still had only one black band. Only on 1st December was the tail moulting into orange, going into the multi-banded appearance of the adult, at the base.

The two *P.p.tongensis* pup commenced their first moult on the nose and hands on day 52; by day 59 the moult line was clearly visible posterior to the eyes. On day 80 the moult saddle was visible on the mid-dorsum and ventrally on the chest. The arms still had to moult only the ventral and inner surfaces. On day 95 the tails became moult-banded (show alternating black and light bands across the tail as hairs start to fall out), and by day 105 the ventral tail surface was orange along the whole length. On day 97 the ventral portion of the saddle had caught up with the dorsal portion, toes had moulted, and the middle portion of the tail was new. The female was slightly slower than the male pup and still showed a saddle reaching to the mid-dorsum and no hindpaw moult by day 105. On day 127 tails had finished moulting and on the bodies only a small area on the hindlimbs still had to moult. This part recommenced moulting on day 197 until day 200. A second moult wave which had commenced on the head on day 147, reached the middorsum by day 211.

In the field, the one juvenile *tongensis* female (Toe 20) born in December 1976, commenced moulting in May and the shoulders were covered by new fur by the 21st May; by the 14th August the midbody had also moulted, and by the 10th November, moult had been completed. A female (Toe 200) started her first moult sometime in the middle of 1976, for when she was first caught on the 21st October, moult had progressed as far as the midbody and by the 23rd January as far as the hips. The second saddle was on the anterior portion of the shoulders and by 25th March it included the hips. Her moult then only recommenced in August together with the study area adults. Three males born in June were moulting on the nose, forepaws and hindpaws on 12th August 1977, and by 9th September moult was in the middorsum.

Juveniles and subadults could be found in moult at any time of the year. They commenced the first moult approximately two months after birth. The first pelt was soft and fluffy and one major difference from the adult pelt was the tail that had only two black bands instead of three or four. The colour of the alternating bands in the tail was darker and thus more cryptic than in the adult. However, the tip of the tail in the juvenile and subadult was made obvious by a particularly long subterminal orange band.

TABLE 95

ENDOPARASITES FROM *P.PALLIATUS* IN KWAZULU

SQUIRREL SPECIES	ENDOPARASITE	LOCALITY
P.palliatus tongensis	Syphacia paraxeri* (non-parasitic)	Lake St.Lucia, Kosi Bay, Lake Sibaya
	Streptopharagus *sp.*	Cape Vidal
P.p.ornatus	Rictularia *spp* Syphacia paraxeri Protospirura muricola	Ngoye Forest,

**Syphacia paraxeri* was present in all caeca of both *tongensis* and *ornatus* specimens. This was also found to be so in all caeca of *P.c.cepapi* (Viljoen, 1975)

TABLE 96

ECTOPARASITES COLLECTED FROM P.PALLIATUS IN KWAZULU

SQUIRREL SPECIES		ECTOPARASITE
P.palliatus tongensis	Phthiraptera	Neohaematopinus sp (St Lucia and Maputa)
	Ixodoidea	Rhipicephalus simus (St Lucia and Maputa) Haemaphysalis spp (St Lucia)
P.p.ornatus (Ngoye Forest, Eshowe District)	Phthiraptera	Neohaematopinus sp Werneckia sp
	Ixodoidea	Rhipicephalus simus

SUMMARY

The biology of *P. palliatus ornatus* from Ngoye forest (28°50'S, 31°42'E) and *P.p. tongensis* from Mkwakwa coastal forest (28°30'S, 32°24'E) are compared and adaptations to habitat of *P.c. cepapi* and *Funisciurus c. congicus* are included to examine niche separation of southern African tree squirrels.

The four species occur where mean annual temperature exceeds 18°C, with a dry winter. *P. palliatus* occurs in frost-free, warm temperate tropical forest. Ngoye forest receives 1868 mm of rain and the KwaZulu coastal plain sand forest and coastal forest where *tongensis* occurs, receive from 600 to 1318 mm. Higher maximum and lower minimum temperatures were recorded outside both of the forest study areas than inside. *P.c. cepapi* and *F.c. congicus* occur in hot and arid Steppe areas. Rainfall for the distributional range of *cepapi* in Southern Africa varies from 74 mm at Tsumeb to 1024 mm at Inhaminga in Mocambique whereas *congicus* largely inhabits the region between the 100 and 300 mm isohyets in SWA/Namibia.

Both *cepapi* and *congicus* inhabit savanna, but the latter species possibly requires a slightly denser vegetation. Plant density estimates (third-nearest individual method revealed that the forests had a significantly higher density of trees with dbh>2,5 cm: 0,29 trees/m^2 in Ngoye forest, 0,16 trees/m^2 in Mkwakwa forest, and 0,04 and 0,05 trees/m^2 in *cepapi* and *congicus* habitat respectively. Percentage vertical cover indicates that visibility is lowest in Mkwakwa coastal forest, which had 58,6% vertical cover and highest in Ngoye forest which had 16,3% cover. In *cepapi* savanna and termitaria thickets the vertical cover was 19,2% and 30,6% respectively. Light intensity measurements were lower in the two forests (152,7 lx in Ngoye and 315,7 lx at Mkwakwa) when compared with the woodland of *cepapi* (2089,0 lx) and *congicus* (3631,0 lx) (values for March at 12h00). Further density estimates (point-quarter analysis)

to compare Ngoye and Mkwakwa forests revealed that the former forest has a denser canopy ($p<0,001$) but less dense subcanopy ($p<0,2$) and a significantly higher canopy ($p<0,001$). Analysis of soil samples from the two forests indicated a high acidity for both areas, but a more leached soil and lower water retaining capacity in Mkwakwa forest than in Ngoye forest.

Phenologically there was a seasonal pattern in all four habitats with flowering in early summer and fruiting peaking in late summer.

Mass and body measurements of squirrels from the study area populations, and cranial measurements of collected specimens and museum skulls are included. The smaller and light-coloured squirrels inhabit the dry forests and the saturated forms inhabit moist forests. Description and measurements of the subspecies are included as well as descriptions of bacula and clitorides. Size differences exist in the body measurements between the four species, a noteworthy difference between the two genuses being that _Funisciurus_ has a relatively longer tail (48% in _Paraxerus_: 52% in _Funisciurus_, of total length).

Observation time in Ngoye forest totalled 845 h and in Mkwakwa forest 657 h. Trap-hours (hours x number of traps) in Ngoye forest were 15394 and in Mkwakwa 14315. Squirrels in the study areas were trapped, marked and released at each visit. Trapping success was 1,88% in Ngoye forest and 0,77% in Mkwakwa forest. This difference is attributable both to a lower population density at Mkwakwa, also to the smaller study area. Trapping records enabled estimates to be made of home range size (minimum area method) and population density (Lincoln index). Telemetry was additionally used on three males of each species to further establish the extent of home range. Home range size of males averaged 3,18 ± 1,72 ha (n=12) for _ornatus_ cf. 4,33 ± 1,34 (n=3) for _tongensis_. Home ranges of females were smaller in both _tongensis_ (o,73 ± 0,10, n=3) and _ornatus_ 2,19 ± 0,93, n=6.

