Nest-building and activity patterns in four sympatric rodent species

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Activity pattern and nest-building in four rodent species, *Aethomys chrysophilus, Praomys natalensis, Otomys angoniensis* and *Lemniscomys griselda,* collected from a single area, were studied in the laboratory. Activity: *Praomys* and *Aethomys* were active primarily during the dark phase of a 12L:12D light regime while *Lemniscomys* was active primarily during the light phase. *Otomys* was individually variable and could not be classified as either nocturnal or diurnal. Nest-building: Each species handled grass in a species-specific manner to the extent to which the leaves were cut into pieces and split lengthwise. These rodents can be placed in the sequence *Praomys, Aethomys, Otomys, Lemniscomys* with regard both to the extent of this cutting and splitting and to the completeness of the resulting nest with *Lemniscomys* using the smallest pieces to produce the best, often spherical, nest. It is suggested that these differences may be correlated with a combination of factors including body mass, time of activity, nest location and extent of sociality, which in turn are correlated with the species' thermal requirements.

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Die aktiwiteitspatrone en nesbouery van vier knaagdierspesies, *Aethomys chrysophilus, Praomys natalensis, Otomys angoniensis* en *Lemniscomys griselda,* almal in een area versamel, was in die laboratorium bestudeer. Aktiwiteit: *Praomys* en *Aethomys* was hoofsaaklik gedurende die donker fase van 'n 12L:12D-ligregime aktief, en *Lemniscomys* hoofsaaklik in die ligfase. *Otomys* het individuele verskille getoon en kan nie as òf naglewend òf daglewend geklassifiseer word nie. Nesbouery: Elke spesie het gras op 'n spesie-spesifieke manier gehanteer veral in dié mate van hoe blare in stukkies gesny en in die lengte geskeur is, in die volgorde *Praomys, Aethomys, Otomys* en *Lemniscomys,* wat ook dui op die volledigheid van die nes, waar *Lemniscomys* die kleinste stukkies gebruik het om die beste, dikwels ronde, nes te bou. Daar word voorgestel dat hierdie verskille gekorrelleer kan word met 'n kombinasie van faktore insluitend liggaamsmassa, tyd van aktiwiteit, posisie van nes en mate van sosialiteit, wat weer gekorrelleerd is met die spesie se temperatuurbenodigdhede.

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Southern Africa is noted for the large number of animal species with similar modes of life that are sympatric in various ecosystems. The ecological and behavioural relationships between the small mammals, especially the rodents, are not well documented even though it is reasonable to suspect that they may represent a significant factor in the overall utilization of resources (Delany 1972; Grant 1978), especially when they occur at high densities. Further, it is common to find several rodent species associated at a site, with the possibility of interspecific competition between them. For example, Kingdon (1974), in his review of the rodents of east Africa, presents data which suggest that *Lemniscomys* is more abundant where neither *Otomys* nor *Arvicanthis* is dominant.

The present work examines some aspects of activity and nest-building in four sympatric species of rodents with the aim of identifying any aspect of the behaviour which would tend to reduce the area of potential niche overlap (Hutchinson 1958; Whittaker *et al.* 1973). Specifically, observations were made on captive animals to determine the pattern in time of daily activity; to compare the character of the nest, specifically its shape or character and the extent of manipulation of component material; and to note any preferences between four species for grass which was provided as nest material. Certain differences in behaviour in the field in relation to trapping were noted incidentally.

Material and Methods

Four species of rodent, the otomyine *Otomys angoniensis* (Angoni vlei-rat) and the murids *Aethomys chrysophilus* (the bush rat), *Praomys natalensis* (the multimammate rat) and *Lemniscomys griselda* (the striped grass-mouse) were trapped on a 1,0 ha site 8 km east of Pietermaritzburg, Natal, in an area of thornveld adjacent to a chicken hatchery. The shrew *Crocidura flavescens* also occurred there.

The traps available for use, built to the design of Meester (1970), were of two sizes, the larger being 28 × 8 × 8 cm and the smaller 25 × 7,5 (high) × 5,5 (wide) cm internal dimensions. The traps, baited with peanut butter and rolled oats, were placed either on a previously established grid at 10 m spacing or at approximately 10 m intervals along lines chosen for convenience. In both cases, two traps, one of each size, were placed within one metre of each other at each site. Trapping was done on an irregular basis between 2 April and 20 August 1975.

