Feeding habits and comparative feeding rates of three southern African arboreal squirrels

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Food utilization by three arboreal squirrels was studied with regard to feeding habits and efficiency, food preferences and chemical analyses of the food. Food selected in the field by the two forest subspecies the Ngoye red squirrel *Paraxerus palliatus ornatus* and the Tonga red squirrel, *P. p. tongensis* are listed. Measurements of lengths of the different parts of their intestinal tracts indicate that the southern African arboreal squirrels are more insectivorous than tropical African squirrels. With regard to feeding efficiency, the tree squirrel *P. cepapi cepapi*, a savanna species, is relatively more adept at handling small seeds and the flesh of fruits, whereas the two forest subspecies mainly concentrate on the endosperm of large fruits. Chemical analyses of fruits and seeds indicate that the fat content is noticeably higher in fruits and endosperm from forests and that the protein content of savanna endosperm is higher than from the forest.

S. Afr. J. Zool, 1983, 18: 378–387

Voedselbenutting deur drie boomeekhorings is met betrekking tot voedingsgewoontes, hanteringseffektiwiteit, voedselvoorkeur en chemiese analieses van die verskillende kossoorte bestudeer. Voedsel wat deur die twee woudsubspesies, die Ngoya rooieekhoring *Paraxerus palliatus ornatus* en die Tonga rooieekhoring *P. p. tongensis* in die veld geselekteer is, word gelys. Afmetings van die lengtes van die verskillende dele van die spysverteringskanaal dui daarop dat die suidelike Afrikaanse boomeekhorings meer insekvretend is as boomeekhorings vanuit tropiese dele van Afrika. Met betrekking tot hanteringseffektiwiteit, is die boomeekhoring, *P. cepapi cepapi* wat 'n savanna spesie is, betreklik meer effektief wanneer dit by klein saadjies en die vrugtevleis kom. In teenstelling, konsentreer die woudsubspesies hoofsaaklik op die endosperm van groot vrugte. Chemiese analiese van vrugte en endosperm dui op 'n hoër vetinhoud vanuit die woudvrugte, maar op 'n moontlik hoër proteïenvlak vanuit savanna-endosperm.

S.-Afr. Tydskr. Dierk. 1983, 18: 378 – 387

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Four species of indigenous arboreal squirrels occur in southern Africa: the tree squirrel, *Paraxerus cepapi*; the red squirrel, *P. palliatus*; the striped tree squirrel, *Funisciurus congicus* and the sun squirrel, *Heliosciurus rufobrachium*. In this paper only the nominate form of the first-named and two subspecies of the second are considered.

Amtmann (1975) listed 10 subspecies of *P. cepapi* from southern Africa, some of doubtful validity, and 11 subspecies of *P. palliatus*. The nominate *P. c. cepapi* was originally described from the Rustenburg district of the Transvaal and has an average mass of 223 g ($n = 69$), and the Tonga red squirrel, *P. p. tongensis* was originally described from the Mangusi Forest, northern KwaZulu, 209 g ($n = 60$). The Ngoye red squirrel, *P. p. ornatus* which occurs only in the Ngoye Forest, KwaZulu is larger than the other two with an average mass of 368 g ($n = 104$). *P. cepapi* is a woodland savanna species, *P. p. tongensis* occurs in xeric to mesic coastal forests and *P. p. ornatus* in evergreen, moist subtropical forest.

Food utilization, which is an important aspect of niche characterization and habitat requirements, was studied with regard to relative feeding efficiency, food choice and chemical analyses of the wild fruits. Food selected by *P. cepapi* has been documented in Viljoen (1977).

Material and Methods

Food selected by the tree squirrel, *P. c. cepapi*, the Tonga red squirrel *P. p. tongensis* and the Ngoye red squirrel *P. p. ornatus* was noted in the field and also in captivity. The amount of time (s) spent feeding by four captive individuals of each of the three squirrels was recorded for 10 fruits of each of 23 species. Fruits were collected in the forests of KwaZulu and refrigerated until used. Feeding times on flesh (exocarp and mesocarp) and seed (endocarp and endosperm) were noted separately and are represented as relative feeding efficiency in percentages. In an attempt to establish possible preferences for different classes of fruits, arbitrary divisions were made between fleshy 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 wet mass, respectively).

