Notes on the activity patterns of 12 species of southern African rodents and a new design of activity monitor

M.R. Perrin
Department of Zoology and Entomology, Rhodes University, Grahamstown

The circadian activity patterns of 12 species of southern African rodents are described under controlled laboratory conditions. Activity was measured in a newly described apparatus, in which rodents, traversing infra-red light beams placed across several arenas and nest-boxes, activated a microprocessor which quantified, and regularly printed data on a recorder. Diel patterns of activity were present in all species and most species were nocturnal. Locomotion, and other behaviours, were continuous or discontinuous (phasic) during activity periods. Short-term periods of activity were most obvious in species with a low body mass and were thought to be associated with a feeding rhythm. Continual diel activity with a regular short-term rhythm characterized *Otomys irroratus*, paralleled that of the microtines, and is believed to be necessitated by specific adaptations to herbivory. Crepuscularity in *Rhabdomys pumilio* may be associated with *Hodotermes* predation, while nocturnalism in (arboreal) *Graphiurus murinus* is believed to reduce competition with diurnal granivorous and insectivorous birds. Notes describe the seasonal change in activity of four species: such differences were less marked than those reported for temperate species.

Die bedrywigheidspatrone per etmaal van 12 spesies van Suider-Afrikaanse knaagdiere onder beheerde laboratorium toestande word beskryf. Die bedrywigheid word gemeet d.m.v. 'n onlangse beskryfde apparaat waarin knaagdiere, sodra hulle oor infra-rooi ligstrale beweeg wat oor verskeie kaste en slaapneste geplaas is, 'n mikroprosesseer-toestel aanskakel wat die data kwantifiseer en dit met gereelde tussenposes d.m.v. 'n opnamedrukker registreer. Dwarsdeur die etmaal is bedrywigheidspatrone by alle spesies waargeneem en die meeste spesies is nagtelik van aard. Beweging en ander gedragspatrone is tydens bedrywigheidstye deurlopend of nie-deurlopend, (d.w.s. dit kom voor in fases). Kortstondige bedrywigheidstye blyk die duidelikste by spesies met lae liggaamsmassa en daar word vermoed dat dit verband hou met die ritme van hul vreetgewoontes. Aanhoudende bedrywigheid met 'n gereelde kortstondige ritme gedurende elke etmaal is 'n kenmerk van *Otomys irroratus*, en loop parallel met die ritme van die genus *Microtus*. Dit word vermoedelik vereis deur spesifieke aanpassings by hul plantvretende aard. Skemertydbedrywigheid by *Rhabdomys pumilio* kan dalk verband hou met die feit dat dit op *Hodotermes* teer, terwyl daar vermoed word dat verhoogde nagtelike bedrywigheid by die boombewoner *Graphiurus murinus* wedywering met diurnale graan- en insekvretende voëls verminder. Die aantekeninge beskryf die seisoenale bedrywigheidswisseling by vier spesies: sodanige wisseling is minder opvallend as die opgetekende wisseling by spesies van gematigde streke.

M.R. Perrin
Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa

The activity patterns of small rodents are governed by several factors, some of them being endogenous, others of an ecological nature (Backlund & Ekeroot 1950). Most rodents display an endogenous circadian rhythm which may be modified by a superimposed short-term feeding rhythm. Activity denotes movement, usually locomotion, although feeding, drinking, elimination and other activities are included (Falls 1968). Ashby (1972) has reviewed some of the patterns of diel activity exhibited in mammals in both the field and laboratory, but it is clear that little is known of the activity phasing of southern African rodents (Choate 1972; Keogh 1973; Nel & Rautenbach 1974; Nel 1975; Christian 1977). The prime objective of this preliminary study was to describe, verify and compare the activity patterns of several species of southern African rodents under controlled laboratory conditions.

The activity monitor described here is capable of sensing the locomotory movements of small mammals, summating the counts of arena, and nest-box (or food-box) activity, and recording data at regular time intervals. Since there are (four) independent arenas, several individuals can be tested simultaneously which permits direct comparison of species, sex, age or social class differences. However, care must be taken to ensure that all subjects of the same species are derived from the same community, unless one is particularly interested in examining shifts in activity phasing caused by niche overlap (different community structure). Results from experimental (e.g. drug-treated) and control (untreated) subjects can be printed sequentially: by extending cables, the responses of subjects to differently simulated environments (temperature, photoperiod) can also be compared.

The microprocessor can be programmed to record counts of activity in any particular area of the arena (e.g. 'wall-walking' versus 'open-field' behaviour) or in nest-boxes and will therefore be particularly useful for studies of exploratory behaviour (Perrin 1971). It has a wide application in small mammal behavioural studies. The results of this study are discussed in relation to habitat and feeding habits, and previous studies.

Materials and Methods

Seven of the 12 species examined (*Graphiurus murinus, Otomys irroratus, Saccostomus campestris, Mus musculus, Praomys natalensis, Aethomys namaquensis* and

Rhabdomys pumilio) were collected from Valley Bush-veld of the Great Fish river valley (Eastern Cape). *Gerbillurus paeba* were caught in coastal sand dunes near Kinkelboss, and their activity pattern compared with two other gerbils, *Desmodillus auricularis* (which occurs in the Great Fish river Valley Bushveld community, Perrin In press) and *Tatera brantsii*; specimens of these two species were obtained from (S.A.I.M.R.) laboratory colonies. The data for *A. namaquensis* were compared with those for *A. chrysophilus* trapped in a coastal forest at Umlalazi, Natal. Finally the activity pattern of laboratory-reared *Mystromys albicaudatus* was considered in relation to that of the obligate herbivore *O. irroratus*, since they are believed to be gastric and caecal fermenters respectively, which might necessitate prolonged feeding and protracted activity phasing.

Activity patterns were recorded by a monitor housed in a constant environment room simulating summertime conditions. A 14L: 10D light regime was employed and temperatures were held constant at 25 ± 1 °C and 15 ± 1 °C during light and dark phases respectively. For *S. campestris*, *P. natalensis*, *A. namaquensis* and *R. pumilio*, a wintertime photoperiod (10L: 14D) and reduced temperatures (18 ± 1 °C : 8 ± 1 °C) were employed, and activity experiments repeated.

Mice placed in activity monitors were allowed 48 h to acclimate before monitoring began; all were captured during the 'same' season as the experimental situation. Monitoring periods were standardized at 7 days, and three replicates used for each species under a single set of conditions. Rat pellets (sunflower seeds, greens) and water were provided *ad libitum*.

The means of activity counts (number of light beams broken per hour) were used to plot activity profiles characteristic of a particular species in captivity. It was very difficult to determine mean values for duration of, and between, short-term bouts of activity, owing to considerable inherent variability and the 'definition' of a bout of activity. It was decided to call periods of activity of less than 1 h duration 'pulses', and longer bouts were called activity 'blocks'. The amplitude or intensity of activity was variable. Future studies must aim to resolve the complication associated with quantification. Szymanski (1918) coefficients were calculated for each species, by dividing the mean daily activity by the mean daily inactivity.

Activity monitor

The recording apparatus comprised a main console and two activity arenas in which monitoring occurred. Each arena consisted of a raised square floor (1 m × 1 m for mice, 1,5 m × 1,5 m for rats), walled (to 25 cm) on all sides, with a circular hole situated in the floor at each corner (Figure 1). These holes allowed access of the subject to four 'nest-boxes' situated directly below the main arena floor. The main arena walls were drilled 25 mm above the floor with 5-mm holes at regular distances apart to permit the emittance of infra-red light beams. The beams were emitted from photo-diodes mounted behind the wall, to photo-transistors mounted (behind the wall) directly opposite. Five such beams ran in a parallel direction across the arena and were transected by five

similar beams running in the opposite direction forming 36 equally sized squares (Figure 1). The nest-boxes were similarly traversed by two beams at right angles to one another. Each arena possessed a power supply for the light transducers, a data interface circuit board and a cable connection to the console.

