

C.N.R.S. Centre de Recherches sur les Zones Arides, Beni-Abbes, Algeria,
and University of Bristol, England

Behavior of *Psammomys obesus* (Rodentia: Gerbillinae) in the Algerian Sahara

By MARTIN DALY and SANDRA DALY

With 7 figures

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I. Introduction

A. *Psammomys obesus*

P. obesus, the "sandrat", is a medium-sized rodent (adult wt 80—200 gm) inhabiting deserts from Mauritania to Palestine. *Psammomys* is one of several genera of gerbils (subfamily Gerbillinae, family Cricetidae), a group mainly confined to the Great Palaearctic Desert, where they comprise the most widely distributed and radiated group of rodents.

Most gerbils are mainly granivorous or omnivorous, and some species, such as *Pachyuromys duprasi* and *Tatera indica*, are highly insectivorous (PETTER 1961, PRAKASH 1962). Desert rodents can subsist on such high-energy dry diets by practising a stringent water economy (SCHMIDT-NIELSEN 1964). However, *P. obesus* has developed a different adaptation, finding ample water in the fleshy leaves and stems of perennials of the family Chenopodiaceae. These plants are found in the wadis (river beds which are only occasionally flooded) and alluvial plains of North Africa. They comprise virtually the entire diet (PETTER 1961, DALY and DALY 1973), and large sandrat populations can be found where these foodplants thrive. Diurnal habits, relatively high population densities, and relatively restricted ranges make *P. obesus* one of the most readily observed and studied of desert rodents.

B. Study Area

This study was conducted in the Wadi Saoura in the northwest Sahara near Beni-Abbes, Algeria (30° 7' N lat, 2° 10' W long). The Saoura varies in breadth from about 300 m to more than a km. Until 1967, it was usually flooded for a few days annually, and its salty soils are more lushly vegetated, mainly with halophytic plants, than the surrounding desert. The Saoura did not flow between 1967 and the time of this study, 1972-73, both because of new dams and because of a drought. At Beni-Abbes, mean rainfall is about 35 mm, but from 1968 to 1972 it was only 20 mm, and periods as long as 8 mo with no precipitation whatever were recorded.

PETTER (1961) has described the climate at Beni-Abbes, the various desert habitats, and the rodents associated with them in some detail. At the time of this study, the distribution of vegetation in the Saoura, and thus that of *P. obesus* as well, was patchier than he described.

Along the Saoura, oases occur at intervals of several km, and support *Tamarix* trees, cultivated date palms, and small gardens. Our main study area was at Ouarourout, a small oasis 7 km west of Beni-Abbes. About 10 ha contained bushes of *Suaeda mollis* (Chenopodiaceae) and these were the areas used by sandrats. This main habitat comprised a roughly rectangular strip 700 m long, bounded by sparsely vegetated dunes and by the very salty wadi bottom, both of which limited *P. obesus*' movement. The population in the study area was not completely isolated, however, as scattered bushes of *Salsola foetida* (Chenopodiaceae), occasionally occupied by the sandrats, extended west along a clay plateau, and *S. mollis* and *S. foetida* were both present in low densities for several km to the east.

A second study area, at Zguilma, about 30 km northwest of Beni-Abbes, consisted of a virtually monospecific stand of *S. foetida* in bushes up to 60 cm high, spread over about 1.5 ha, and isolated from any other concentration of vegetation by several hundred m. Tall trees, numerous at Ouarourout, were absent at Zguilma.

II. Methods

A. Field Observations and Trapping

The Ouarourout study area was visited on 121 days from Dec. 1 1972 to Apr. 30 1973, and Zguilma on 14 days between Dec. 27 and Mar. 15. At the study areas, a trapping programme was combined with direct observation of the rodents.

Animals were captured in traps baited with fresh green parts of their food plants and placed at their burrow entrances. Since sandrats use runways to the virtual exclusion of other routes, trapping by geometric grids is inappropriate.

We began by marking all animals in one part of the study area, and expanded over the first 2 mo to include the whole area. Thereafter, traps were laid for any unmarked animal seen, or wherever there were signs of activity by unknown animals. 83 sandrats were marked at Ouarourout and 7 at Zguilma.

Most sandrats were deliberately retrapped. We tried to capture each adult ♀ about every 2 wk, to keep track of reproductive condition, and often trapped at much shorter intervals to attempt to pinpoint an imminent delivery. Pups were trapped at short intervals in order to obtain growth data. Adult ♂ were retrapped at intervals of about a month to refresh marks and to check for further growth.

In general, we trapped as little as was consistent with our aims, for trapping entailed a risk of mortality (1.4%) and consumed time during the hours best suited for field observation. Capture frequencies are presented in Table 1.

Table 1: Capture frequencies of marked sandrats

No. of captures	14	13	12	11	10	9	8	7	6	5	4	3	2	1
No. of individuals	1	1	2	0	1	1	3	5	11	7	10	15	17	16
Totals: 90 animals trapped 365 times														

Trapped sandrats were sexed, measured, inspected for reproductive condition (testicular descent, vaginal opening, lactation, late pregnancy), marked for permanent identification by claw clipping and ear nicking, marked for field observation by cutting away patches of the outer fur revealing the dark underfur in distinctive patterns and loci, and were then released.

Observation was conducted both with the naked eye and with binoculars. We attempted to identify as many individuals as possible daily, and to record their locations. Behaviour recording was mostly opportunistic; systematic data on the behaviour of litters or individuals were occasionally collected and are described in the relevant sections below.