Prior to testing in the laboratory, the animals were housed individually in conventional rat cages in a room with natural illumination and some heating which prevented their exposure to the lowest ambient temperatures on winter nights. All experiments were conducted in a windowless, airconditioned room where the temperature was maintained at 18 ± 2 °C. The only illumination was provided by a 200 W incandescent bulb suspended 1,5 m above the activity chamber and controlled through a time clock to provide a 12L:12D regime with the light on between 06h00 and 18h00. The experimental work was performed between 18 May and 5 September 1975.

The activity chamber consisted of a plywood box 120 cm (square) × 50 cm (high) fitted with a lid of mesh chicken-wire. The floor of the chamber was covered with soil to a depth of approximately 4 cm. Internally, the area was subdivided equally into four, by two intersecting 20 cm high partitions.

Each of the four subdivisions was in communication with the two adjacent ones through a 5 cm wide gap in the partition near the outside wall. A microswitch was mounted at each of these so that the activating lever was horizontal and level with the bottom of the gap. The switches were wired in series and connected to an Esterline-Angus event recorder. The frequency of switch activations per hour was manually transcribed from the chart paper and these values were taken as representing activity during each hour. To encourage movement between sections, the four subdivisions were provided, respectively, with (1) a water bottle, (2) food pellets scattered on the ground, (3) two galvanized metal nest boxes 12 × 12 × 20 cm long with approximately one cm of sawdust on the floor and (4) a pile of dirt in the outside corner which was moistened at the start of each test and into which an animal could burrow. Rodent were tested individually in this chamber for periods of four days.

The cages for the nest-building experiments each consisted of a wooden box 58 × 29 × 28 cm with the front closed by a wire grille through which grass could be pulled from a cardboard reservoir mounted on the outside. Attached externally and opening into one end of the cage was a nest box measuring 10 × 10 × 10 cm. Four species of grass were collected daily from the trapping area: *Eustachys paspaloides* (Vahl.) Lanza and Mattei, *Chloris gayana* Kunth, *Themeda triandra* Forsk. var. *trachyspathea Goosens* and *Digitaria macroglossa* Henr. Although the material actually used in building nests in the field is unknown, these grasses were chosen from amongst the numerous species in the area because they reflect the morphological array of the more prominent grasses present and grew in scattered, pure stands so that single species samples could be harvested efficiently. Table 1 shows the mean values of certain measurements of the leaf and culm which might influence the rodent's choice. Replicate measurements of height were not made because the rodents attack the base, not the apex. Culm diameter was recorded only for three species, *Digitaria* being a densely tufted grass without culms or seed heads at the time of the study. In a series of replicate experiments, the four rodent species were supplied with the four grasses in a randomized order over four days in an effort to eliminate any effect of time. The cages and nest boxes were examined daily and the location and character of any formed nest recorded. These nests and any grass in the cage were removed and weighed to the nearest 0,1 g. Food and water were available *ad libitum* in all cases.

Results

Field observations

Preliminary trapping indicated that few animals entered the traps during the daytime and consequently the traps were usually examined only once per day early in the morning. On the six occasions when traps were checked both early morning and late afternoon (474 trap half-days), a total of 27 rodents was found in the mornings and five in the afternoon, three *Praomys* and two *Otomys*. Comparable morning collections yielded 16 *Praomys* and five *Otomys*. Neither *Aethomys* nor *Lemniscomys* was trapped during the day.

The trapping results, summarized in Table 2, suggest a differential response in relation to trap size. A chi-square test indicates a significant lack of homogeneity in these data ($\chi^2 = 7,96$ with 3 d.f.; $p < 0,02$). *Praomys* entered the larger traps more frequently ($\chi^2 = 6,07$ with 1 d.f.; $p < 0,001$) and *Lemniscomys* less frequently ($\chi^2 = 4,45$ with 1 d.f.; $p < 0,002$) than the smaller traps. No comparable difference was evident in either *Aethomys* or *Otomys*. This differential response is apparently not related to body size (Table 2) because although *Praomys* is the smallest of the four species, *Lemniscomys* is not much larger and both are significantly smaller than *Aethomys* and *Otomys*. Comparable results were obtained by Delany (1964) in Uganda.