The lengths of stomachs, small intestines, caeca and large intestines were measured in the fresh state to obtain an estimate of frugivory/insectivory of the different squirrels. Permission to collect squirrels was difficult to obtain, and traps had to be used. No stomach content analyses of the trapped squirrels were recorded as the ingestion of the bait would have affected the results.

Proximate analyses (moisture, ash, fibre, protein, fat and carbohydrate values of the mesocarp and endosperm, i.e. peeled flesh and dehusked seed) were made of various species of fruits in order to obtain information on the energy and quality of food available in the different habitats.

Results

Observations on feeding habits

Field records of food of *P. p. ornatus* and *P. p. tongensis* are listed in Tables 1 and 2 respectively. Both subspecies fed on large and small fruits, and in captivity, preferred fruits that had a large endosperm such as *Harpephyllum caffrum* and *Garcinia* spp. In the wild they searched for ripe fruits, but if these were not available they would take unripe fruits and even extract the endosperm through the germination pore.

Close observation revealed that they gnaw by holding the top incisors steady, pressing the nut against them, and moving the lower incisors rapidly in order to make the incision. They either opened the nut at the germination pore or sometimes split it open. *Sapium integerrimum* nuts have three seed-vessels, and were opened at the three pores by *P. c. cepapi* and *P. p. tongensis* but *P. p. ornatus*, which is the largest of these squirrels and has a superior gnawing ability, severed off one of the three hard seed-cases to get at the seeds.

Surplus seeds were scatter-hoarded (i.e. buried individually)

Table 1 Feeding records[a] of *P. p. ornatus* from April 1976 to May 1978 in Ngoye forest (tree species except where otherwise stated)

Plant part utilized	Species	Month and year
Mesocarp and endosperm	*Trichilia dregeana*	6/76; 5/78
	Solanum mauritianum	6/76; 1/78
	S. geniculatum	1/78
	S. giganteum	1/78
	Oxyanthus speciosus	6/76
	Harpephyllum caffrum	11/76; 10/77
	Flagellaria guineense — climber	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 speciosus — climber	6/76; 5/78
	Dalbergia armata — climber	6/76
Leaf	Tree orchid	1/78

[a]Number of observation hours: 845.

after removing the exocarp and mesocarp. Preferred hoarding sites were against a tree trunk or rock, or in a hole in a tree, but food was sometimes wedged between two branches. No large food stores were assembled. Only large seeds were hoarded by *P. p. ornatus* such as those of *Drypetes gerrardii, Syzygium guineense gerrardii, Garcinia gerrardii, Harpephyllum caffrum* and *Trichilia dregeana*. *P. p. tongensis* hoards the seeds of *Ziziphus mucronata*, and *Inhambanella henriquesii*. Arboreal squirrels are omnivorous (Viljoen 1977), and have been recorded on occasion to take fledglings (Stutterheim, pers. comm.). This was not recorded during the present study and probably is a rare occurrence. However, a glossy starling was observed to attack an Ngoye red squirrel *P. p. ornatus* and a black-crowned tinker barbet a Tonga red squirrel *P. p. tongensis*, suggesting that these birds are apprehensive towards squirrels. Hand-reared squirrels ate raw liver and biltong but in the wild, fed on the flesh and kernels of fruits and invertebrates which together form the greater part of the diet. In captivity the squirrels displayed hunting behaviour, following ants and chasing and reaching up for moths and winged termites. They often scratched underneath bark to extract insects and also obtained larvae from parasitized seeds such as those of *Milletia sutherlandii* and *Protorhus longifolia*. Of 556 *P. longifolia* seeds, 87,6% were parasitized, and captive *P. p. tongensis* fed on the seed as well as on the larvae of the parasites. The skin of the fruit and husk of the kernel were discarded by all three squirrels and the forest squirrels frequently discarded the flesh.

Fruit supply is to a large extent seasonal (Viljoen 1980). The result is that both savanna and forest squirrels are opportunistic feeders. *P. c. cepapi* took nectar, chewed aloe leaves, licked pollen and ate green shoots, new leaves and termites (Viljoen 1977). At certain times the squirrels had to feed almost exclusively on a single plant species. *P. p. ornatus* fed on berries of the shrub *Solanum mauritianum* in June 1976 and on *G. gerrardii* in April 1977. The forest subspecies moved widely through the home range even though they could have found enough food in one tree. This is probably both for social reasons and in order to familiarize themselves with the ripeness of various foods throughout the range.

