BEHAVIOURAL STUDIES ON SOME RHODESIAN RODENTS

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ABSTRACT

Field studies (Lake Kariba shoreline and Salisbury) and experiments with a captive colony of 12 species of Rhodesian rodents were undertaken for a period of three years. Comparative behavioural data are presented here with special reference to den and nest behaviour, group and territorial behaviour, reproductive and juvenile behaviour, and activity pattern. No species was found to be truly gregarious except *Dendromus mesomelas*, but *Praomys (Mastomys) natalensis, Lemniscomys griselda, Tatera leucogaster*, and *Aethomys chrysophilus* were found to tolerate crowded conditions in captivity. Nipple dragging of young was found in both species of *Aethomys* and in *Acomys*, with the remainder observed to utilise mouth carrying behaviour. It was noted that especially in *Rhabdomys* and *Praomys (Mastomys)*, and also in *Lemniscomys*, young have a strong tendency to scatter in all directions from a disturbed nest, even before their eyes open. The significance of nipple dragging, scattering and crowding behaviour and correlation to survival and tendency to irrupt are discussed. All species were found to be nocturnal (usually with irregular sub cycles of activity) except *Rhabdomys* (largely diurnal), *Lemniscomys* (diurnal/crepuscular) and *Otomys* (nocturnal/crepuscular).

A number of books and papers deal with the taxonomy of rodents in southern Africa but little behavioural information is included in most of them and none specifically deals with Rhodesia. It is the purpose of this paper to deal with several species of rodents at the same time so that comparison between them can be made with regard to each topic studied. The two species of *Aethomys, Praomys (Mastomys) natalensis, Rhabdomys pumilio* and *Tatera leucogaster* will be emphasised throughout, as the majority of field and laboratory observations have been made on them. Where possible, data will be given on *Saccostomus campestris, Lemniscomys griselda, Acomys spinossisimus, Dendromus mesomelas, Graphiurus murinus, Otomys angoniensis* and *Cricetomys gambianus* but the samples for this latter group were often very small. In cases where limited field data were obtained, laboratory observations are given but no implication is made that the behaviour would be the same in the field.

Comparative consideration will be given to den and nest behaviour, grouping and territorial behaviour, courtship, parental and juvenile behaviour and activity patterns. The quantitative and detailed studies of the ecological and display patterns of individual species will be published elsewhere, as they would detract from the purpose of this paper, namely the emphasis of broad comparative aspects.

PROCEDURE

The observations both from field and laboratory work reported herein were collected over three years from April 1968 to April 1971. Field studies centred on the Nuffield Lake Kariba Research Station at Sinamwenda on the southern shores of Lake Kariba in the Chete Game Reserve. Vegetation on the predominantly basalt substrate is mainly *Colosphermum mopane* woodland. Live trapping indicates that the dominant rodent species here are *Aethomys chrysophilus* and *A. namaquensis, Acomys spinossisimus, Praomys (Mastomys) natalensis* and *Tatera leucogaster.*

Graphiurus murinus and *Lemniscomys griselda* occur sparsely. At least a hundred live-trap-nights in each of five study sites were run three or more times per year (normally at 3–4 month intervals), providing over a thousand captures or recaptures from which behavioural data were derived. Sample sizes vary with each species and topic so are reported individually in the text.

The same live trapping pattern was followed at Salisbury where most of the other field work was carried out. The two main substrates here are red clay-loam soil and black vlei soil, the former occupied by *Brachystegia* woodland and the latter by vlei grassland. The main species in the Salisbury study area were *Rhabdomys pumilio, Praomys (Mastomys) natalensis, Saccostomus campestris, Otomys angoniensis, Dendromus mesomelas,* and *Cricetomys gambianus.*

A laboratory colony of all these species was established at the University of Rhodesia. No less than 100 individuals were studied in the case of the five important species. Other sample sizes are reported in the text. Nearly all the animals were kept as pairs or families in wire cages of from 0,028–0,057 m^3 capacity containing a nest box with cotton wool and wood chips. Later behavioural observations were facilitated by the development of a glass-fronted "double-storey" cage which made pairing, encounters and photography of behaviour easy (Fig. 1). Tests of grouping and agonistic behaviour of the five most abundant species were staged on a "neutral" table of 0,37 m^2 surface area (details of these experiments are not reported here). Animals were normally housed in a partially temperature-controlled room and at least a dozen individuals of most species have been housed for over a year in a controlled light and temperature room with 12 hours red and 12 hours white light. Observations were usually recorded on tape and often made through one-way glass. Activity was recorded in both field and laboratory with a 10 channel Goertz Miniscript event recorder. The solenoids were operated by foot treadles which could be set off by a 5–10 g force.

DEN AND NEST BEHAVIOUR

Few direct observations on behaviour of wild mice were gathered during the first two years of this study. The obvious reasons for this being the nocturnal nature and inaccessible dens of most of the species. No special effort was made to dig out dens, but a few were found belonging to most species. Most of the following observations are supplemented with notes on animals breeding under artificial laboratory conditions.

a) Aethomys namaquensis commonly makes large nests of grasses in niches between large rocks or in hollows of live or fallen trees. The average height above ground for 17 nests was 82,3 cm with the lowest being 42,7 cm and the highest 1,4 m. All but five of these were between horizontally lying rocks which averaged 1,8 m in diameter. These observations are in general agreement with those of Ansell (1960) and Roberts (1951). Within these grass nests there are several tunnels and some had more than one chamber. Faeces was often widespread, but six nests showed evidence of regular toilet areas. In five nests more than two adults were found, but of 12 others, reasonably fully dismantled, only three contained mice but some may have escaped. Two of the latter were occupied by a pair of adults (one with young) and in one, only a lone male was found. Thus from these few examples, it seems that nests in this species may contain solitary animals, pairs and larger groups of up to four adults. This is in agreement with a variety of notes in the literature e.g.