Both *cepapi* and *congicus* move over smaller areas (0,4 to 1,26 ha) indicating the clumped nature of their resources and also the smaller body size.

Female *tongensis* defend an area with several nest trees within which they rear their litters. There appears to be a greater overlap of movement in *ornatus* and less defence of area. *P.c.* *cepapi* defends a group territory and it is possible that *F.c.* *congicus* has a similar system. Distance between vocalisation clashpoints in Ngoye forest was 432,9 m ± 131,68 (n=12) and in Mkwakwa forest, 216,66 ± 48,16 (n=6). Both in Ngoye forest and at Mkwakwa forest, 71% of all vocalisation was given at the clashpoints.
Population density estimates and biomass figures are the highest for Ngoye forest at 4,32 squirrels/ha or 1659,8 g/ha. Nest groups average 2,98 ± 1,39 (n=50) in Ngoye forest and 3,1 ± 1,17 (n=20) in Mkwakwa (difference NS). Nesting behaviour showed that the forest squirrels are extremely wary close to nests at nesting time and that nest groups are flexible. In habitat of *cepapi* and *congicus* nestholes are at a premium and nest groups are consistent in number throughout the year with very little movement between nests. The only species to build dreys is *congicus*.

Tree squirrels communicate extensively by means of visual, olfactory and auditory signals. Descriptions of these are mainly for the three *Paraxerus* spp, but in the sonographic analyses *congicus* has been included. Visual signals include pilo-erection of tail hair and tailflicking. *Tongensis* tailflicks more than the other species, and *congicus* is the only species to carry the tail over the head. Foot-stomping, earwagging and other body movements as well as head-bobbing eye-narrowing and scrotal movements also serve as visual signals. Olfactory signals are evident in urine, mouth-wiping, flehmen and analdragging.

Auditory signals were more intensively investigated. Murmurs (contact-seeking calls), growls (defensive calls), and a continuum of sounds rising in the alertness scale starting with soft clicks, given at an increasing rate with increasing excitement, and sometimes proceding into a trill (alarm and spacing context) are included in the sonagraphic analyses. Barks by the forest species and whistles by the savanna species serve a warning function in extreme alarm.

Differences between calls in the open and closed habitats lie in the fundamental frequency, but between ornatus and tongensis the main difference is one of frequency of calling, i.e. ornatus is much more vocal than tongensis. During 731 h in Ngoye forest 1,98 squirrels / h were noticed of which 86,5% vocalised, but in 657 h in Mkwakwa forest 1,03 squirrels / h were noticed of which only 38,4% vocalised. Cepapi are also relatively unvocal and in 69 h 2,26 squirrels / h were noticed of which only 18,6% were calling.

Food utilisation was studied with regard to relative feeding efficiency, food choice and proximate analyses of wild fruits. Feeding records from the two forest habitats are given (28 for each squirrel species). It appears as though the forest tree species have fruits with a higher energy yield both in the mesocarp and endosperm than those from savanna. With regard to feeding efficiency, ornatus is relatively more effient on the medium and larger seeds when compared to tongensis and cepapi, feeding in 59,5% and 66,7% of the time of tongensis and in 36,7 and 41,4% of the time op cepapi.

Lengths of the different sections of the intestines, indicate that southern African tree squirrels are much more insectivorous than tropical squirrels. These lengths differ significantly between the studied species.

Reproduction data were derived from breeding condition of trapped squirrels, histological sections of ovaries and testes of seven ornatus and 10 tongensis. Breeding is seasonal both in captivity and in the field for both species, occuring from about August to about March. In captivity the contact-seeking male mating call was given more frequently during the breeding period and males had diminished scrotal size when this call was absent.

Breeding of P. palliatus in captivity commenced only after about two years and indicated a litter size of 1,69 ± 0,48 for tongensis (n=13) and 1,60 ± 0,52 (n=10) for ornatus. Gestation period was 59 d in ornatus (n=1). The small litter size of the four southern African tree squirrel species and the long gestation period is accompanied by a more precocial state of development at birth than in temperate tree squirrel species. Early postnatal growth curves were computer-fitted.

Energy metabolism was investigated for all four of the squirrel species. They are all adapted to hot regions, reflected in the oxygen consumption which is lower than the expected Brody-Proctor prediction. The two forest squirrel species (moist habitat) have a VO_2 closer to the expected, indicating adaptation to less extreme conditions. The smallest species, F.c. congicus has the highest thermal conductance (0,21 ml/g.h.°C) The two forest squirrel species show heat stress at 34°C ambient temperature, contrary to the two open habitat squirrel species. Regression fits for ambient temperature against VO_2 for each of the species were calculated.

In Appendix 1 a description of moult progression and timing and in Appendix 2 the ecto- and endoparasites identified from the P. palliatus of the present study, have been included.

SAMEVATTING

Die biologie van *Paraxerus palliatus ornatus* in die Ngoyewoud ($28^{\circ}50'$S, $31^{\circ}42'$O) en *P.p. tongensis* in Mkwakwa kuswoud ($28^{\circ}30'$S, $32^{\circ}24'$O) vergelyk en aanpassing by habitat van *P.c. cepapi* en *Funisciurus c. congicus* is ingesluit om nisskeiding van suider Afrikaanse boomeekhorings te beklemtoon.

Al vier die spesies kom voor waar die gemiddelde jaarlikse temperatuur 18°C oorskrei en waar die droë seisoen in die winter val. *P. palliatus* kom in rypvrye gebiede voor met óf warm gematigde reën- óf tropiese reën-klimaatstoestande, in tropiese woude. Ngoyewoud ontvang jaarliks 1868 mm reën en die KwaZulu kusvlakte waar die kuswoud voorkom, ontvang jaarliks van 600 tot 1318 mm reën. Buite beide die woudstudiegebiede in KwaZulu is hoër maxima en laer minima aangeteken as daarbinne. *P.c. cepapi* en *F.c. congicus* kom voor in warm dor Steppe gebiede. Reënval vir die verspreidingsgebied van *cepapi* in suider Afrika wissel van 74 mm by Tsumeb tot 1024 mm te Inhaminga in Mosambiek, terwyl *congicus* die gebied bewoon tussen die 100 en 300 mm isohyets in SWA/Namibia.

Beide *cepapi* en *congicus* bewoon savanna, maar laasgenoemde spesies verg moontlik 'n effens digter plantegroei. Plantdigtheidsramings (derde-naaste individuele metode) het getoon dat die woude 'n merkbare hoër boomdigtheid gehad het (dbh> 2,5cm): 0,29 bome/m^2 in Ngoyewoud, 0,16 bome/m^2 in Mkwakwawoud en 0,04 en 0,05 bome/m^2 respektiewelik in *cepapi* en *congicus* habitat. Persentasie vertikale dekking toon dat sigbaarheid die swakste is in die Mkwakwawoud met 58,6% dekking, en is in die Ngoyewoud 16,3% dekking. In *cepapi* savanna en termitariabosse was die vertikale dekking 19,2% en 30,6% respektiewelik. Metings van ligintensiteit was laer in die twee woude (152,7 lx in Ngoye en 315,7 lx in Mkwakwa) in vergelyking met 2089 lx in *cepapi* habitat en 3631,0 lx in *congicus* habitat, vir Maart om 12h00.