B. Laboratory Maintenance

For observation in captivity, wild-caught and captive-born sandrats were maintained in the laboratory at Beni-Abbes, in glass-and-metal aquaria or wood-and-metal cages. Floors were covered with sand which was changed daily (entirely or in part), and soft shredded paper was provided as nest material.

Natural foods were provided daily, mainly *Traganum nudatum*, *S. foetida* and *S. mollis*, and occasionally *Salsola longifolia*, *Salicornia fruticosa* and *Atriplex halimus*. These Chenopod

plants were the only diet and water source. 12 to 15 hr light a day were provided by natural and artificial lighting.

III. Use of Habitat

Sandrats live in multi-entranced burrows directly under their food plants. The burrows are usually deep and organized at several levels. Drawings and descriptions of excavated systems have been published by PETTER (1952, 1961).

It was typical in our study areas for the rodents to exploit several food bushes, usually of the same species, at once. The degree of utilization of different plant species has been described elsewhere (DALY and DALY 1973). The ground between the bushes is completely bare of vegetation, as is a majority of the terrain in the Wadi Saoura; *P. obesus* moves rapidly between the plants on well-worn paths. This behaviour contrasts with the much more variable and exploratory movements of the other rodents of the vicinity.

Activity above ground is primarily diurnal (PETTER 1961, HUSSEIN, BOULOS and ESSA 1969). In December, there was often frost on the low dunes in the Saoura at dawn, and we found that *P. obesus* did not emerge until an hour or two after sunrise on such cold mornings. In December and January, when the average daily maximum and minimum in the shade were 17° and 4°, the sandrats spent long periods basking in the direct rays of the sun at all hours of the day. Feeding occurred throughout the day, and food was cut and taken to the burrow in large quantities, usually within the last 3 hr before sunset, presumably to be eaten after dark. FRENKEL, SHAHAM and KRAICER (1972) found captive *P. obesus* to eat most of their food during the night. The wide-ranging activities of adult ♂♂, described below, were especially frequent at dusk, and we often had to abandon observation due to darkness when the animals were still busy. Young sandrats, still living with littermates, almost never emerged except where there was direct sunlight.

By April, the shade maximum and minimum at Beni-Abbes are up to 28° and 14°. By that month, *P. obesus* has switched to primarily crepuscular outside activity, although sorties occur at a low frequency throughout the day. Major bouts of food hoarding occur around dawn and dusk. In July and August, temperatures surpass 40° daily and occasionally reach 47°; the crepuscular activity pattern presumably continues until autumn. This seasonal activity pattern has been described in Egypt by HUSSEIN, BOULOS and ESSA (1969).

IV. Social Behaviour Patterns

A. Direct Interactions

P. obesus is basically solitary. An adult ♂ can often be found in a burrow with a ♀ with or without young, but the pairs do not stay together. The ♂ may visit the same ♀ on several successive days, especially when she is near parturition, but we never saw evidence of a couple remaining in the same burrow for even a few hours. Light winds during the night often erased all tracks and made it possible to observe burrows at about dawn with the certainty that any activity seen was the first of the day. No adult ♂ was ever observed to have spent the night in a ♀'s burrow. The only animals to live together were mothers with nursing young, and recently weaned littermates.

Intraspecific encounters in the field are described in section VI. The ontogeny of antisocial reactions is treated further in section IX. Sexual behaviour is described in detail in section VII. A. Other social behaviour patterns are few.

Social "grooming" was only observed between mother and offspring and among littermates. It involved a brief pawing of the other's head and was

usually ignored, though it occasionally led to the groomee's turning on his back with a fight (or a "play fight" in young animals) ensuing.

In fighting, both antagonists stand up on their hind legs and tails, and leap and paw and bite mainly at the opponent's head and ears. If one animal attempts to flee, both will run on all fours and the chasing rodent may bite the other's rump, but if both animals are aggressive, the upright stance is held until one is thrown off balance and is immediately resumed. Although one animal might be thrown on its back and freeze there with the other standing over it, we never saw the sort of rolling together and mutual flank-biting that occurs in many rodents. This kind of tussling is precluded because neither animal will abandon a mouth-to-mouth orientation. A similar fighting posture has been described in *Tatera indica* by BLAND (1969). It is a preliminary to less ritualized fighting in *Meriones persicus* (EIBL-EIBESFELDT 1951) and *M. unguiculatus* (NYBY, THIESSEN and WALLACE 1970).

Fights observed in the field always ended with one animal fleeing to another bush and the winner (not necessarily the original inhabitant, see sections V.B. and VI.) staying at the scene of the fight.



Fig. 1: Sidling. The ♂, at right, moves sideways toward the ♀ and places his right rear foot on her flank

An animal "sidles" towards another by presenting the flank and advancing sideways with short steps. The hair on the advancing flank and haunch is erected and the body raised on that side. The sidling animal may lift his foot to actually step on the other's back and may hold this posture (Fig. 1). Sidling was seen only in heterosexual encounters and was more often performed by the ♂. It may have olfactory significance, and may be followed by agonistic or sexual behaviour. The identical pattern occurs in *Meriones lybicus* (our observations) and in *M. unguiculatus* (NYBY, THIESSEN and WALLACE 1970).

B. Behavior Patterns with Probable Olfactory Significance

1. Urination and Urine-balls

Sandrats urinate frequently in small amounts. They then dig a little sand under the body with 2 quick simultaneous strokes of both forepaws, and this sand absorbs the liquid. By the wetting of a small area of sand, a "urine-ball" is formed which maintains its integrity even after drying. Sandrats may pick up urine-balls in both forepaws and sniff them, often with an exaggerated up-and-down movement of the snout that gradually breaks up and scatters the urine-ball. In the laboratory, ♂♂ exhibit especially prolonged intense sniffing of the urine-balls of oestrus ♀♀.

