BEHAVIOUR OF THE VLEI RAT, *OTOMYS IRRORATUS* (BRANTS, 1827)

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ABSTRACT

This paper is a contribution to the poorly known subject of wild rodent behaviour. Observations were conducted in the field and laboratory on the vlei rat, *Otomys irroratus*, as part of a comprehensive study of its ecology and life history.

Individual behaviour, social behaviour, and post natal development are described and discussed. It was found that the vlei rat is very shy and retiring in captivity. It can be considered as crepuscular, but activity tests conducted in the field and laboratory indicated some activity throughout the day and night.

Interactions of adults were tested and they were found to be very antisocial, with intrasexual aggression occurring when caged. Complex threat and communication patterns exist, a feature of asocial behaviour. Mating failed to occur in captivity, probably also a result of their antisocial nature.

Marking behaviour is very distinctive in this species and, combined with urination and possibly defecation, would appear to be useful in delimiting territories. It is concluded from their social habits, marking behaviour, and considerable overlap of home ranges that in nature their interactions with conspecifics are represented by a dominance hierarchy.

Several litters of young were reared. They are very precocial at birth and development proceeds rapidly. At birth the incisors are erupted, enabling them to cling firmly to the nipples of the mother. Most adult behaviour patterns are developed before weaning at 13 days.

Behavioural studies of rodents have been primarily concerned with the laboratory rat and mouse, *Rattus norvegicus* and *Mus musculus*, and to lesser extent with the golden hamster, *Mesocricetus auratus*, and guinea pig, *Cavia porcellus*. Behaviour studies of wild rodents are seldom comprehensive, usually being confined to a specific aspect. Comparisons of rodent behaviour are often made between taxonomically and ecologically unrelated species because few comprehensive studies of representative species are available.

A detailed description and comparison of all aspects of adult behaviour of two species of *Peromyscus* and of the heteromyid rodents are presented by Eisenberg (1962 and 1963). The only African rodent to have been extensively studied behaviourally is the African giant rat, *Cricetomys gambianus* (Ewer 1967).

The behaviour of the vlei rat, *Otomys irroratus* (Brants), is described in this paper from observations in the field and laboratory. This study was undertaken as part of a comprehensive study of the ecology and life history of a local population of these animals.

PROCEDURE

The study area is in the Van Riebeeck Nature Reserve (Rietvlei Dam), 20 km SE of Pretoria, where field observations were conducted and animals later utilised in the laboratory were trapped. Animals were maintained in a variety of cages, aquaria being utilised for observations on maintenance behaviour, maternal care, and development of the young. Animals were primarily fed fresh green lettuce supplemented with fresh carrots, carrot tops, cabbage, and standard mouse cubes. Drinking water was not provided as water was never taken when offered. Since these

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animals are active during the day most observations were made during daytime.

Descriptions of postures and movement sequences were recorded in notebooks and on a tape recorder. An attempt was made to photograph various postures and behavioural patterns. The animals were marked for easy identification during observation by either clipping or painting the ears.

Behavioural interactions and activity studies were conducted in an observation chamber similar to that described by Brown (1964). The main chamber was 60 cm square with 60 cm runways (10 cm wide) leading away from all four sides. To the ends of each runway were attached 30 cm square nest boxes. This chamber was constructed of wood and Masonite (hardboard) with clear plastic covering all upper surfaces for observational purposes. This enclosure was kept in an environmental control room with constant temperature and humidity and lighting regulated on a 12-hour on-off cycle.

For study of adult behavioural interactions two males and two females were placed in the observation chamber, each in a separate nest box. After a period of acclimatisation dividing partitions were removed and interactions observed.

Activity periods were recorded in the same enclosure by means of a photoelectric cell placed midway in each runway and connected to a multichannel Esterline Angus event recorder. In order to avoid the effect of social contact upon normal activity, animals were either tested individually or with dividing partitions placed in the central chamber, thus isolating them. This latter procedure proved the most efficient as four animals could be tested simultaneously.

GENERAL ECOLOGY

The vlei rat, *Otomys irroratus,* belongs to the small subfamily Otomyinae which has recently been placed in the family Cricetidae (Misonne 1969). This species has a very discontinuous distribution in South Africa and is limited to the eastern escarpment in Rhodesia. *Otomys tropicalis* Thomas, considered by Delany and Neal (1966) to be a conspecific of *O. irroratus,* is found in tropical Africa: Congo (Kinshasa), Uganda, and Kenya. An isolated race, *O irroratus burtoni* Thomas, occurs in the grasslands of the Cameroun Mountain (Rosevear 1969). There exists an uncertainty regarding the status of *O. tropicalis* and *O. i. burtoni,* so for the present they will thus be considered as distinct from *O. irroratus* of southern Africa.

Otomys irroratus is moderate-sized, with a short, stout-looking body, blunt face, large, rounded, well-haired ears, short tail, and long, soft, shaggy pelage. The general dorsal colour is a dark slate-grey suffused with buffy and brown. The underparts are slightly paler and more grey. They are also chracterised by very large, yellow, deeply grooved incisors. The means and extremes of external measurements of 20 adult study specimens from the study area are as follows: total length, 270 (252–303) mm; tail length, 103 (92–117) mm; hindfoot length (with claws), 32 (29–34) mm; ear length (notch), 21 (20–23) mm; total weight, 141 (100–204) g.

In interpreting the behaviour of wild animals in the laboratory it is important to have some ecological knowledge of the individuals concerned. Very little has been reported in the literature on the ecology of *O. irroratus* and some of it is conflicting. As the common name implies, the vlei rat inhabits areas consisting primarily of lush grasses, sedges, and herbaceous vegetation associated with wet soil and sometimes shallow, standing water near rivers, streams, and in marshes. Being

most abundant in these habitats, populations therefore do not seem to be randomly distributed over a given area, but appear to have a patchy distribution.

Vlei rats are terrestrial, the soil often being too wet for burrowing, and they make intricate, well-defined, runway systems under and through the vegetation. The nest is normally open and shaped like a shallow bowl. The nest consists of shredded grasses placed directly on top of the ground, and is covered over with a heavy growth of vegetation. They feed primarily on green vegetable matter and the pith of herbs and grasses, which are cut into short lengths and the outer layer stripped away, the debris being deposited in little piles along runways. They have been reported as being diurnal (Thomas and Schwann 1905; Roberts 1951), and by others as primarily nocturnal (Hewitt 1931; Shortridge 1934).

The vlei rat has been found to breed nearly throughout the year in the study area, June and July being the exceptions. Asdell (1964) reports it as being polyoestrous, breeding about three times per year, and for the first time at about four months of age. Data from the study area indicate that it normally breeds three to four times per year and occasionally as often as five times, while the first indications of breeding occur as early as two to three months of age. The number of offspring per litter has been reported to vary from two to five, the usual being two or three (Powell 1925; Shortridge 1934; Roberts 1951). Examination of 11 gravid females and records of 20 litters show a mean number of 2,4 foetuses or offspring with variation from one to four. The offspring are born in a precocial state, being furred and mobile, and either at birth or soon thereafter have functional eyes and ears.

In captivity vlei rats are very shy and retiring, making observations often difficult. They have also proven reluctant to breed in the laboratory.

INDIVIDUAL BEHAVIOUR

The following individual behaviour patterns refer to adults only. For juvenile behaviour and its development see the section on Postnatal Development.

Locomotion and Exploration

The vlei rat is quadrupedal and in walking and running uses the diagonal sequence of alternate limb movements. Walking is the main form of locomotion and is frequently interrupted by hesitations. Running is very quick and the body is kept close to the floor in a flat posture, seemingly adapted for rapid movement through runways.

These animals are capable of swimming but do not appear to take readily to water. Shortridge (1934) states that they enter water to cross from one reed patch to another. One marked individual was found to have crossed a flowing stream approximately 5 m in width.