The console consisted of a (C.D.P. 1802) microprocessor based microcomputer, power supplies, a 16 column drum printer, and various option selection switches and other controls (Figure 2); 25-pin plugs connected the data and control lines to the activity arenas.
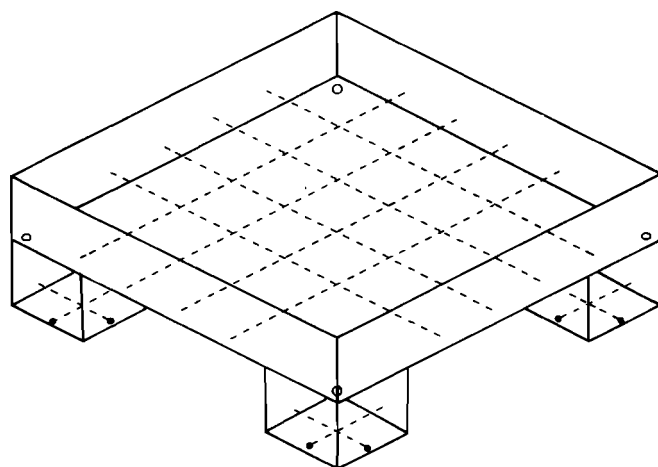

Figure 1 A diagrammatic representation of a single activity tank to show the arrangement of the upper arena and the four lower nest-boxes. Circles represent access points to the nest-boxes from the arena, and dashed lines represent the paths of intersecting infra-red light beams.

Operation

Activity was monitored in either or both of the (potentially four) arenas simultaneously, for any number of runs, each of a duration (from 1 min to 1 h) selected by the operator. Having selected run time and arena, the operator depressed a 'Reset' button to reset all accumulators, run counts and previous options selected, and the 'Run' button, whereupon the new run time and arena selects were read and monitoring of the arena data buses commenced immediately. ('Buses' are wires carrying units of binary-coded information, called 'bits'). The arena data buses selected were read sequentially.

The information from the 14 photo-transistors ('beam open' = logical 1, 'beam occluded' = logical 0) was for presentation to the microprocessor on the eight bit data bus; six data bits pertained to upper arena conditions, and two bits to nest-box conditions. Any change in one of the eight bit values between two consecutive readings of an arena data bus was interpreted as one movement and added to the accumulating number in the relevant upper or lower arena accumulator.

When the run time selected had elapsed, the printer was started and the data temporarily stored in the memory were printed. Arena and run number, and activity counts for both upper and lower arenas were recorded. At commencement of printing the accumulated data were moved to a temporary storage location in the microprocessor to enable data collection to continue. The run
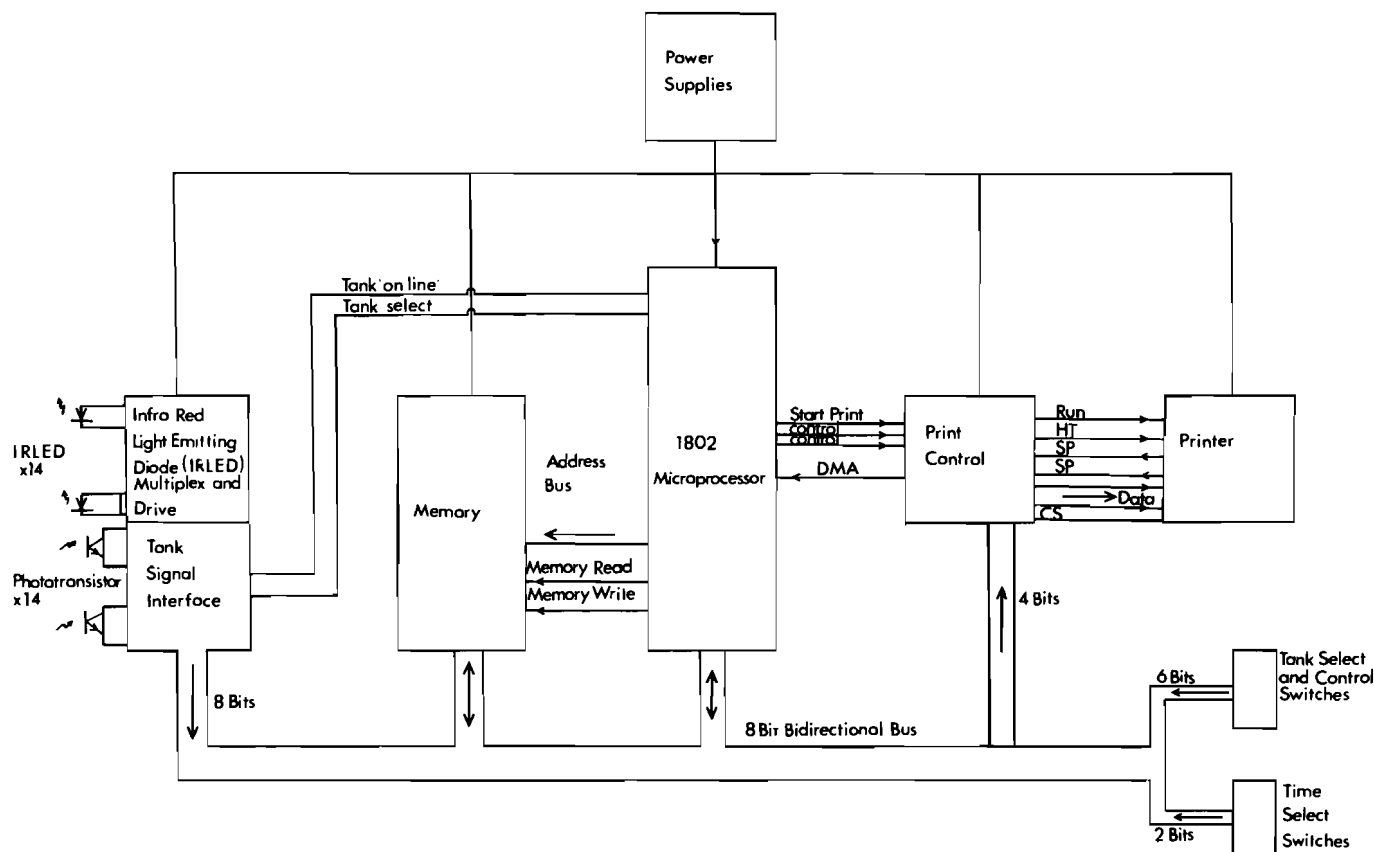
Figure 2 A circuit diagram of the activity monitor demonstrating the layout of various components including infra-red light emitting diodes and phototransistors, microprocessor and memory, print control and printer, and various control switches.

number was incremented by one and the process continued until the 'stop' button was depressed.

Results

Preliminary considerations

First, the apparatus allowed for the monitoring of locomotory, arena (terrestrial) activity and non-locomotory, nest-box (subterranean) activity. The two measures gave slightly different results, as might have been expected, and as is shown for *A. namaquensis* in Figure 3; the overall pattern was similar for both sets of data. All remaining activity profiles report data from the locomotory activity recorded in the (terrestrial) arena. Nest-box activities were therefore excluded from the (locomotory) activity profiles of the various species examined.

Secondly, there were individual differences in activity profiles. Figure 4 shows the difference in the intensity of activity of two male *R. pumilo* each recorded over seven days. The temporal sequence (pattern) of locomotory activity was the same for each individual, but the distance travelled (amplitude) was very different. Some attenuation in activity score occurred on successive daily trials and it was therefore essential to test naive animals sequentially over a seven-day period and to examine the mean of the results collected.

Finally, there were within-individual differences in the timing of activity bouts. Such temporal shifts of periods of activity are exemplified by the results for *D. auricularis* in Figure 5. The shifts of activity bouts were contained within the essentially nocturnal pattern characteristic of this species (see later), and summation produced a typical
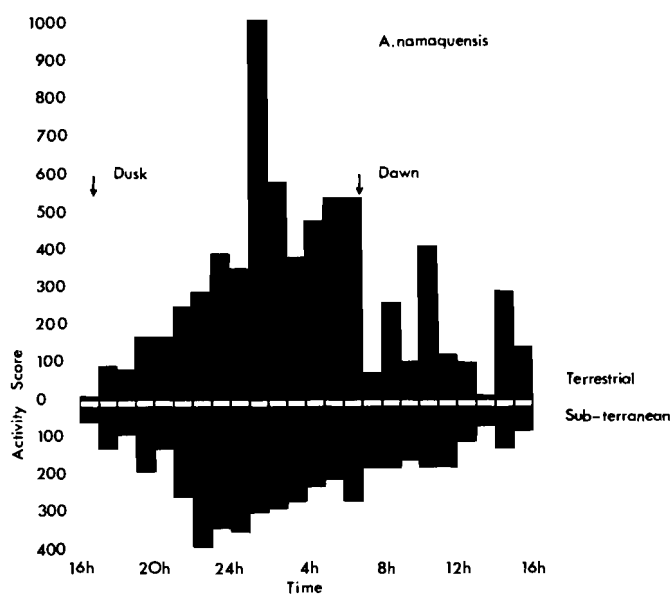

Figure 3 Activity profiles of *A. namaquensis* indicating the differences in data collected from the arena (terrestrial activity) and nest-boxes (subterranean activity).

profile. Mean values (composite species profiles) do not always demonstrate such differences and can lead to generality and disguise underlying detail.