Verdere digtheidsramings ('point-quarter analysis') het getoon dat Ngoye 'n digter blaredak het maar 'n yler sub-blaredak. Terselfdertyd is die blaredak aanmerklik hoër. Ontleding van grondmonsters uit die twee woude toon 'n hoë suurgehalte vir albei gebiede maar die Mkwakwawoud het 'n meer uitgeloogde bodem met laer voghoudende vermoë as die Ngoyewoud.

Fenologiese waarnemings in al vier gebiede het 'n seisoenspatroon getoon met bloeityd in die vroeë somer en vrugtyd in die laat somer.

Massa en ligaamsafmetings van die eekhorings van die studiegebiedbevolkings en skedelafmetings van versamelde en museum skedels, is geneem. Die kleiner en ligter-gekleurde diere bewoon die droë woude terwyl die groter en donkerder vorme die vogtige woude bewoon. Beskrywing en afmetings van die subspesies word ingesluit asook beskrywings van bacula en clitorides. 'n Merkwaardige verskil tussen die twee genusse is die feit dat Funisciurus 'n betreklik langer stert het (52% van totale lengte) wanneer vergelyk met die Paraxerus spp. (48% van totale lengte).

Waarnemingstyd in die Ngoyewoud het in totaal 845 h beloop, en in die Mkwakwawoud 657 h. Lokvalure (ure x getal valle) was 15394 in Ngoye en 14315 in Mkwakwa. Eekhorings in die studiegebiede is by elke besoek gevang, gemerk en weer vrygelaat. Vangste-slaagsyfer was 1,88% in Ngoye en 0,77% in Mkwakwa. Die verskil is toe te skrywe beide aan 'n laer bevolkingsdigtheid by Mkwakwa, sowel as aan die kleiner studiegebied. Opgawes van vangste het ramings van tuisgebied moontlik gemaak (minimum gebiedsmetode) asook van bevolkingsdigtheid (Lincoln index). Bykomstig is telemetrie in die geval van drie mannetjies van elke spesies gebruik om die tuisgebied nader te bepaal. Die tuisgebied vir mannetjies was 3,18 ha ± 1,72 (n=12) vir ornatus, cf. 4,33 ± 1,34 (n=3) vir tongensis. Die kleiner gebiede wat deur beide cepapi en congicus bewoon word (0,4 tot 1,26 ha) dui op die kollerige aard van die verspreiding van lewensbronne asook op die kleiner liggaamsgrootte.

Die wyfie *tongensis* verdedig 'n tuisgebied met etlike nesbome waarin sy haar werpsels grootmaak. Dit skyn asof daar 'n groter oorvleueling van beweging, en minder verdediging van gebied, by *ornatus* voorkom. *P.c. cepapi* verdedig 'n groepsterritorium en dit is moontlik dat dieselfde sisteem by *F.c. congicus* voorkom. Afstand tussen volkale botspunte in die Ngoyewoud was 432,9 m ± 131,68 (n=12) en in Mkwakwawoud 216,66 m ± 48,16 (n=6). Beide in Ngoye- en Mkwakwawoude het 71% van alle vokalisasie by hierdie botspunte geskied.

Ramings van bevolkingsdigtheid het getoon dat Ngoyewoud 'n gemiddelde van 4,32 eekhorings/ha het; d.w.s. 'n gemiddelde biomassa van 1659,8g/ha. Nesgroepgrootte toon 'n gemiddelde van 2,98 ± 1,39 (n=50) in Ngoyewoud en 3,1 ± 1,17 (n=20) in Mkwakwa. Dit blyk dat die woudeekhorings saans gedurende nestyd uiters lugtig is in die nabyheid van die nes en dat nesgroepgrootte heelwat wissel. In die habitat van *cepapi* en *congicus* is nesgate skaars en nesgroepgrootte is konstant; beweging vind selde plaas tussen neste. Die enigste spesies wat blaarneste in die blaredak van bome bou is *congicus*.

Boomeekhorings kommunikeer op groot skaal deur middel van visuele, reuk- en hoorbare seine. Die ingeslote beskrywings hiervan geld meestal vir die drie *Paraxerus spp*. maar by sonografiese analieses word *F.c. congicus* ingesluit. Sigbare tekens sluit in pilo-ereksie van die sterthare en 'n op -en-af wip van die stert. *Tongensis* wip die stert meer dikwels as die ander spesies en *congicus* is die enigste spesie wat die stert oor die kop gebuig dra. Voetestamp, oorbewegings en ander liggaamsbewegings, kopknik, vernouing van die oë en beweging van die scrotum, dien almal as sigbare tekens. Reuktekens is te bespeur in uriene-uitskeiding, bekveeg, "flehmen" en anaalsleep .

Klanktekens is meer intensief ondersoek. Sagte kontaksoekende roepe ('n binnesmondse bromgeluid), verdedigingsgroepe (grom) en 'n kontinue reeks van klanke op 'n stygende waaksaamheidskaal, (dit begin met sagte klikke, gegee teen 'n toenemende tempo met toenemende opgewondenheid, en slaan soms oor in 'n trilklank, in die woudeekhorings, en in 'n geratel in cepapi), is sonografies geanaliseer. Skor blafgeluide word geuiter deur ornatus en tongensis in uiterste gevaar, maar cepapi en congicus gee fluitgeluide in soortgelyke uiterste gevaar.

Die verskille tussen roepe van die eekhorings in die savanna en woud, lê in die fundamentele frekwensie; maar tussen ornatus en tongensis is die hoofverskil dié van aantal roepe: ornatus is meer vokaal as tongensis. Gedurende 731 uur in Ngoyewoud, is 1,98 eekhorings per uur aangeteken waarvan 86,5% geroep het, maar gedurende 657 uur in Mkwakwawoud is 1,03 eekhorings per uur aangeteken waarvan slegs 38,4% gevokaliseer het. Cepapi is ook betreklik swygsaam: oor 69 uur is 2,26 eekhorings per uur aangeteken met net 18,6% roepende.

Voedselbenutting is bestudeer m.b.t. relatiewe doeltreffendheid van voeding, voedselkeuse en ontledings van wilde vrugte. Dit wil voorkom asof die boomspesies in die woude van KwaZulu oor 'n hoër energie-lewering beskik beide in die mesokarp en die endosperm van hul vrugte, as in vrugte vanaf savanna boomspesies. Wat betref voedingsdoeltreffendheid, is ornatus relatief meer bedrewe op die medium en groter sade vergeleke met tongensis en cepapi: vergeleke met tongensis, vreet ornatus in 59,5% en 66,7% van die tyd, en vergeleke met cepapi in 36,7% en 41,4% van die tyd. Lengtes van die verskillende dele van die ingewande, toon dat suider Afrikaanse boomeekhorings veel meer insektevretend as die tropiese eekhorings is. Hierdie lengtes verskil beduidend tussen die bestudeerde spesies.

Data i.v.m. voortplanting is verkry van die teeltoestand by vangste in die studiegebiede, van histologiese snitte van ovaria en testes van sewe ornatus en 10 tongensis. Beide in gevangenskap en in die veld is teling seisoengebonde, en geskied wel vanaf om en by Augustus tot en met Maart. In gevangenskap word die mannetjies se kontaksoekende paringsroep dikwels geuiter en by afwesigheid van hierdie roep, het die mannetjies verminderde skrotumgrootte getoon.