Ansell (1964), Davis (1962), Powell (1925), Roberts (1951), and Shortridge (1934). In captivity more than one male was rarely tolerated but a pair shared a simple nest together with their immature offspring (73 matings). A dark nest box improved the frequency of parturition but was not required for reproduction.

b) Aethomys chrysophilus nests were not examined in the field due to inaccessibility but this species was found to occupy burrows (eight instances), rock niches (six instances) and the base of a tree (one instance). In at least three of the former cases, trapping and tracks showed the burrow to be used also by *Tatera leucogaster* but it was not possible to determine which species was truly resident in the burrow. Under captive conditions *A. chrysophilus* bred freely in the absence of nesting material or a dark chamber, but built lined hollows when material was offered (143 pairs, 105 litters). Both sexes participated in building in most instances but the female in a few cases forced the male to remain outside the nest, especially when she had young. The field observations generally agree with the foregoing authors and Smithers (1968).

c) Praomys (Mastomys) natalensis nests were only found four times in the field, two of these being in burrows and two in crevices (one rock and one tree base). Several other pregnant females were traced to burrows but not investigated further. The nests found consisted of simple, lined chambers about 11,4 cm in diameter at the end of variable runways from 0,46–1,67 m in length, but within 0,6 m of the ground surface. Lining materials varied from grass and leaves, through dry roots (?) to hair.

Captive animals brought all available materials (wood chips, cotton wool, vegetables, food pellets) to the nest and built large piles between the darkest corner and the opening (119 pairs, 70 litters). Sometimes materials were lodged between the wires so as to block the light. Both sexes indulged in nest making and light-blocking behaviour and in some cases a mated pair was joined in these actions by juveniles or even other adults living in the same cage (similar to Plate 11, Barnett 1963). This species was the only one in this study which successfully reared young in a small cage with several males and females present (21 litters). *A. chrysophilus* could do so with one male and several females, but the others were usually successful only in pairs. Field observations show that *Praomys (Mastomys)* burrows sometimes contained more than a pair of adults as well as some juveniles. This agrees with Ansell (1960) but not fully with Shortridge (1934) who says they are not gregarious.

d) Rhabdomys pumilio: This species usually nests above ground, as indicated by the locations of nine surface grass nests during the study, and only two each in crevices and burrows. One pregnant female was known to live in a burrow but she was not recaptured there after the date young were expected (see Choate (1971) for gestation and other reproductive information). However one family with recently weaned young shared a burrow with at least one *Praomys (Mastomys) natalensis.* A typical situation for a nest was at the end of a covered runway in deep grass, and two were placed alongside large tussocks with slight excavations dug beneath the grass nest proper. Above ground grass nests resemble birds nests (e.g. *Prinia*) being about 15,2 cm in diameter (range 10,1–20,3 cm) with a single 3,2 cm entrance hole leading to a 7,6 cm diameter chamber in the centre, lined with fine grasses. Females and young were found in all but one occupied nest, the

remaining one containing a young adult male.

In captive conditions females built nests of available materials and frequently, but not always excluded males once young were born (81 pairs, 49 litters). However, both in one wild nest and several captive nests, weaned young were allowed to remain with newly born young (3–4 weeks younger – resulting from post-partum copulation). New nests could be constructed within 24 hours as evidenced by a female with six young whose nest was disturbed during field investigations and was found in a new one 2,13 m away the following morning. No evidence supports the idea that *Rhabdomys* is communal (put forth by Powell 1925 and supported by Walker 1968) and two males placed together are usually very intolerant (see groups).

e) Tatera leucogaster: Only one nest of this species was found, as the extensive burrow systems of the Sinamwenda study area were left intact. No evidence was found of *Tatera* living anywhere except in burrow systems which were occupied by families or even several adults (in 20% of 65 colonies studied). The single nest dug up was in an unlined chamber 11,4 cm in diameter, 76,2 cm below the surface, off a complex of tunnels, 1,5 m from the nearest entrance. Three young (about 7 days old) were in the nest, but no *Tatera* adults were caught in this case.

In the laboratory, several pairs failed to breed in open cages even when nesting material was supplied (grass nests are built by some Gerbils and Jerboas, Happold 1970). Two pairs were put in aquarium tanks, one filled with damp sand, the other with clay-loam soil. Both pairs burrowed extensively and the pair in soil built a nest chamber of 10,1 cm diameter at the furthest point away from the entrance (61,0 cm). They had conceived young during the 3 weeks before their burrowing collapsed the nest chamber. Four young were born 3 weeks later in a very shallow hole and three were raised largely on the surface after one was buried in another collapse. The descendants of these two pairs have continued to breed in cages with little nest shelter, forming small mound nests out of wood chips and other available material (48 pairs, 30 litters). The male is sometimes excluded from the nest area, but not always, and on a few occasions the male assisted in nest building.

f) Other species: No nests have been found belonging to *Saccostomus campestus*, although it lives in burrows in the study areas. *Lemniscomys griselda* likewise has not been directly observed although a grass nest was found on a runway used by this species. One *Acomys spinossisimus* nest was found under a very large rock.

The chamber was poorly lined and located about 1,1 m from the entrance, nearly level with the ground surface. Two large mice escaped when the rock was lifted but no young were seen. Twenty three pairs of this species have been identified in the vicinity of specific holes, and only six additional adults have been caught at the same localities, giving a fair indication that most *Acomys* live in rock niches in family-sized units only. They are poor nest builders in captivity and rarely have given birth (18 pairs, four litters).