Species activity profiles

G. murinus was completely nocturnal (Figure 6, Table 1) and showed no short-term periodicity in its activity pro-
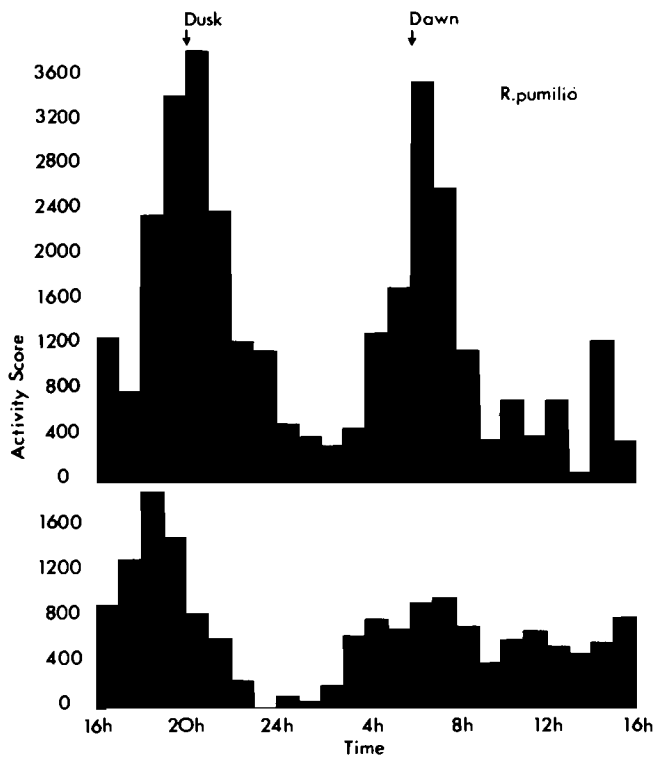
Figure 4 Activity profiles of two male *R. pumilio* to demonstrate similar activity phasing but dissimilar intensity of activity.

Figure 5 Five (i – v) daily activity profiles of a single *D. auricularis* to show temporal shifts in, and the variable duration of short-term periods of activity.

file, while *D. auricularis* was predominantly nocturnal but with some crepuscular activity (Figure 7, Table 1). Short-term activity bouts were present but were irregular in duration and varied in intensity (Figure 5). *G. paeba* was clearly nocturnal and had no short-term periodicity in its activity phasing but there was a tendency for increased post-dusk and pre-dawn activity (Figure 8, Table 1). Total nocturnalism characterized *T. brantsii's* behaviour, but crepuscular peaks were present also (Figure 9).

O. irroratus was the only species to exhibit a predominantly diurnal activity profile and a definite short-term activity rhythm (Figure 10). *M. albicaudatus*, however, was nocturnal with no short-term activity bouts and no crepuscular activity, although there was a tendency for a reduction in mid-night activity (Figure 11, Table 1). *S. campestris* was somewhat intermediate in that it was predominantly nocturnal but exhibited some diurnal activity (Figure 12); the activity bouts were of variable length (Table 1).

Activity was nocturnal in *M. musculus* and *P. natalensis*: the former exhibited no short-term phasing (Figure 13, Table 1) while the activity profile of the latter comprized a number of pulses of variable duration (Figure 14, Table 1).

Both *Aethomys* species were nocturnal but the activity pattern of *A. chrysophilus* lacked a short-term component (Figure 15, Table 1); that of *A. namaquensis* contained activity pulses of variable length (Table 1) and much of the activity was concentrated after dusk (Figure 16).

R. pumilio, like *O. irroratus*, was diurnal, but predominantly crepuscular; blocks of activity were of considerable duration (Figure 17, Table 1).
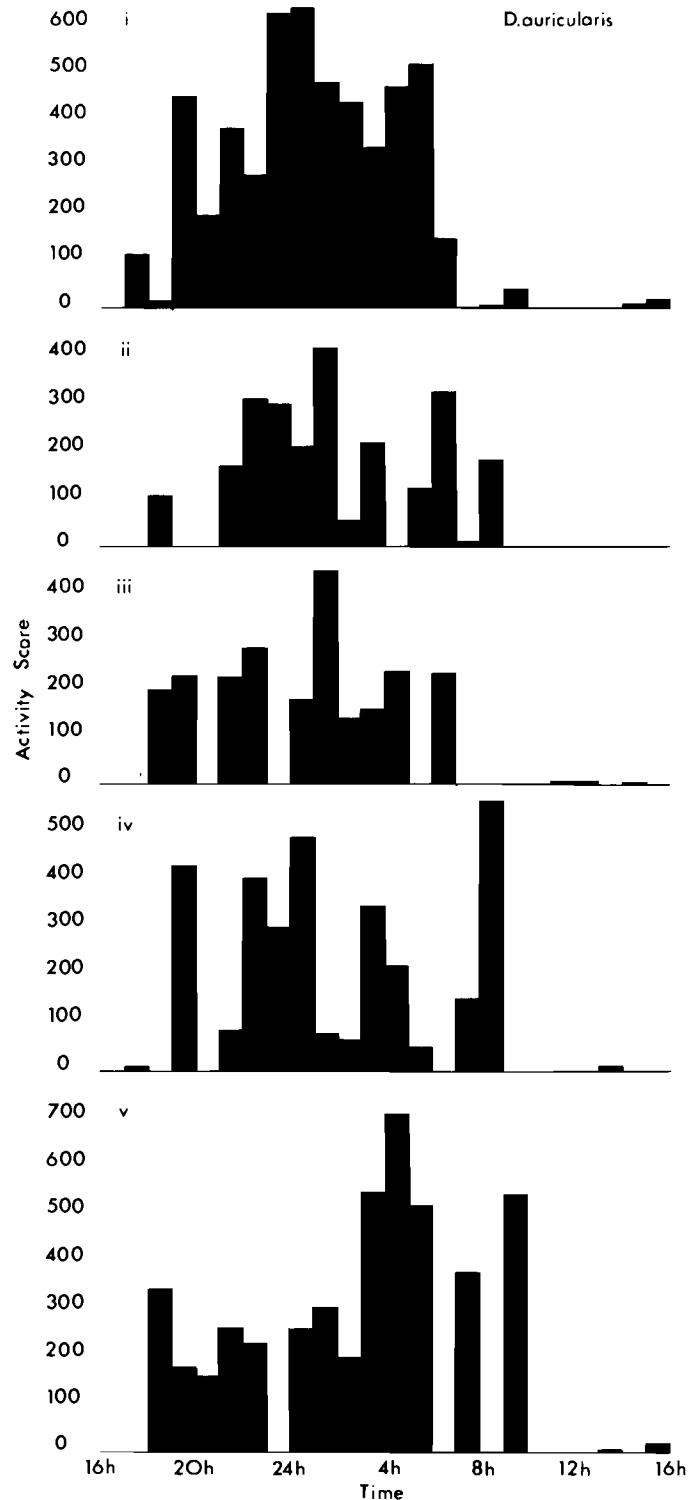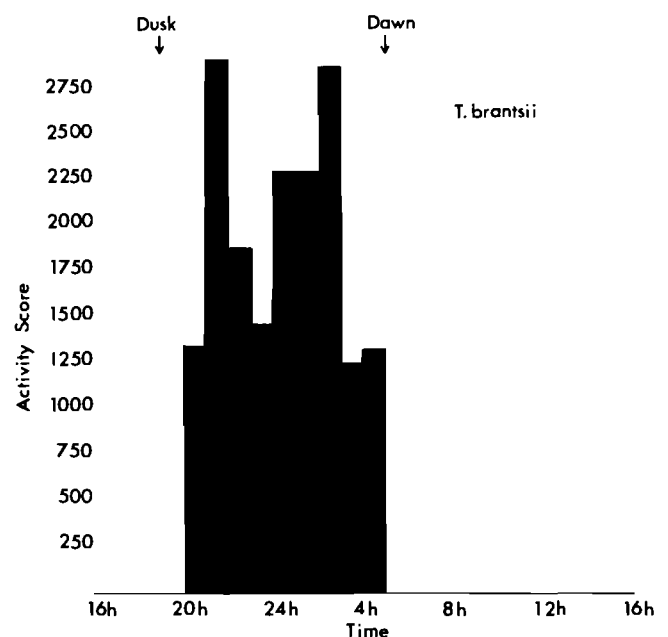
Seasonal changes in activity patterns

There was a slight increase in nocturnal activity in *S. campestris* during winter and the duration of the active phase was partially extended (Figure 18). The variable-length summertime pulses also occurred in winter but were accompanied by longer blocks of activity (Table 3).

