Activity parameters relative to habitat in four southern African tree squirrels

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Activity measurements were aimed at quantifying the most obvious interspecific differences. Analyses of variance were made on the parameters of tailflicking, grooming, movement, murmuring, time spent motionless and time spent feeding. The two species from open habitats, *Paraxerus c. cepapi* and *Funisciurus congicus* have a lower level of activity than the two subspecies from forested habitat, *P. palliatus ornatus* and *P.p. tongensis*. The former two species move less frequently and over shorter distances. The largest species *P.p. ornatus* is the most active. The two forest subspecies are more efficient in handling food and feeding. The two open habitat species allogroom more frequently than selfgroom when compared to the forest subspecies. This is related to a closer group structure.

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Aktiwiteitsmetings is op die ooglopendste verskille tussen die spesies toegespits. Variansie-analises is gedoen op die metings van stertgebruik, pelsskoonmaak, beweging, kontakroepe, tyd wat die dier bewegingloos is asook tyd om te eet. Die twee spesies afkomstig van savanna-habitat, *Paraxerus c. cepapi* en *Funisciurus congicus* toon 'n laer aktiwiteitsvlak as die twee subspesies van inheemse subtropiese woud, *P. palliatus ornatus* en *P.p. tongensis*. Die eersgenoemde twee spesies beweeg minder dikwels en oor korter afstande en verlaat die nes later en keer vroeër daarna terug. Die grootste subspesie *P.p. ornatus* is die aktiefste. Die twee woudsubspesies is meer effektief met betrekking tot voeding en hantering van voedsel. In vergelyking met die skoonmaakgedrag van die woudsubspesie maak die twee savanna-spesies mekaar se pelse meer dikwels skoon. Hierdie aspek is verwant aan 'n hegte groepstruktuur in die savanna-spesies.

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Four species of tree squirrels occur in SWA/Namibia and South Africa: the western striped squirrel, *Funisciurus congicus* (average adult mass = 112 g, n = 20) in arid savanna of north-western SWA/Namibia; the yellow-footed bush squirrel, *Paraxerus cepapi cepapi* (223 g, n = 69), in north-eastern SWA/Namibia, northern and eastern Botswana and in the north of the Transvaal Province of the Republic of South Africa; the Tonga yellow-chested squirrel, *P. palliatus tongensis* (209 g, n = 60) on the southern tip of the Mozambique plain in subtropical xeric to mesic coastal forests; and the Ngoye red squirrel, *P.p. ornatus* (368 g, n = 104), also on the eastern seaboard, but isolated in the evergreen, moist, subtropical Ngoye forest which covers an area of 2 900 ha.

Initial observations revealed that the activity levels of the two forest species are higher than those of the two species from open woodland. Activity measurements were aimed at detecting and quantifying, where possible, the most obvious interspecific differences. Therefore, although weather variables such as temperature, wind, rainfall and light intensity do influence the activity of tree squirrels (Hicks 1949; Bahnak & Kramm 1977; Golightly & Ohmart 1978; 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 measured parameters were: movement, grooming, tailflicking, murmuring and time spent motionless and feeding. Grooming, tailflicking and murmuring frequencies would indicate behavioural adaptations to habitat, whereas movement and duration motionless and feeding time, would additionally indicate energy expenditure.

Methods

Observations on general activity throughout the day (divided into 2-h periods) were made both in the field and in captivity. Field observations were made throughout the year on *P.p. ornatus* and *P.p. tongensis*; and on *F. congicus* in April 1978 (Viljoen 1978). The three *Paraxerus* subspecies were monitored in captivity but *F. congicus* specimens were obtained too late to be included.

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 murmuring (a close-contact call) and tailflicking.

The squirrels were caged out of doors (12 m^3) and were tame but could not be handled. Five minutes were allowed before commencing observations. Recordings were then made for 15 min on one individual, recording all the parameters on a data 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 variations in day length and climate respectively. These recording sessions were made at different times of the year in between field trips to the study areas in KwaZulu (Viljoen 1980).