In gevangenskap het aanteel eers na ongeveer twee jaar begin; 'n werpselgrootte van 1,69 ± 0,48 (n=13) is vir tongensis en 1,60 ± 0,52 (n=10) vir *ornatus*, aangedui. Draagtyd by *ornatus* was 59 dae (n=1). Die getalgeringe werpsel en lang draagtyd van die vier suider Afrikaanse eekhoringspesies gaan gepaard met 'n meer gevorderde stadium van ontwikkeling by geboorte en selfstandigheid teen byna die helfte van die ouderdom, vergeleke met die Nearktiese en Palearktiese eekhoringspesies. Groeikurwes vir die vier bestudeerde eekhoringspesies is met die rekenaar bepaal.

Energiemetabolisme is ondersoek by al vier die eekhoringspesies. Hulle is almal aangepas by warm streke, soos blyk uit die suurstofverbruik (VO_2) wat laer is as die verwagte Brody-Proctor voorspelling. Die twee woudeekhoringspesies het 'n VO_2 nader aan die verwagte, wat dui op aanpassing by minder uiterste toestande. Die kleinste spesie, *F.c. congicus* het die hoogste hitte-geleidingsvermoë (0,21 ml O_2/g.h.°C) en kan dus makliker van oortollige hitte ontslae raak. Die twee woudspesies toon by 'n omringende temperatuur van 34°C, uiterste gevoeligheid vir hitte, in teenstelling met die twee eekhoringspesies uit savanna. Regressiekurwes vir omringende temperatuur teenoor VO_2, is bereken vir elke spesie.

Ingesluit in die eerste Bylae , is 'n beskrywing van verharing van *P. palliatus*, en in die tweede Bylae is die geïdentifiseerde ekto- en endoparasiete vanaf *P. palliatus*.

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ADDENDUM

MADOQUA, VOL. II, NO. 2, 1978 (119–128)

Notes on the western striped squirrel *Funisciurus congicus* (Kuhl 1820)

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CONTENTS

ABSTRACT

Information on *Funisciurus congicus congicus* was obtained during eight days spent in the field at Otjitambi (20° 15′S, 15° 15′E) and from museum records. Distribution and habitat preferences of this squirrel and the bush squirrel, *Paraxerus cepapi* are clarified. Vegetation on a study area inhabited by *F. congicus* is described, a density estimate for trees is given, and plants are listed. Nine food items are recorded together with the time spent feeding on them. Two ticks are identified to generic status; mass and measurements, range of movement and population density are given. Aspects of reproduction are mentioned and a preliminary description of activity and basic behavioural patterns (grooming, alertness, vocal and visual communication, group structure) are given. The possible use of the tail in thermoregulatory behaviour is mentioned.

1 INTRODUCTION

Two tree squirrels occur in South West Africa, both limited to the north of 21°S: *Funisciurus congicus*, the western striped tree squirrel (Shortridge 1934), or Kuhl's tree squirrel (Amtmann 1966a), hereafter referred to as the striped squirrel; and *Paraxerus cepapi*, the bush squirrel of yellow-footed squirrel. According to Amtmann (1966b), *F. congicus* includes *F. poolii*, and the subspecies *congicus*, *flavinus*, *interior*, *oenone* and *damarensis* of earlier authors are invalid. Apart from brief distributional notes and observations by early workers (Sclater 1899; Shortridge 1934; and Roberts 1951), very little is known about this squirrel. As a result the description by Sclater (1899) is here relevant: "general colour above yellowish brown, brighter on the shoulders, below very pale yellow, hairs of the back black at the base, and many of them with black tips; along the sides from shoulder to hindlimbs runs a narrow pale yellow stripe, below which is a similar dark one; an incomplete white ring around the eye; ears moderate; whiskers black; limbs pale, toes covered with long hairs nearly concealing the claws; tail a little shorter than the head and body, bushy, with hair half an inch long". Additions to this description from the present study are that the ventrum and sidestripe are white to cream rather than yellow; ears have white hairs and both ears and eyes are larger relative to head-size than those of the genus *Paraxerus* in southern Africa (the white ring around the eye makes the large eyes particularly obvious); the bands on the tail from the centre outward are: Yellow-black-yellow-black; and the tail is slightly longer than head and body calculated from museum skins, animals trapped in the field and by reference to figures in Roberts (1951) and Shortridge (1934). (See: Mass and Measurements).

PLATE 1: *F. congicus* feeding on a mopane worm, *Gonimbrasia belina*.

Native names of bush squirrel and striped squirrel (Shortridge 1934, except where otherwise mentioned):

Paraxerus cepapi — Onjéri — Herero and Ovambo
Sipepe — Bechuana, from where the specific name

Funisciurus congicus — Onjéri-mbidíwa — Herero
Ephuku — Herero (present study)
Onjéri-shikwénga — Ovambo
Haridadob — Nama (present study)
Durus — Nama (present study)

2 MATERIAL AND METHODS

Information on distribution was obtained from specimens in the Windhoek and Transvaal Museums, as well as from various sources: Sclater (1899), Shortridge (1934), Hill and Carter (1941), Roberts (1951), Walker (1964), Amtmann (1966b), Coetzee, Schlettwein and Tinley (pers. comm.). Data on mass, standard body measurements and moult were obtained from museum specimens and records; from some of the above-quoted references, as well as from animals trapped in the field. Museum specimens were aged according to tooth wear (Viljoen 1976a) to make information more relevant. Eight days (8 April to 16 April 1978) were spent on the farm Otjitambi (20° 15′S, 15° 15′E), during which time animals were trapped along one kilometre on either side of a dry water course. Fifteen live traps (Have-a-heart type, 30 cm × 13 cm × 13 cm), baited with apple and a peanut-butter/muesli mixture, were placed on branches or rocks where the animals had been seen to move. These were attended to five times per day, every three hours from sunrise to sunset. Trapped animals were aged according to mass and external reproductive characteristics. (Females have four well-developed black inguinal nipples, adult males have enlarged scrota and often have bare chin patches). The animals were marked with Nyanzol D fur dye (Giles 1971), and ticks were collected and preserved in 70 % alcohol. Recaptures and observations on some of these squirrels enabled collection of data on their feeding, range of movement and behaviour. A vegetation transect through the study area was made (third-nearest individual method of McNeill, Kelly and Barnes (unpubl.) which they found less biased than other plotless methods in estimating density in Rhodesian woodland habitat) to give an idea of density of woody individuals (dbh more than 2,5 cm) as well as plant species present. The method entails the following: along a straight line, points are put out every 15 m where the distance to third-nearest neighbour in each of the 180° sectors along the line of travel is measured, species noted, as well as height, canopy diameter and diameter at breast height (dbh). The only difference in this instance was that the line of travel was not straight but hugged the water course at a distance of 5 m from the edge of the bank and curved with it, thereby following the distribution of the vegetation type to be sampled. In addition, a list of the plants in the study area was compiled.