When an animal is placed in a strange enclosure it demonstrates its extremely shy and retiring habits by moving to a side wall or near corner, positioning itself with face toward the middle, and then often not moving for as long as several hours on end. When it finally decides to investigate its surroundings the body is tense and in an elongate posture. In this posture the body is very much extended and flattened, the tail very stiff, sticking straight out behind or with slight upward tilt, and the ears erect and slightly forward (Fig. 2). The animal moves with very slow, cautious steps, occasionally stopping to rise on its hindlimbs and test the air. The nose and vibrissae are constantly

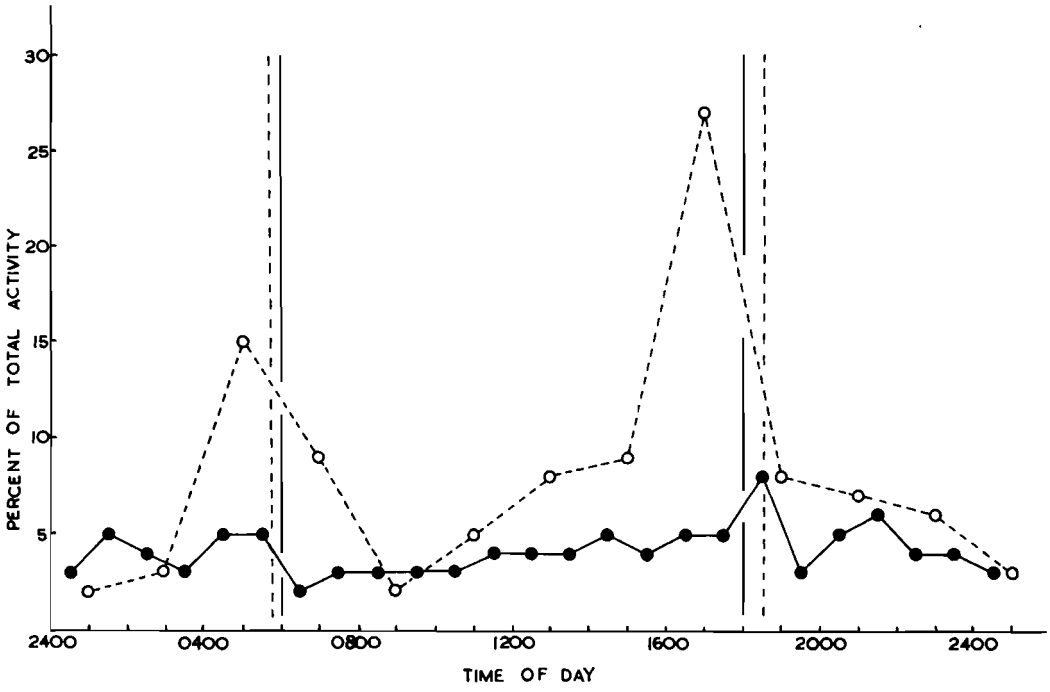

FIGURE 1
Summary of activity in the field and laboratory. Activity during each one- or two-hour interval is represented as a percent of the total recorded activity during a 24-hour period. Dashed lines indicate field activity, solid lines laboratory activity, vertical dashed lines actual sunrise and sunset, and vertical solid lines laboratory "sunrise" and "sunset"

exploring and testing the air, substrate, and any object in its path. Any slight sound or movement causes it to make a hasty retreat and a long time may elapse before it resumes exploration. Occasionally it may suddenly retreat without any evident cause.

After becoming familiar with its surroundings the animal moves with a more relaxed posture, the body being higher off the floor, with more rounded body contours, and the tail more relaxed, dipping slightly at the base and giving the appearance of being dragged.

Investigative behaviour was tested by subjecting an animal to a new object in familiar surroundings. The elongate posture is resumed when contacting these new objects. Motivation for investigation of a new object is seldom immediate or a direct action but arises during a regular reconnaissance of its surroundings, which apparently "refreshes its memory" and helps keep a check on its environment. Shillito (1963) and Ewer (1967) found this same behaviour in *Microtus agrestis* and *Cricetomys gambianus* respectively.

Rest and Sleep

The resting animal normally adopts an elongated posture with the hindlimbs under the body, the forelimbs forward and curled under the neck, and the chin resting on the floor. Occasionally an

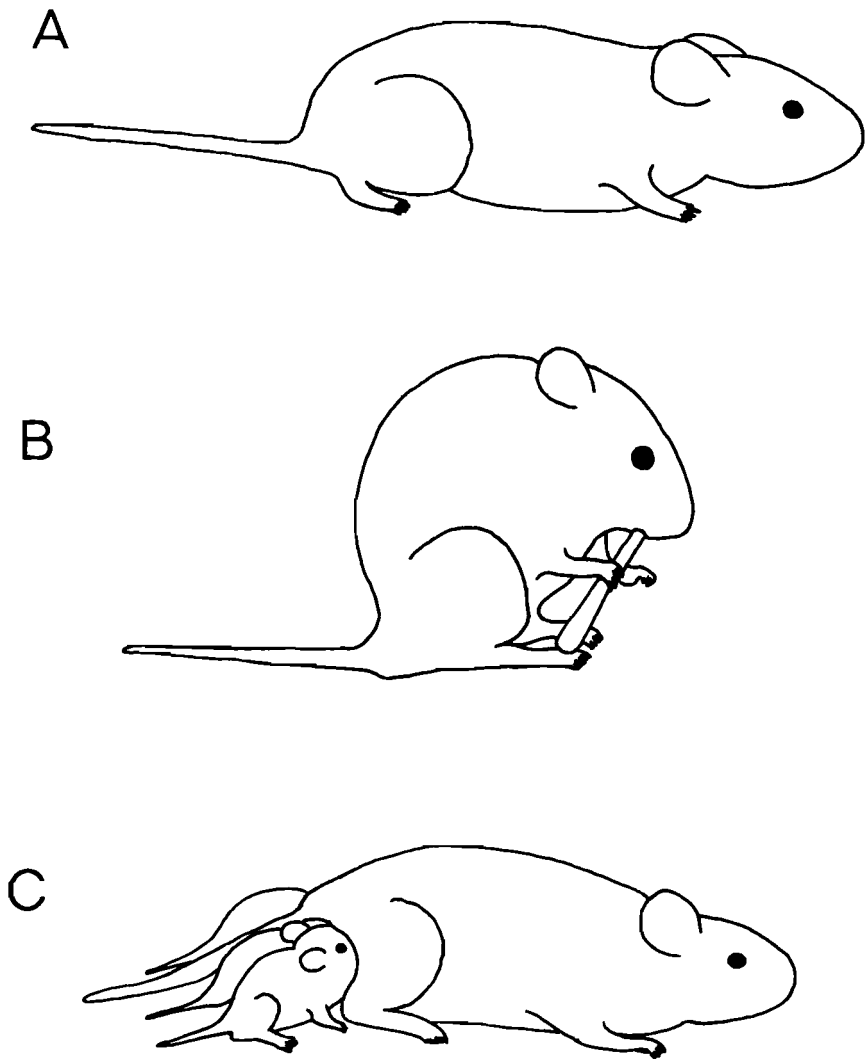

FIGURE 2
Behavioural postures: A, elongate posture; B, feeding posture; C, mother transporting nipple-clinging young.

individual will rest on its side in a slightly curled posture with hindlimbs out to the side.

The typical sleeping posture resembles the latter, the only difference being that the eyes are closed. Individuals sometimes sleep like many other rodents, in a sitting posture with the head tucked slightly ventrad. The tail comes forward but it is not curled around the body. During sleep the eyes are seldom closed for more than a few seconds to minutes at a time, and with the slightest disturbance they are immediately opened.

Stretching, by extending the limbs and de-arching the back, usually occurs as the animal leaves

the nest upon awakening or after rest. Stretching is not always followed by grooming as in *Peromyscus* (Eisenberg 1962) but is often accompanied with yawning.

Grooming

Washing begins with several rapid alternate motions of the forepaws under the mouth. This is followed by several rapid movements of the arms and paws, usually simultaneously, up the face to the level of the eyes and back down to the nose. This motion is interrupted often to repeat washing of the paws. After repeating this sequence several times the arms and paws are extended back behind the ears. Accompanying the action of the arms and paws over the face is a bobbing motion of the head. Washing of the sides, flanks, and inguinal region frequently follows face washing. This action involves combing the fur with the forepaws while mouthing the same area with rapid head bobbing. Cleaning of the tail as in *Cricetomys gambianus* (Ewer 1967) and *Peromyscus* (Eisenberg 1962) has never been observed. Washing is always done while sitting slightly upright with the weight on the hindlegs.