One nest each of the tree-dwelling species *Graphiurus murinus* and *Dendromus mesomelas* have been observed to date. The former was in a faeces and shredded vegetation-lined cavity 3 m up the trunk of a dead tree and contained a female and four young only. The latter was a grass nest occupied by approximately 11 adults of both sexes in a fork of a branch 1,8 m off the ground. It was not clear whether they had taken over a bird's nest or built the 25,4 cm diameter structure

themselves. In the laboratory both species make nests of available materials but *Graphiurus* seems more adept at constructing a strong chamber (sample of three each). *Lemniscomys*, and *Saccostomus* have so far failed to make much use of nesting materials placed in their cages (34 and 25 pairs respectively). Only the former will normally tolerate more than a mate in a small cage with it (see below).

GROUP SIZE, TERRITORY AND INDIVIDUAL DISTANCE

a) Aethomys namaquensis: Under captive conditions this species is moderately aggressive and in cages ranging from 0,028–0,057 m^3 capacity, two adult males could not be housed together without serious fighting which usually resulted in the death of one. Even when juvenile males were housed together after weaning (about 30 days) fighting erupted within a month and social dominance was established in every case (23) by the end of the second month. In some cases siblings would kill each other but more commonly sub-dominant males would carry extensive wounds along the neck, back and tail but survive for weeks, usually occupying the most distant corner of the cage. These wounded animals eventually died or were removed for humane killing and in 14 out of 16 cases a new "scapegoat" developed among the remaining juvenile males (average of three). In only one instance was the damaged animal a female. There was evidence of increased aggression between the males in mixed groups after the third month when females began to be sexually receptive (this agrees with Scott 1951).

Home range and territoriality data (to be published elsewhere) from field studies indicates that groups (usually a family) had a minimum "exclusive" space of 100 m^2 centred on the nest. In captivity, groups or individual adults which had been undisturbed in cages for more than a few weeks developed a territorial type of attachment to their space and in a few cases defended some distance around it. Most marking, defence and aggression was shown by males and on seven occasions males which had escaped from their cages were observed to threaten or "fight" males of adjacent cages through the bars. Strangers were usually attacked when placed in the cage regardless of sex and age. Furthermore 50 tests on neutral ground (to be published later) showed decreased dominance and lack of space-orientated aggression in the same, formerly "territorial" males, but fight winners nearly always marked objects in the new area with urine ("crawl over object" of Grant and Mackintosh, 1963). The relatively exclusive territoriality apparent in *A. namaquensis* does not agree with the comments by Roberts (1951) and others implying a degree of communal living.

Solitary males sometimes even wounded females in oestrus severely (five of 22 cases), but this seemed to depend on "personalities", as in one instance a female in oestrus which had been living alone defeated a male in his own cage (see Archer, 1970 for effect of solitude). Groups of up to seven females were raised to adulthood together and fighting developed in only two of 11 cases. Adult females could be placed together as strangers in relatively few instances and when successful these were the result of live-trapping wild animals and simultaneously placing them together in a cage. Pairs could be formed from strange adult males and females in this fashion as long as they were sufficiently stressed by live-trapping. The trauma of capture appears to have suppressed the aggressive components of the encounter and pairing behaviour (19 instances). This is perhaps allied to the suppression of aggression in pairs of animals recovering simultaneously from certain

anaesthetics (Cherkin & Meinecke 1971).

b) Aethomys chrysophilus: The limited field data indicate relatively wide spacing of pairs and only a few instances of more than two adults occupying a burrow or crevice. In the laboratory, wild-caught adults were frequently very aggressive, not only to conspecifics but to other rodents and even humans. Threatening displays (details to be published elsewhere) were made at the boundaries of all sizes of cages, especially by males, and this usually accompanied investigation of disturbances. This tendency to investigate, patrol, urine-mark and threaten at cage boundaries is taken as an indication of territoriality. However, a considerable reduction in this behaviour was noted with time and after four months in captivity, all but one of 21 males (17 paired with females) had ceased threatening humans and animals in adjacent cages. They did persist in full investigation and aggressive display toward animals placed in their cage including those of other species (see under *Rhabdomys*). Two such males meeting on neutral ground nearly always showed complete agonistic sequences (25 cases – to be detailed elsewhere).

It is possible that because the captive colony developed from the offspring of five (out of 10) wild-caught females, many of which were not full adult weight, there was selection of less aggressive (or more adaptable) strains. Subsequent generations (more than 250 individuals) tolerated considerable crowding provided they were siblings or placed together shortly after weaning. Up to 13 females occupied 0,057 m^3 cages with minimal strife (but a social order developed) and one male would live and reproduce with several females and their young in these cages. Young males were tolerated through to adulthood provided they retained their subordinate status (perhaps "psychological drubbing" of Calhoun 1963), but groups of males seldom were strife-free even if raised together. Low-ranking and defeated males usually showed mutilations from fighting or persecution but were much more rarely killed than in *A. namaquensis*. Groups of three to six males have been maintained together for over a year with only minor strife (provided resources are abundant) once a ranking is established.

c) Praomys (Mastomys) natalensis has been successfully raised in captivity by a number of workers (Davis 1963). Both in the field and in the laboratory several adults will live together with little aggression even in cages of less than 0,028 m^3 capacity. In low density field areas the nest unit seems to be a family but even two adult males have been found together. Females with young will tolerate other adults and juveniles in the nest box under captive conditions, provided they are companions of long standing. In larger cages there is some evidence of voluntary maintenance of groups ("In Groups" of Calhoun 1963).