Table 2 also probably reflects the relative population densities in the study area with *Praomys* being the most abundant.

Table 1 Comparison of certain measurements ($\bar{X} \pm$S.D.; n = 50) of the four grasses provided as nesting material

Species	Diameter of culm 10 cm above ground (mm)	Leaf length (mm)	Leaf width at base (mm)	Height (cm)
Digitaria macroglossa	–	404,2 (± 53,6)	4,89 (± 1,31)	~ 20
Themeda triandra	1,32	162,6 (± 57,1)	5,20 (± 0,73)	~ 60
Chloris gayana	2,61	361,5 (± 63,7)	3,90 (± 0,89)	~ 80
Eustachys paspaloides	1,77	267,3 (± 47,7)	3,07 (± 0,41)	~ 70

Table 2 Comparison of body mass and frequency of capture in two different-sized traps of four species of rodent

Species	n	Body mass (g) ($\bar{X} \pm$ S.D.)	No. in large traps	No. in small traps
P. natalensis	60	37,7 ± 12,49	41	19
L. griselda	11	43,5 ± 4,95	2	9
A. chrysophilus	18	83,6 ± 13,51	10	8
O. angoniensis	12	121,3 ± 4,73	7	5

Bait preference was not part of this study, but it is worth noting that, although Dippenaar (1974) failed to trap *Praomys* or *Otomys* with a mixture of peanut butter and rolled oats, that bait was successful here. It remains to be determined whether this is due to a difference in behaviour in response to bait or to trap.

Activity

Three males and three females of each species were studied to determine the temporal pattern of their activity in the laboratory. Preliminary trials showed that the amount and pattern of activity during the first day sometimes differed from subsequent days, presumably reflecting heightened exploratory behaviour in the novel surroundings, and activity in general then declined after four days to extremely low levels. Therefore, the results from days two to four only were utilized and were graphed as the percentage of the total activity occurring each hour for these days combined.

The patterns of activity were consistent within species except for *Otomys*. *Praomys, Aethomys* and three of the *Otomys* were more active during the dark phase and *Lemniscomys* during the light phase. An example for one individual of each sex of each species is shown in Fig. 1.

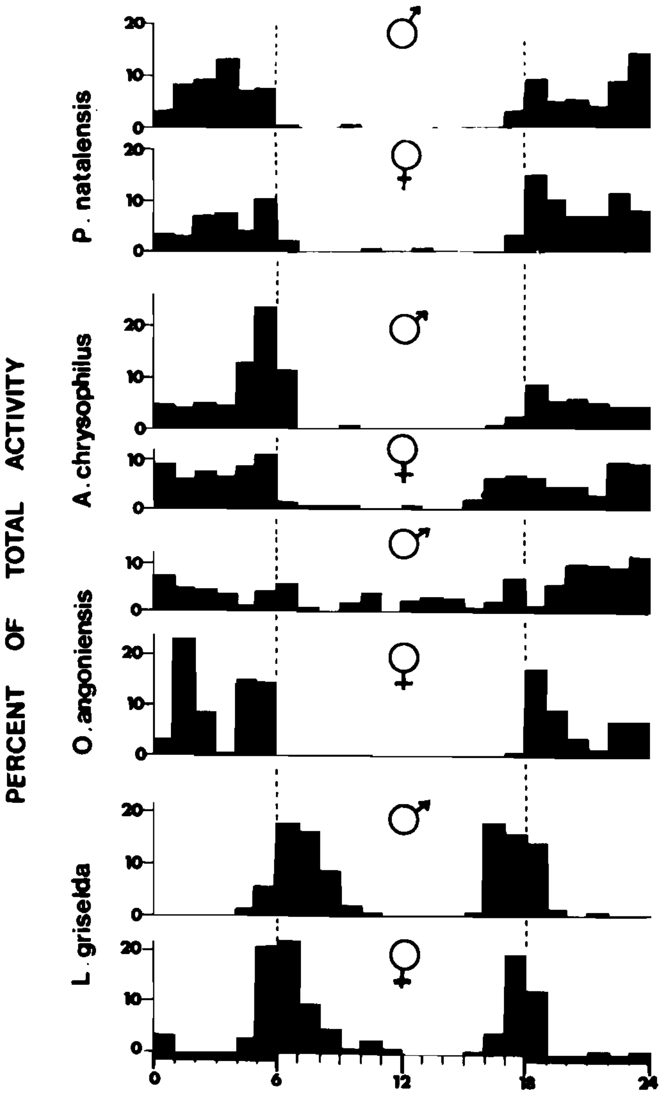

Fig. 1 Temporal pattern of activity in the laboratory of individual animals of each sex, plotted as the percentage of the total activity occurring each hour.