Scratching of the head, ears, sides, and back is done with the hindfoot and from a three-point stance. Scratching of the back is accomplished by ventrally shifting the skin of the back and side, thereby exposing it to the reach of the hindfoot. Biting at the claws of the hindfoot following scratching occurs occasionally.

Feeding

Food is picked up with the teeth and lips and then held in the well-equipped forepaws while sitting in the typical hunched upright position (Fig. 2). This upright posture is not as erect as that of a squirrel but more like that of the cane rat, *Thryonomys swinderianus* (Ewer 1968), or the woodrat, *Neotoma floridana* (Poole 1940), with the forelimbs barely raised above the ground. Small items of food are sometimes held with only one forepaw while the other rests on the ground, again as in *T. swinderianus* (Ewer 1968). Feeding is usually followed by a period of grooming.

The vlei rat is predominantly a grass eater. In feeding it bites through the grass close to the ground, picks up the cut piece in the mouth, sits back on its haunches, grasps the grass on either side of its mouth with a paw, and bites off a 2-5 cm piece. If the piece is young and tender it sticks the end in its mouth, bites off a series of small pieces, and then chews with its molars. If the grass is very coarse it moves the piece through the mouth from one end to the other, stripping off the outer part to get at the tender pith.

Tell-tale piles of grass cuttings are left along runways, some of which are the result of attempts to get at and eat the tender upper parts of vegetation. In typical vlei rat habitat a piece of grass cut at the base will not topple over, which makes it necessary to continue chopping off basal pieces until the more tender parts are reached.

When fed sunflower seeds and oats in the laboratory, lengthwise pieces of shell are stripped off with the teeth until the kernel is reached, as is also done by the golden hamster, *Mesocricetus auratus*, the striped mouse, *Rhabdomys pumilio*, and the red veld rat, *Aethomys chrysophilus*.

Coprophagy, the eating of faeces, is very common in the vlei rat and has also been recorded in many rodents, lagomorphs, and shrews. From the hunched, upright, feeding position the faeces are removed from the anus with the teeth and then eaten. This habit is very important in vegetarian species during transition from milk to solid food in the young, in order to obtain the proper

bacterial flora for digestion from the adults. It has also been shown to be a source of vitamins. Coprophagy appears to be more common during absence of food. When an abundance of food is present faeces are discarded after removal from the anus. Eating of faeces when there is a lack of food may therefore have additional survival significance during the winter months when there is a shortage of green vegetation.

In the laboratory food is consumed sporadically throughout the day with peaks coinciding with activity peaks (see Activity Periods and Fig. 1).

Elimination

During defecation no special posture is assumed nor is there any specific place for this activity. It appears to occur at any time while walking or feeding. Defecation also occurs in the nest and faeces are rarely cleaned out (Powell 1925; pers. obs.).

In the field faeces are found scattered everywhere as in captivity, and occasionally an abundance of faeces can be found on a small bare spot or flat rock about 10 to 30 cm in diameter. These accumulations are similar to but not as extensively displayed as in the woodrat, *Neotoma floridana* (Poole 1940). Faeces are also very commonly deposited on top of traps. The significance of these faeces accumulations is unknown unless they may serve as a means of marking.

Urination generally occurs in a specific corner in captivity, which indicates its possible use as a marking device. During urination the animal backs into the corner with his tail extending up the corner and remains motionless until finished.

Owing to the food habits of vlei rats copious amounts of wastes are produced and cages with solid bottoms and absorbent floor litter are quickly soiled.

Marking

A prominent marking movement becomes evident when an individual is placed in a new or clean cage. This movement is unlike the perineal drag of many other rodents and is performed by placing the region of the tail base against a side wall. By extending and lowering the hindlimbs this area is rubbed up and down on the wall. This behaviour is problaby associated with the occurrence of prominent paired anal glands.

The possible use of faeces and urine as a means of marking has been discussed above (see Elimination).

Nest Building, Runway Formation, and Burrowing

Nests are usually open and shaped like a shallow bowl, approximately 15 cm in diameter and 3 cm deep, with normally two runways leading away. They are composed of the most readily available vegetation which is chopped, shredded, and placed directly on top of the substrate. Shortridge (1934) states that in grassveld and vleis vlei rats dig shallow holes in which to nest. In the eastern Cape Province, where reed-beds are scarce, they often live in burrows or crab holes near the edges of rivers (Shortridge 1934). The use of shallow burrows or crab holes has not been observed in the study area, but this could be the result of a high water table or unsuitable soil. In captivity a similar type of nest is formed with carrot tops or shredded paper or lettuce (finely shredded with the teeth), which is placed in shallow depressions in the soft litter. The

nesting material is either carried to the nest in the mouth or simply pulled into the nest and under the animal with the forelimbs. Final placement of nesting material is performed with sideways and backward motions of the forelimbs, and undesirable items are discarded from the nest with the mouth.

Runways are probably formed as a direct result of feeding, the individuals more or less eating their way through the vegetation. The tops of the cut vegetation are sometimes left and help to form a protective covering. In captivity vlei rats often first eat the underside and then the inside of a head of lettuce, which provides them with a hollowed-out, protective canopy. They have also frequently been seen pushing vigorously upwards with head and shoulders as they crawled under vegetation. This activity no doubt aids in formation of runways.

Digging takes place with alternate motions of the forelimbs. After a small pile of floor litter has developed under the body from this movement a concerted effort of the hindlimbs expels the material with considerable force. A characteristic sideways motion of the forelimbs may be useful in eliminating debris from a runway.

Activity Periods

Otomys irroratus has been described by some authors as diurnal (Thomas & Schwann 1905; Roberts 1951) and by others as nocturnal (Hewitt 1931; Shortridge 1934). Although Hewitt (1931) and Shortridge (1934) state that it is primarily nocturnal, they do say that it is often out during the daytime. Shortridge (1934) suggests that period of activity may vary according to season or locality. Further support for the statement that they are nocturnally active comes from the abundant presence of their remains in barn owl pellets (Davis 1959; de Graaff 1960). Evidence from owl pellets found in the study area indicates that vlei rats are a common prey of grass owls living in the area. Also on two separate occasions in the trapping grid a marked vlei rat was discovered being consumed by a grass owl.

Checking traps in the field every two hours for 24-hour periods in October 1970 and February 1971 showed activity to occur throughout most of the day but with two prominent peaks of activity, the first (smaller) between 0400 and 0600 h and the major peak between 1600 and 1800 h (Fig. 1). These two peaks of activity account for 42 per cent of the total recorded activity. Despite the fact that the early morning peak is shown occurring before official sunrise it does begin to become light well before this time. The light intensity during these peaks would appear to be closely comparable. Judging from these data *O. irroratus* could be considered primarily crepuscular. It would be interesting to ascertain whether this activity pattern is maintained during winter as well.

The activity of eight animals over a total period of 33 days was tested in the laboratory (Fig. 1). The activity occurring between 0400 and 0600 h, although not forming a distinct peak, is sustained for a longer period than at most other times of the day. The most distinct peak of activity occurred between 1800 and 1900 h. Both of these active periods are followed by a sharp decline in activity, similar to that recorded in the field. Although activity periods under controlled laboratory conditions are not as easily discernible as in the field, they correspond closely. An obvious feature of activity in the laboratory was the immediate decrease in activity when the lights came on and the sudden increase when they went out. This fact combined with more evident periods of activity in the field, indicates that the controlling factors of activity are multiple and complex.

SOCIAL BEHAVIOUR

Social behaviour includes any behaviour patterns involving two or more interacting individuals.

Communication

Communication is by means of the following senses: visual, auditory, olfactory, and tactile. The eyes of the vlei rat, although very large, appear to be rather ineffective, as individuals are not visibly affected by the activity of others in directly adjoining glass-sided cages nor by slow movements of an observer only 30 to 60 cm away.

Observations on response to sound, involved sounds only within the range of human hearing, but there was nothing to suggest the occurrence of frequencies above that range. Only two adult sounds were heard, the first being an alarm squeal heard infrequently from animals held for measuring. The second was a metallic "chit" repeatedly uttered, primarily during conflict, as a threat directed by the upright individual at an approaching animal. The closer the individual approached the more rapid and intense become the "chits". Hearing appears quite keen but only loud noises and an imitation of the "chit" elicited immediate response. Chattering of the incisors together, very common in many murid and cricetid rodents (Ewer 1968), was not observed. Ewer (1968) suggests that this behaviour is absent in species which rarely attack by biting, possibly being replaced by vibration of the tail. This would not appear to be the case in the vlei rat as both tail shivering and biting attack occur.