The activity profiles of *P. natalensis* were essentially the same during summer and winter (Figure 19) and comprized variable-length, nocturnal pulses (Table 3). The duration of the active period was extended.

Table 1 Degree of nocturnalism and short-term activity profiles of the rodents studied

Species	% nocturnal activity	Szymanski coefficient	Short-term profile	Literature records
G. murinus	99	0,01	Continual nocturnal activity	Principally[d] nocturnal[a,b,c,e]
D. auricularis	75	0,33	Complex pulses and blocks	Mainly[d] nocturnal[i]
G. paeba	92	0,09	Continual nocturnal activity	Nocturnal[d,i]
T. brantsii	100	0,00	Crepuscular blocks. Nocturnal	Strictly[g] nocturnal[d,i]
O. irroratus	37	1,70	Regular short-term rhythm	Partly nocturnal[a], predominantly nocturnal[b,c], mainly nocturnal[d,g], crepuscular[e], diurnal[f,h]
M. albicaudatus	99	0,01	Continual nocturnal activity	Nocturnal[d,g]
S. campestris	86	0,16	Variable nocturnal pulses	Nocturnal[b,c,d,i]
M. musculus	87	0,26	Continual nocturnal activity	Mainly[a,d] nocturnal[b,i]
P. natalensis	96	0,04	Variable nocturnal pulses	Nocturnal[c,f,i]
A. chrysophilus	95	0,05	Continual nocturnal activity	Nocturnal[c,e,f,i]
A. namaquensis	84	0,19	Variable nocturnal pulses	Nocturnal[b,c,e,f,g,i]
R. pumilio	33	2,03	Crepuscular blocks	Mainly[b,f,i] diurnal[d,g]

[a]Rosevear 1969. [b]Delany 1975. [c]Ansell 1960. [d]Walker 1975. [e]Kingdon 1974. [f]Shortridge 1934. [g]Roberts 1951. [h]Meester & Setzer 1971. [i]Smithers 1971
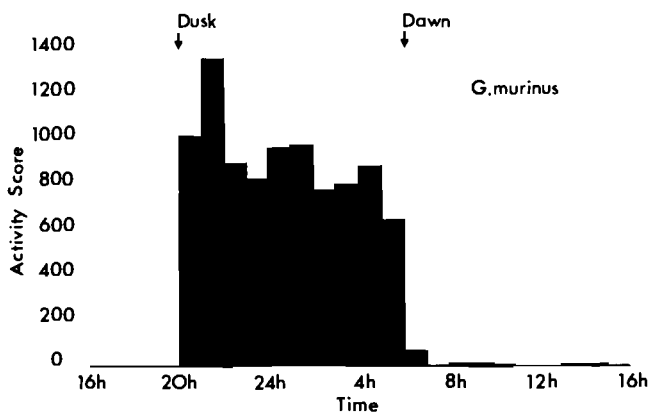
Figure 6 Summertime activity profile of *G. murinus*.
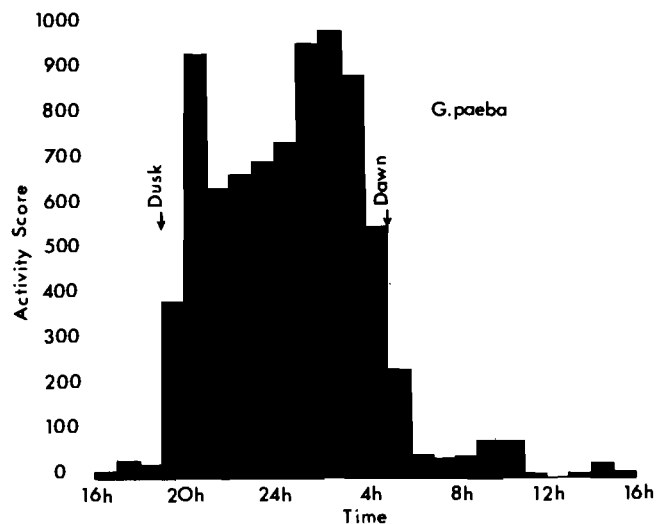
Figure 8 Summertime activity profile of *G. paeba*.
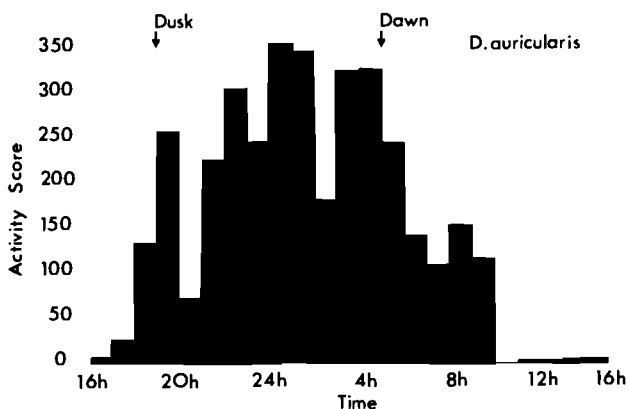
Figure 7 Summertime activity profile of *D. auricularis*.

There was a reduction in nocturnal activity in *A. namaquensis* in winter (Figure 20) causing the activity profile to change quite markedly. Some short-term activity pulses were extended to form blocks of longer duration (Table 2). Diurnal activity pulses gave rise to a polyphasic appearance and reduced nocturnalism.

A crepuscular pattern was apparent in both seasons in *R. pumilio* (Figure 21); in winter aggregated pulses ten-
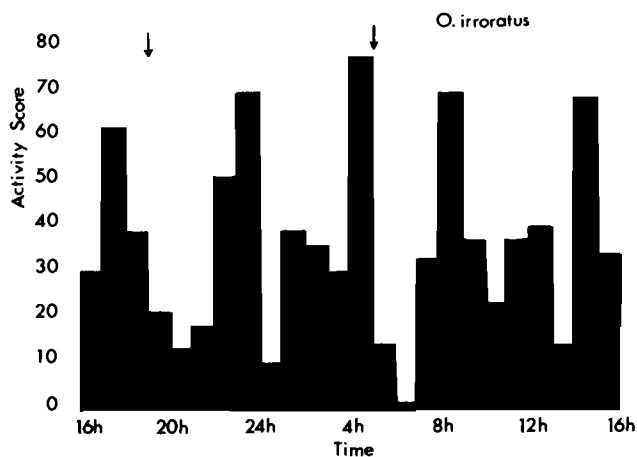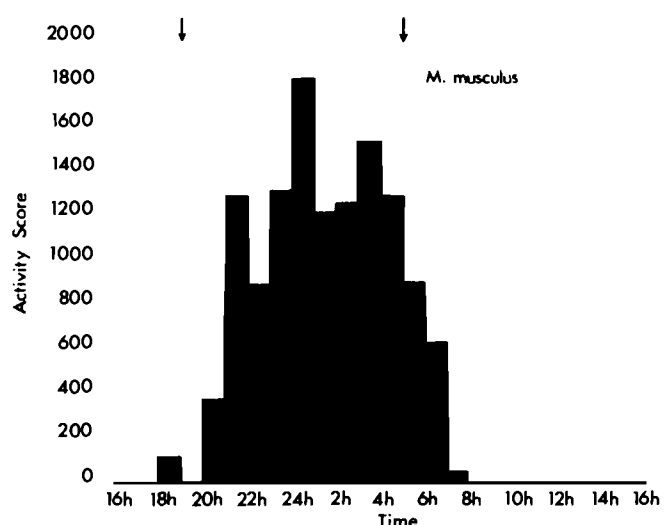

Figure 9 Summertime activity profile of *T. brantsii*.

Figure 10 Summertime activity profile of *O. irroratus*.

Figure 11 Summertime activity profile of *M. albicaudatus*.