Both in captivity and in the wild squirrels drank water, often obtaining a supply from holes in trees. However, they do not appear to be dependent on a water supply for they occur in areas where it is not always available.

Food preferences

The divergent tastes and feeding abilities of the different species of squirrel make it impossible to use certain fruits and seeds in the comparison of feeding rates (Table 3).

— Many of the forest plant species have fruits and seeds which are unattractive to or too hard to open for *P. c. cepapi*. The softer seeds of mopane, *Colophospermum mopane*, a bushveld tree species, were taken by *P. c. cepapi* and *F. congicus*, but not by the forest squirrels.

— *P. c. cepapi* sometimes feeds on the flesh of fruits (e.g. *Diospyros* spp.) which are totally ignored by *P. palliatus*.

— A further discrimination was shown by *P. p. ornatus* against small seeds. In captivity they showed little interest in the seeds of *Apodytes dimidiata, Allophylus natalensis, Rinorea angustifolia, Phyllanthus discoideus, Croton sylvaticus, Cassipourea gummiflua, Trema orientalis* and *Rhus chirindensis*, even though most of these were taken in the field.

— The flesh of certain fruits was very sticky or highly aromatic

Table 2 Feeding records[a] for *P. p. tongensis* in Maputaland

Plant part utilized	Species	Month & year	Reference[b]
Mesocarp	*Strychnos spinosa*		I.F.G.
	S. madagascariensis		I.F.G.
	S. innocua		I.F.G.
	Monanthotaxis caffra — shrub		I.F.G.
	Balanites maughamii		I.F.G.
	Vitex sp. — shrub		I.F.G.
	Uvaria caffra — shrub		I.F.G.
	Diospyros natalensis		p.s.
	Landolphia kirkii — climber		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 leptoclada — shrub	2/78	p.s.
	Artabotrys monteiroae — shrub	6/77	p.s.
	Trema orientalis	4/76	R.T. & F.J.
	Parinari capensis incohata — shrub		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. — shrub	11/75	p.s.
	Celtis africana	11/75	p.s.
Roots	Tree fern		p.s.
Lichen			p.s.

[a]Number of observation hours: 657. [b]I.F.G. I.F. Garland (No dates available), R.T. R. Taylor, F.J. F. Joubert, p.s. Present study.

Table 3 Preference and rejection of captive *P. p. tongensis, P. p. ornatus* and *P. c. cepapi* towards certain plant species[d]

Plant species	Habitat collected[a]	Preference shown by[b]	Behaviour during feeding and/or reason for rejection
Landolphia kirkii	T	T O	Outer seed coat too hard for C[a] to open
Strychnos madagascariensis	T	T O	Outer seed coat too hard for C to open
Garcinia gerrardii	O	T O	C merely sniffs
G. livingstonei	T	T O	C feeds on flesh, but drops nut
Trichilia dregeana	O	T O	C merely sniffs
T. emetica	T O	T O	C merely sniffs
Syzygium guineense gerrardii	O	T O	C merely sniffs
Linociera peglerae	T	T O	C merely sniffs
Pancovia golungensis	T	T	O clears throat; C merely sniffs
Inhambanella henriquesii	T	T	O drops; C merely sniffs
Parinari curatellifolia	T	T O C	C only on flesh
Chrysophyllum viridifolium	O	None[b]	Flesh elicits mouthwiping, very sticky
Diospyros lycioides	C	C	C feeds on flesh, seed only tasted
D. natalensis	T	None	C feeds on flesh, seed only tasted
Mimusops spp.	T O	None[c]	C feeds on flesh, seed only tasted
Teclea natalensis	O	None	Merely sniff; aromatic?
Erythrina spp.	T O	None	Merely sniff
Xeromphis sp.	T	None	Very aromatic? Squirrels merely sniff
Phoenix reclinata	T	None	Taken by T&O, but never finished
Hyphaene ventricosa	T	None	Too hard to penetrate
Colophospermum mopane	C	C	T and O merely taste then mouthwipe
Acorns (exotic)	–	T O C	Much sought after

[a]T = *Paraxerus palliatus tongensis*, O = *P. p. ornatus*, C = *P. c. cepapi*. [b]Seeds when offered clean, are taken. [c]Soft young seeds are eaten. [d]10 seeds of each plant species offered.