Although the olfactory sense appeared to be the most highly developed, the role of glandular secretions, urine, and faeces in olfactory communication is not fully understood. An intruder, actively smelling everything, did not seem overly interested in investigating these means or areas of communication. Recognition of conspecifics was naso-nasal and very rarely naso-anal. When individuals (male and female or mother and young) were returned to their cleaned cage there normally existed a period of non-recognition, confusion, and threat. Recognition did not take as long as in new encounters but they had to repeat all sequences, and only when the "new" cage had been fully explored did confusion cease. If this same procedure was repeated but with familiar floor litter returned to the cage recognition of each other was immediate, indicating that unfamiliar surroundings caused breakdowns in recognition patterns.

Although defecation and occasional urination are indiscriminate these would occur more often in the most actively used runways, which would help to mark the pathways most frequently used. Because of abundant interconnecting runways, the aforementioned accompanied by marking with the anal glands probably serves only as an indication of the use of specific runways and not as a deterrent to conspecifics. Despite the lack of positive evidence several of the above mentioned activities (see also Elimination and Marking) indicate that olfactory communication may exist in one form or another.

Tactile communication by use of the vibrissae appeared to be a means of supplementing olfactory information when investigating new surroundings and objects. The vibrissae probably aid the animal when moving rapidly through the narrow runways. Contact of the vibrissae did not occur in social nose to nose contact.

Adult-Offspring Behaviour

Because breeding in the laboratory has not been successful to date, behavioural interaction between father and young has not been observed. Meester (personal communication) made brief observations on one successfully bred pair and their young in which the male appeared to be fully tolerated by the female, often huddled with the female while the young were suckling, and seemed oblivious to the young.

For the first few days after birth a high-pitched squeak was emitted by the young when separated from the mother. This squeak could be heard for long distances and probably served as an aid in finding lost and helpless youngsters. A few very young and helpless babies were found squeaking and wandering aimlessly in the study area, possibly because the mother had been captive in a trap and was therefore absent from the nest for a longer period of time than normal.

Nipple-clinging by the young, a phenomenon known in *Aethomys, Tatera, Thallomys, Mystromys,* and *Neotoma* (Lawrence 1941; Hamilton 1953; Meester & Hallett 1970) among others, was very prominent in the vlei rat and was aided by the presence of incisors at birth. Even though the young were mobile at birth their clumsiness caused them to be dragged about on the inguinal mammae. As their legs quickly co-ordinated they are soon seen running along behind the mother while firmly attached to the nipples (Fig. 2). For the first few days the young were seldom found unattached but it does not seem likely that the female transported the young while foraging for food. Instead they are presumably left in the nest. On a few occasions a mother with a nipple-clinging baby was captured in a trap. Because these cases involved the mother and only a single, advanced young it appears more likely that the youngster followed the mother into the trap and was not transported there. The discovery of very young and helpless individuals wandering aimlessly in the study area also gave credence to their detachment, even at a very early stage.

While suckling the young the mother would crouch over them with her back arched and the hindlegs extended, or lie on her side with the upper hindlimb raised to accommodate the young. The mother detached the young by very slowly rising and moving off the nest like *Peromyscus* (King 1963). When detached in such a manner the young remained very quiet and undisturbed in the nest, but if startled they remained firmly attached to the nipples. The mother was never observed mouth-carrying the young as has been seen in species producing large litters, such as *Rhabdomys pumilio* and *Praomys natalensis* (Meester & Hallett 1970).

When the young were returned to the cage after measuring, the mother seldom made an attempt to collect them, but because of their mobility they would soon locate her. There was apparently olfactory recognition on the part of the mother after which the young were pulled under her body with the forepaws. This pulling-in action was identical to that used in nest building. The young were then groomed very briefly, possibly because they were capable of grooming themselves at a very early age. By the age of three to four weeks there was a reversal of roles, after which the young were often seen grooming the mother.

When the young began actively eating solid food they often came into conflict with the mother over a particular food item. The result would be a brief tugging match with the mother rather violently jerking the food from the young, then sometimes turning the back to eat the morsel undisturbed. Occasionally one of the young would become perturbed over a conflict with the mother and give a threatening "chit", but to no avail.

Adult Interaction

The behaviour patterns and postures discussed in the following categories are essentially the same for both sexes, unless otherwise stated. Allowance has been made for a certain amount of individual variation.

1. Approach behaviour. Approach is conducted with the body in an elongate posture. This elongate posture is characterised by the body being tense, extended, somewhat flattened, with the tail rigid and horizontal, the nose and vibrissae active, and the posterior margin of the ears extended outward to direct the ear pinnae more forward (Fig. 2). Movements are normally very slow, with much hesitation.

2. Contact behaviour. Contact is made in the elongate posture and is nose to nose. Naso-anal contact only seldom manifests itself in male-female encounters and such close proximity is never allowed in male-male or female-female encounters. Any naso-anal contact is initiated by the male from the elongate posture with the female in a threatening upright posture. Unlike several other rodents (Eisenberg 1962 and 1963) naso-anal contact is infrequent and no change in the opening of the eyes has been noted in the vlei rat.

During initial contacts lateral shivering movements of the tail are usually displayed. This behaviour is manifested in a number of rodents and represents a high state of general excitement (Ewer 1968). These movements are of a large amplitude in the house mouse, *Mus musculus*, and create a rustling sound against the substrate which constitutes a threat to a rival (Clark & Schein 1966; Ewer 1968). In some rodents this movement is a sign of aggression, but in male *Thryonomys* it is a sexual display during courtship (Ewer 1968). Tail shivering is definitely associated with a high state of excitement in the vlei rat but any association with mating behaviour is unknown. Because it occurs during conflict situations and is primarily demonstrated by dominant individuals it probably serves as a threat in the vlei rat.

3. Grooming behaviour. Owing to either the antisocial behaviour of the vlei rat or a very low or non-existent motivational intensity, social grooming has seldom been observed in either inter- or intrasexual encounters. In certain animals there exist body areas of specialized sensitivity which they enjoy being groomed. Scratching and rubbing the vlei rat just under the chin will cause it to turn the head, close the eyes, and remain motionless until manipulation is stopped. A similar area of sensitivity under the chin exists in *Thryonomys* (Ewer 1968) and in the blacktailed prairiedog, *Cynomys ludovicianus*, (King 1955). Ewer (1968) states that this area is briefly groomed when two friendly cane rats meet and that this behaviour forms a sort of greeting ceremony. Grooming of this area, along with general social grooming, has been frequently witnessed between juvenile littermates but appears nearly non-existent in adults, perhaps as a result of a breakdown of sexual behaviour in captivity (see Sexual Behaviour).

Displacement grooming is very common in conflict situations and is usually displayed by the dominant individual.

4. Upright postures. The upright posture is normally associated with defensive threat and submissiveness and is often accompanied by a threatening "chit". When the upright posture becomes mutual (Fig. 3), boxing and pushing ensue after which dominance and submissiveness are normally established. In the upright position the angle of the body to the substrate depends upon the amount of aggression involved or upon the persistence of the aggressor. Usually the more vertical the body, the greater the level of submissiveness. When the angle of the body with the

substrate is near 45 degrees the forepaws are held together and close to the body; when more vertical the forepaws are outstretched to ward off attack. A female, when approached by a male, readily goes upright but seldom into the vertical position. Attack is seldom initiated from an upright posture. Eisenberg (1962) states that in *Peromyscus* the upright posture is transitory and followed by flight or maintained as a defensive posture. This appears to be the case in the vlei rat but it is also transitory for a third one, that of submissive appeasement (see Submissiveness).