2. Scent-marking

P. obesus possesses a midventral gland like that of other gerbils (SOKOLOV and SKURAT 1966), and will rub it over objects placed in its cage. There is also a glandular area under the chin, which is prominent in large ♂♂ and is rubbed against branches. Specific scent-marking of objects (as opposed to sand-bathing, see below) was only observed in adult ♂♂.

Two prolonged bouts of marking were seen in the field. Both were performed by ♂ 51 (a dominant ♂, see section V.B.1.). Once, 51 chin-marked extensively in a bush which had been occupied by a young ♂ (22) whose testes had just descended. 22 was meanwhile some 20 m away at a bush occupied by a female littermate. He had presumably been chased there by 51, who was often observed to chase young ♂♂ from their burrows, and to occupy them himself for a few days. On another day, 51 exhibited a long bout of chin-marking, ventral-marking, and urine-ball sniffing in bushes which were occupied by a 78-day-old ♀, possibly in her first oestrus.

3. Sand-bathing

Like many desert rodents, sandrats sand-bathe by alternately rubbing each flank on the substrate. This side-rubbing may be preceded by forepaw digging movements. We observed this type of sand-bathing only once in the wild. In the laboratory, it was most frequent immediately upon the provision of fresh sand.

Long low body-stretching with ventral rubbing on the sand was a more common type of sand-bathing. Such stretching was seen only near the home burrow.

Prolonged, elaborate bouts of sand-bathing were seen in *Meriones libycus* and *Gerbillus nanus*, but not in *P. obesus* maintained in the same laboratory.

C. Foot-thumping

A conspicuous behaviour of presumed social function is audible foot-thumping. When startled, *P. obesus* usually dashes down its burrow, and may thump loudly in doing so. If an observer approaches, the animal may thump about every 3 sec, then at increasing intervals, and stop after about a min. A startled sandrat's first thump often accompanies a high-pitched squeak.

Thumping is also common in intraspecific encounters, especially ♂-♀ interactions, both sexual and agonistic. A few individuals thumped persistently in traps while being handled.

M. libycus also foot-thumped. These jirds live solitarily at much lower densities than *P. obesus* (PETTER 1961, and personal observations). They were much more persistent thumpers than sandrats: one thumped steadily for 23 min, a total of 371 thumps, while an observer stood quietly near his hole.

Foot-thumping by gerbils has been described in popular writings as an alarm signal to which whole "colonies" react by dashing below. Although another sandrat was often within earshot, we never saw one show a clear response to an other's thumping. Occasionally one animal would thump, run below, and continue thumping, while another fed or moved about obliviously within 3 m.

Often a gerbil was first detected because it was thumping, especially in the case of *M. libycus*, whose burrow entrances may be hidden. Potential disadvantages of such conspicuous behaviour seem obvious. Further observation may reveal a redeeming social function.

V. Home Ranges

In many small mammal studies, a "home range" (HR) is measured for individual animals. Comparisons are then drawn between sexes, age-classes, and, occasionally, species.

To eliminate dispersing juveniles (see IX. D.) from consideration, adults are here defined as ♀♀ who have conceived their first litter, and ♂♂ with prominent testicular development and tails 110 mm or more in length. To compute HRs, only those adults who were positively identified in the field on at least 10 different days are considered. These were 7 ♂♂ and 11 ♀♀.

Areal measures of HR seem inappropriate in a habitat that is mostly bare and unused, so our HR measure is Range Length (RL), defined as the straight-line distance between the 2 most distant points where the animal was recorded.

Mean ♂ RL = 189.6 m. Mean ♀ RL = 75.8 m. This difference is highly significant (Mann-Whitney U = 6, $p < .001$), despite more individual-day records for the ♀♀ (Means 39.0 v 23.6 days), and a longer total duration from first to last record for the ♀♀ (Means 13.7 v 9.0 wks), both of which factors introduce bias in the direction of relatively inflated RLs for the ♀♀.

A. Use of Range by ♀♀

The case of one reproductive ♀ is illustrative. Fig. 2 shows all the bushes visited by ♀ M2 in the period Jan. 19 to Apr. 30. This period included her first pregnancy and the rearing of her first 2 litters. She moved her first litter from A to F on Mar. 1, the estimated conception date of the second litter. On about Mar. 25, their delivery date, she left her first litter at F and moved to N. At 2 to 3 wk of age, the second litter was moved to K, 2 wk later to L, and finally to M.

Each move except the first was into a burrow which the mother had dug under a bush already in her food-gathering range. All the lettered bushes were visited for food, but no more than 5 were ever in use at once. For example, only J, K and N were in use from Apr. 1 to 7 and only K, L and M from Apr. 23 to 30.