Choate (1972) reports similar patterns in the same species of *Praomys, Aethomys* and *Lemniscomys* from Rhodesia, although it is unclear from his paper whether his animals were from sympatric populations. Although not graphed in the same time units, the activity of these three species is not as evenly distributed throughout the active period in the present work when compared to Choate's (1972) figures. This is particularly true for *Lemniscomys* which Choate (and Hubbard 1972) characterizes as diurnal. My animals were relatively inactive during the middle of the light period, suggesting a tendency towards crepuscularity.

The behaviour of *Otomys* appears to be variable. My results show patterns ranging from nocturnality bordering on crepuscular to near uniform activity regardless of light phase. Similar variability is reported by Choate (1972) in Rhodesia. This apparent variability requires further study in relation to the temporal organization and/or resource requirements of potential competitors and predators in different ecosystems. It would be of interest to determine also whether the holders and non-holders of territories (Davis 1972) are active at the same or different times.

Even with limited opportunities for digging (a pile of soil in one chamber only) all *Praomys* tested dug tunnels and used the resulting burrow for shelter, as found also by Kingdon (1974).

Nestbuilding

For unknown reasons, some animals did not attempt to build nests on some days in either the nest-box or the cage proper (i.e. removed less than 1,0 g of material from the grass reservoir) or else sheltered in grass on the cage floor, with or without manipulating the grass into a nest cup, and transported no grass to the nest-box. Stiemie and Nel (1973) showed that in *Aethomys* and *Praomys* the amount of nest-building was related to temperature, but that factor alone cannot explain these results. Instances of this sort were too few to permit statistical analysis but there was no evident trend in this regard in relation to either grass species, animal species or sex, or day in the study sequence. The result, however, was an unequal number of samples in each part of the replicate series. Consequently, the following analysis utilizes one-way analysis of variance rather than three-way analysis of variance.

When the data for animal and grass are pooled and compared between days, there is no statistical difference between days in mean mass of grass either in the nest-box (F = 0,697; 3 & 152 d.f.) or in the total removed from the grass reservoir, i.e. found in nest-box plus cage (F = 1,031; 3 & 205 d.f.). Therefore, the variable 'day' was disregarded in the subsequent analyses.

When the data for animal and day are pooled and the mass of the different grass species is compared, there is no statistical difference between the mean amounts transported to the nest-box (F = 1,47; 3 & 152 d.f.) or between the means of the total removed from the reservoir (F = 2,259; 3 & 204 d.f.). In view of the differences between grasses (see Table 1) in such parameters as presence or absence of culm and leaf width and length, it would appear that all of these rodents could be considered opportunistic in their selection of nest material.

When the data for grass species and day are pooled and

Table 3 Mass of grass (A) used in nest construction within the nest-box and (B) removed from the reservoir, with the percentage of total moved actually used in nest construction and the results of an analysis of variance

	(A) Used			(B) Removed			
Species	n	$\bar{X} \pm$ S.D.		n	$\bar{X} \pm$ S.D.		%
P. natalensis	36	3,47	1,81	54	26,21	17,33	13,2
A. chyrophilus	48	6,46	2,65	62	31,24	20,18	20,7
O. angoniensis	28	3,50	1,82	41	14,81	10,94	23,6
L. griselda	44	3,74	1,94	51	10,25	7,62	36,5
F.		20,188			21,567		
d.f.		3 & 152			3 & 204		
p		< 0,005			< 0,005		