3 DISTRIBUTION

The distribution of the two South West African tree squirrels has been mapped by Tinley (unpubl. manuscript 1970). He shows that the bush squirrel intrudes from the east (Botswana) reaching its most westerly distribution points at Otavi (19°45′S, 17°20′E) in the south, and at Ruacana falls (17°20′S, 14°15′E) in the north. At these two localities the bush squirrel overlaps with the striped squirrel. However, in between, the bush squirrel occurs around the east of the Etosha saline, and the striped squirrel along the west. There is a large amount of overlap in western Ovamboland, where the striped squirrel extends as far south as the forest belt between Ondongwa and Ukuambi (Shortridge 1934); and also just north of the South West African border, where the striped squirrel follows the Kunene River, and the bush squirrel occurs up to Mossamedes and Capelongo close to the coast (Hill and Carter 1941). In regions of overlap, the two species can be found in the same tree (Shortridge 1934). The bush squirrel is represented by two subspecies, the southerly population being *P. c. kalaharicus*, *vide* Smithers (1968), and the northerly pale-coloured Ovamboland population being *P. c. phalaena*, which also occurs in the south of Angola. In the Etosha National Park the bush squirrel can be seen in mopane-veld and occurs both at the Halali and Namutoni rest camps.

The genus *Funisciurus* ranges as far west as Southern Nigeria and Sierra Leone, and through the Northern Congo to Lake Tanganyika and Ruwenzori in the east; the species which concerns us here, occurs up to the Congo river where the type specimen was collected (Shortridge 1934). Amtmann (1966b) mentions them in the Katanga district of the Congo and says that they are probably to be found in eastern and north-eastern Angola. They are numerous in the west of Angola (Hill and Carter 1941) and occur right up to the seaboard as far south as Benguella and then angle south-eastwards to be distributed down the mountain range in Kaokoland to the Ugab river (20°45'S, 15°15'E) (Coetzee, pers. comm.), from there turning east, still to follow the mountain range and the *Commiphera/Kirkia* and *Colophospermum mopane* vegetation types mapped by Tinley (1969).

4 ECOLOGY

4.1 Habitat preferences

Walker (1964) notes the genus in palm groves, palm scrub, savanna and in forests up to an altitude of 2 175 m. Hill and Carter (1941) mention the striped squirrel occurring from plateau country in Angola and to the edge of the desert. Moreover, on the coast they are commonly found in palm groves, in the bushes of the savanna and also in the trees on the sides of cliffs. Shortridge (1934) notes that they prefer mopane and mixed forest, as well as dry river courses where the trees attain a larger size than elsewhere. Tinley (pers. comm.) associates them with granite outcrops, and not with open plains; and Schlettwein (pers. comm.) has also seen them frequently along dry water courses and on rocky outcrops, especially where some large trees are to be found close to these koppies. Both Schlettwein and Tinley surmise that the animals move seasonally, occurring in the wet season on the koppies and in the dry season along the river courses. All indications are that the striped squirrel requires a slightly denser vegetation type than the bush squirrel, the latter occurring both on the plains and hills, and the former not on the open plains. The bush squirrel is twice as heavy as the striped squirrel, although it is not much longer in body length, and covers large distances between patches of vegetation and trees on the ground, whereas the striped squirrel (mean adult mass of 100 g) prefers to move from twig to twig and branch to branch, even though they do spend a substantial amount of time on the ground when feeding. Frequency of sightings (n = 211) in different layers of vegetation was as follows: ground — 39 %, subcanopy (up to 2,5 m) — 42 %, and canopy (higher than 2,5 m) — 18 %. They are in the habit of jumping considerable distances between branches which *Paraxerus* prefers not to do. An additional attraction to the rocky outcrops might be a slightly warmer micro-climate, which could be critical to such a small animal in winter. In addition they seem to be better able to cope with warmer conditions than the bush squirrel. (See: Behaviour).

According to the isohyet map of SWA (Tinley 1971), the striped squirrel inhabits the region between the 100 mm and 300 mm isohyets down the western length of its distribution, but in Ovamboland and also south of Etosha where they range up to Tsumeb, they cross the 400 mm and 500 mm isohyets. Giess (1971) maps mopane savanna (his vegetation type 5) and mountain savanna and karstveld (his type 6) over this region; and the more detailed description of De Sousa Correia (1976) of the Kaokoland, indicates *Colophospermum mopane/Spirostachys africana* savanna; *C. mopane/Terminalia prunioides/Acacia* spp. savanna with *Terminalia sericea*, *Lonchocarpus nelsii*, *Combretum apiculatum*, *C. imberbe* and *Kirkia acuminata*; *C. mopane/T. prunioides* savanna; sub-desert steppe with *C. mopane* and *T. prunioides*; and escarpment area with rocky hills. (His types 9, 10, 12, 13 and 14.) Overlap between the two squirrels are in his vegetation types 2, 3 and 4.

4.2 Vegetation of study area

The study area could be divided into three different habitat types namely rocky outcrops, vegetation alongside the dry river courses and open savanna. Work during the present study was limited to the former two habitat types as this had been indicated as the preferred habitat of the striped squirrel by Schlettwein and Tinley (pers. comm.). The following plants were collected from these two habitat types in the study area: (concentrating on tree species)

Dry water courses — *Acacia heteracantha*, *A. mellifera* var. *detinens*, *A. hebeclada*, *A. reficiens*, *A. tortilis*, *Boscia albitrunca*, *Colophospermum mopane*, *Combretum apiculatum*, *C. imberbe*, *Commelina* sp., *Commiphora crenatoserrata*, *C. mollis*, *C. pyracanthoides*, *Croton gratissimus* var. *subgratissimus*, *Cucumis angurea* var. *longipes*, *Dichrostachys cinerea*, *Grewia bicolor*, *G. flavescens*, *G. villosa*, *Justicia matammensis*, *Lonchocarpus nelsii*, *Maytenus senegalensis*, *Mundulea sericea*, *Terminalia prunioides*, *Ziziphus mucronata*.

Rocky outcrops — *Acacia nilotica*, *A. mellifera* var. *detinens*, *Boscia albitrunca*, *Colophospermum mopane*, *Combretum imberbe*, *C. apiculatum*, *Commiphora mollis*, *Croton gratissimus* var. *subgratissimus*, *Cardiospermum pechuylii*, *Cissus nymphaeifolius*, *Grewia* *bicolor*, *G. flavescens*, *G. villosa*, *Maytenus senegalensis*, *Mundulea sericea*, *Securinega virosa*, *Solanum* sp., *Sterculia quinqueloba*, *Steganotaenia araliacea*, *Tinnea juttae*, *Terminalia prunioides.*