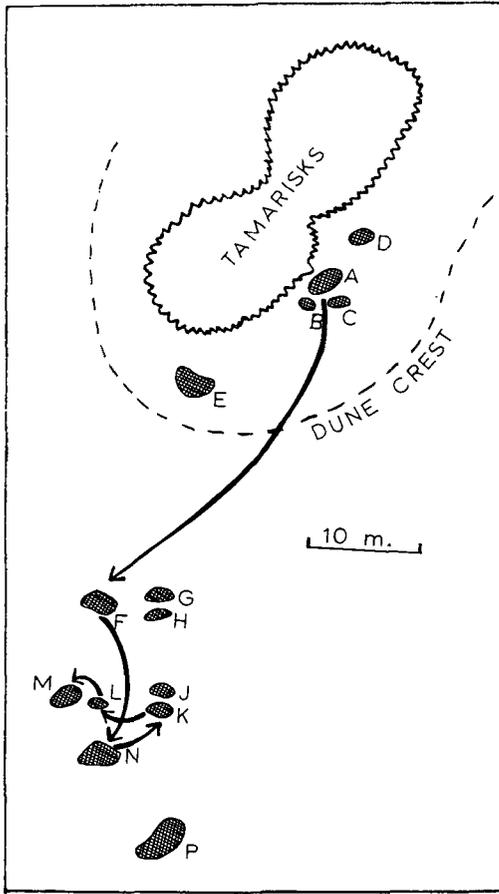


Fig. 2: Areas used by ♀ M2. Lettered bushes are food sources (*Suaeda mollis* and *Traganum nudatum*). Arrows connect successively occupied burrows

Records for other reproductive ♀♀ were similar. Adult ♀♀ generally exploited small ranges containing several food bushes, carrying bundles of food to the home burrow. Tracks showed that excursions outside this small domain of exploitation were very rare.

This small HR "drifted" over days: one bush, regularly visited, would be abandoned, sometimes upon exhaustion of its edible growth, and another added to the range. Some ♀♀ returned to exploit bushes they had abandoned weeks earlier. Others did not.

B. Use of Range by ♂♂

1. Subordinates

Most ♂♂ at Ouarourout tended to stay in one burrow for several days, as did ♀♀. However, when they moved, they were likely to move greater distances, and residencies were on average briefer than those of ♀♀. Of 40 instances where an adult ♀ occupied a single burrow for a week, she occupied it for more than 2 weeks 26 times (65%). Of 13 instances where an adult ♂ occupied a single burrow for a week, he occupied it for more than 2 weeks only twice (15%). This is a significant difference ($\chi^2 = 7.9, 1 \text{ df}, p < .01$).

The attraction exerted by a litter make ♀♀ more sedentary than ♂♂, but two other conspicuous factors favoured short-term residencies in ♂♂. First, the bushes with the best food supplies were usually occupied by ♀♀, and a young adult ♂ sometimes ate himself out of a home in about a wk. Secondly, a few dominant ♂♂ with large "true HRs" (see below) often attacked and evicted younger adult ♂♂.

2. Dominants

A smaller number of dominant ♂♂ moved about over relatively large HRs, repeatedly visiting the same areas; this is the sort of behaviour usually implied by the term HR.

At Ouarourout, there were two phases. ♂ M6 was dominant over a large area in the west in Dec. and Jan. and then disappeared from the population. ♂ 51 and ♂ S1 were then dominant over adjacent ranges, maintaining a stable boundary which was never violated until the end of the study (Apr. 30). Fig. 3 shows the locales where M6, 51 and S1 were seen in temporal sequence.

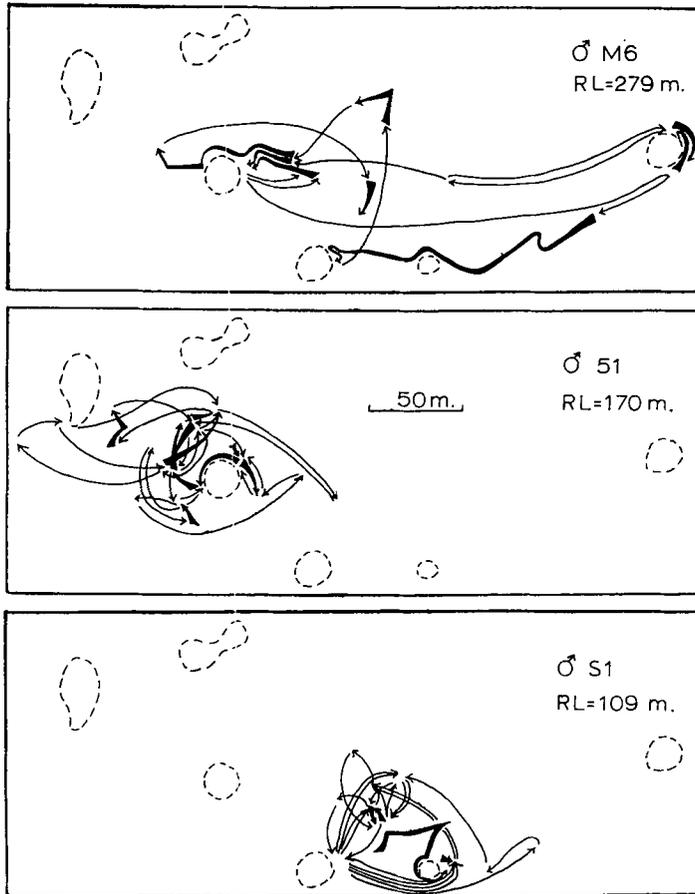


Fig. 3: Areas ranged by 3 dominant ♂♂. Dotted lines enclose *Tamarix* trees. Thin arrows connect successive points at which the animal was observed. Thick arrows represent movements which were directly observed

Each of these ♂♂ visited every resident ♀ within his HR at least every few days, and sometimes visited several daily. In one hr 40 min at dusk on Jan. 29, for example, ♂ M6 visited and interacted with 3 widely separated ♀♀ within his range, proceeding 76 m and 52 m between the successive burrows. None of the 3 was sexually receptive. He stayed 1 hr with one ♀ who was very near term, and less than 5 min with each of the others.

Besides visiting ♀♀, these dominant ♂♂ attacked and chased other ♂♂ over about 7 wk of age whenever they encountered them. Interactions are described in more detail in section VI.