Strangers are more readily accepted into groups by this species than any other studied but this is also the most nervous species with respect to the investigator. The highly-strung and fearful attitude of wild-caught adults and juveniles was never fully lost even after a year of conditioning, but breeding commenced after only a month or two in captivity provided that dark nestboxes were available (for behaviour details see Veenstra 1958).

d) Rhabdomys pumilio: Most observations in the field indicate that males occupy well-separated areas. In captivity a fairly wide range of individuality was observed, with most adult males not tolerating other males in their cages. However, some individuals were tolerant, especially when

freshly caught or when placed in frightening, neutral environments. Similarly, some females would accept strangers in their cages and more frequently would do so in neutral cages, but the majority were aggressive and females with high aggression scores dominated males with low aggression scores when placed in neutral cages (data to be published elsewhere).

In cases where males and two to three females were settled together the females and sometimes the males shared parental duties (see below) and showed minimal aggression. Sibling males would frequently remain together without serious fighting once sexually mature, but social ranking was established and the lowest animal was frequently scarred on the back from bites. When a female was raised in such a group, and especially if she was introduced as an adult, the resultant conflict between males normally resulted in the death of the "lowest" male (not necessarily sexual combat, Barnett 1963, p. 84 and 195).

Some long isolated males regularly damaged or killed females placed with them, even if in oestrus. This may be an extension of the concept of increased aggression shown by mice raised in isolation (Kahn 1954). One such male was placed with an aggressive *Aethomys chrysophilus* male and was immediately submissive to his threats. After a week the individual distance had so narrowed (inter-specifically) that they were found resting together in the same corner of the 0,028 m^3 cage. Older males of this species also showed "cage territoriality" and in addition moved to adjacent cages (if given the opportunity) and threatened residents through the bars. This was greatly strengthened if an oestrus female was inside and in two instances resulted in three-way fighting: the presence of the extra male disrupting peaceful relations between the resident pair. It is possible to interpret this, however, as simple "behavioural contagion" (Dimond 1970, p. 130).

e) Tatera leucogaster: As indicated above, these were found to be somewhat communal in the field, even accepting other species in the burrow upon occasion. Nevertheless, in small cages (0,028 – 0,057 m^3), the most successful group was the pair, and extra individuals of any sex and age were often only tolerated if they were all simultaneously placed in a strange cage after some severe "psychological shock" (such as after initial capture in the wild) or if raised together from weaning age. Some exceptions to this were noted, but none of these bred successfully, implying some form of inhibition within such a group. Strong "freezing" or flight behaviour was shown by recently caught animals which never fully ameliorated, even in their offspring. When held firmly in the hand *Tatera* would usually cease to struggle and would not bite.

Individuals of both sexes, if sufficiently large and mature, would treat cages as "territories" by marking, drumming and threatening strangers and neighbouring individuals. In this respect they showed similarity to *A. chrysophilus* but rarely developed similar tolerant ("harem") breeding groups in captivity. Foot drumming, interpreted as defence/threat, was performed by both sexes but some individuals were never observed to drum. Males usually urine marked cages, especially in the presence of strangers, regardless of whether a fight ensued or not.

f) Other species: Saccostomus campestris was found to be extremely intolerant in captivity and strange adults were rarely successfully housed together. A pair in a "double-storey" cage (Fig. 1) had the levels connected only for mating. Adolescent siblings in both single sex and mixed groups developed fighting behaviour (seven of 12 litters) which usually ended in severe injury or death to one participant. This species shows remarkable convergence with hamsters, not only in