The vegetation analysis is the same as that completed in the habitats of other southern African tree squirrels which will be used later for comparative purposes (Viljoen, unpubl.). From this analysis and from the lists of plants from one daily range (Table 1), the vegetational requirements of the squirrel on Otjitambi can be approximated. The vegetation density estimate (D) was 0,05 individuals/m^2

$$\left\{ D = \left(\frac{2}{\pi \times N}\right) \times \left(\sum_{i=1}^{N} \sum_{k=1}^{2} \frac{1}{r_{ik}^{2}} \right) \right\}$$

where k = 2 (the number of sectors) and N = 50, the number of points sampled

4.3 Feeding records

Squirrels fed on the following items: *Colophospermum mopane* (green seeds) *Commelina* sp. (shoot/stem), *Commiphora mollis* (fruits), *Cucumis angurea* var. *longipes* (fruit), *Grewia bicolor* (fruits and seeds), *G. flavescens* (fruit and seeds), *Gonimbrasia belina* (the mopane worm, not on the live worms but when they had been recently dead, and still soft, the exoskeleton discarded), *Justitia matammensis* (leaf/shoot), *Berchemia discolor* (fruits) and galls on trees. Time spent feeding on some of the items was as follows: *Colophospermum mopane* (n = 22), 290,45 seconds (S.D. = 97,71) taking 100 seconds to peel it first; *Commiphora mollis* (n = 5), 160 seconds (S.D. = 24,49) taking 60 seconds of this time to peel it; *Grewia bicolor*, (n = 14) 65 seconds (S.D. = 17,76); *Gonimbrasia belina* (n = 9), 360,0 seconds (S.D. = 183,10). They were twice seen to bury dry mopane seeds, so they can be expected to scatterhoard. *Grewia bicolor* stores were found on some rocks.

4.4 Trapping results

During the eight days (88 trap hours) 16 squirrels (10 adults; 6 subadults) were caught, an average of 2,0 per day (± 0,76 S.D.). Seven of the trapped squirrels were females (5 adults) and nine were males (5 adults).

4.5 Ectoparasites

No lice were collected on these animals, but ticks were found on three individuals and were identified as *Haemaphysalis* sp. and *Rhipicephalus* sp.

4.6 Mass and Measurements

Table 2 shows mass and standard measurements calcalculated separately for museum specimens (Windhoek and Transvaal Museums); reference to Shortridge (1934) and Roberts (1951); and the present study. Hindfoot measurements are *cum ungue*, and where specimens had stunted tails, the tail measurement was not used. Subadult animals in the present study (probably around six months old) had a mean mass of 75,0 g, ear length was close to adult size, but hindfoot, head-body, and especially tail length were still markedly less than those of adults. The tails measured slightly longer than head-body throughout.

4.7 Range of movement

Determination of nesting sites, observation and retrapping of marked animals and the following of a group for one whole day, enabled a calculation of six groups for a length of 1 000 m along a dry water course. The animals were not utilizing more than 10 m on either side of the river bank, i.e. where the home ranges were stretched along the length of the river (three of the groups just seemed to touch the river for about 100 m). If 20 m is then taken as the width of the range (excluding the width of the dry river), the study area included 2,0 ha, less than 0,5 ha per group. One group, followed for a whole day, moved 200 m on both sides of the river course, bringing their range of movement in one day to 0,4 ha. However, the next day they also moved 50 m in the opposite direction, so that their total home range will be somewhat more than the daily range. In another group the range calculated over the whole week's study, was slightly more than 279 m along the river, yielding a range of 0,56 ha. They certainly move over a limited area e.g. one morning at 10h00 the two subadults were still only 20 m from the nest tree and at 12h00 they were 60m off, less than for the two adults who had then already moved at least 130 m away from the nest tree.

4.8 Population density

The size of groups averaged four individuals (i.e. number of squirrels emerging from the nest in the morning) but new litters had just been added throughout the study area which would probably push the group size up to six, resulting in a variation in population size from 24 in January to 36 from April onwards (i.e. on 2 ha). Subadults of the year could be chased out of their groups by September if the social system is at all similar to that of *P. cepapi cepapi* (Viljoen, 1977). The biomass would then vary from 400 to 600 g/ha depending on the time of year. It must be emphasized that all these figures are based on a very short period of study.

4.9 Moult

The eight adult animals encountered in the study area were all moulting their tails except for one female which had a moult line between the eyes. The eight subadults displayed no moult.

5 REPRODUCTION

Shortridge (1934) records juveniles just old enough to run about in the trees, collected from March to August. According to the museum specimens, juveniles (0 – 4 months old) and young subadults (4 – 7 months old) could be collected throughout the year, but there were two peaks of occurrence, one from October to January, and the other from April to June. During the present study, subadults estimated to be six months old were caught in April and newly born litters were then again in the nest – there seemed to be birth synchronization in the study area population with all the subadults very close to 75,0 g, and the adult females lactating again. Births therefore probably occurred early in October (middle of the hot-dry season), and in March (end of the hot-wet season), i.e. if the seasons in northern SWA are considered as follows: Hot-dry from 16 August to 15 December, hot-wet from 16 December to 15 April, and cold-dry from 16 April to 15 August (Berry, pers. comm.). At Lake Kivu, Rahm (1970) also found two peaks of breeding in *F. anerythrus*, one in August/October, at the end of the dry and into the long wet season, and a small peak in April at the end of the wet season. Although the above figures are fragmentary, it does seem as if this squirrel can be expected to breed twice a year, once in the spring and once in the autumn. During the present study an adult male with small testes was caught on one occasion and scrota from museum skins also indicate that testes of adults might not always be enlarged. The measurement from just behind the penis to the posterior tip of the scrotum was 20,85 mm in the two subadult males, and 30,92 mm in the adults. However, one adult male (adult mass) measured much shorter at 21,10 mm, indicating either a degenerated or a developing testis. Litter size deduced from three nesting groups in the present study was two in each case (two litters of one male, one female, and one litter of two females).

6 BEHAVIOUR

The striped squirrel is a contact species (deduced from the large amount of allogrooming, and the contact that is kept vocally), with a cohesive group and they might therefore be territorial as found in the bush squirrel (Viljoen 1977). However, no active chasing between any squirrels was seen, only vocalisation that might signify social spacing calls, was heard. The number of squirrels seen together on 24 occasions was 1,88 (S.D. 1,03) and ranged from one to four. Even though squirrels were often seen on their own they were usually within vocal contact distance and when one moved, another would often follow it shortly afterwards. This group cohesion is necessary in an open habitat where individuals are highly vulnerable to both ground predators when crossing open stretches, and to raptors.
(See: Alarm behaviour).

6.1 Grooming

Both auto- and allogrooming could be seen at any time of the day, the former taking up twice as much time as the latter. However, not enough time was available to make any accurate assessment of grooming.

6.2 Vocalisation

This is described as a cricket-like chattering by Shortridge (1934). It consists of very high-pitched, sharp staccato sounds reminiscent of and easily mistaken for a bird, and were used in the following contexts:

1. Contact between members of groups: an adult male was once seen to move up to the two subadults (subadults were slightly smaller than adults and noticeably more playful) of the group whilst giving a series of chirps. He was answered by the one squirrel and then first went to the one subadult, and after a naso-nasal identification sniff, moved to the other individual. Subsequently, such chirps were often heard just before one squirrel would approach the others of the group. After then meeting, they would either move off on their own again, or together with one of the group. Once, shortly after releasing a male squirrel, the chattering sounds came from his direction. It therefore seems as if they 'test for company' which usually lasts for about two minutes or less and is given at six chirps per 30 seconds. This contact or maintenance call sometimes develops into a duet, once heard between an adult male and adult female sitting 20 m apart, taking turns, 37 chirps (each a double note) per minute for each individual, lasting for 18 minutes. The male had a more dominant lower frequency to his vocal quality. The chirping can be heard at 110,6 m (n = 3) when the animals are perched about 6,0 m above ground. This is a reasonable distance for an animal with 200 m length to its home range. This call also attracts other members of the group and was once given by an adult male immediately after he discovered a *Cucumis* fruit and might also serve to attract others to food. (It is sometimes given together with tailflicks, when a squirrel is about to descend onto the ground, possibly testing for hidden danger).
2. Sporadic chattering, as far as determined only given by adult males for no obvious reason. This could

be a spacing or territorial call. Once, a subadult male in a trap next to me (from a different area in which I was at that moment), answered an adult male which I was watching and caused him to continue vocalising for 13 minutes, each time responding to one another.