C. Sex Comparisons of Short-term Range Use

Three rather different patterns of HR use can thus be described. Reproductive ♀♀ have a small "drifting" HR, subordinate ♂♂ a small frequently "shifting" HR, and dominant ♂♂ a large "true HR".

Since the total adult RLs computed above (♂: 189.6 m, ♀: 75.8 m) included HR drifts and shifts, a short-term measure was also computed. This is Mean Weekly RL (MWRL), averaging the RLs for all weeks in which the individual was located on at least 2 different days, for the same 7 ♂♂ and 11 ♀♀. ♂ MWRL = 67.7 m, ♀ MWRL = 11.7 m ($U = 0$, $p < .0001$).

The ♂ MWRL is 36% of the total ♂ RL, but the ♀ MWRL is only 15% of the total ♀ RL. When this percentage is computed for each individual, the sex difference is again significant ($U = 8$, $p < .01$). In other words, in an average week, ♂ range over a significantly larger proportion of their significantly larger total range than do ♀♀.

If these data were based on trapping an unobservable species, the obvious conclusions would be that ♂♂ have a greater HR and that ♂♂ actively patrol their HR more than do ♀♀. However, direct observation points to 2 different mechanisms with the same apparent result: 1) the "true HR" behaviour of dominant ♂♂, and 2) the suboptimal locales and aggression experienced by subordinate ♂♂ causing frequent moves.

D. Utility of the Home Range Concept

These patterns of range use present a difficulty for the HR concept. Many authors have differentiated "shifts of HR" or "dispersal movements" from movements within the HR. However, such a dichotomy does not encompass the "drifting" HRs of female sandrats.

The soundness of the HR concept varies with species. Water voles (*Arvicola terrestris*) visit virtually all of a bounded HR daily, and shifts of range are easily discriminated from activity within the range (STODDART 1970). Other species do not patrol their ranges with any regularity, and the HR may be considered as a region within which the animal may be found with declining probability at increasing distances from a centre of activity (HAYNE 1949).

Increasingly sophisticated methods have been brought to bear on the problem of HR measurement, always assuming the HR to exist and our problem to be that of minimizing estimation errors. However, the drifting HR of a ♀ sandrat can only be quantified with reference to an arbitrary time interval. We can thus compare sexes or age-classes, but cannot attach much importance to the exact magnitudes of the HR estimates.

VI. Intraspecific Encounters

The basic solitariness of *P. obesus* is evidenced by the rarity of observed interactions between adults. In approximately 1100 observer-hours in the field, many hundreds of interactions between mothers and their young, and between littermates or young of successive litters, were seen but only 58 interactions between known animals outside immediate family groups.

If the animals involved are categorized as adult ♂♂, adult ♀♀, juvenile ♂♂ and juvenile ♀♀, then the 58 interactions can be broken down as follows:

Adult ♂ — Adult ♀:	27 — 2 copulations; 3 interactions with elements of receptive and aggressive behaviours; 7 purely agonistic (ended by ♂ fleeing 5 times, ♀ fleeing twice); 15 neutral contact or briefly aggressive with no clear resolution. 25 of these 27 interactions involved the 3 dominant ♂♂, M6, 51 and S1.
Adult ♂ — Adult ♂:	2 — dominant ♂ defeats and chases subordinate from home burrow.
Adult ♀ — Adult ♀:	0
Adult ♂ — Juvenile ♂:	17 — 3 neutral; 4 juvenile follows adult, squeaking; 10 adult chases juvenile(s) (all 10 including ♂51).
Adult ♂ — Juvenile ♀:	8 — 6 neutral; 2 juvenile follows adult, squeaking.
Adult ♀ — Juvenile ♂:	1 — adult chases juvenile.
Adult ♀ — Juvenile ♀:	1 — adult chases juvenile.
Juvenile ♂ — Juvenile ♂:	2 — neutral.
Juvenile ♂ — Juvenile ♀:	0
Juvenile ♀ — Juvenile ♀:	0

In addition to these direct observations, there were instances where an interaction could be inferred from the displacement of one animal by another. The original resident was often seen around the periphery of his former range for a day or two before establishing another burrow.

There were 5 clear cases of a reproductive ♀ evicting a resident animal to take over its burrow and food bushes. The displaced animals were a young adult ♂, a juvenile ♀ and 3 adult ♀♀. In 2 of these latter cases, the displaced ♀ apparently lost a nursing litter. There were several cases of a dominant ♂ suddenly turning up in the burrow of a young adult or juvenile ♂, with the original inhabitant being found elsewhere. In such cases the dominant ♂ usually only stayed a day or two.

When adult ♂♂ visited ♀♀ with young litters (less than 6–7 wk) there were no interactions observed between ♂♂ and pups. In the laboratory, we tried placing an adult ♂ in a 4-wk-old litter's cage. Both parties engaged in obvious active avoidance and there was not a single close approach in a half hour's observation.

VII. Reproduction

Adult ♀♀ were pregnant, lactating or both throughout the study period. These 5 months (Dec. to Apr.) were the season of maximal reproduction in captive Israeli sandrats (FRENKEL, SHAHAM and KRAICER 1972) but litters were born in all months.

In Beni-Abbes, according to local people, young can be found in any month. The leaf diet of perennial shrubs should free *P. obesus* from the seasonal cycles of food availability experienced by granivores but adequate data are lacking.

A. Sexual Behaviour

According to the classification of mammalian copulation devised by DEWSBURY (1972), *P. obesus*, like most Cricetid rodents, exhibits pattern no. 13: multiple intromissions and multiple ejaculations with neither repeated thrusting at each intromission nor a lock.