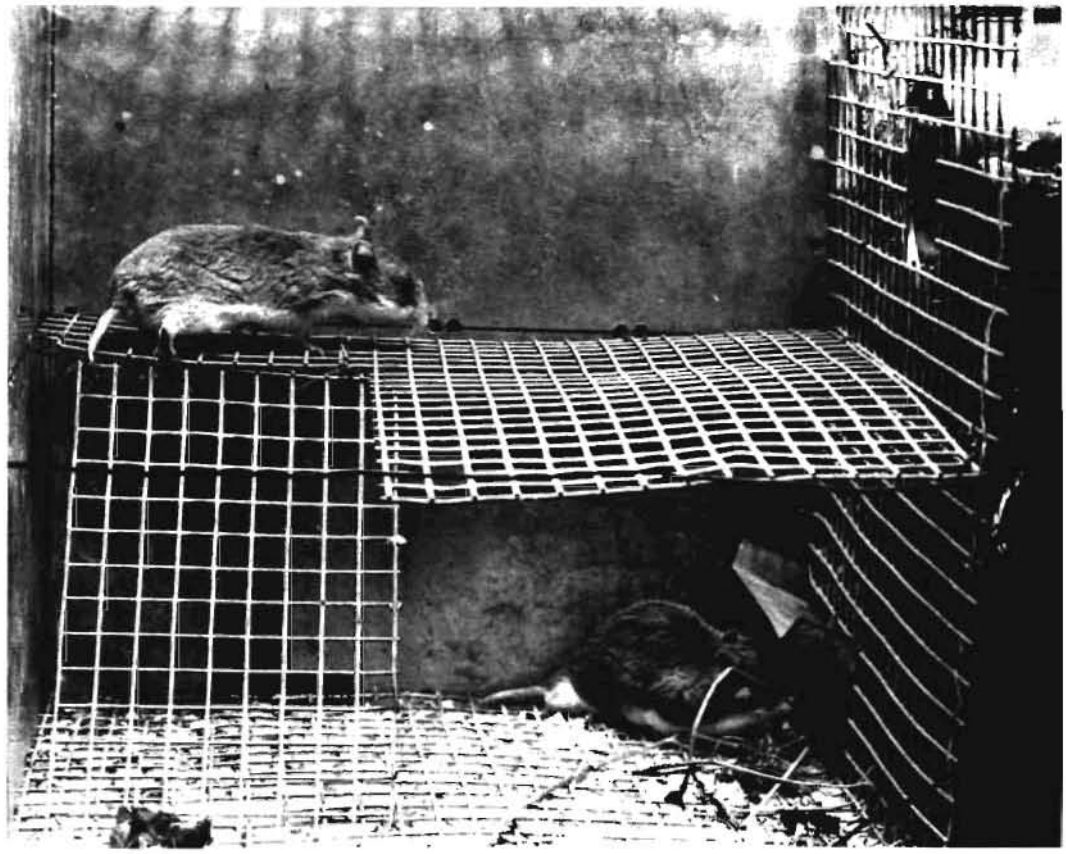

FIGURE 1
The two storey, 0,028 m^3 observation cage with a glass wall, containing a pair of *Saccostomus campestris*.

morphological but ethological characters. For example, despite their docile nature with humans, the only reliable period when male and female could be placed together was during the height of her oestrus and even then some fighting took place before coitus (this agrees with Eibl-Eibesfeldt 1953). The female usually dominated even on neutral ground and most successful matings were effected by putting the female into the male's cage.

Lemniscomys griselda showed considerable fright behaviour in the form of "freezing" when newly caught and groupings could be made at this time. However social order was soon established and thereafter intolerance was shown, but aggressive encounters seldom resulted in severe injury and several adult groupings, especially of mixed sexes, have been successful. All juveniles raised together stayed peaceful, though with mild social order developing after about 40 days (sample of over 50). Parents would tolerate their young until nearly grown with the adult male showing the first intolerance towards young males (inconsistently and only after testes descent).

Acomys spinossissimus seems to be a fairly intolerant species, which not only shows evidence of fixed home range in the field (occupied by one or rarely two males), but males fight each other in 0,028 m^3 cages regardless of breeding condition. In four instances juvenile males were persecuted by their fathers to the extent that most of the spines were lost on the back and two failed to obtain more than 75% of normal adult size in six months. Polygamous groups and pairs were usually peaceful but rarely bred in small cages.

Dendromus mesomelas shows nearly the opposite behaviour to the foregoing, with the three groups studied containing all sexes and ages including several sexually mature males. Unfortunately, young have not been born in these gregarious groups so evidence is lacking on the effect of mating and young on colony behaviour.

Graphiurus murinus, Otomys angoniensis and *Cricetomys gambianus* have all been kept in captivity but without successful raising of young. None of these three seems to be tolerant of groups and show well developed threat toward strangers in the cage and even mates (particularly in the case of *Cricetomys*).

COURTSHIP, PARENTAL AND JUVENILE BEHAVIOUR

a) Aethomys namaquensis: Courtship activities were seen to occur at all times of the year with peak births occurring in summer (field data also support the latter). Both parents participate in nest building and young are born in the same nest used for daily activities. Post-partum heat is common and aggression may occur shortly after birth. In a few cases where young were available (not attached to the nipples of the mother) they were killed by the male. During the first three days, and sometimes thereafter, young removed from the nipple for examination were occasionally killed by the mother, rather than replaced on the nipple by her. The safest procedure was to place the teat in the baby's mouth to which it immediately attached.

Nipple dragging is the rule in this species until about three weeks of age (this agrees with Meester 1958 and 1970). After about two weeks, when the eyes are open, the young may be found detached upon occasion; but even when four weeks old may rush to the teat during fear provoking situations. There are a few instances recorded where the female discouraged this in order to travel by herself after the young were three weeks old. In the field, the only time a baby was found attached to the teat of a trapped female it had probably entered the trap unattached as it was recaptured alone the following night.

b) Aethomys chrysophilus shows a similar reproductive pattern except that less fighting was observed between males and in captivity they bred more readily throughout the year. However, females with young sometimes excluded the male from the nest box (but did not otherwise show aggression) when they had young attached to the nipples. This species has a similar slow maturity of over four months and full reproductive potential seemed to be reached in the second year (highest litter frequency, data to be published elsewhere). Males and females of this species were not seen to kill their young and usually accepted them back after temporary removal. Both females and males groomed their young more frequently in this species than in *A. namaquensis*.

c) Praomys (Mastomys) natalensis has been described by several authors and comparative data are shown in Meester (1960). Observations on our colony indicate similar parental behaviour with the following additional notes: post-partum heat is very common and litters may be born throughout the year with mid-winter lowpoint. This agrees with Coetzee (1965) in part, but not with Delany (1969). With successive litters born, the young are not evicted from the nest and up to three litters comprising 25 young plus the parents were seen to live together. At this point there were no further post-partum pregnancies which may indicate density regulation. Furthermore, disturbed females often ate their young, especially in the first few days after birth.