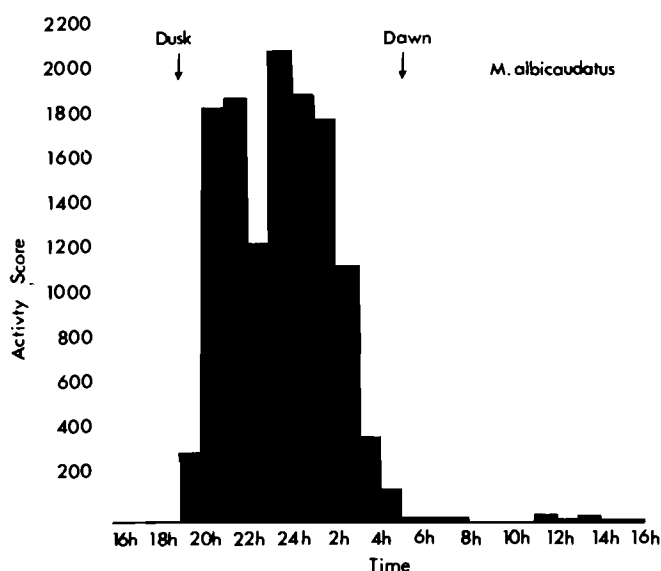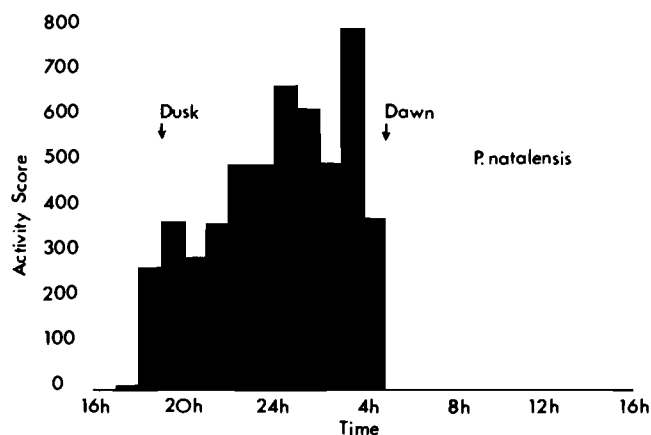**Figure 12** Summertime activity profile of *S. campestris*.

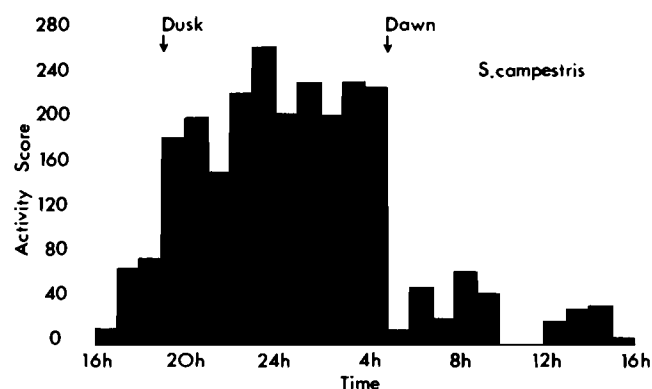**Figure 13** Summertime activity profile of *M. musculus*.

Figure 14 Summertime activity profile of *P. natalensis*.
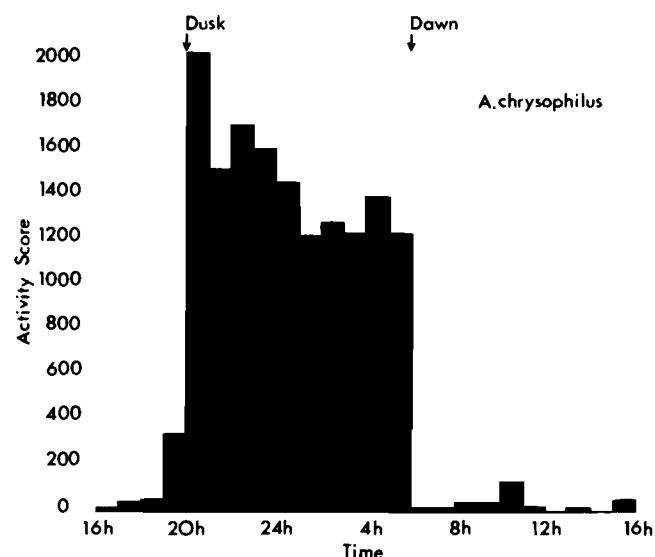

Figure 15 Summertime activity profile of *A. chrysophilus*.

ded to replace activity blocks (Table 3). The separation of dusk and dawn activity peaks was extended.

Activity patterns within a small rodent community

Seven of the species studied were from a single community, and of these, five were nocturnal (Table 4). None exhibited short-term pulses of activity but activity phasing

altered in other ways. Nocturnal activity was normally distributed in *S. campestris* and *M. musculus*, skewed forwards towards dusk in *G. murinus* and *A. namaquensis*, and skewed backwards towards dawn in *P. natalen-*
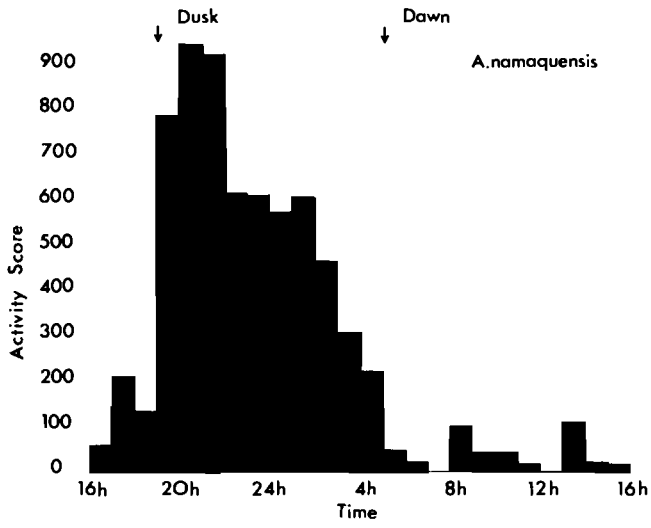
Figure 16 Summertime activity profile of *A. namaquensis*.

Figure 17 Summertime activity of profile of *R. pumilio*.

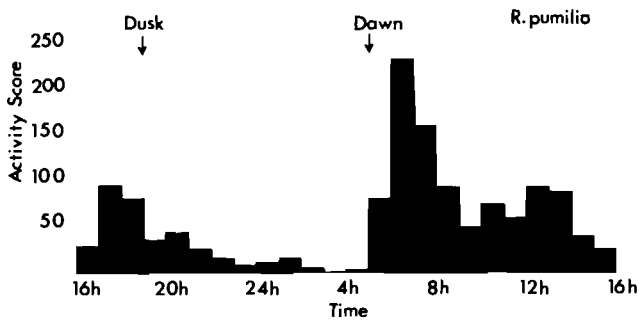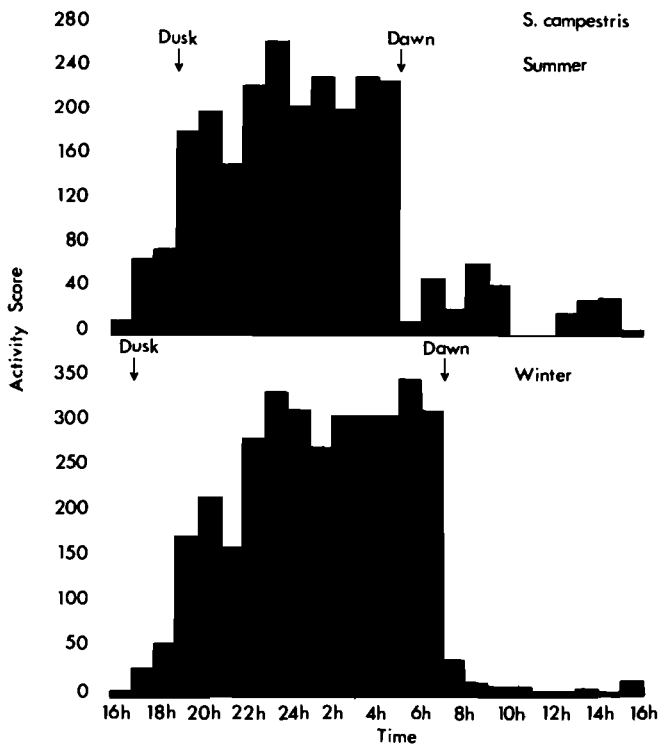**Figure 18** Activity profiles of *S. campestris* recorded in summer and winter.