Table 4 Intestinal tract measurements (mm) of three *Paraxerus* spp. (means and levels of probability of *T*-tests for two means)

	C[a]	T[a]	C	N[a]	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	

[a]C = *Paraxerus cepapi*, n = 31; T = *P. palliatus tongensis*, n = 10; N = *P. p. ornatus*, n = 7.

(e.g. *Chrysophyllum viridifolium*, and *Teclea natalensis* respectively) and even though some of the seeds were taken the rest of the fruit was discarded.

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 4). *P. c. cepapi* had a longer large intestine and shorter small intestine than *P. p. tongensis*. The mean adult mass of these two species, however, was similar. Table 5 shows that the southern African arboreal squirrels have comparatively short, small intestines and caeca.

Feeding efficiency

All the fruits tested were indigenous except *Solanum mauritianum* which occurs extensively in KwaZulu and was taken by *P. palliatus*, and *Melia azedarach* which was taken by *P. c. cepapi*. The flesh of the various fruits varied in mass from 0,07 g for *Ozoroa obovata* to 25,46 g for *G. gerrardii* and the seeds from 0,09 g for *Grewia occidentalis* to 10,25 g for *G. gerrardii*. To obtain an idea of the size of the seeds taken by the three squirrels from the different habitats, measurements of the diameter of seeds were taken from Coates-Palgrave (1977). This showed that *P. c. cepapi* took seeds with a diameter of 13,0 mm ± 10,08 (*n* = 13); *P. p. tongensis* 17,58 ± 10,69 (*n* = 24) and *P. p. ornatus* 20,77 ± 8,06 (*n* = 14). Measurements from the present study are presented in Tables 6 and 7. The measurements of seeds from the bushveld did not include grass seeds which are normally part of the diet of

Table 5 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 and Hb[a]		Small intestine	Caecum
Protoxerus stangeri	293	1103	360
Heliosciurus rufobrachium	255	1246	331
Funisciurus carruthersi	216	771	176
F. pyrrhopus	198	2036	286
Paraxerus alexandri	105	2067	433
P. boehmi emini	135	2571	439
F. anerythrus	186	2821	359
Paraxerus c. cepapi	185	350	18
P. palliatus tongensis	188	631	24
P. p. ornatus	221	948	22

[a]Hb = Head-body length (mm).

P. c. cepapi. Therefore the average size of seeds taken by *P. cepapi* would be much smaller than the above estimate.

There are great differences in texture, taste, hardness of husk, and searching time with the result that there is no relationship between seed size and the time spent in feeding. Examples of two fruit species of the same flesh mass (0,3 g) but with different squirrel feeding rates (means of 10 trials) are *Apodytes dimidiata*, where the mesocarp took *P. p. ornatus* 51 s to consume, *P. p. tongensis* 67 s and *P. c. cepapi* 75 s, and *Trichilia emetica* where the aril took *P. p. ornatus* 126 s, *P. p. tongensis* 220 s and *P. c. cepapi* 255 s. *P. c. cepapi* was a relatively more efficient feeder on small seeds than on large seeds, sometimes even feeding in a shorter time than *P. p. tongensis* and being nearly as quick as *P. p. ornatus*. Similarly, with small seeds *P. p. tongensis* is sometimes more efficient than *P. p. ornatus*. However, *P. p. ornatus* fed more efficiently on the medium and large-sized seeds than *P. c. cepapi*. Compared with *P. c. cepapi* both *P. p. tongensis* and *P. p. ornatus* fed more efficiently on large seeds than on fruits.

To obtain a comparative estimate of feeding efficiency, the feeding time of the larger species of squirrel was calculated as a percentage of that of the smaller species (Tables 6, 7 & 8). The closer to 100% the more equal are the two species in feeding rate, and the lower the percentage, the more efficient is the larger squirrel species. Generally, the larger *P. p. ornatus* fed at a quicker rate than *P. p. tongensis* and both these forest species fed more efficiently than *P. c. cepapi*, even though *P. p. tongensis* does not differ significantly in size from *P. c. cepapi* (Viljoen 1980).