Analyses of variance were carried out on the results from both wild and captive squirrels to ascertain any interspecific differences. For the field data these analyses were employed to test the number of squirrels heard and noticed (i.e. the two Kwazulu species either seen or heard) during all hours of the day for the months of January, March, June, August and November 1977, and May 1978. For observations in captivity two different analyses of variance were carried out, the first, testing the seven activity parameters for all hours of the day between the three *Paraxerus* subspecies for the months February, April, July and October 1977 and July 1978; and the second, testing for only five parameters (tailflicking and murmuring excluded) between *P.p.tongensis* and *P.p.ornatus* through all hours of the day for the months February, April, July and October 1977, August, October and December 1976 and July 1978. This latter test included data from 1976 when *P.c.cepapi* had not yet been monitored. 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 late afternoon are summarized in Table 1 for wild *P.p.ornatus* and *P.p.tongensis*. Both species leave the nest shortly after sunrise and return some time before sunset, 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 statistically tested between the different species. *F.congicus* and *P.c.cepapi* leave considerably later and return earlier than *P.p.ornatus* and *P.p.tongensis*. This is evident from Table 2 where the former two species were still in the nests for the first monitored hour and is probably related to their overall lower activity levels and greater degree of energy conservation (Viljoen 1980).

Field observations

During 731 h in Ngoye forest, 1 446 *P.p.ornatus* were either seen or heard, i.e. 1,98 squirrels/h. In Mkwakwa forest in 660 h, 674 *P.p.tongensis* were either seen or heard i.e. 1,02/h. The numbers of squirrels vocalizing were 1 249 or 1,71/h for *P.p.ornatus* and 259 or 0,39/h for *P.p.tongensis*. Therefore, 86,4% of the *P.p.ornatus* that were noted,

Table 1 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*	
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 ± 0,0	(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 ± 0,19
Dec	(13)0528 ± 0,08	(14)1810 ± 0,23			

Table 2 Activity recorded in April of *F.congicus* (F) in the field and *P.c.cepapi* (C), *P.p.tongensis* (T) and *P.p.ornatus* (N) in captivity

Time of day	Activity parameter / 15 min															
	Distance moved (m)				No. of times moved				Feeding (s)				Motionless (s)			
	F	C	T	N	F	C	T	N	F	C	T	N	F	C	T	N
0700	–[a]	–[a]	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

[a]Not yet out of nest

vocalized but only 38,4% of the *P.p.tongensis*. Both the numbers heard and the total numbers seen and heard indicate a higher level of activity for *P.p.ornatus* than for *P.p.tongensis*.

The analysis of variance for the field data indicated differences for the following periods (T) of the day: T_1 = 05h00 – 07h00; T_2 = 07h00 – 09h00; T_3 = 09h00 – 11h00; T_4 = 11h00 – 13h00; T_5 = 13h00 – 15h00; T_6 = 15h00 – 17h00; T_7 = 17h00 – 19h00. The differences were as follows: T_1,$P<0,01$; T_2,$P<0,01$; T_3,$P<0,05$; T_4,NS; T_5, NS; T_6,$P<0,05$; T_7,$P<0,05$. The overall conclusion is that significantly more *P.p.ornatus* were either seen or heard during a day than *P.p.tongensis*. This might not necessarily indicate only a difference in activity, but also points to a difference in behaviour as *P.p.tongensis* are a more cryptic, shy and less vocal species. The lesser difference at T_4 and T_5 could be related to a lull in activity which is apparent in *P.p.ornatus* but not so apparent in the cryptic *P.p.tongensis*, and similarly the increased difference ($P<0,05$) at T_6 and T_7 could be related to renewed activity during which *P.p.ornatus* is once again more obvious.

During 69 h spent in *P.c.cepapi* habitat at Naboomspruit, 156 squirrels were noted (2,26/h) of which only 34,6% vocalized (0,78/h). The large numbers of *P.c.cepapi* noted are indicative of the greater visibility (Viljoen 1980). In addition, however, they are not as vocal as *P.p.ornatus*.

During 29 h in *F.congicus* habitat, 53 squirrels were noted (1,83/h) of which 62,3% vocalized (1,14/h). Visibility is also good in *F.congicus* habitat (Viljoen 1980), but they appear to be more vocal than *P.c.cepapi*. Although sample size and time spent in *F.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* subspecies in captivity and those of *F.congicus* in the field (Table 2) shows that *P.c.cepapi* and *F.congicus* are less active than the two *P.palliatus* subspecies from forests. The only data available for *F.congicus* are from the field, but as this species is extremely tame, I 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 the captive squirrels.