3. Alarm vocalisation: Once a trapped squirrel chirped when I approached it and when I picked it up, it urinated, obviously alarmed. They often seemed to vocalise shortly after suddenly noticing me such as when I came around a corner. They have been seen to mob a snake in a group (Schlettwein pers. comm.), and in the present study two subadults also once mobbed a snake. This mobbing consists of peering down to the ground, whilst tailflicking and chirping, and every now and again moving around the tree. They were also seen to mob once for 10 minutes, the calls attracting the adult male to the group, but the cause could not be determined. However, the next day a large lizard was seen in this spot, and the reptilian movement could have caused them to start calling. In response to birds of prey the chattering was of a higher frequency with almost no audible inter-pulse breaks, sounding like a whistle. This is allelo-mimetic and causes the squirrels to freeze instantly. This call is reminiscent of that of the bush squirrel alarm behaviour towards raptors (Viljoen 1977) and quite different from the situation in forest squirrels which give a low-pitched bark (Viljoen unpubl.). A scops owlet was once chased off by the adult female in the group (two subadult squirrels were with her). She rushed at it with an excited series of chirps causing it to fly off.
4. Juvenile vocalisation: A lactating female, released next to her nest tree, gave two chirps, and was answered after a few moments by juvenile barking from the drey. She immediately rushed towards the nest. These barks are very similar to those given by pups of the genus *Paraxerus* (Viljoen 1977).

6.3 Alarm and alertness

The animals are particularly tame compared to forest squirrels, both when one approaches them and when one holds them in the hand (they do not attempt to bite as squirrels of the genus *Paraxerus* do). They can move past you at 3,0 m distance, being aware of as they obviously peer at you, but do not take fright. On one occasion one was disturbed at a trap when I came to within 2,0 m of it, and when I turned and walked off to a distance of 8,0 m, he returned to the trap trying to extricate the food from the back. This might be an adaptive strategy in the particularly open habitat where they would be better off freezing where they are (they are cryptically coloured and difficult to distinguish when motionless) than to move off. Also, as regards conservation of energy in a hot environment, it would be beneficial for them to spend as little energy as possible. They are often seen on the ground, but flee to trees at the slightest disturbance. They are also very tame at nesting time, when forest squirrels are usually extremely wary and ready to move to another nest at the least disturbance. In *Funisciurus* habitat it would be impossible to have numerous nests to choose from and the best would be not to move off. When alert the hairs on the tail are spread, and the tail is flicked. Tailflicks are sporadic jerks, with the tail still in the questionmark shape.

6.4 The tail and thermo-regulatory behaviour

The animal does not carry its tail loosely as recorded by Shortridge (1934) but carries it in a questionmark reminiscent of overseas squirrels, over the head (Figure 1). When raising the tail over the back thus, the undersurface of the tail, which is very light when compared to the back, fits neatly in between the two white side-stripes presenting a light-coloured reflecting surface to the sun. It is also remarkable that the distal part of the tail very often throws a patch of shade over the animal's head. This squirrel is adapted to arid open and hot regions and the method of carrying the tail is in sharp contrast to that of *Paraxerus*, which carries it loosely and curls it around the body in cold weather (Viljoen 1975). The hairs on the tail of *Paraxerus* are also longer than those of *Funisciurus congicus*. *Xerus*, another squirrel from an arid, hot environment, is also quoted as using its tail for thermoregulatory purposes (Marsh, Louw and Berry 1978), and Golightly (1976) found that Aberts squirrels (*Sciurus aberti*) raised the tail above the body in response to elevated body temperature.

6.5 Nests

The striped squirrel differs once again from the bush squirrel and other members of the genus *Paraxerus* in utilising dreys in addition to natural holes in trees. In the study area, some squirrels were using holes in trees and others were using leaf-nests (Table 3). Perhaps they move from leaf-nests in the summer to holes in trees in winter. Nest-building was seen on one occasion in the morning when an adult lactating female moved 150 m in 23 minutes whilst she fetched bundles of nesting material from a disused drey (eight trips) and carried it each time to the hole in the tree which they were at that time using for nesting. The leaf-nests are placed in a fork in the branches, and from the outside are covered with grass and twigs. Emmons (1975) records leaves and bark fibres as nesting material for *Funisciurus* in Gabon.

6.6 Activity

Sunrise was at 07h05 and sunset at 19h00; sun rays first appeared on the trees at 07h20 on a clear day. The squirrels' emergence from nests ranged from

07h20 to 08h15 (light intensity around 1400 lux, measured with incidence dome on Luna Six 3 light meter) depending on whether it was a clear or an overcast day. They left the next tree soon after leaving the nest. They returned to the nest in the late afternoon from 18h00 to 18h53, but mostly before 18h40, well before sunset (light intensity around 700 lux).

Table 4 presents distance travelled per 15 minutes throughout the day, periods spent dozing motionless, as well as time spent feeding and temperatures throughout the day. Distance and number of times moved indicate that they were most active early in the day. However, the early mornings were already chilly and they were probably generating heat by movement. Golightly (1975) monitoring Aberts squirrels (*Scuirus aberti*) with temperature sensitive transmitters, found that the degree of hyperthermia was directly related to the intensity of activity. The relatively long time motionless early in the day was preferably spent basking in the sun and this also suggests that the striped squirrels needed heat. Time spent feeding dropped towards 16h00, as did all other measurements of activity. They could be seen or heard at any time of the day (Table 5).

7 DISCUSSION

This short project forms part of a broader comparative study of the eco-ethology of southern African tree squirrels. *F. congicus* is a west African species and differs in various respects from the only other southern African genus *Paraxerus*. The building of dreys is a habit alien to both *P. cepapi* and *P. palliatus*. It has, however been found in other species of *Funisciurus* (Walker 1964; Emmons 1975), and could have evolved in a habitat where nest-holes are at a premium. This might also hold true for the American grey squirrel, *Sciurus carolinensis* where Burger (1969) found that placement of artificial nest boxes increased the population size, indicating a shortage of natural nest-holes in certain habitats. The other southern African woodland species, *Paraxerus cepapi*, is limited to fire controlled habitat and this probably caused their exclusive nesting in natural holes in trees.