P. c. cepapi was more adept in handling small seeds and the flesh of fruits, whereas *P. p. ornatus* and *P. p. tongensis* concentrated mainly on kernels. When feeding times on 10 species of small seeds and 11 species of medium to large seeds were compared, *P. p. ornatus* and *P. p. tongensis* were both more efficient than *P. c. cepapi*. On average *P. p. ornatus* and *P. p. tongensis* fed in 41,4% and 59,5% of the time respectively than *P. c. cepapi* does on medium to large seeds, and in 69,2% and 78,6% of the time, respectively, on the small seeds. *P. p. ornatus* fed in 100,3% of the time that *P. p. tongensis* did; but *P. p. ornatus* was more efficient when dealing with larger seeds and fed in 66,7% of the time taken by *P. p. tongensis*. The smallest species, *F. congicus* fed consistently slower than *P. c. cepapi* on *C. mopane* seeds (290,5 ± 97,7 s, *n* = 22; *cf.* 223,1 ± 52,9 s, *n* = 15).

Food analyses

Analyses of fruits of 17 and seeds of 10 plant species from

Table 6 Feeding rates of *P. p. ornatus, P. p. tongensis* and *P. c. cepapi* on seeds from KwaZulu forest tree species[d] (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[b] *cepapi*
1	*Teclea natalensis*	1,12	19,2 × 12,0	20,7	87,3	18,0
1	*Melia azedarach*	0,37	9,7 × 7,8	38,6	50,5	19,5
3	*Sapium integerrimum*	0,90	19,0 × 16,0	15,9	129,2	20,6
5	*Chrysophyllum viridifolium*	0,45	15,9 × 11,2	23,9	124,4	29,8
1	*Diospyros natalensis*[a]	0,19	9,9 × 5,4	62,3	54,5[a]	33,8[a]
1	*Harpephyllum caffrum*	1,10	22,2 × 10,6	48,4	72,1	34,9
1	*Canthium inerme*	0,12	7,0 × 3,4	65,6	69,0	45,6
1	*Ozoroa obovata*	0,16	6,0 × 4,3	64,2	71,4	45,9
1	*Apodytes dimidiata*	0,11	8,2 × 6,4	107,4	43,7	46,9
1	*Ziziphus mucronata*	1,16	12,5 × 12,5	87,1	60,4	52,6
1	*Mimusops obovata*	0,26	12,6 × 6,2	64,7	83,0	53,9
3	*Grewia occidentalis*	0,09	6,2 × 3,5	129,3	46,3	59,9
1	*Syzygium guineense gerrardii*[a]	1,09	12,0 × 11,0	64,3	95,7	61,6
1	*Cassine aethiopica*	1,76	16,4 × 13,8	52,5	125,6	65,8
5	*Trichilia dregeana*	1,38	24,0 × 11,3	118,3	67,1	79,3
1	*Dialium schlechteri*	0,09	15,9 × 10,9	162,6	56,2	91,3
1	*Sideroxylon inerme*	0,14	6,1 × 5,8	59,8	158,4	94,7
1	*Linociera peglerae*[a]	1,48	17,8 × 12,7	[a]	28,4	[a]
1	*Garcinia gerrardii*[c]	10,15	29,6 × 27,3	[a]	[a]	[a]
1	*Colophospermum mopane*[a]	0,77	28,1 × 18,9	101,8	[a]	[a]
1	*Rhus englerae*	0,03	3,0 × 3,0	49,8	[a]	[a]
1	*Olea capensis*	0,87	15,5 × 13,9	29,3	81,5	23,9
1	*Phyllanthus discoideus*				126,0	

[a]Refusal to feed by one or both of the species, either consistently, or occasionally. [b]Arranged for most efficient feeding of *P. p. ornatus*. [c]Squirrels never finish this large kernel. [d]10 fruits of each species.