5. Threat. Two types of threat, offensive and defensive, can be defined. Offensive threat is displayed by the dominant, approaching individual and characterised by the low, elongate posture (Fig. 2), with ears flattened against the head, shivering of the tail, and occasionally a slight exposure of a side to the rival. This lateral display (Fig. 3) is a transition behaviour occurring only briefly between mutual upright and approach followed by direct attack (see Intrasexual encounter). As in *Peromyscus* (Eisenberg 1962), the elongate posture during offensive threat appears similar to that during investigation and in both cases is expressed by "confident" individuals.

Defensive threat is demonstrated by the approached animal and is posed from an upright posture (Fig. 3) accompanied by the vocal "chit", the intensity of the vocalisation being dependent upon the amount of aggression involved, male-female encounters eliciting less aggression than male-male or female-female encounters.

6. Chasing. This consists of the dominant animal running after the submissive one, making frequent attempts to bite the rump, resulting in numerous minor wounds and much fur loss from this area. Damage does not seem to be inflicted upon the tail and there is never any shift to sexual behaviour with attempted mounts as in *Peromyscus* (Eisenberg 1962) and some other rodents. If the individual being pursued makes a sharp turn or quick stop the pursuer often loses contact with him. This disappearance of the releaser stimulus (the fleeing animal) results in a shift of behaviour by the pursuer to such displacement activities as feeding and grooming.

7. Fighting. Fighting generally occurs following a chase when the pursued animal is caught. Fighting is characterised by rolling and struggling about on the floor, head to head, with bodies adpressed. It is of short duration, ending with one having a bite hold on the rival's shoulder, cheek, or lip. They then break apart and chasing again ensues. Unlike some other rodents during locked fights, serious wounds are often inflicted and there does not appear to be a struggle for a superior position.

Eisenberg (1963), referring to heteromyid rodents, states that locked fighting is more common in quadrupeds while sparring predominates in the more bipedal *Dipodomys* and *Microdipodops*. In the confined conditions of the laboratory there does not appear to be any predominance of either locked fighting or sparring in the quadrupedal vlei rat. During agonistic tests a submissive female was killed by the dominant female and a submissive male was so badly wounded by the dominant male that it had to be destroyed, the major wounds occuring during locked encounters. Although occasional individuals in the field, usually large males, have similar wounds it seems likely that under natural conditions locked fighting, and especially mortal wounds, would occur less frequently as opportunities for escape would not be limited as in the laboratory. Impressive verbal displays of threatening "chits", similar to those heard during sparring bouts, have been heard a few times in the study area.

8. Dominance. Several characteristics are associated with dominance in vlei rats. Dominant

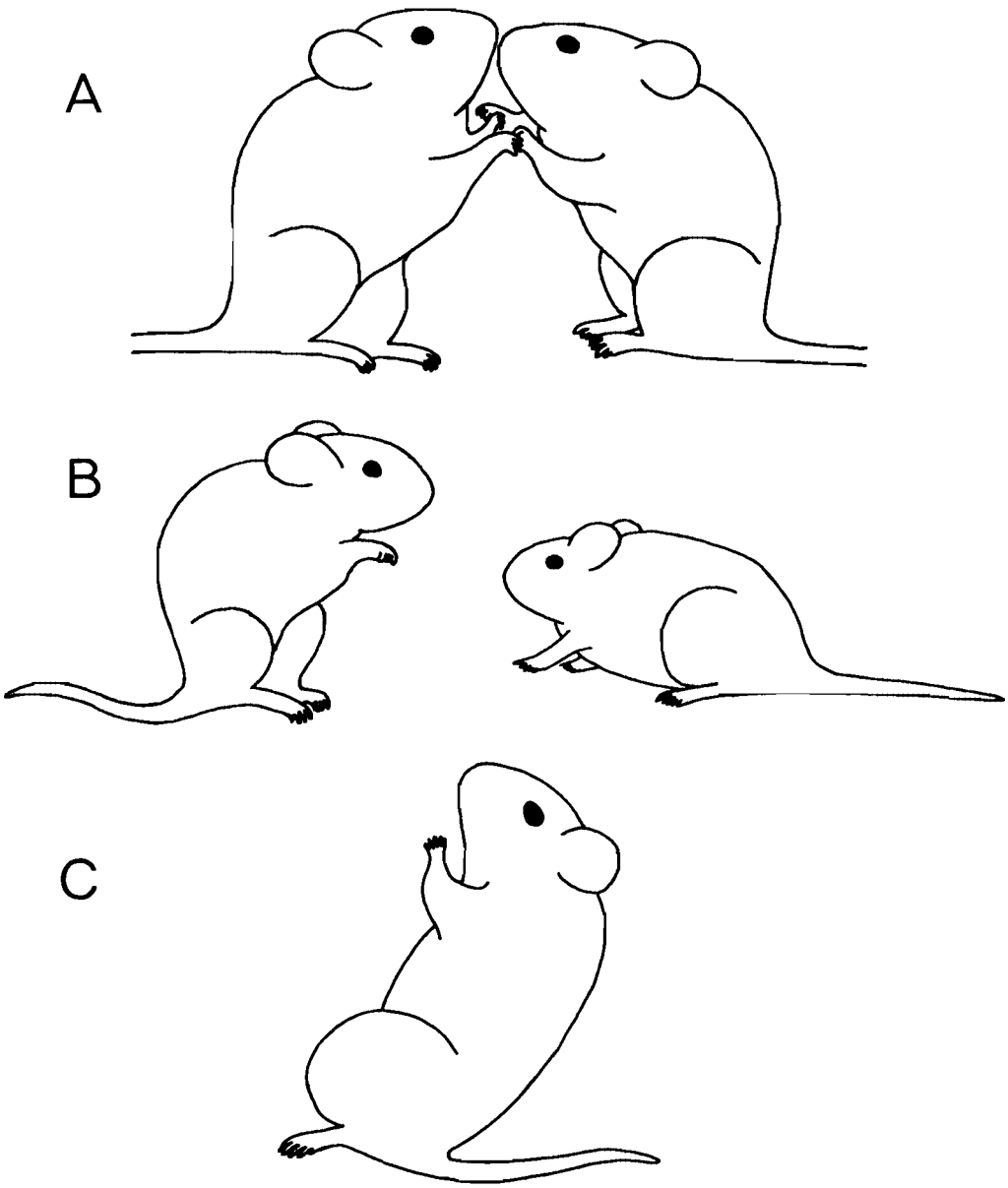

FIGURE 3
Behavioural postures during encounters: A, mutual upright with sparring; B, upright ward (defensive threat) by the animal on the left and lateral display (offensive threat) by the animal on the right; C, submissive appeasement.

animals approach a rival in the elongate posture, with ears flattened against the head. This approach by the dominant animal is sometimes followed by a lateral display (see Fig. 3 and Threat), but more often by an outright attack. No variation in degree of eye opening has been observed as in other rodents. Tail shivering and displacement grooming predominate in dominant animals. Usually individuals with the greater body weight will be dominant over lighter ones, but on one occasion a male with 15 per cent lower body weight proved far superior to his heavier rival. Males are generally dominant over females.

9. Submissiveness. Submission is characterised by the upright ward posture (Fig. 3) accompanied by chittering, similar to that seen in defensive threat. The more vertical the body posture and more extended the forelimbs the more submissive the animal. Appeasement sometimes follows the vertical upright and is demonstrated by nearly falling over on the back, exposing the vulnerable belly (Fig. 3). When this occurs even a persistent attacker will desist and move away. A similar type of appeasement posture is also found in the golden hamster and the vole, *Microtus agrestis* (Clarke 1956). Although evidence is not conclusive, submissive animals appear to lose more weight than dominant ones during encounter tests of one week duration.

Sequences of Behaviour During Encounters

Particular behaviour patterns in male-male and female-female encounters are essentially the same, differing only occasionally in frequency. Sequences in intersexual encounters are different in some respects and will be described separately.

Because of the shy and retiring nature of the vlei rat several weeks of acclimatisation to laboratory conditions are necessary before tests can begin, and when animals are placed in a mutually unfamiliar enclosure another period of two to three days is required to again acclimatise.