Although the behavioural contexts of vocalisation in the different squirrels are similar, the birdlike chirrups of the striped squirrel differ from the more raucous clicks and rattles of squirrels of the genus *Paraxerus*. Striped squirrel vocalisations possibly take up less energy and in open habitat these sounds will also carry over a sufficient distance, whereas the sounds of *Paraxerus* can penetrate either denser vegetation (such as in the forest species *P. palliatus*) or carry over larger distances (as in woodland species *P. cepapi*). However, the two vocal reactions of extreme alarm i.e. the raptor alarm whistle (also found in *P. cepapi*) and the alarm barks of a yet dependent pup in the nest (found in all the squirrels encountered) are very similar. This is probably parallel evolution of the most efficient survival vocalisation under these circumstances.

The carrying of the tail over the back and head indicates an animal adapted to an open hot environment. Golightly (1976) monitoring Abert's squirrels (*Sciurus aberti*) with temperature-sensitive transmitters, found that they raised the tail above the body in response to elevation of body temperature, and that the white ventral side of the tail has a higher reflectance (58 per cent at 750 nm) than the grey dorsal body pelage (10 per cent at 750 nm). He suggests that the tail is used as a shading device that moderates solar radiation striking the body.

The striped squirrel has a completely different rat-like smell from any of the other squirrels here considered. The significance of this is not clear, as very little is known of their olfactory communication.

Kingdon (1974) regards *Paraxerus* as a subgenus of *Funisciurus*. However, in the light of the above-mentioned differences between *F. congicus* and two different *Paraxerus* sp. studied (Viljoen unpubl.) they are here given separate generic status. The small size of the striped squirrel, pale colour and cohesive group structure all indicate an animal adapted to an open environment. Although it does overlap with *P. cepapi* in certain areas, they still show preference for a slightly different niche. The latter animal is better adapted to moving some distance over open ground, the former to slightly denser habitat enabling them to move from twig to twig on thinner branches than *P. cepapi*. The colour of these two open habitat squirrels is very similar and sometimes, at a glance, they might even be mistaken for one another. But the pale side-stripe, white ventrum and limbs as well as the relatively large eye of the striped squirrel are distinctive. Compared to other species of the genus, *F. congicus* is also much lighter coloured. The range of movement fits the small size of the animal. The home range is slightly smaller than that of the slightly larger (142 g and 300 g respectively) *F. lemniscatus* (0,94 to 1,24 ha) and *F. pyrrhopus* (1,0 to 5,17 ha) in Gabon (Emmons 1975).

Feeding as in most other tree squirrels is opportunistic, and similar to habits found in the bush squirrel (Viljoen 1976b).

The small litter size of two is consistent with litters in other African squirrels (Emmons 1975; Viljoen 1975), and contrasts with Nearctic and Palearctic tree squirrels that have more young born in a more altricial state of development.

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TABLE 1: Numbers of the different tree species in one daily range (4 000m^2) of a group of *F. congicus.*

Tree species	Total	Shrub	Sub-Canopy	Canopy
Acacia mellifera var. *detinens*	12	8	4	
A. reficiens	31		27	4
Boscia albitrunca	1		1	
Colophospermum mopane	179	150	5	24
Combretum apiculatum	24	11	12	1
C. imberbe	2			2
Commiphora pyracanthoides	1	1		
Croton gratissimus var. *subgratissimus*	4	4		
Dichrostachys cinerea	31	31		
Grewia bicolor	87	87		
G. flavescens	62	62		
G. villosa	7	7		
Lonchocarpus nelsii	24	8	10	6
Maytenus senegalensis	7	7		
Mundulea sericea	2	2		
Terminalia prunioides	19	17	2	
Ziziphus mucronata	6	3	3	
Total	499	398	64	37

TABLE 2: Mass (g) and standard body measurements (mm) of the western striped squirrel, *F. congicus* (mean and standard deviation).

	Head and body	Tail	Hindfoot (c.u.)	Ear	Mass
Present study:					
(April 1978)					
Subadults (n = 5)		154,80 ± 3,27	38,30 ± 1,27	14,48 ± 1,03	75,40 ± 2,88
Adults (n = 6)		160,20 ± 4,76	38,57 ± 1,04	15,12 ± 1,71	108,17 ± 5,88
Museum specimens:					
Juvenile (n = 7)	123,75 ± 8,54	140,71 ± 12,96	35,71 ± 2,75	13,29 ± 2,69	—
Subadult	140,0 ± 5,90 (n = 7)	149,33 ± 11,34 (n = 9)	39,33 ± 0,82 (n = 9)	15,33 ± 2,12 (n = 9)	66,75 ± 3,86 (n = 4)
Adult	146,91 (n = 23)	161,08 ± 9,10 (n = 26)	40,18 ± 2,13 (n = 17) 37,83 ± 2,18 (s.u.) (n = 18)	15,84 ± 2,42 (n = 45)	113,0 ± 7,78 (n = 13)
Shortridge (1934):					
Juvenile (n = 1)	98	107	31	12	
Adults (n = 49)	155,94 ± 6,63	169,90 ± 10,04	40,23 ± 1,08	16,66 ± 0,60	
Roberts (1951):					
Juveniles (n = 1)	120	130	34 (s.u.)	16	
Adults (n = 8)	148,3	169,33	38,67 (s.u.)	15,33	

TABLE 3: Description of nestholes and dreys of the western striped squirrel, *F. congicus.*

	Tree species	Height of nest-hole or drey and dimensions of drey	Direction of entrance
Nestholes	*Colophospermum mopane*	1,75 m (tree 4 m high)	West
	C. mopane	2 m (tree 9 m high)	West
Dreys	*C. mopane*	12 m (14 x 22 cm)	
	C. mopane	9 m (14 x 25 cm)	
	Lonchocarpus nelsii	5 m (15 x 20 cm)	East
	Combretum imberbe	11 m (15 x 20 cm)	

TABLE 4: Activity of striped squirrels, *F. congicus* throughout the day. (Sample size in parenthesis)

Shade temp. °C (n = 2)	Time of day	Distance travelled/ 15 minutes (metres)	No. of times move/15 minutes	Time motionless (seconds)/15 minutes	Time spent feeding (seconds)/15 minutes
13 – 19	07h00 – 09h00 (n = 9)	41,67 ± 20,05	11,75 ± 5,76	210±222,49	86,67±216,67
19 – 27,9	09h00 – 13h00 (n = 10)	25,24 ± 16,39	7,70 ± 4,66	159,43 ± 127	43,21 ± 59,35
27,9 – 29	13h00 – 16h00 (n = 12)	17,63 ± 15,21	6,25 ± 4,47	222,50 ± 376,5	175,83 ± 194,50
29 – 23,8	16h00 – 19h00 (n=6)	11,10 ± 9,90	2,29 ± 3,82	326,56 ± 398,38	46,88 ± 87,62

TABLE 5: Numbers of squirrels *F. congicus* encountered throughout the day.

Shade temp. °C (n = 2)	Time of day		Total no. of squirrels either seen or heard	Total no. of squirrels heard
13 – 19	07h00 – 09h00	(n = 7)	2,4	0,86
19 – 24,5	09h00 – 11h00	(n = 6)	2	0,17
24,5 – 27,9	11h00 – 13h00	(n = 4)	2,5	1,75
27,9 – 28,6	13h00 – 15h00	(n = 6)	1,5	1,17
28,6 – 28,4	15h00 – 17h00	(n = 7)	1,14	1,00
28,4 – 23,8	17h00 – 19h00	(n = 5)	3,0	2,00