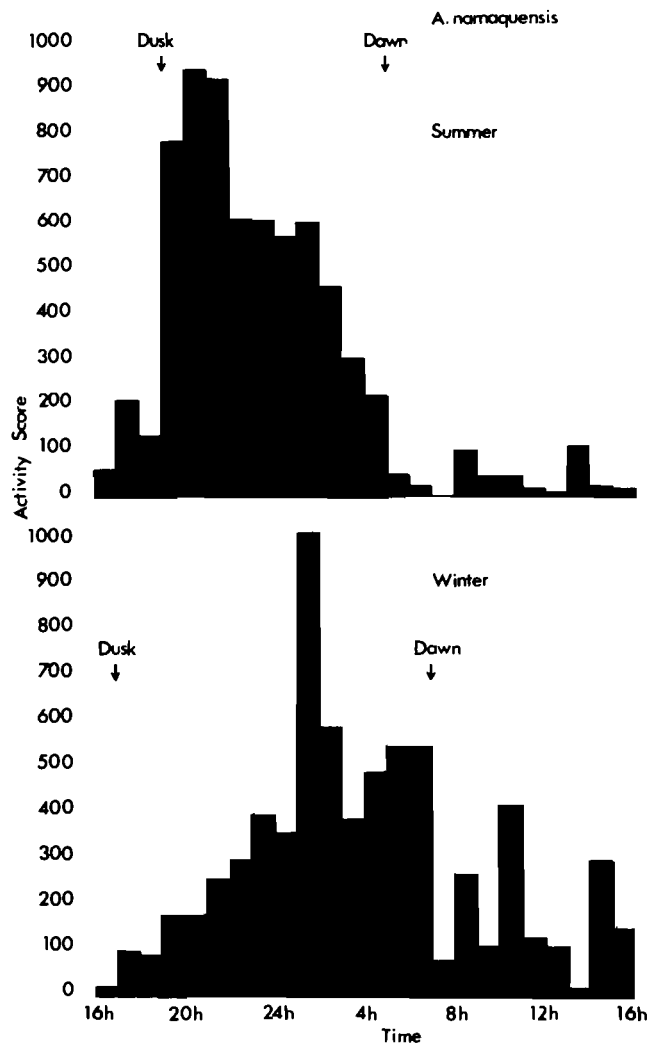**Figure 19** Activity profiles of *P. natalensis* recorded in summer and winter.

Figure 20 Activity profiles of *A. namaquensis* recorded in summer and winter.

Table 2   Habitat, range and feeding tactics of the rodents studied as reported in the literature

Species	Habitat	Range in sub-sahara Africa	Feeding habits	Trophic niche
G. murinus	Wide tolerance[c,e,l]	Widespread[b,c,g,j]	Insects, fruits, seeds[b,e,f]	Insectivore/granivore
D. auricularis	Xeric[c,g,i]	Southern Ethiopian[b,g,l]	Seeds, insects[a,c,g]	Granivore/insectivore
G. paeba	Xeric[a,c,g,m]	South-western[a,b,l,m]	Seeds[c,m]	Granivore/graminivore
T. brantsii	Xeric[a,c,e]	Southern Ethiopian[a,b,l]	Seeds, vegetable matter[a,c,e,g,i]	Vegetarian
O. irroratus	Mesic[a,e,g,i,j,k]	Discontinuous[b,i,k]	Green vegetation[a,d,e,f]	Herbivore
M. albicaudatus	Xeric tendency[g]	Southern savanna grass-lands[b,l]	Seeds, vegetable matter[a,g]	Vegetarian
S. campestris	Xeric[a,f] tendency[e]	Widespread[b,e,g,l]	Seeds, fruits, insects[a,c,e,f,g]	Granivore/insectivore
M. musculus	Xeric[i] tolerance[g]	Widespread[c,e,g]	Seeds, insects, plants[c,i]	Omnivore
P. natalensis	Xeric[e] tolerance[c,j]	Widespread[b,e,k,l]	Seeds, insects, plants[a,e,f]	Omnivore
A. chrysophilus	Xeric[c] tendency[a,e]	Southern savanna grass-lands[b,e,i,l]	Seeds, fruits, leaves, buds[a,e]	Vegetarian
A. namaquensis	Xeric[g] tendency[g]	Southern Ethiopian[b,i,l]	Seeds, fruits, leaves, buds[a,e]	Vegetarian
R. pumilio	Xeric[c] tendency[g]	Widespread[b,e,g,l]	Green vegetation, seeds, insects[a,d,e,f]	Omnivore

[a]Roberts 1951. [b]Meester & Setzer 1971. [c]Smithers 1971. [d]Perrin 1980a. [e]Kingdon 1974. [f]Delany 1975. [g]Walker 1975. [h]Hewitt 1931. [i]Shortridge 1934. [j]Ansell 1960. [k]Rosevear 1969. [l]Davis 1974. [m]Stutterheim & Skinner 1973

Table 3   Seasonal changes in nocturnalism and short-term activity periods of four rodent species

Species	Summer			Winter		
	% nocturnal activity	Szymanski coefficient	Short-term profile	% nocturnal activity	Szymanski coefficient	Short-term profile
S. campestris	86	0,16	Variable pulses	97	0,03	Pulses and blocks
P. natalensis	97	0,03	Variable pulses	100	0,00	Variable pulses
A. namaquensis	84	0,19	Variable pulses	77	0,30	Pulses and blocks
R. pumilio	33	2,03	Crepuscular blocks	40	1,51	Grouped crepuscular pulses
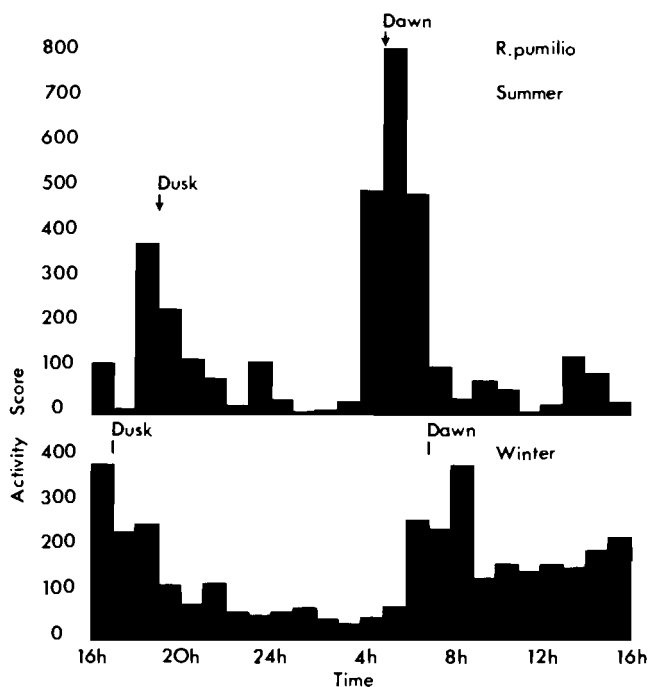
Figure 21   Activity profiles of *R. pumilio* recorded in summer and winter.

sis. Pre-dusk activity occurred in most species but post-dawn activity was far less common (Table 4). Of the two diurnal species within the community, *O. irroratus* was

polyphasic and *R. pumilio* was crepuscular. Dawn activity in *R. pumilio* was in phase with, but dusk activity was out of phase with, that of the activity peaks of *O. irroratus*.

Discussion

The results of the present study confirm and extend the accounts of activity patterns of southern African rodents reported in the literature (Table 1). Most species studied were nocturnal and have been recorded as such, but there has been little recording or quantification of short-term (feeding) activity phasing. Apparent ambiguities in, and conflicting reports of, activity patterns of several (diurnal) species have appeared in the literature. This is partly due, perhaps, to limited visual (daytime) observations in the field, but is largely induced by variation in activity phasing caused by competition, predation pressure, commensalism, and lunar rhythms (Ashby 1972).

In some rodents, short-term rhythms of activity of approximately constant periodicity occur within the overall daily periodicity (Davis 1933). There is an obvious need to distinguish between the short-term feeding rhythm and the circadian locomotory rhythm.

Species profiles

All gerbil species were nocturnal, substantiating the reports of Choate (1972), Keogh (1973) and Stutterheim & Skinner (1973). Nocturnalism is often associated with high daytime temperatures in arid environments and the

Table 4 Details of activity phasing of five coexisting small rodents

Species	Pre-dusk activity	Activity distribution	Post-dawn activity
G. murinus	None	Skewed forwards: early	Little
S. compestris	Considerable	Normal distribution	Some
M. musculus	Very little	Normal distribution	Considerable
P. natalensis	Some	Skewed backwards: late	None
A. namaquensis	Considerable	Skewed forwards: early	Little

need to conserve water (Schmidt-Nielsen & Schmidt-Nielsen 1953). A short-term rhythm was only present in *D. auricularis* which is considerably larger than *G. paeba*, yet their feeding tactics appear similar. The absence of a short-term feeding rhythm was not unexpected in *T. brantsii* owing to its larger mass and more generalized feeding habits. The presence of a short-term rhythm in *D. auricularis* is probably correlated with foraging trips to collect and hoard seeds. The absence of a similar rhythm in *G. paeba* may indicate the necessity for continued searching for small seeds in an extensive sand dune ecosystem (Stutterheim & Skinner 1973).