A number of matings were observed in the laboratory. None took place without some agonistic behaviour.

A highly receptive ♀ approaches the ♂, usually from the side, with forequarters held low and head pointing slightly up, emits a brief squeal and quickly turns to present her rear. She may step forward 1 or 2 steps, and then almost always digs briefly in a full sequence of forepaw digging followed by hind kicks, showering the ♂ with sand. She then holds the lordosis posture, with the forequarters very low and posterior raised, for a few seconds.

The ♂ steps forward, seizes her flanks and mounts, attempting intromission with a single thrust. The ♀ usually turns, often vocalizing, and strikes or bites at the ♂'s genitals

or head. If the ♂ jumps back with each dismount, no aggressive contact need occur. The ♀ may exhibit the initial receptive behaviour, but turn on the ♂ when touched, preventing copulation; the ♂ usually loses interest quickly.

Ejaculation can be recognized as a deeper thrust, often evoking a more violent reaction from the ♀. That ejaculation has occurred is then confirmed by the ♂'s refractory interval, and by his prolonged bouts of grooming his genital region. The ♀ may continue to approach the ♂ sexually, then groom herself, sand-bathe, eat or engage in other activity. Between copulatory series, ♂♂ frequently scent-mark with both the chin and ventral glands, sniff urine-balls and eat.

When the ♀ is highly receptive, intermount intervals may be less than 10 sec. A less receptive ♀ will initiate fights, and mounts may occur only every min or two, necessitating as long as 20 min to complete a series. Either animal may sidle vigorously, but this is rarer after mounting has begun.

The number of mounts required to reach ejaculation shows no clear trend over successive series: in 4 trials pairing different animals, these were 3-4-8; 14-13-14; 5-5-5; 26-11-12; (hyphens separate successive series within a trial and semi-colons separate different mating trials). The refractory period increases over series: in the same 4 trials, successive refractory periods in min were 3-11-15+; 3-6-20+; 3-19; 6-16-24+. These trends are similar to those observed in other rodents (see references in DEWSBURY 1972). The relatively variable behaviour seen here may depend on using natural oestrous periods or on using wild-caught animals. The quickest first series observed required only 3 mounts at intervals of 25 and 17 sec, producing ejaculation less than 3 min after the animals were placed together. In the slowest first series observed, 9 mounts were spaced over 14 min, interspersed with much aggressive behaviour by the ♀.

2 copulations were observed in the field. Both occurred at the ♀'s home bush and were performed by the dominant ♂ whose range overlapped hers. The stereotyped approach behaviour of the ♀, with squealing, turning and digging, was identical to that observed in the laboratory. The first copulation occurred at dusk. 10 mounts were observed in a single series, and intermount intervals varying from 13 to 50 sec were recorded. One brief fight occurred between mounts as the ♀ turned on the ♂ and forced him onto his back. After ejaculation, the ♀ approached sexually several times but the ♂ ignored her while grooming himself, whereupon she walked away to eat elsewhere in the bush. The ♂ continued grooming, occasionally sniffing urine-balls and foot-thumping frequently.

The second copulation was observed shortly before dawn. Only a single intromission was observed, evidently ejaculation. The ♀ then turned, vocalizing, upon the ♂ who ran to a nearby palm and later continued to a distant part of his range. All the observed features of copulation in the field suggest that the phenomena observed in the laboratory are not greatly distorted by the unnatural confinement.

The subreceptive sequence of sexual approach followed by aggression by the ♀ was twice observed in the field. In both instances, the ♂ remained at the ♀'s bush only a few minutes longer.

B. Gestation Periods and Postpartum Matings

A single laboratory ♀ was mated in an observed trial and was observed to deliver. Pregnancy lasted 24.8 days, with mating at dusk and parturition in the early afternoon. Gestation periods of 23—25 days have been reported in sandrats from Tunisia, Egypt and Israel (CHOUMOVITCH 1954; PRANGE, SCHMIDT-NIELSEN and HACKEL 1968; FRENKEL, SHAHAM and KRAICER 1972).

5 ♀♀ who delivered litters in the laboratory were paired with ♂♂ in a neutral cage between 6 and 36 hr postpartum. All mated but none produced a litter.

The field data provide one demonstration of fertile postpartum oestrus. The only 2 observed copulations involved the same ♀ and took place at an interval of 24.5 days. The next day, she was trapped and had large nipples. 26 days later pups were seen with her. The second copulation must have occurred in a postpartum oestrus. Unfortunately this was too near the end of the study for the next litter to be observed, but 32 days after the second copulation, with the litter weaned and the mother having moved to a nearby burrow, she was again trapped and was apparently in a state of advanced pregnancy.

This raises the question of extended gestational periods during lactation. With no litters from laboratory postpartum matings, there was no direct evidence. However trapping of the mother and early growth data for the pups (see section VIII.C.) permitted estimations of birth dates for successive litters. The estimated interlitter intervals were 36, 42, 35, 36, 37 and 44 days. A 36-day interval coincides with an old report of the gestation period of *P. obesus* (DEHNE 1914). In the Indian gerbil (*Tatera indica*), lactation causes a delay of implantation, lengthening the gestation period from 22.3 to 36 days (BLAND 1969).