Results from the analysis of variance between the three *Paraxerus* subspecies in captivity, indicate that the distance that the three species moved as well as the time spent motionless differed significantly with *P.p.ornatus* being the most active and *P.c.cepapi* the least active ($P<0,01$). This was to be expected and is also evident from Tables 2 to 4. Feeding times did not differ significantly in the analysis and Tables 2 to 4 also show that of the two savanna species, *F.congicus* takes longest to feed and *P.c.cepapi* takes almost the same time as *P.p.ornatus* and *P.p.tongensis*. This is probably related to a lower efficiency of feeding in the savan-

Table 3 Activity in captivity of three tree squirrel species throughout one day

	Distance (m)			No. of times moved			Feeding (s)			Motionless (s)		
	C[a]	T[a]	N[a]	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

[a]C = *P.cepapi cepapi*, T = *P.palliatus tongensis*, N = *P.p.ornatus*

Table 4 Activity in captivity of two tree squirrel species throughout one day

	Distance (m)		No. of times moved		Feeding (s)		Motionless (s)	
	T[a]	N[a]	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

[a]T = *P.palliatus tongensis*, N = *P.p.ornatus*

na species (Viljoen 1980). Tables 3 and 4 show that *P.p.tongensis* probably also spends slightly more time feeding than *P.p.ornatus* does even though it is only half the mass. This also indicates that *P.p.tongensis* is a less efficient feeder than *P.p.ornatus*. As far as grooming is concerned, there was a significant difference in autogrooming frequency between the *Paraxerus* subspecies. This was also anticipated and the magnitude of the difference is reflected in Table 5 with the 'contact' species *P.c.cepapi* doing by far the most allogrooming. Both the frequencies of tailflicking and murmuring also differed significantly between the three subspecies ($P<0,01$). Viljoen (1980) showed that *P.c.cepapi* seldom tailflicks and that *P.p.tongensis* and *P.p.ornatus* frequently do so. Murmuring is also a slightly depressed behaviour parameter in *P.c.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 (Viljoen 1980).

Table 5 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	–[a]	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

[a]No observations.

The second analysis of variance which tested five parameters between *P.p.tongensis* and *P.p.ornatus*, shows that the differences found above, were mainly between *P.c.cepapi* and the two forest subspecies and not between the latter two subspecies. There was, however, a significant difference ($P<0,01$) between the distances moved, with *P.p.ornatus* moving further, 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 subspecies were compared there. Table 4 also indicates that *P.p.tongensis* is only slightly less active than *P.p.ornatus*.

Time spent feeding in this second analysis between captive *P.p.ornatus* and *P.p.tongensis* did not differ significantly and this indicates that *P.p.tongensis* is probably a less efficient feeder as it is much smaller than *P.p.ornatus*. For allogrooming there was no significant difference between these two subspecies as can also be seen from Table 5. Therefore the difference in allogrooming indicated by the first analysis of variance was also between *P.c.cepapi* and the two forest subspecies. There was a significant difference for grooming in the different months. The comparison of grooming data (Table 5) shows that *P.p.tongensis* and *P.p.ornatus* spend less time allogrooming (10,6% and 12% respectively of grooming frequency) than *P.c.cepapi* (33% of grooming), and that they spend slightly more time autogrooming. From field observations it appeared that *F.congicus* also allogrooms more requently (34% of grooming frequency, $n = 38$) than the two forest subspecies. The two open habitat species have a closer group cohesion (Viljoen 1980), probably maintained by the extensive allogrooming.