Nipple dragging was not present and females, males and even other cage residents participated in transfer of young to a new site after disturbance. A strong tendency to evacuate the nest was noted in young over one week old, even though their eyes had not yet opened. Scattering of many young in differing directions probably has a high survival value, and vocalizing by such "lost" young did not begin immediately. After about 15 days of age violent escape jumping and hiding or "on bars" (Grant and Mackintosh 1963) were all well developed.

d) Rhabdomys pumilio: Both parents are usually present at birth and participate in nest building and post-partum copulation with a high frequency. In a number of cases, however, the male was excluded from the nest box (or ball) by the female and in one case a sexually frustrated male tried to mount fleeing juveniles in the cage and showed masturbatory (?) scrotum dragging. Disturbed females and males killed their young, especially in the first week. Nipple dragging is not present but nest evacuation by young is extremely well developed. Within the first week they would wriggle out of sight under nest materials anddurin g the second and third weeks run considerable distances from the nest. A special squeak after 10–20 minutes caused retrieval by both parents.

e) Tatera leucogaster: Although males were frequently allowed in nest boxes by females after birth, post-partum pregnancy was less common in this species than the other four and less aggression occurred between the pair during this period, possibly indicating lack of oestrus. Field data indicate breeding only during summer. Killing of newborn young by either sex was rare. However, females seemed to require up to a year to reach optimum maternal activity and inexperienced mothers were seen to use young as nest material rather than to place them in the centre as special objects. Males participated very little in parental care. It is notable that this species moved young by mouth carrying virtually exclusively as opposed to teat dragging seen in other species of *Tatera* (Meester and Hallett 1970). Young clung to the teats more firmly than in *Rhabdomys* and *Praomys* but females usually specifically pushed them off the nipples when leaving the nest. Young still attached to the mother after a hurried exit generally fell off before the other side of the 0,057 m^3 cage was reached and were eventually carried back to the nest by mouth. Audible calls by young were as frequently made in the nest as when dropped outside, as in *Praomys (Mastomys)* and some *Peromyscus* (King 1963). Evacuation (scattering) behaviour of young was not seen in this species.

f) Other species: Saccostomus campestris, as mentioned above, is rather hamster-like and usually males were not tolerated by females except at oestrus. Therefore they were not allowed to participate as parents and the females raised the rather altricial young by themselves, and retrieved

them by mouth carrying as expected. Post-partum heat was only observed in a single case and excessive fighting in the typical "rolling-ball" fashion prevented copulation. This tendency to turn over when threatened was seen in juvenile play as early as three weeks.

Lemniscomys griselda showed a pattern fairly similar to that of *Rhabdomys* except that slightly lower numbers of young were born under more gregarious conditions. They developed rapidly, unattached to the teat, in nests largely constructed by females and both sexes retrieved displaced young. Their escape behaviour was not as well developed as the adults.

Acomys spinosissimus: The male is tolerated by the female during birth and post-partum copulation occurred in two cases but seems uncommon. Young are large at birth and immediately attached firmly to the teat. They could be seen free at times after only two weeks but took as much as four months to reach adult size. Breeding in both laboratory and field was restricted to summer (November – March). Also in the field there is evidence that juveniles do not breed until the following summer at about nine months old.

ACTIVITY RHYTHMS

A series of activity rhythm recordings from cages containing pairs or individuals of the seven main species were made under natural light conditions in February and March. Normal activity of three or four individuals of five species was recorded simultaneously for 24 hours. Replicate recordings were made of at least 6 other individuals for at least four other 24 hour periods. The 10 cages being recorded at any one time were by necessity within sound (but not sight) range of each other. There is thus some likelihood of mutual stimulation in the records, but diurnal and nocturnal species were always run together and their recordings seem largely independent in character.

Fig. 2 shows a typical (not composite) record of this series in which a pair and an individual of each of five species were tested. The difference in height of the activity bars represents a different total of activity in the 20 minute periods extracted from the continuous record. For each species the histogram with the greatest average height was produced from the cage with two animals in it, e.g., the upper for *Praomys (Mastomys).* No difference in the pattern produced is detectable between the two histograms for *Praomys (Mastomys), Tatera* and *Aethomys chrysophilus.* However, slightly more continuous activity was shown by *Aethomys namaquensis* and *Lemniscomys* in the two-animal cages, suggesting a mild degree of social facilitation. As noted earlier, none of the seven species whose activity graphs are presented show true social grouping in the field and often remain intolerant in captivity.

Apart from the diurnal pattern apparent in *Lemniscomys* all these species show a clearly nocturnal pattern. This is in general agreement with Ansell (1960, 1964), Roberts (1951), Shortridge (1934) and Walker (1968). However, a number of subsidiary peaks are shown within the general activity period of most individuals tested. *Praomys (Mastomys)* seems to show early, middle and late activity peaks. *Tatera* is more continuously active than the other examples. The two species of *Aethomys* both have two or three resting periods of an hour or less with some tendency for quietness near midnight. The histograms for *Lemniscomys* show a strong crepuscular activity with only short, irregular activity periods during midday. This is not mentioned in the available literature.