The cricetomyid *S. campestris* resembles *D. auricularis* in its body mass, habitat preference, feeding habits and activity pattern (nocturnalism and phasing) which may be of significance. It suggests that unrelated species with similar ecological requirements, or under similar selective pressures, may adopt similar patterns of activity behaviour. *S. campestris* collects large numbers of seeds which are transported back to the nest in cheek pouches.

The other two cricetids, *O. irroratus* (otomyinid) and *M. albicaudatus* (cricetinid) are similar-sized herbivores with marked adaptations of their alimentary canal for caecal and gastric microbial fermentation respectively (Perrin & Curtis 1980, Maddock & Perrin 1981). However, their activity patterns differ markedly in both the degree of nocturnalism and short-term phasing. The xeric tendencies of *M. albicaudatus* might explain its nocturnal activity (*O. irroratus* is a mesic-adapted species) but not the absence of a short-term rhythm. This is explicable in terms of forestomach carbohydrate storage supplementing liver glycogen reserves. The blood glucose levels of the laboratory rat remain high for 12 – 16 h post-feeding (Peters & Gärtner 1973) and similar mechanisms are most probably highly developed in *M. albicaudatus* (Maddock & Perrin 1981). Aylett (1962, 1968) has described the relationship between food passage and antagonism between plasma insulin and glucagon levels, but has not confirmed the feedback mechanism between blood sugar levels and feeding rate.

The continual day and night activity of *O. irroratus* with its regular short-term rhythm is very similar to that of temperate microtines (Davis 1933; Erkinaro 1969; Lehman 1976), which are also advanced grazers with caecal microbial fermentation and obligate herbivory (Watts 1968). The short-term phasing is the result of a feeding rhythm that is closely dependent on metabolic demands (Lehman 1976).

O. irroratus has been described as diurnal (Thomas & Schwann 1905; Roberts 1951) and predominantly nocturnal (Hewitt 1931; Shortridge 1934) but with some daytime activity. Nocturnal activity has been confirmed by barn owl predation (Davis 1959; Perrin In press). Davis (1972) described the species as being crepuscular with some activity through the day and night, on the basis of field and laboratory studies, and suggested controlling factors of activity are multiple and complex. This is undoubtedly true.

Nel (1975) has suggested that diurnal arid zone species live in colonies as an antipredator mechanism. However, the prolonged diurnal activity of *O. irroratus* is more likely related to a feeding rhythm (Lehman 1976). Nel & Rautenbach (1974) suggested that the more strictly diurnal activity pattern of *Parotomys brantsii* than of *O. irroratus* was caused by differences in social structure and behaviour. Social organization, like predation and refuges (Nel 1975), may influence the evolution of activity phasing but foraging patterns and digestive physiology might be of greater fundamental significance.

Each of the species of *Aethomys*, which have similar feeding habits and distributions, was nocturnal; but exhibited different short-term activity profiles. Choate (1972) recorded continual nocturnal activity in both species. The cause of the short-term phasing difference recorded in this study may be attributable to body mass. The considerably smaller *A. namaquensis* (body mass 47 g against 90 g for *A. chrysophilus*) may require frequent energy input and therefore a pulsed activity profile. Alternatively the cause may relate to dissimilar foraging patterns in different environments, since *A. namaquensis* is predominantly rupicolous while *A. chrysophilus* is terrestrial and partly arboreal (Ansell 1960).

The arboreal, seed and insect predator *G. murinus* was also nocturnal and exhibited no short-term phasing. It is difficult to explain why this species is nocturnal (confirmatory evidence from Choate 1972) since a visually orientated predator/forager of woodland canopies might be expected to be diurnal. Nocturnalism may contribute to reduce predation, but this is probably low in arboreal species in any case (Perrin In press): its prime cause may be to allow predation on inactive insects at night and to reduce competition from granivorous and insectivorous (diurnal) birds.

Mus musculus and *Praomys natalensis*, two small commensal murids with similar ecologies, were both nocturnal. This may represent an adaptation to human disturbance and predation, or to an essentially deserticolous way of life (Green, Keogh, Gordon, Pinto & Hartwig 1980; Keogh & Price In press). The short-term phasing record for *M. musculus*, but not for *P. natalensis*, may reflect its relatively larger energy demands because of its smaller size. No short-term activity rhythms were demonstrated for *P. natalensis* by Choate (1972).

It must be remembered that the apparent absence of

short-term rhythms may be caused by an over-riding locomotory circadian rhythm. However, none of the larger rodents, with the particular exception of *O. irroratus* (see above), exhibit a short-term rhythm.

There have been several conflicting reports of the activity profile of *R. pumilio*. Walker (1975) and Smithers (1971) reported primarily diurnal activity, the latter noting occasional nocturnal activity and a tendency towards crepuscularity. Choate (1972) found *R. pumilio* to be active mainly during midday under laboratory conditions with some extension of activity into an artificial night, while Christian (1977) demonstrated continuous diurnal activity in *R. pumilio* with no tendency towards nocturnal or crepuscular behaviour.

In this study, *R. pumilio* was unique in being the only species with crepuscular activity, a behaviour it shares with several species of the closely related *Lemniscomys* genus (Petter, Chippaux & Monmignaut 1964; Choate 1972). The only cause which can be suggested for this particular activity pattern, other than equable temperatures and humidities (Brooks 1974), is predation on harvester termites (*Hodotermes* sp.) which also have a predominantly crepuscular activity pattern (Skaife 1979). Termites have been shown to be important in the reproductive biology of natural populations of *L. striatus* (Field 1975) and *R. pumilio* (Perrin 1980b). It would be interesting if the effect of moonlight could be tested for this and other species. Smithers (1971) trapped *R. pumilio* between 21h00 and 24h00 and Shortridge (1934) observed them on warm, moonlight nights.

Seasonal changes

Many authors have reported extended and increased general activity in small rodents during winter (Orr 1959; Grodzinski 1963). Falls (1968) in his review of nocturnal activity of *Peromyscus* concluded that on short summer nights activity is sustained at a high level and there is usually a single peak in the evening; on long winter nights, activity is less continuous and the average pattern shows two major periods of activity early and late in the night.

In *S. campestris* and *P. natalensis* there was an increase in the duration of nocturnal activity in winter, while in *R. pumilio* there was a greater night-time separation of crepuscular activity peaks, agreeing with general theory. The activity profile of *A. namaquensis* was considerably altered between the seasons; diurnal activity increased in winter and the onset of activity became very indistinct. The cause of these changes is unknown.

Nocturnal activity was discontinuous (except for *R. pumilio* in summer) and there was considerable variability in the duration of activity periods (excluding those of *P. natalensis*) which changed between the seasons. This situation is obviously complex and apparently less precisely influenced by photoperiod (and temperature) than in temperate regions where environmental variables have marked seasonal effects on activity patterns (Falls 1968; Lehman 1976). Calhoun (1945) documented the lability of activity rhythms in small mammals, and Ashby (1972) concluded his review by stating that patterns of diel activity of rodents vary greatly with environmental variables.

Activity patterns within a small rodent community

There was very little temporal overlap of active phasing between the two diurnal species, or between them and the nocturnal species. Differences in activity rhythms of the nocturnal species may have lessened niche overlap along a temporal axis, by skewing activity times or by differing degrees of crepuscularity. More information, and controls, are required to develop such an idea satisfactorily.

In the wild many factors affect the activity of small rodents. The seasonal composition (Watts 1968) and caloric content (Grodzinski 1962) of the diet, lactation (Gelmroth 1970), age (Gurnell 1972), social factors (Bovet 1972; Nel 1975) and interspecific interactions are some important factors. The apparatus used to study activity here provides much useful information on many of these.

References

ASHBY, K.R. 1972. Patterns of daily activity in mammals. *Mamm. Rev.* 1: 171 – 185.

ANSELL, W.F.H. 1960. Mammals of Northern Rhodesia. Government Printer, Lusaka.

AYLETT, P. 1962. Gastric emptying and change of blood glucose level, as affected by glucagon and insulin. *Clin. Sci.* 22: 117 – 178.

AYLETT, P. 1968. The effect of changes in blood glucose levels on the gastric emptying rate. *Am. J. Dig. Dis.* 13: 1035 – 1046.

BACKLUND, H.D. & EKEROOT, S. 1950. An actograph for small terrestrial animals. *Oikos* 2: 213 – 215.