Table 7 Feeding rates of *P. p. ornatus, P. p. tongensis* and *P. c. cepapi* on fruits from KwaZulu forest tree species[b] (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	11,8 × 11,6	41,0	38,8	15,9
Cassine aethiopica	4,45	23,9 × 23,6	64,9	54,0	35,0
Ziziphus mucronata	2,01	18,0 × 18,0	75,7	56,1	42,4
Syzygium guineense gerrardii	3,15	17,8 × 17,7	102,6	44,8	45,9
Solanum mauritianum	0,99	13,3 × 11,6	94,0	50,4	47,3
Diospyros natalensis	0,37	10,6 × 8,3	61,6	93,8	57,8
Linociera peglerae	2,35	21,8 × 18,6	109,1	59,2	64,6
Sideroxylon inerme	0,45	9,8 × 9,7	67,5	96,5	65,1
Apodytes dimidiata	0,30	10,9 × 7,3	90,7	75,0	68,0
Harpephyllum caffrum	2,70	24,0 × 16,0	94,8	75,0	71,1
Melia azedarach	0,36	12,7 × 12,3	78,6	102,7	80,8
Ekebergia capensis	1,44	19,7 × 16,2	87,8	100,0	87,8
Sapium integerrimum	6,03	24,0 × 22,0	100,8	113,6	114,4
Dialium schlechteri	0,22	21,1 × 14,6	[a]	50,6	[a]
Trichilia emetica	0,58	20,1 × 12,6	[a]	90,7	[a]
Trichilia dregeana	0,31	20,4 × 13,0	[a]	62,3	[a]
Canthium inerme	0,51	10,1 × 6,1	81,6	[a]	[a]
Colophospermum mopane	0,75	Only skin	267,9	[a]	[a]
Mimusops obovata	1,32	15,0 × 12,0	62,5	102,8	64,2
Ozoroa obovata	0,07	6,5 × 4,4	[a]	[a]	[a]

[a]Refusal to feed by one or both of the species. [b]10 fruits of each species.

the savanna habitat (CSIR data, Table 9) are compared to fruits of 33 and seeds of 35 plant species from the forest habitat (data from present study and from CSIR , Tables 10 & 11). These data indicate a higher energy content for both fruits and en-dosperm 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.

Table 8 Feeding rates on fruit and seed combined for *P. p. ornatus*, *P. p. tongensis* and *P. c. cepapi* (feeding time of the larger squirrel species[b] as 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	0,77	111,0	[a]	[a]

[a]Refusal to feed by one or both of the species. [b]Mean adult mass: *P. p. ornatus* 368 g, *n* = 104; *P. p. tongensis* 209 g, *n* = 60; *P. c. cepapi* 223 g, *n* = 69.

Table 9 Proximate analysis of fruits and seeds from tree species in habitat of *P. cepapi*

	g/100 g dry weight					Energy
	Ash	Protein	Fat	Fibre	COH	kJ/100 g
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
Vangueria infausta	3,8	3,7	0,4	13,2	78,9	1405
Ziziphus 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

Differences between values for *P. p. tongensis* and *P. p. ornatus* habitats do not appear significant apart from the higher carbohydrate value for the seeds eaten by *P. p. ornatus*.

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 & Svendsen 1978). Winter is the crucial time of food scarcity.

Table 10   Proximate analyses of fruits and seeds of forest tree species (g/100 g) on a moisture-free basis in order of energy content (kJ/100 g)

Species	Ash 1[a]	Ash 2[b]	Fibre 1	Fibre 2	Protein 1	Protein 2	Fat 1	Fat 2	Carbohydrates 1	Carbohydrates 2	Energy 1	Energy 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 abovata (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) ± S.D.		3,48 ±1,79		17,39 ±16,13		11,91 ± 6,22		21,68 ±19,59		45,32 ±26,75		1772,4 ± 536,9
Additional fruits only												
Euclea natalensis	3,7		2,4		2,3		0,7		90,9		1592	
Landolphia kirkii	4,5		3,2		3,2		1,9		87,3		1592	
Ximenia americana	5,7		8,8		21,0		6,3		58,3		1570	
Salacia kraussii	5,6		4,3		6,8		2,5		80,9		1568	
Mimusops caffra	4,3		6,3		2,8		2,0		84,6		1544	
Dialium schlechteri	4,2		5,3		3,0		0,8		86,7		1537	
Scutia myrtina	4,5		5,3		2,3		0,4		87,5		1524	
Ochna sp.	1,8		18,2		13,6		9,0		55,2		1496	
Olea capensis	3,8		11,5		4,2		1,0		79,6		1446	
Cassine aethiopica	4,5		14,3		3,3		1,2		76,9		1392	
Solanum mauritianum[c] (a)	2,4		29,0		11,0		10,2		47,7		1369	
Ficus vogelii[c]	7,9		21,7		4,6		3,3		62,5		1252	
Antidesma venosum	17,5		14,3		6,4		2,1		59,9		1193	
Mean (n = 33) ± S.D.	5,33 ± 3,04		10,73 ± 8,24		7,41 ± 4,70		8,43 ±13,11		66,87 ±17,96		1582 ± 299,9	