1. Intrasexual encounter. After being placed in the observation chamber there is a long period of quiet. Finally one animal begins to slowly move about in the elongate posture making a thorough investigation. After becoming frightened and racing back to the original place a few times it finally makes contact with another animal. Because no overt aggression exists at this point the first contact with the other animal by the approaching individual usually results in a hasty retreat. There now remains curiosity on the part of both individuals which may cause the inactive animal to begin investigating. During the highly excitable periods of initial approach both animals come nose to nose in an elongate posture with much retreating, reapproaching, and tail shivering. Eventually one individual, usually the more "confident."(who began investigating first), presses the approach too close, causing the other to go upright and begin chitting. This may happen once or twice, followed by retreat of the approacher, but eventually ends in a mutual upright posture with much sparring. Sparring may occur several times until it appears that one animal becomes more sure and aggressive and the other either goes into the appeasement posture or flees, usually the latter. When the appeasement posture occurs the rival usually retreats, but when one animal flees, chasing is initiated in the other, resulting in one of the following: locked fighting, a return to a threatening posture by the submissive animal, or escape. The dominant animal continues his elongate posture approaches with tail shivering and at this stage may be seen performing the lateral display. This seldom seen exposure of the side is usually a precursor to a direct attack. From a certain point in the sequence the lateral display is eliminated entirely and approach leads to direct attack. The submissive animal maintains an upright defensive threat posture during approaches and

lateral displays by the dominant, but is ready to make a quick escape leap when the approacher gets too close or attacks. During approach the dominant animal may suddenly stop his aggressive activities and begin displacement grooming or feeding or turn and leave in a relaxed walk to resume eating or grooming elsewhere. Aggressive activity may return as quickly as it ceased, however, causing the animal to return to the rival. This sudden cessation of aggressive activity may be due to a low level of aggression at that time, absence of aggression-stimulating movements on the part of the rival, or a combination of both. In time the aggression level appears to dwindle in the dominant animal and it tries to investigate the rival more closely. The tension becomes too great and the submissive animal assumes a threat posture, thereby causing conflict to be renewed. The dominant animal continues to persecute the other and such other activities as social grooming never occur, even after seven days of mutual exposure.

2. Intersexual encounter. Male-female encounters begin in the same way as the intrasexual encounters just discussed, the essential difference being a much lower level of aggression following recognition. Recognition appears to occur in the nose to nose position, because once that contact has been made no attack follows. The male is generally the one approaching and shows much interest. The male assumes the elongate posture when approaching the female and shows a great amount of nervousness in the form of tail shivering. The female rises upright, "chits", and, if the male approaches too close, attempts to ward him off with the forelimbs. The male attempts to sniff the genital area but the threat of the female becomes too great and he retreats. The assumption of typical agonistic postures, but with no hostile action, is similar to that seen in *Cricetomys gambianus* (Ewer 1967). The male appears greatly interested and moves persistently closer until the female develops a tolerance. Very brief and infrequent mutual grooming on the neck and head has been observed but there have been no attempted mountings. Following this there develops what could be referred to as a mutual tolerance or platonic relationship, during which the two animals merely rest and sleep huddled together.

Sexual Behaviour

Very little information regarding sexual behaviour can be contributed as mating has not occurred under laboratory conditions. Meester (personal communication) has knowledge of a successful mating in the laboratory, but the act was not observed nor is any history of the adults available. Davis (1963) reported that *O. irroratus* failed to breed in the laboratory.

On a single occasion a three-week old juvenile was observed to climb onto the back of one of its siblings. It rather aggressively bit at the fur of the neck and head of the youngster underneath which struggled to escape but for a moment ceased its struggles and closed its eyes. Although these animals were far from sexually mature this action could well represent a development of sexual behaviour, as grooming the female about the head and neck during courtship occurs in a number of rodents.

Reproductive success was found to increase in captive pine voles, *Microtus pinetorum*, with length of time in captivity (Kirkpatrick & Valentine 1970). Vlei rats have been kept in captivity for as long as six months and maintained as pairs for periods of one to six weeks during which no successful matings occurred. Kirkpatrick and Valentine (1970) suggest the following factors as contributing to non-breeding: the presence of and disturbance by humans, change in food, restricted area of activity, and maintenance of a paired rather than colonial status. Eisenberg (1967) states that solitary species, when forced to live in pairs in a small cage, even though

compatible, do not reproduce, as a result of inhibition of the female reproductive cycle. He suggests that the failure of the female cycle is apparently the result of social contact above some minimal level, this tolerance level being exceeded by only pair association in intolerant and some semi-tolerant species. It has also been stated that less tolerant species will sometimes breed if provided with a larger space or if paired during oestrous only (Eisenberg & Isaac 1963). Donat (1933) found success in breeding *Neotoma fuscipes* only after greatly increasing the enclosure size.

Because of the shy and retiring habits of the vlei rat disturbance by humans could easily be a factor causing non-breeding. The fact that food habits are not precisely known and the difficulty of obtaining adequate supplies of their "normal" food, as well as the use of rather small enclosures, could be contributing factors. The maintenance of animals in colonies would certainly create difficulties due to the antisocial character. Maintaining unbalanced sex ratios has also been considered but data from the trapping grid indicate a balanced sex ratio and such unbalanced ratios would undoubtedly also lead to conflict. In the vlei rat constant pair association in captivity would appear to create a situation which causes a breakdown of mating behaviour in both sexes, and merely the effect of being in captivity itself may be enough to inhibit the oestrous cycle. It is interesting to note that reproductively inactive animals (non-perforate females and non-scrotal males) when placed together show signs of becoming reproductively active by becoming perforate or scrotal. Maintaining litter mates in pairs as a means of reducing social conflict has been attempted but these individuals have failed to develop reproductively. Eisenberg (1967) reports this method as ineffectual in several species of typically solitary rodents.

Territorial Behaviour

The territory of an animal is accepted as a defended area and differs from the home range, which is an area of mutual tolerance frequented while foraging. In the vlei rat the marking behaviour and the habit of urinating in specific places could be a means of defining a territory by odour.

An attempt was made in the laboratory to define territoriality during tests of adult interactions. Prior to these tests the individual animals were placed in the observation chamber separated by barriers for periods varying from two to seven days. After removing the barriers a check was kept during the testing period as to the nestbox preference of each animal and its relationship to the original area occupied. It was found that the longer the animals were kept separated the greater the preference for a specific nestbox. The dominant male appeared to have the strongest preference for his original nestbox.

Because of a relatively high population density of *O. irroratus* in the study area, determination of territoriality from trapping records is rather difficult. If one considers only the very large and extremely scrotal males (usually over 160 g) there appear to be mutually exclusive areas occupied by conspecifics of similar size and sex. The data of females do not seem to be as conclusive and may depend upon their reproductive state. Trapping results show great overlap of home ranges and suggest that several individuals may use the same runways, as found also in *Microtus californicus* (Pearson 1960). This would mean that if an area is defended, defence affects only certain runways and more than likely only those in the close vicinity of the nest.

The occasional presence of regular defecation spots (see Elimination) is not understood unless these belong to the dominant individual of an area. The more usual habit of indiscriminate defecation and the presence of faeces from animals of all sizes on top of traps raises doubts as to the use of faeces in defining territories.

POSTNATAL DEVELOPMENT

For study of the growth and development of young *O. irroratus*, gravid females from the study area were live-trapped and brought into the laboratory. This proved very satisfactory considering the difficulties encountered in attempts at breeding in the laboratory. Thirteen gravid females were brought in and from these were born 36 young (two to four per litter, mean 2,8). Four individuals were born dead and two litters (five young) were premature and did not survive. Several instances of premature birth occurred in traps and those in the laboratory were within two days of capture, indicating that abortion resulted from stress caused by capture or captivity. As can be noted from the number of individuals utilised each week for determining weight increase (Fig. 4) a disproportionate number of young died or stopped growing, probably as a result of captivity. A brief description of physical appearance and development is included for better understanding of behavioural maturation (see also Figs. 4 and 5).

General Description

The young of *O. irroratus* are very precocial at birth with head and body well furred, eyes and ears sometimes functional, incisors erupted, vibrissae long (13 mm), ambulatory, and toes free and clawed. The mean weight of 28 young at birth (day 0) was 12,5 g and varied from 9,6 to 15,5 g (Fig. 4). The eyes are usually open by day two but in a few individuals were open either at birth or only as late as day four. The auditory meatus is open at birth, and although weak, a response to sound is present, hearing becoming acute by day two. The incisors are erupted to enable the young to cling fast to the mammae (see Adult-Young Behaviour). Solid food is eaten by the second day but does not become a regular part of the diet until day six or seven. Weaning appears to be nearly complete by day 13. The young grow very rapidly during the first eight weeks of life, showing an average weight increase of 9,4 g per week (a mean total increase of 75 g).