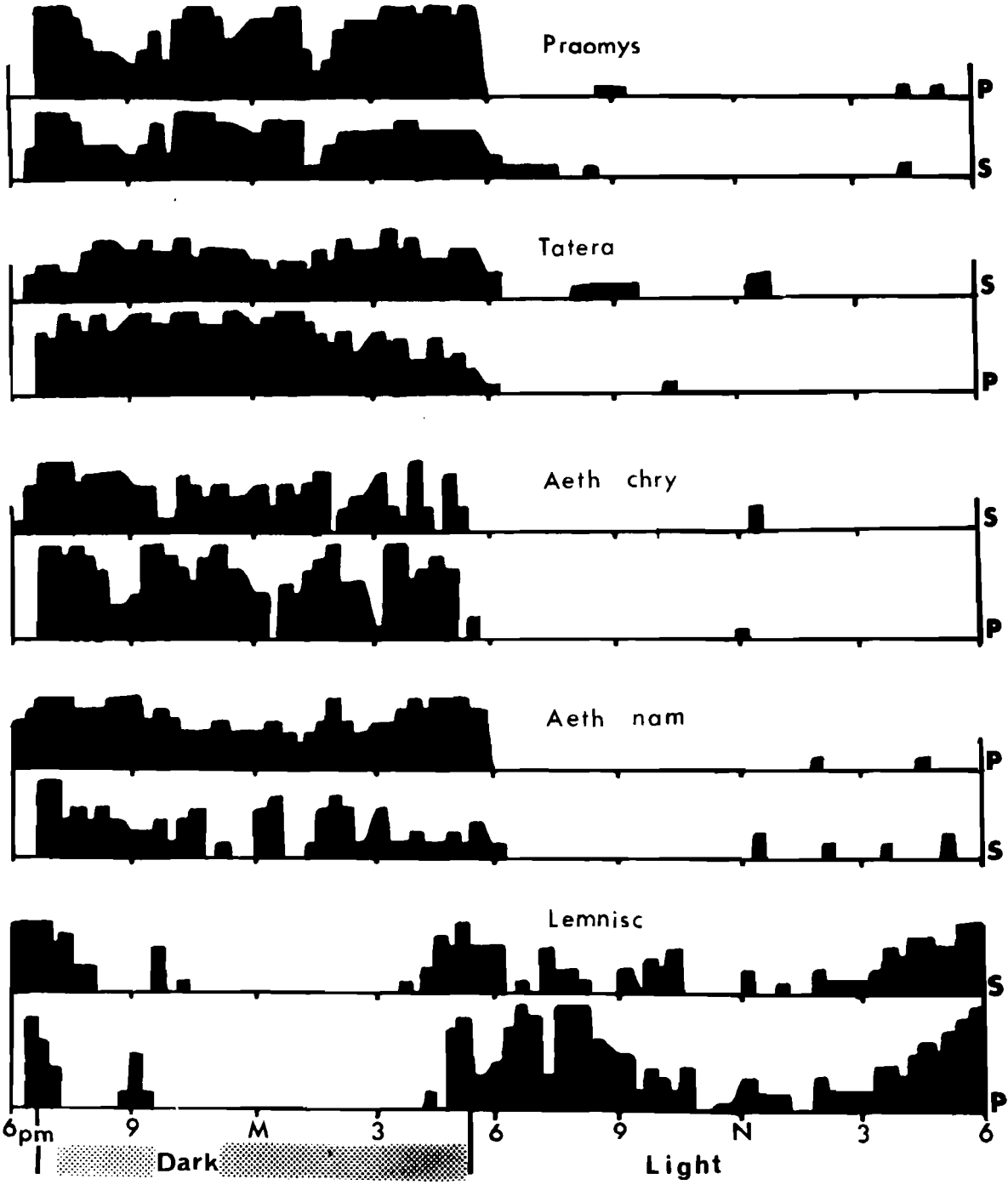

FIGURE 2

Activity patterns of five rodent species under natural light, February, 1970. P and S. refer to a pair or a single animal in the cage recorded.

During the same February–March period pairs of each of the seven species were recorded under 12 hours of red and 12 hours of white light phased about 2 hours earlier than natural light (Fig. 3 shows typical activity records). Note that the nocturnal species (in Fig. 2) responded similarly to the red light as to darkness and shows no sign of awareness of actual outside light conditions. *Saccostomus campestris* falls in this class, although not shown in Fig. 2. *Lemniscomys* maintains its crepuscular activity peaks but shows a spreading of activity into the red light "night". It seems able to awaken more than an hour before the white light, as it does naturally before dawn (Fig. 2). *Rhabdomys pumilio* shows a similar tendency to extend its activity over about half the night and anticipate the white light but is more active at midday. Although not shown in Fig. 2, *Rhabdomys* is quiet during most of the night and for three or four short periods during the day under normal light conditions. It is suggested that an ability to see in the red light and thus failure to adapt to it as "night" (despite a month's previous exposure) accounts for this apparent nocturnal activity in *Lemniscomys* and *Rhabdomys*. Field trapping never revealed nocturnal activity in either species. An internal "clock" mechanism must be present, however, to account for the awakening of activity an hour or two before the white light turns on (and well before they awakened under natural light).

Other species were studied in which insufficient individuals were kept in captivity for a reliable activity study. These include *Acomys spinosissimus, Graphiurus murinus, Dendromus mesomelas, Otomys angoniensis* and *Cricetomys* gambianus. Of these, all showed purely nocturnal activity except *Dendromus* and *Otomys. Dendromus* (the only sociable species and thus the sample of 24 was in three groups) was active crepuscularly, emerging an hour or so before dark from the communal nest. Since groups of eleven, eight and five lived together they showed fairly synchronous activity, probably as a result of mutual facilitation and therefore each group could be considered as only one sample of activity. *Otomys* (sample of eight in four pairs) occasionally showed diurnal activity, but was primarily crepuscular and nocturnal. The four (two pairs) kept under red/white lighting were seldom active except under red light. Thus the variable nature of *Otomys* activity shown in the literature (see Walker 1968) is apparently confirmed but this species requires further study.

Field recordings were made at seven den sites over a period of five days and served mainly as confirmation of the nocturnal nature of *Acomys*, both *Aethomys, Praomys*, and *Tatera*. Data are not shown as it was not known how many animals made the recordings.

DISCUSSION

It was found that all species (except *Dendromus* which is truly social) showed some aspects of agonistic, territorial-type behaviour although much of the evidence comes from captive conditions. Such behaviour was well marked in aggressive species such as *Aethomys namaquensis* and *Rhabdomys pumilio*. It is notable that the most nervous and defensive species towards humans, *Praomys (Mastomys)*, was one of the more tolerant of its own kind, especially if part of the family group. This supports the concept of independence of these two forms of behaviour (Barnett 1963).