Discussion

The purpose of the present study was to determine interspecific differences in activity where possible. Results indicated that the two smaller species from open habitats are less active. *P.c.cepapi* is the least active of the three subspecies of *Paraxerus*, moving about less and spending longer periods motionless. In addition, the metabolic rate of *P.c.cepapi* (Viljoen 1980) indicates that it is well adapted to conserving energy, correlating with the low activity level. Similarly, *F.congicus* lives in a habitat where efficient heat exchange is essential, and therefore also has a low level of activity. The difference in movement between *P.c.cepapi* and *F. congicus* probably reflects the artificiality of captivity, as *P.c.cepapi* is recorded as having a similar number of moves but moving a shorter distance. *P.c.cepapi* which is approximately twice the mass of *F. congicus* probably moves over a similar or slightly larger area than *F.congicus*. Viljoen (1978) calculated a home range of 0,56 ha for *F. congicus* whereas *P.c.cepapi* was found to move over 0,31 ha in *Spyrostachys africana* termitaria thickets (Viljoen 1977) and over 1,26 ha in *Burkea africana* sandveld (Viljoen 1980).

P.p.tongensis and *P.p.ornatus* with their higher activity levels occur in the less exacting habitats as far as moisture and temperature are concerned. The average rainfall at Ngoye forest was 1698 mm for the studied year and at Cape St Lucia, it was 1466 mm (mean of 17 years). In contrast, rainfall in the distribution areas of *F.congicus* and *P.c.cepapi* was 351,6 mm at Ohopoho ($n = 36$ years), 53 mm at Ghanzi ($n = 27$ years) and 723,6 mm at Louis Trichardt ($n = 66$ years). The mean maximum temperature measured at Eshowe (near Ngoye forest) was 24,4 °C over 35 years, and at Cape St Lucia 25,4 °C over 31 years. At Ohopoho in S.W.A./Namibia the mean maximum temperature ($n = 36$ years) was 30,9 °C and at Tsumeb where both *F.congicus* and *P.c.cepapi* occur, the mean maximum temperature ($n = 39$ years) was 29,2 °C. The extreme minimum temperatures also fall below zero in the distribution areas of *F.congicus* and *P.c.cepapi*.

P.p.ornatus is the most active, moves the furthest, and the most frequently, and spends the least time motionless. *P.p.tongensis* is only slightly less active than *P.p.ornatus* and spends a similar amount of time motionless but does not move as far. The home range of *P.p.ornatus* males (3,18 ha ± 1,72; $n = 12$) did not differ significantly from that of *P.p.tongensis* males (4,33 ha ± 1,34; $n = 3$), and neither did the average distance that the males moved (Viljoen 1980). However, the *P.p.ornatus* females had a larger range

(2,19 ha ± 0,93; $n = 6$) than did the *P.p.tongensis* females (0,73 ± 0,10; $n = 3$) and also more than twice the average distance of movement. The forest habitat, with food resources which are widely scattered, no doubt requires a greater degree of movement. The home range measurements of *P.p.ornatus* and *P.p.tongensis* were much larger than those for the savanna squirrels, *F.congicus* and *P.c.cepapi*. The volume of habitat is also much greater in the forests, especially in Ngoye where the canopy height averages 21 m (Viljoen 1980). It would therefore be more time and energy consuming to locate and assess the ripeness of fruit in the forests. In contrast to the two forest subspecies which do not stay long in one tree even when the tree has sufficient fruit, *P.c.cepapi* (Viljoen 1977) will stay in a small clump of *Grewia* or *Euclea* for the whole day. This difference probably also relates to the territoriality of *P.c.cepapi* — they can not move far without transgressing on neighbouring territory and being chased back. *P.p.ornatus* moves over a home range and there is much overlap of movement (Viljoen 1980).

The time spent feeding does not necessarily reflect activity but does indicate that *P.p.tongensis* and *P.p.ornatus* feed at a quicker rate (more efficiently) than do *P.c.cepapi* and *F.congicus*. *F.congicus* is the least efficient feeder (Viljoen 1980). Unfortunately no data are available on the abundance and distribution of food but chemical analysis indicated that the lipid content, and therefore the total energy content of both fruit and endosperm from the forest plant species are higher than from the savanna plant species (Viljoen 1980). This would be necessary to support the high energy needs of the forest squirrels. Measurements from the intestinal tracts indicated that *P.p.cepapi* is more insectivorous than the *P.palliatus* subspecies (Viljoen 1980). This could indicate a different food preference and a more predictable resource which does not necessitate as great a degree of movement as would a predominantly fruit diet.

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