the mean mass of grass transported to the nest-box (n = 156) and the amount removed from the reservoir (n = 208) are compared between animal species, there are significant statistical differences. These values are shown in Table 3 along with percentage of the total amount of grass removed and which was found in the nest-box. The difference between species in the amount found in the nest-box is due solely to the greater amount transported by *Aethomys*. In contrast, a comparison of the means by the L statistic of Dixon and Massey (1969 p.167) of the total removed from the reservoir indicates that there is no difference between *P. natalensis* and *A. chrysophilus* or between *O. angoniensis* and *L. griselda*. The high value of F from the analysis of variance is due to the relatively large amount moved by *Praomys* and *Aethomys* when compared to *Otomys* and *Lemniscomys* (L = 8,67). The data also suggest differences in what might be termed 'efficiency' in that, of the total removed from the reservoir, *L. griselda* transferred more to the nest-box (i.e. 36,5%) than the others, particularly when compared to *P. natalensis* (i.e. 13,2%).

The difference between the rodent species in their handling of potential nest-building material is demonstrated by more than just these mass values. There are also differences in the extent to which they cut (crosswise) and split (lengthwise) the material as well as in character or completeness of the resulting nest.

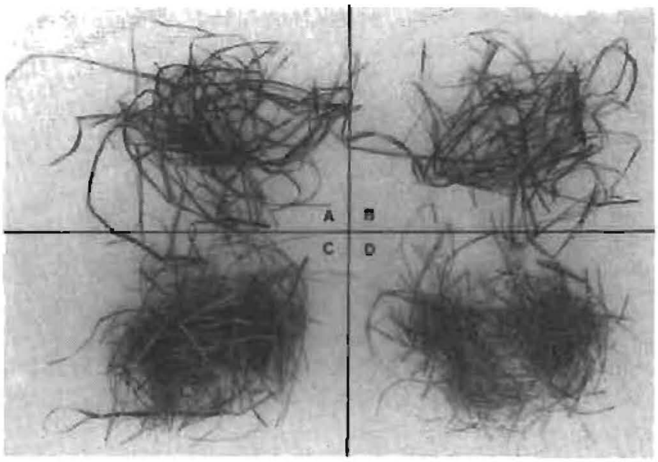

Fig. 2 An example of the variation in the character of the tow removed from nests built by (A) *Praomys natalensis*; (B) *Aethomys chrysophilus*; (C) *Otomys angoniensis*; and (D) *Lemniscomys griselda*. The grass in each case is *Digitaria macroglossa* and the magnification is identical.

The extent to which the four grass species were cut into segments and split lengthwise varied between rodent species. Figure 2 illustrates the typical character of the tow, derived from the grass *Digitaria*, produced by each of the rodent species. *Praomys* did not cut or split the grass leaves except for the cut necessary to free the leaf from the culm in the reservoir. Similar results are reported by Veenstra (1958). *Aethomys*, *Otomys* and *Lemniscomys* successively, in the order named, cut and split the grass into smaller and smaller pieces. Table 4 shows the mean width and an estimate of the modal range of the length of grass fragments removed from nests built in the nest-boxes. Lengths were not measured because of the difficulty of selecting objectively which to measure; for example, *Aethomys* nests contained many small fragments, particularly near the base, but the bulk of the construction consisted of long pieces. A few individuals, all males, specifically two *Lemniscomys*, one *Otomys* and three *Aethomys*, included split pieces of culm from the three grasses with culm (Table 1) in the nest. The apparent sexual differences and relatively low frequency of occurrence of this behaviour cannot be explained from the present data.

This behaviour of cutting and splitting the grass was observed only in material found in the nest-boxes. The material removed from the reservoir and found in the cage was not dissected, not even in the 27 instances (11,1% of the trials) when some form of nest was found in the cage.

The character of the tow comprising the nests was sufficiently species-specific to provide reliable identification of unoccupied nests — a technique which might be developed for future field studies.