VIII. Development

A. Individual Development

Development was systematically observed in 4 laboratory-raised litters. Each was observed daily for one 15-min trial, with the mother removed, from the first day postpartum until 23 days of age. All action patterns (APs) observed were listed and a topographical description of all APs still undergoing development was attempted. Conspicuous aspects of morphological development were also noted. Litter sizes in captivity were 2, 3, 3, 4 and 5. (One litter of 3 was not raised by the mother.) The chronologies for all 4 litters were similar despite growth differences (see below) and are combined in the summary below.

At birth *P. obesus* lacks visible hairs except for vibrissae and is darkly pigmented dorsally and pink ventrally. Limb and trunk movements are uncoordinated and jerky. The hind toes can touch the body and the forepaws can touch the head.

By 2 days of age a tendency to rest belly-down is seen, and self-righting both by forward and lateral rolls occurs. Long forepaw strokes are evident, especially in "boring" down between littermates. Lifting the head is occasionally seen on day 3 and repeated hind-foot kicks are first seen then. Development after this age is most conveniently described by functional behaviour categories plus morphological change.

1. Morphological development

Fine white hair appears on the back by day 2 and white tufts may also be seen on the forelegs. By day 3, the back fur is turning brown and it darkens to a rich brown with some black hairs by day 5 or 6. Sparse white hair begins to appear on the ventrum about day 5, as does hair on the tail. By day 7, hair covering appears fully adult except for a large bare ano-genital region, naked soles, naked pinnae, and sparsely furred forelegs. The soles and ano-genital region show fur by day 10 and the pinnae soon after.

At birth, the claws are not obviously differentiated from the digits, the pinnae are attached flat, and the incisors are invisible. By day 2 or 3 the claws are conspicuous. Both lower and upper incisors may pierce the gums as early as day 3 and were erupted by day 6 in all animals. The pinnae become detached by day 4 or 5 and by day 6 manifest a concavity where the ear will open.

2. Locomotion and Forays

The body may be dragged about by the forepaws pulling together or in alternation by day 4. Crawling with the forequarters elevated was seen on day 5, and support of the level

and body gradually improves until true walking appears on about day 11 with a slightly erratic "trot" synchrony (i.e. roughly simultaneous steps by diagonally opposite limbs). The "gallop" synchrony (forelegs simultaneous and backlegs simultaneous) is not seen until about day 15 and only occurs at high speeds, but by adulthood it is far more frequent even at slow speeds than the trot which is mainly used in crawling under low obstructions or into tunnels.

Pups first leave the nest and walk about on day 11. They sniff around their cages and rear unsteadily up the wall by day 13. From about day 14 to 20 a great deal of jerky running and darting and shivery hops are seen, often in conjunction with urination and with whole-body shakes.

On day 21, at the earliest, a sudden wariness is seen. This mainly involves hiding behind whatever cover is available in the cage and freezing prolongedly or playing "peekaboo" by starting out and dashing back repeatedly usually while fixating the observer. Foot-thumping is also first seen at day 21 in conjunction with the peekaboo behaviour which disappears by about day 30.

3. Feeding

Mouth movements may be seen with the forepaws resting limply near the mouth as early as day 3; chewing movements with the forepaws held at the mouth corners are only evident about day 7. By day 9, biting at a twig while pawing it, and by day 10, similar biting with two-handed holding, were recorded. Only on day 11 was unmistakable eating first recorded. By day 16 animals are dragging food to the nest and eating sitting up, with separate use of the 2 forepaws. On day 17, pups cut leafy twigs from larger branches, and by day 18, climb branches to do so. A pup first perched on a branch to eat at 23 days.

Suckling continues until about day 20 but only in the nest. Pups may try to wriggle under the mother outside the nest, but she always moves away.

Direct coprophagy from the animal's anus ("refection") was first observed on day 22.

4. Grooming

A forepaw was wiped forward along the cheek as early as day 5. Chewing movements with tense forepaw postures gave rise both to eating, and to pawlicking and snout grooming at about the same age. Small circling snout-wipes were seen on day 9 and the sequence of increasing amplitude movements to a full overhead wipe on day 11.

Scratching with the hind foot begins as slow movements which may contact the flank or neck on about day 3 but the rapid rhythmic kicking of mature scratching then appears on day 4 or 6 with little or no body contact before neck, head and shoulder begin to be accurately scratched. The flank, cheek and chin are added by about day 9 and the top of the head and high on the back by day 10.

On day 12, grooming bouts combining scratching and forepaw wiping were seen. Body combing with forepaws and incisors was first seen then and was incorporated into the bouts, as was whisker-pulling. Foot-licking was first seen on day 12 and on day 13 scratching bouts alternating scratches and foot-licking. Combing the outside of the thigh was not seen until day 18, and pups were still not finishing grooming bouts with the usual mature tail-grooming sequence by day 23.

5. Digging and Nest-building

Although long forepaw strokes were common from about day 3, there was no real forepaw digging (that is, moving sand or other material with forepaw strokes while the bulk of body-weight rests on the hindlegs) before day 14 when complete digging with hindkicks, in a mature bout including gnawing behaviour, suddenly appeared. The hindkick with the forepaws firmly planted was seen in isolation once on day 12. Long bouts of mature digging were common after day 20.

Pups first held and chewed bits of nest-paper on day 13. Scraping back a little nest material and tucking it under the chest just before leaving the nest was first recorded on day 16.

6. Social Behaviour

Pups are in constant contact with littermates when very young but none of their behaviour is truly "social". The first signs of any mutual responsiveness occur only after the young have begun to move about outside the nest. At day 13, 2 pups encountering each other sniff briefly nose-to-nose and move on. By day 16, "greeting" is more elaborate: one or both may tilt his head and the two "kiss" briefly; one or both forepaws may be lifted and the sib pawed at, and the animals may shut their eyes as they push their noses toward one another.