[a]1 Exo- and mesocarp except where noted (a) in which case analyses only of mesocarp. [b]2 Endocarp and endosperm except where noted (b) in which case analysis of endosperm only. [c]Analysis of total fruit including the many pips.

Table 11 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

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 which is the habitat of the tree squirrel, the main seeding-time is from January to May, and in northern KwaZulu, where two subspecies of the red squirrel, *P. palliatus* occur, the bulk of fruits is available from December to August with peaks mainly in January but also in June (Viljoen 1980). The prime time for insects to emerge in South Africa, is from January to March (De Villiers, pers. comm.) even though the social insects such as the Termitidae are available as food throughout the year (Viljoen 1977).

Tree squirrels are omnivorous and are opportunistic to a large extent (Shorten 1951; Rahm 1972; Emmons 1975; Viljoen 1977). 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 also 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 rain-forest squirrels along a spectrum of size and hardness; and MacKinnon (1978) working on nine squirrel species in a Malayan tropical forest, found divergence facilitated by differential use of forest strata associated with differences in locomotor adaptations, dietary specializations, activity times, and foraging patterns resulting from major differences in body size and also in differences in social organization and spatial distribution. Among temperate woodland squirrels sympatry can occur where two species show dietary differences (*Tamiasciurus hudsonicus* and *T. douglasii*; Smith 1970) or despite close similarity in diet, where species show different spatial use of the habitat (*S. carolinensis* and *S. niger*; Smith & Follmer 1972). MacKinnon (1978) found that the competing red and grey squirrel in Great Britain had similar dietary preferences (seeds and hard food mast) and that they also had a similar social organization and spatial distribution with overlapping individual home ranges. The grey is ousting the red squirrel in most of its natural habitats, not as a result of dietary differences but because of a higher intrinsic rate of increase. 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 squirrels *P. c. cepapi*, *P. p. tongensis* and *P. p. ornatus* studied in KwaZulu and the Transvaal show decided preferences and varying efficiency of feeding on seeds of different texture, hardness and size despite the similar mass of two of the species (*P. c. cepapi* and *P. p. tongensis*). *P. p. ornatus* is the larger and more efficient feeder (stronger jaw action) on the hard and large kernels, whereas *P. c. cepapi* feeds relatively faster on the smaller seeds and fruits than on the medium and large seeds.

Both from field records and observations on captive squirrels it is clear that the three *Paraxerus* subspecies differ in their utilization of mesocarp and endosperm. *P. p. ornatus* prefers larger seeds such as *G. gerrardii* but, if these are unavailable, as in captivity, they feed on small fruits and seeds. In captivity *P. p. tongensis* prefers the same foods as *P. p. ornatus* even though the fruits and seeds available to it in its natural habitat are smaller than those in the natural habitat of *P. p. ornatus*. *P. c. cepapi* has smaller seeds available in its natural habitat and also prefers these in captivity. *P. c. cepapi* feeds on grass seeds, herb leaves, nectar, pollen and leaf tips, in which *P. p. ornatus* has no interest. The inefficiency of *P. c. cepapi* in handling some of the forest fruits would make it difficult for them to survive in forest. They lack the physical ability that *P. p. ornatus* has to move through a large area of forest to detect ripe fruits. Generally the smaller the seeds of a plant are, the more seeds it produces and *vice versa*. Species whose seedlings become established in shade also have heavier seeds (and fewer) than those whose germination 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 & Moore 1970). It is relatively easy, therefore, for *P. c. cepapi*, in its habitat of 'colonizing' species to remain in one small clump of trees and shrubs (30 × 5 m, i.e. 150 m^2) for a whole day and obtain sufficient food (unpublished observations). This is also true for the striped squirrel *F. congicus* (Viljoen 1978). In contrast, the large *P. p. ornatus* in habitats with plants in later successional stages, can move over 5,64 ha per day (Viljoen 1980), probably not only in search of food but also to 'test' trees about to fruit where food resources are not clumped but spread over a wider area.