Two groups emerge from examination of parental behaviour, those which drag young by the

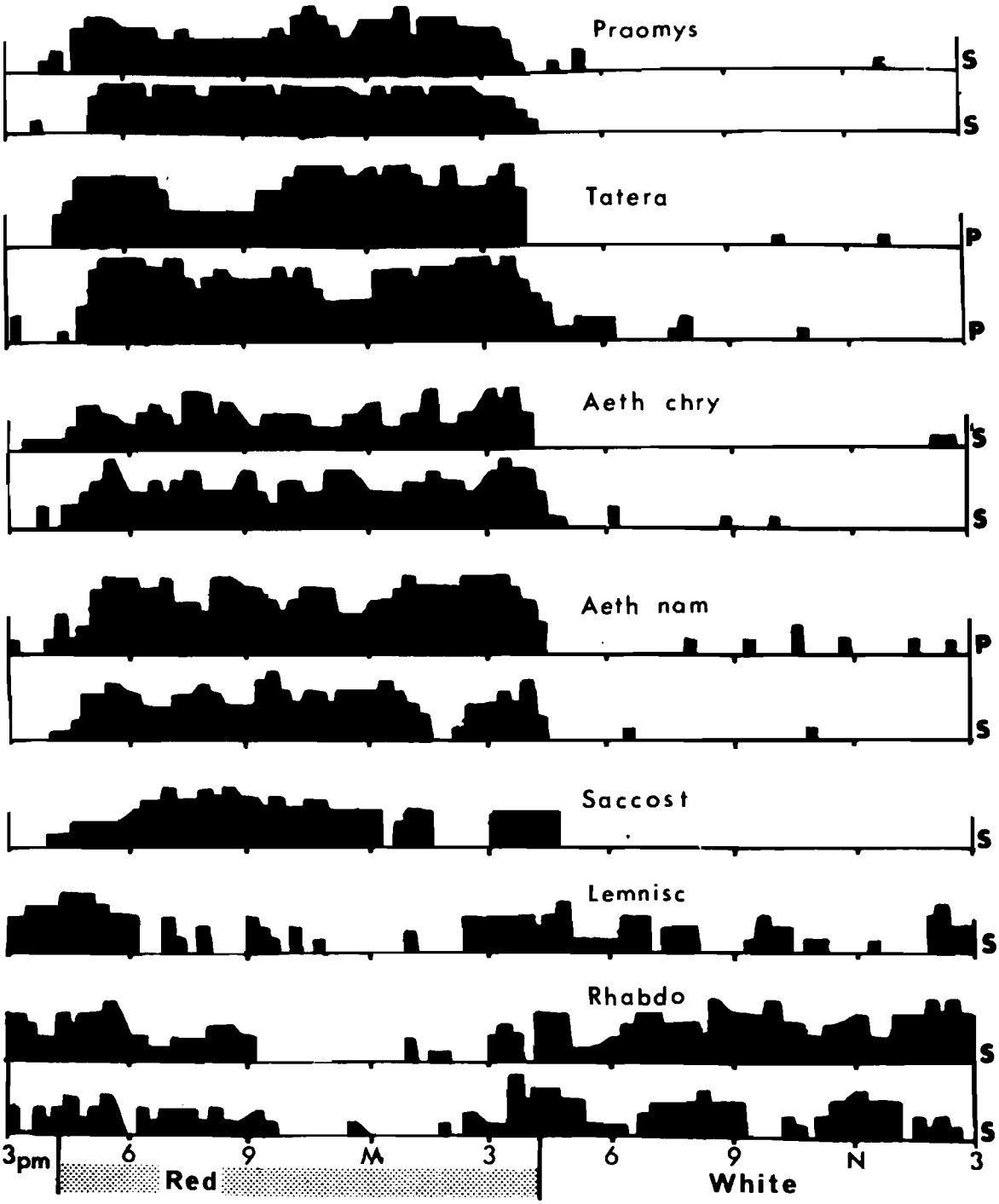

FIGURE 3
Activity patterns of seven rodent species under 12 hours red and 12 hours white artificial lighting, February.

teats (both species of *Aethomys* and *Acomys*) and those leaving them in the nest with mouth carrying *(Rhabdomys, Praomys, Lemniscomys, Saccostomus). Tatera leucogaster* falls in this latter group as an exception to other members of the genus. Meester and Hallett (1970) suggest that nipple dragging is found among those species with low litter size and equate this with better parental care. The results of this study support this in part but provide exceptions such as *Tatera leucogaster.* Since species such as *Aethomys namaquensis* are not good parents if the young are not attached to the nipples, but other species are, even though they are not attached, there may be other or additional survival values implicated in this behaviour. One possibility is the care of young in emergencies (King 1963). *Aethomys namaquensis* and *Acomys spinossissimus* live in rocky habitats where scattering of the young may be disadvantageous but nipple dragging advantageous and this might similarly apply to tree and certain burrow dwellers. *Rhabdomys, Praomys* and *Lemniscomys* which are more likely to live in grassland and sometimes nest above ground, show large litter sizes and a tendency for young to scatter when disturbed. The reason for the lack of both behaviour patterns in *T. leucogaster* is not apparent.

Finally, in several cases of Rhodesian irruptions of rodents, among the commonest species have been *Praomys (Mastomys), Lemniscomys* and *T. leucogaster* (details to be published elsewhere). There may be an important correlation between social tolerance and tendency to irrupt as these three species show the greatest group sizes and most compressible individual distance of the species studied, (except perhaps *Aethomys chrysophilus* which does not seem to be especially tolerant in natural conditions). *Praomys (Mastomys)* is the worst in this regard because of its high reproduction rate in addition to the above characters (Oliff 1953). If this is so, *Rhabdomys* would not be as likely to irrupt, despite its high reproductive rate, because of its relative intolerance. Future research should hopefully provide a test of this hypothesis.

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