Development of Individual Behaviour

Young vlei rats at birth are capable of locomotion with the body partly raised off the substrate. The hindlimbs are splayed out and movement is very unco-ordinated until about day five. By then the hindlimbs are under the body and the young are capable of a co-ordinated run. The righting response is immediate at birth. A strong grasping reflex of the forepaws exists at birth enabling the young to climb.

As in most rodents co-ordination for locomotion purposes develops in an anterior to posterior direction, the forelimbs becoming fully co-ordinated before the hindlimbs. An interesting difference in limb co-ordination occurs in *Otomys*, the appearance of the scratching reflex with the hindfoot (day 0) prior to face washing (day two). Even cleaning the hindfoot with the teeth following scratching was observed as early as day two. Regular grooming sessions commence from the seventh day.

When the young are placed in a group a weak form of investigational behaviour begins by day one or two, probably associated with the opening of the eyes.

Play is an independent activity consisting of racing about the cage, often while carrying an object in the mouth. This begins during the first week and is a common activity by the end of the second week.

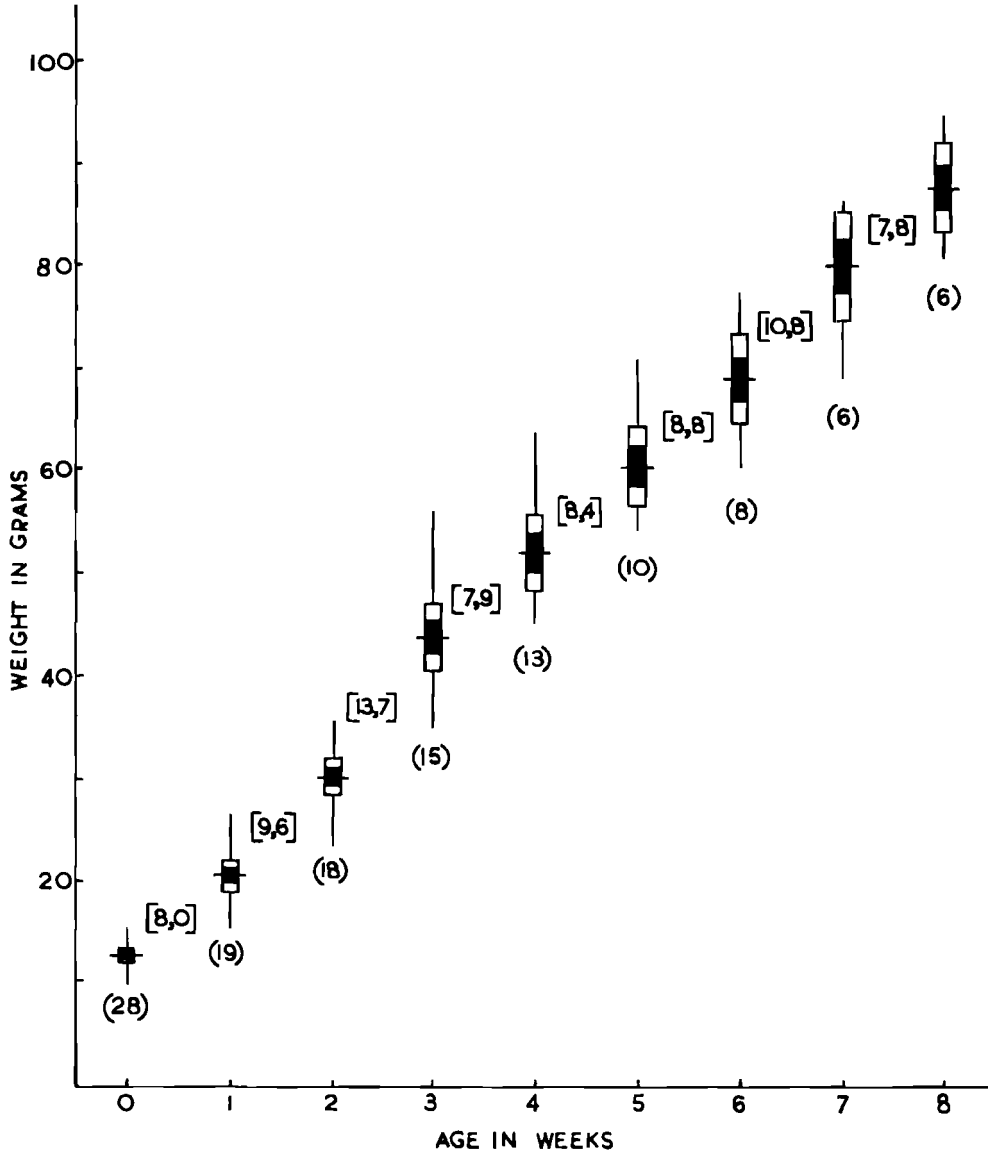

FIGURE 4
Summary of weight increase from birth to eight weeks of age. Vertical lines represent the range, horizontal lines the mean, solid bars one standard error, open bars two standard errors, figures in brackets the mean weight increase per week, and figures in parentheses the sample number.

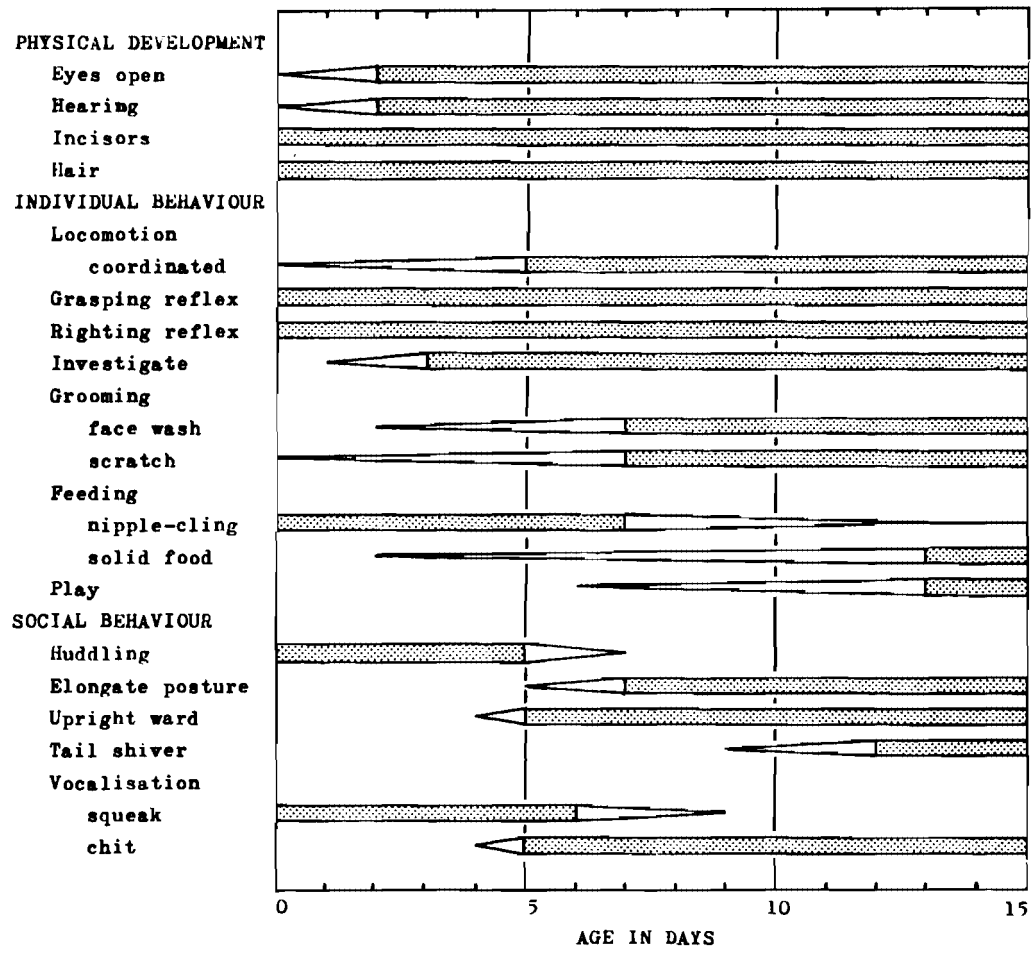

FIGURE 5

Summary of physical and behavioural maturation rates from birth to 15 days of age. Shaded bars indicate the mean appearance or disappearance of characters and activities and their duration. Open wedges indicate the difference between the time when a character or activity was first or last seen in any individual to or from the time of mean appearance or disappearance.