It is more advantageous for *P. p. ornatus* to feed on larger seeds. Smith (1975) states that if predation rates are proportional to seed size, then the percentage of the day needed for feeding increases at a geometric rate with decreasing seed size. From the present analyses of fruits and seeds it is also clear that a large kernel is the 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* seed, 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).

Smith (1975) lists five general patterns according to which seed predators can interact with seeds. He found that *T. hudsonicus* chooses lodge pole pine trees with large numbers of seeds per pine cone but also affecting the choice are various traits that make cones difficult to remove from trees. However,

this species has co-evolved closely with conifers and hoards up to 16 000 cones in one cache (Rusch & Reeder 1978). In contrast, the sub-tropical squirrels tend to be omnivorous, they scatter-hoard, and take whichever species is available but are deterred by hardness of husk and texture of fruits of certain species [Smith's methods 1; 3 and 4 (discriminating against either seed size or species)].

Squirrels are well documented as dispersal agents (Ridley 1930; Baker 1972; Smith 1975). Tropical (Emmons 1975) and subtropical squirrels of the genus *Paraxerus* and *Funisciurus*, scatter-hoard. By hoarding, squirrels 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 germination (see appendix) and less rot, and when hoarding they 'plant' it against a tree or rock. The larger forest squirrel subspecies will be more efficient in carrying the heavy and large forest fruits and conversely it would not pay them to trade only in the 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 give rise to seedlings.

Feeding on and dispersal of the very large *Strychnos* spp. by *P. palliatus* squirrels are probably similar to those described for *Sciurus granatensis* or *Scheelia* sp. (Smith 1975). These have an impermeable exocarp and a fleshy mesocarp within, which surrounds hard seeds. This mesocarp has the same energy value as the seed, and supplies nutrition to the animals at the same 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 energy 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* (appendix) is also warranted as *P. p. ornatus* seems to be the major dispersal agent for the fruit in the 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, the 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 *P. p. ornatus* and *G. gerrardii*, in the Ngoye forest. In other areas of *G. gerrardii* distribution there has to be some other dispersal agent as *P. p. ornatus* occurs only in the Ngoye forest.

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

Although many factors can influence the lengths of the different portions of intestinal tracts (Perrin & Curtis 1980), it does seem as if squirrels of the genus *Paraxerus* are unusually insectivorous, particularly *P. c. cepapi*. Viljoen (1977) analysed stomach contents of *P. c. cepapi* from the Transvaal and found that 79% contained insect material which at times contributed up to 100% of the contents. Rahm (1972) set a standard for large intestine length, and calculated the relative lengths of small intestines and caeca of seven species of tree squirrels. He concluded that the more frugivorous *Funisciurus carruthersi*, *Pro-*

toxerus stangeri and *Heliosciurus rufobrachium* have relatively longer caeca and small intestines. The more insectivorous *Paraxerus boehmi emini* and *Funisciurus anerythrus* have relatively short small intestines and caeca. When the South African squirrels of the genus *Paraxerus* are compared with these tropical squirrels they appear to be much more insectivorous (Table 5) with *P. c. 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.

Acknowledgements

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Appendix

Activity levels rise when *G. gerrardii* nuts are presented to captive *P. p. ornatus* and *P. p. tongensis* and they obviously need distance to bury them away from feeding mates. In the field *P. p. 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.

To establish how well these nuts could last and how soon they germinate, 230 seeds were planted on 20 June 1978. In December, 13 could be transplanted, in January 1979 another 7, 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 had germinated i.e. 45,2%. Half of the seeds had husks when planted and the other half were dehusked as peeled by *P. p. ornatus*. Of the husked seeds 37,6% germinated, whilst 62,4% of the dehusked seeds germinated indicating that *P. p. 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 58% germination rate whereas the two and three class seeds had 35% and 37% germination rates respectively.