BOVET, J. 1972. On the social behaviour in a stable group of long-tailed field mice (*Apodemus sylvaticus*). II. Its relation with distribution of daily activity. *Behaviour* 41: 55 – 67.

BROOKS, P.M. 1974. The ecology of the four-striped field mouse *Rhabdomys pumilio* (Sparrman 1784), with particular reference to a population on the Van Riebeeck Nature Reserve, Pretoria. D.Sc. thesis, University of Pretoria.

CALHOUN, J.B. 1945. Diel activity rhythms of the rodents, *Microtus ochrogaster* and *Sigmodon hispidus hispidus*. *Ecology* 26: 251 – 273.

CHOATE, T.S. 1972. Behavioural studies on some Rhodesian rodents. *Zool. Afr.* 7: 103 – 118.

CHRISTIAN, D.P. 1977. Diurnal activity of the four-striped mouse, *Rhabdomys pumilio*. *Zool. Afr.* 12: 238 – 239.

DAVIS, D.H.S. 1933. Rhythmic activity in the short-tailed vole, *Microtus*. *J. Anim. Ecol.* 2: 231 – 238.

DAVIS, D.H.S. 1959. The barn owl's contribution to ecology and palaeoecology. *Ostrich suppl.* 3: 144 – 153.

DAVIS, D.H.S. 1974. The distribution of some small southern African mammals (Mammalia: Insectivora, Rodentia). *Ann. Transv. Mus.* 29: 135 – 184.

DAVIS, R.M. 1972. Behaviour of the vlei rat, *Otomys irroratus* (Brants, 1827). *Zool. Afr.* 7: 119 – 140.

DELANY, M.J. 1975. The rodents of Uganda. British Museum (Natural History). London.

ERKINARO, E. 1969. Der Phasenwechsel der lokomotorischen Aktivität bei *Microtus agrestis* (L.) *M. arvalis* (Pall.) und *M. oeconomus* (Pall.). *Aquilo, Ser. Zool.* 8: 1 – 31.

FALLS, J.B. 1968. Activity. In: Biology of *Peromyscus* (Rodentia), (ed.) King, J.A., Inst. edn, ch. 14, Am. Soc. Mammalogists. U.S.A.

FIELD, A.C. 1975. Seasonal changes in reproduction, diet and body consumption of two equatorial rodents. *E. Afr. Wildl. J.* 13: 221 – 235.

GELMROTH, K.G. 1970. Wer den Einfluss verschiedener ausserer und innerer Faktoren auf die lokomotorische Aktivität der Waldmaus (*Apodemus sylvaticus* L.). *Z. wiss. Zool.* 180: 368 – 388.

GREEN, C.A., KEOGH, H., GORDON, D.H., PINTO, M. & HARTWIG, E.K. 1980. The distribution, identification, and naming of the *Mastomys natalensis* species complex in southern Africa (Rodentia: Muridae). *J. Zool., Lond.* 192: 17 – 23.

GRODZINSKI, W. 1962. Influence of food upon the diurnal activity of small rodents. *Proc. Int. Symp. Meth. Mammal. Invest. Brno, 1960:* 134 – 140.

GRODZINSKI, W. 1963. Seasonal changes in the circadian activity of small rodents. *Ekol. Polska Ser. B.* 9: 1 – 17.

GURNELL, J. 1972. Studies of the behaviour of wild woodmice, *Apodemus sylvaticus* (L.). Ph.D. Thesis. University of Exeter.

HEWITT, J. 1931. A guide to the vertebrate fauna of the Eastern Cape Province. Part 1. Mammals and birds. Albany Museum, Grahamstown.

KEOGH, H.J. 1973. Behaviour and breeding in captivity of the namaqua gerbil *Desmodillus auricularis* (Cricetidae: Gerbillinae). *Zool. Afr.* 8: 231 – 240.

KEOGH, H.J. & PRICE, P.J. In press. The multimammate mouse: a review of its ecology, distribution, present status and importance in medical research. *Proc. Int. Lab. Anim. Congr.*

KINGDON, J. 1974. East African Mammals: an atlas of evolution in Africa. Vol. 2(B), Hares and rodents. Academic Press, London.

LEHMAN, U. 1976. Short-term and circadian rhythms in the behaviour of the vole, *Microtus agrestis* (L.). *Oecologia* (Berl.). 23: 185 – 199.

MADDOCK, A.H. & PERRIN, M.R. 1981. A microscopicial examination of the gastric morphology of the white-tailed rat *Mystromys albicaudatus* (Smith 1834). *S. Afr. J. Zool.* 16: 237 – 247.

MEESTER, J. & SETZER, H.W. (Eds.), 1971. The mammals of Africa: an identification manual. Smithsonian Institution Press, Washington.

NEL, J.A.J. 1975. Aspects of the social ethology of some Kalahari rodents. *Z. Tierpsychol.* 37: 322 – 331.

NEL, J.A.J. & RAUTENBACH, I.L. 1974. Notes on the activity patterns, food and feeding behaviour of *Parotomys brantsi* (Smith, 1840). *Mammalia* 38: 7 – 15.

ORR, H.D. 1959. Activity of white-footed mice in relation to environment. *J. Mammal.* 40: 213 – 221.

PERRIN, M.R. 1971. Exploratory behaviour as related to trapping results and population estimation of the vole *Microtus agrestis hirtus* (Bellamy 1839). Ph.D. Thesis, University of Exeter.

PERRIN, M.R. 1980a. The feeding habits of two co-existing rodents, *Rhabdomys pumilio* (Sparrman, 1784) and *Otomys irroratus* (Brants, 1827) in relation to rainfall and reproduction. *Acta Oecologia Oecol. Gener.* 1: 71 – 89.

PERRIN, M.R. 1980b. The breeding strategies of two co-existing rodents, *Rhabdomys pumilio* and *Otomys irroratus*: with a brief review of some pertinent life history ideas. *Acta Oecologia Oecol. Gener.* 1: 383 – 410.

PERRIN, M.R. In press. Prey specificity of the barn owl, *Tyto alba*, in the Great Fish river valley of the Eastern Cape Province. *S. Afr. J. Wildl. Res.*

PERRIN, M.R. & CURTIS, B.A. 1980. Comparative morphology of the digestive system of 19 species of southern African myomorph rodents in relation to diet and evolution. *S. Afr. J. Zool.* 15: 22 – 33.

PETERS, K. & GÄRTNER, K. 1973. Untersuchungen zur Funktion des Vormagens der Muriden. I. Passage fester und flüssiger Futterbestandteile, pH-Wert und α-Amylaseaktivität im Vormagen der Ratte. *Zbl. Vet. Med. A.* 20: 233 – 243.

PETTER, F., CHIPPAUX, A. & MONMIGNAUT, C. 1964. Observations sur la biologie, la reproduction et la croissance de *Lemniscomys striatus. Mammalia* 28: 620 – 627.

ROBERTS, A. 1951. The mammals of South Africa. Trustees of 'The mammals of South Africa' Book Fund, Johannesburg.

ROSEVEAR, D.R. 1969. The rodents of West Africa. Trustees of the British Museum (Natural History). London.

SCHMIDT-NIELSEN, K. & SCHMIDT-NIELSEN, G. 1953. The desert rat. *Sci. Am.* 189: 73 – 78.

SHORTRIDGE, G.C. 1934. The mammals of South-West Africa. Heineman. London.

SKAIFE, S.H. 1979. African insect-life. Struik. Cape Town.

SMITHERS, R.H.N. 1971. The mammals of Botswana. Trustees of the National Museums of Rhodesia, Salisbury.

STUTTERHEIM, D.J. & SKINNER, J.D. 1973. Preliminary notes on the behaviour and breeding of *Gerbillurus paeba paeba* (A. Smith, 1834) in captivity. *Koedoe.* 16: 127 – 148.

SZYMANSKI, J.S. 1918. Die Verteilung der Ruhe-und Aktivitätsperioden bei weissen Ratten und Tanzmäusen. *Arch. ges. Physiol.* 171: 324.

THOMAS, O. & SCHWANN, H. 1905. The Rudd exploration of South Africa. II. List of mammals from the Wakkerstroom District, south eastern Transvaal. *Proc. zool. Soc. Lond.* 1905(1): 129 – 138.

WALKER, E.P. 1975. Mammals of the World. 2 vols, 3rd edn. The John Hopkins University Press. Baltimore.

WATTS, C.H.S. 1968. The foods eaten by wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in Wytham Woods, Berkshire. *J. Anim. Ecol.* 37: 25 – 41.