Development of Social Behaviour

Nipple-clinging is nearly constant during the first seven days and the young are seldom seen unattached. To remove them for measuring it was necessary to block off the nasal openings, together with a gentle but constant pull on the animal. During the first week this detachment took an average of 30 seconds, but soon they became detached in only 10 seconds and occasionally fell off of their own accord.

During the first five days of life the littermates huddle when they come in contact, pushing and crawling over and under each other. When separated during this period a sharp squeaking noise is

produced which aids in bringing them together and would enable the mother to locate them if lost. As this contactual urge begins to diminish around day five there ensues the defensive upright warding and threatening "chit" as found in adults. The elongate posture is seen about day seven and well coordinated tail shivering by day 12. Social grooming of littermates and the mother was observed as early as day four but did not become a common activity until day 14.

GENERAL DISCUSSION

Few of the individual behaviour patterns of *O. irroratus* differ from those of other rodents, especially quadrupedal species, variations being primarily related to environmental conditions.

Nipple-clinging is a very prominent feature of young vlei rats during the first two weeks of life. The principal adaptive value of nipple-clinging has been suggested to be the reduction of litter losses through predation (Davis 1963; King 1963; Layne 1968). This would be especially true in an animal using an open, unprotected nest such as *O. irroratus.* The rodents reported to use nipple-clinging (see Adult-Offspring Behaviour) have been found to have small litters. Most of these rodents also produce young that experience a long period of dependence. Davis (1963) noted that the survival rate of the young in the nipple-clinging *Mystromys albicaudatus* was high, attributing this to nipple-clinging. If this is the case the survival rate of *O. irroratus* young should be very great as the young are not only nipple-clingers, but are few in number (2,4 per litter) and become independent very early.

The absence of sexual behaviour and the failure to mate in the laboratory, as well as strong intrasexual aggression during encounter tests, demonstrates that *O. irroratus* is antisocial and tends toward adult isolation. The existence of marking behaviour and the probability of territoriality, especially in dominant individuals, also gives further support to their asociality. It has been shown that the more asocial rodents have evolved complex threat and communication patterns to avoid contact except during mating (Eisenberg 1963), and this definitely appears to be the case in the vlei rat. Mutual upright posture and sparring are methods of fighting to avoid drawing blood, except in captivity where persecuted animals may be severely wounded. "Chitting" and tail shivering are both rather sophisticated mechanisms for threatening without physical contact, as is sand kicking in *Dipodomys deserti* and tail flagging in *Perognathus penicillatus* (Eisenberg 1963).

In areas of excellent habitat, as in certain parts of the study area, the population density of the vlei rat gets rather high during the latter part of the breeding season. In these areas of high density it would be very reasonable to assume that animals in a given area are familiar with their conspecifics and that their interactions are well represented by a dominance hierarchy.

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REFERENCES

ASDELL, S.A. 1964. *Patterns of mammalian reproduction.* London: Constable.

BROWN, L.N. 1964. Ecology of three species of *Peromyscus* from southern Missouri. *J. Mammal.* 45 : 189–202.

CLARK, L.H. and M.W. SCHEIN. 1966. Activities associated with conflict behaviour in mice. *Anim. Behav.* 14 : 44–49.

CLARKE, J.R. 1956. The aggressive behaviour of the vole. *Behaviour,* 9 : 1–23.

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

DAVIS, D.H.S. 1963. Wild rodents as laboratory animals and their contribution to medical research in South Africa. *S. Afr. J. med. Sci.* 28 : 53–69.

DE GRAAFF, G. 1960. A preliminary investigation of the mammalian microfauna in pleistocene deposits of caves in the Transvaal system. *Palaeont. afr.* 7 : 59–118.

DELANY, M.J. and B.R. NEAL. 1966. A review of the Muridae (Order Rodentia) of Uganda. *Bull. Br. Mus. nat. Hist., Zool.* 13 (9) : 297–355.

DONAT, F. 1933. Notes on the life history and behavior of *Neotoma fuscipes. J. Mammal.* 14 : 19–26.

EISENBERG, J.F. 1962. Studies on the behavior of *Peromyscus maniculatus gambelii* and *Peromyscus californicus parasiticus. Behaviour,* 19 : 177–207.

EISENBERG, J.F. 1963. Behavior of heteromyid rodents. *Univ. Calif. Publs. Zool.* 69 : 1–102.

EISENBERG, J.F. 1967. A comparative study in rodent ethology with emphasis on evolution of social behavior. I. *Proc. U.S. natn. Mus.* 122(3597) : 1–51.

EISENBERG, J.F. 1968. Behavior patterns, p. 451–495. In:J.A. King (ed.), *Biology of* Peromyscus *(Rodentia), Spec. Publs. Am. Soc. Mammal.* (2) : 1–593.

EISENBERG, J.F. and D.E. ISAAC. 1963. The reproduction of heteromyid rodents in captivity. *J. Mammal.* 44 : 61–67.

EWER, R.F. 1967. The bevaviour of the African giant rat *(Cricetomys gambianus* Waterhouse). *Z. Tierpsychol.* 24 : 6–79.

EWER, R.F. 1968. *Ethology of mammals.* London: Logos Press.

HAMILTON, W.J., JR. 1953. Reproduction and young of the Florida wood rat, *Neotoma f. floridana* (Ord). *J. Mammal.* 34 : 180–189.

HEWITT, J. 1931. *A guide to the vertebrate fauna of the eastern Cape Province. Part I. Mammals and birds.* Grahamstown: Albany Mus.

KING, J.A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairiedog town in the Black Hills of South Dakota. *Contr. Lab. vertebr. Biol. Univ. Mich.* (67) : 1–123.

KING, J.A. 1963. Maternal behavior in *Peromyscus,* p. 58–93. *In* H.L. Rheingold (ed.), *Maternal behavior in mammals.* New York: Wiley.

KIRKPATRICK, R.L. and G.L. VALENTINE. 1970. Reproduction in captive pine voles, *Microtus pinetorum. J. Mammal.* 51 : 779–785.

LAWRENCE, B. 1941. Incisor tips of young rodents. *Fld. Mus. nat. Hist., Zool. Ser.* 27 : 313–317.

LAYNE, J.N. 1968. Ontogeny, p. 148–253. In J.A. King (ed.), *Biology of* Peromyscus *(Rodentia), Spec. Publs. Am. Soc. Mammal.* (2) : 1–593.

MEESTER, J. and A.F. HALLETT. 1970. Notes on early postnatal development in certain southern African Muridae and Cricetidae. *J. Mammal.* 51 : 703–711.

MISONNE, X. 1969. African and Indo-Australian Muridae. Evolutionary trends. *Annls Mus. r. Afr. cent. Ser. 8vo., Zool.* (172) : 1–219.

PEARSON, O.P. 1960. Habits of harvest mice revealed by automatic photographic recorders. *J. Mammal.* 41 : 58–74.

POOLE, E.L. 1940. A life history sketch of the Allegheny woodrat. *J. Mammal.* 21 : 249–270.

POWELL, W. 1925. Rodents. Description, habits, and methods of destruction. *S. Afr. Dep. publ. Hlth.* (321) : 1–21.

ROBERTS, A. 1951. *The mammals of South Africa.* Johannesburg: Trustees of "The mammals of South Africa" Book Fund.

ROSEVEAR, D.R. 1969. *The rodents of West Africa.* London: Trustees Br. Mus. nat. Hist.

SHILLITO, E.E. 1963. Exploratory behaviour in the short-tailed vole *Microtus agrestis. Behaviour,* 21 : 145–154.

SHORTRIDGE, G.C. 1934. *The mammals of South West Africa.* London: Heinemann. 2 vol.

THOMAS, O. and H. SCHWANN. 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.