Table 4 Width ($\bar{X} \pm$ S.D.) and, in brackets, estimated modal length of grass fragments (mm) removed from nests of the three rodent species who cut the tow; and the value of F and level of probability from an analysis of variance within grass and between rodent species

Species	*Digitaria macroglossa* n = 40	*Themeda triandra* n = 30	*Eustachys paspaloides* n = 30	*Chloris gayana* n = 30
Aethomys chrysophilus	1,06 ± 0,44 (270 – 330)	1,14 ± 0,53 (125 – 170)	1,96 ± 1,02 (160 – 255)	0,85 ± 0,46 (175 – 230)
Otomys angoniensis	0,92 ± 0,32 (150 – 200)	1,11 ± 0,39 (90 – 120)	1,10 ± 0,50 (40 – 150)	0,96 ± 0,46 (60 – 120)
Lemniscomys griselda	0,68 ± 0,23 (30 – 60)	0,56 ± 0,21 (30 – 80)	0,71 ± 0,31 (30 – 100)	0,71 ± 0,25 (50 – 100)
F	13,07	19,68	25,77	2,87
p	< 0,005	< 0,005	< 0,005	No significance

The character or 'completeness' of the nests in the nest-boxes also varied between rodent species under the conditions of the experiment. Preliminary observations indicated that it would be impossible to score the nests for 'completeness' by a single numerical value. While the nests varied between those consisting only of loose grass not woven or shaped into any form to those forming a complete hollow ball, some consisted of a poorly defined cup but with some strands of grass over the top as a rudimentary roof. Therefore, the character of the nest cup and the extent of the roof coverage were scored separately and then the two scores summed. The cup was scored between one and six, with one indicating grass present but loose or unshaped as a cup, and then progressive development of a cup shape until six indicated a high-walled cup with the wall at least as high as the animal's body. The roof was classed as absent, Type A ($<$ 10% coverage), Type B (10% to 50%) or Type C ($>$ 50%), and these classes were given point values of zero to three respectively. Instances where no grass or less than 1,0 g was found in the nest-box were not scored and were not included in the calculations indicating nest character.

The scores for extent of cup development were examined for differences between sex within species but no differences were found. This contrasts with the observations of Stiemie and Nel (1973) who found that female *Praomys* and *Aethomys* built 'better' nests than males when cotton-wool was provided as the nesting material.

Table 5 summarizes the data for 248 nests, showing the frequency of the various classes of roof, and the mean scores for roof and cup development and their sum. This sum is meaningful only in a comparative context in that it allows the species to be ranked. These results show that *Praomys* produced the poorest nest with regard to both the extent of cup and roof. *Otomys* produced a better nest both in the extent of the cup walls and the frequency and completeness of the roof. *Aethomys* and *Lemniscomys* both had relatively high scores for cup character, reflecting not only the height of the cup wall but also how well the material was put together. The latter two species differ, however, in the extent of roofing; *Lemniscomys* frequently put together a tightly woven roof which completely obscured the animal when the nest-box lid was removed. These results are in general accord with the observations of Stiemie and Nel (1973) who compared nest-building with cottonwool at three temperatures by *Aethomys* and *Praomys* (and *Rhabdomys pumilio*) and who found that under all conditions tested *Aethomys* tended to construct more complete nests than *Praomys*. They report that *Rhabdomys* removed the most cottonwool and built better nests than the other two species. The latter observation is relevant to the present work in that a *Rhabdomys* nest that I was shown in Rhodesia was indistinguishable from those made by *Lemniscomys* and described above.

Table 5 Comparative scores for the character of the 248 nests found in the nest-boxes (see text for details of scoring)

	Roof					Mean	Total
	Frequency of class				Mean	cup	nest
Species	Abs.	A	B	C	score	score	score
Praomys	60	7	2	–	0,16	2,73	2,89
Otomys	34	1	4	2	0,37	3,29	3,66
Aethomys	58	7	9	–	0,34	4,38	4,72
Lemniscomys	40	–	8	16	1,00	4,11	5,11

Discussion and Conclusions

Although we do not know the thermal neutral zone or the insulative value of the pelage or adipose tissue for these rodent species, nor the role of the substrate in influencing the location (Kingdon 1974 p.567) of nests, it is interesting to speculate on the various interactions which may influence nest character. In this connection, Table 6 summarizes our knowledge of nesting behaviour in the rodents studied and the following discussion refers to this table, with numbers in brackets indicating the column.

It will be noted that the species pairs within which there is no statistical difference in the amount of nesting material moved (2), *Praomys* and *Aethomys* on the one hand and *Lemniscomy* and *Otomys* on the other, are of disparate mean body mass (1). Thus, the similarities in the amount of nesting material moved must have behavioural and/or physiological significance.

If the amounts of nesting material used in nest construction (4) and removed from the reservoir (2) are converted to percentage of mean body mass, the data can be related to metabolic size. When this is done, an even greater disparity is evident in the amount removed (3), with *Praomys*, the smallest species and on a metabolic scale the most sensitive to cold, moving two to five times more on a body mass basis than the other species. However, the amount actually used in nest construction as a percentage of mean body mass was similar for *Praomys*, *Aethomys* and *Lemniscomys* but considerably less for *Otomys*, the largest species.

The species which pair on the basis of the amount of material moved also pair in other regards. *Praomys* and *Aethomys* are both active primarily at night (6), are reported to nest in burrows or other sheltered position which would provide some thermal insulation (7), and formed the poorest nest roofs (8). Conversely, *Lemniscomys* and some *Otomys* are relatively inactive at night and hence more susceptible to low night temperatures than species active then, formed the best nest roofs and are reported to nest, at least in some places, on the surface.

There are, however, certain parameters in which the members of these pairs do not match. *Aethomys* used more grass in nest construction than *Praomys* (4) although the amounts were similar on a body mass basis (5). On this same basis, however, *Lemniscomys* and *Otomys* are disparate in that *Otomys* used much less and, in fact, used less than all other species (5).

These rodents also differ in their sociality (9), ranging between very social (*Praomys*) to antisocial and territorial (*Otomys*). This is relevant to the present context because huddling can constitute a thermoregulatory activity (Gebczynska & Gebczyski 1971) in more highly social forms such as *Praomys*.

Consequently, it is suggested that the nesting behaviour observed in this study may be interpreted primarily in terms of thermal requirements along the following lines.

Praomys natalensis, which is of small size, is active during the night and retires to a communal, underground nest site during the day (Choate 1972). The underground

Table 6 Summary of data correlating nesting with other species characteristics

		Amount nesting material							
		Moved		Used					
Species	Mean body mass (g) (1)	In (g) (2)	As % body mass (3)	In (g) (4)	As % body mass (5)	Active time (6)	Nest locations (7)	Nest scores + roof cup total (8)	Sociality (9)
Praomys natalensis	37,7	26,21	69,5	3,47	9,2	Dark	Burrows, natural crevices, etc. (a)	0,16 2,73 2,89	Very social (d)
Lemniscomys griselda	43,5	10,25	23,6	3,74	8,6	Light	Surface (a), (b)	1,00 4,11 5,11	Not gregarious (b)
Aethomys chrysophilus	83,6	31,24	37,4	6,46	7,7	Dark	Burrows, rock niches termitaries (a)	0,34 4,38 4,72	Pairs, oo intolerant (a)
Otomys angoniensis	121,3	14,81	12,2	3,50	2,9	Light & dark	Surface or burrows (b), (c)	0,37 3,29 3,66	Anti-social, territorial (c)

(a) = Choate 1972; (b) = Kingdon 1974; (c) = Davis 1972; and (d) = Veenstra 1958.

location and the opportunity for communal huddling would reduce the need for extensive nesting material for thermoregulatory purposes — hence the low values in column 8.

Lemniscomys griselda, which is also small but is active during the day, and is non-gregarious and surface-nesting (Kingdon 1974), would require a much more elaborate nest and did produce the most complete and probably the best insulated nest among the species studied — hence the high values in column 8.

Aethomys chrysophilus resembles *Praomys* in most regards but is much less social (Choate 1972). It is also larger in size and hence less sensitive to cold than *Praomys* and requires, therefore, only a moderate nest (i.e. good cup but poor roof); hence the intermediate value in column 8.

Otomys angoniensis resembles *Lemniscomys* in several regards but builds a nest consisting of little more than an open cup. This suggests that *Otomys,* the largest species studied, may be approaching a size which can rely more upon physiological rather than behavioural means to maintain body temperature.

In conclusion, it is suggested that, in terms of the broad concept of the niche as developed by Hutchinson (1958) and Whittaker *et al.* (1973), possible niche overlap in these four species is reduced not only because of differences in time of activity as this may relate to feeding or other behaviour, but also because of differences in the behaviour of nest building as an outcome of different insulative needs arising directly as a result of differences in body size and the attendant metabolic consequences.

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