By day 18 "playfights" appear, brief bouts of fighting behaviour that are terminated abruptly with neither a victor nor aftereffects like freezing or cowering. The mature upright fighting posture was first seen on day 23. Social grooming was observed in pups of the same age and it often provoked playfighting. Rearing up against a sib's back occurs occasionally and might be from behind. Something more like real sexual mounting in orientation and in grasping the flanks was observed in one litter at 25 days of age, but the sexes of the animals were not determinable. Nothing like ♀ receptive behaviour was ever seen in pups.

7. Other Action Patterns

Yawning was first observed on day 8. It may have been in the repertoire sooner, for it was very rarely observed, and not at all in 2 litters. Stretching occurred with yawning as early as day 18.

Dragging out the hind legs and thus rubbing the ventrum on the nest edge while leaving the nest was once seen in a 16-day-old pup. A full stretch with ventral rub on the sand was seen on day 19. More elaborate sequences of stretching were not observed in pups, nor was lateral sand-bathing, nor ventral marking of objects, nor chin-marking.

8. Comparative Discussion of Development

This early development of behaviour can be described as a process of differentiating patterns and occasional integration of movements into complex APs like mature digging or grooming bouts.

The chronology is remarkably similar to that observed in hamsters (DALY 1974), rodents of a different subfamily (Cricetinae) but the same family (Cricetidae) as the gerbils (Gerbillinae). The several stages of the different kinds of grooming and their later integration into bouts are identical, for example. The APs that differ in mature sandrats and hamsters tend to be relatively late developing ones (after 2 wk), such as scent-marking, fighting postures and ♀ receptive behaviour. That evolution operates by accumulating small changes acting late in development (WADDINGTON 1966) is an embryological principle that often applies to postnatal behavioural development as well.

Table 2 presents the postnatal ages at which various developmental landmarks have been observed in Gerbillinae. The exact figures may not be strictly comparable due to variations in maintenance and observation conditions; such simple handling manipulations as those involved in weighing pups can significantly accelerate rodent development (see review by DALY 1973). However postnatal development of *P. obesus* appears generally accelerated even though the *P. obesus* pups were not handled before 20 days of age. Differences in tooth eruption and feeding seem particularly large and striking. An acceleration of

Table 2: Age (days) of developmental landmarks in Gerbillinae

	Incisor Eruption	Ear Erection	Eye Opening	Feeding	Nest Departures
<i>Psammomys obesus</i>	3- 5	3- 5	13- 15	11	11- 12
<i>Meriones shawi</i> (PETER 1961)		5- 6	16- 20		
<i>M. tristrami</i> (PETER 1961)	11- 12	5- 6	13- 18		
<i>M. vinogradovi</i> (PETER 1961)	12	6- 7	19- 20		
<i>M. libycus</i> (PETER 1961)	7- 9	4- 6	12- 17		
<i>M. persicus</i> (EIBL-EIBESFELDT 1951 ; PETER 1961)	13	4	19	13- 15	13
<i>M. unguiculatus</i> (McMANUS 1971 ; KAPLAN and HYLAND 1972)	12- 15	5- 6	17- 20	17- 18	14- 19
<i>M. hurrianae</i> (PRAKASH 1964)	2nd wk	4- 5	15- 16	by 18	
<i>Tatera indica</i> (BLAND 1969 ; PRAKASH, JAIN and PUROHIT 1971)	2nd - 3rd wk	1st wk	14- 21, 20		
<i>Pachyuromys duprasi</i> (PETER 1961)	11- 15	5- 8	20- 21		
<i>Gerbillus pyramidum</i> (PETER 1961 ; HAPPOLD 1968)	15- 18	5- 7	18- 20	22	
<i>G. campestris</i> (PETER 1961)	13- 16		13- 16		
<i>G. nanus</i> (KIRSCHOFER 1958 ; PRAKASH and JAIN 1971)	10- 11	10- 11	13- 14, 20- 22		13- 14

the ability to exploit solid foods may be related to time-budgeting constraints imposed upon lactating ♀♀ by the low-energy diet (DALY and DALY 1973).

B. Mother-Pup Interactions

Pups began feeding on solid food at 11 days of age in the laboratory but suckling continued until at least 3 wk. In the field, litters from 3 to 5 wk of age emerged from their burrow to sit in the sun and eat in the entrance holes. However, they seldom or never collected their own food at this age. The mother, still living with the pups, hoarded large quantities of food to the burrow entrances. At this stage, the mother may be cutting and collecting 3 to 4 times as much food as her own requirements (DALY and DALY 1973).

This often involved exploiting nearby bushes and shortly before the delivery of her next litter the mother sometimes moved into a burrow under one of these, or alternatively moved her older litter to the new burrow and dropped the new litter in her old burrow. At least once, a second litter was dropped and nursed in the same burrow with the first litter and was moved some days later. When successive litters were intact in nearby bushes, the mother occasionally visited her older pups and sometimes cut and hoarded food to their burrows as well as her own. By the time a new litter was delivered the 5-wk-old pups had begun to eat in the bush above their burrow and to cut and hoard food.

The demands of subsequent litters probably play an important part in the decline of mother-pup contact. One ♀ with no subsequent litter lived with the sole surviving daughter of her last litter until the latter was 87 days old. They stopped living in the same burrow at about 2 mo but were occasionally seen to groom one another and to bask side by side on subsequent days. When the pup was 77 days old, the mother conceived and then emigrated 10 days later. (The emigration covered 170 m, by far the longest move recorded for an adult ♀.) The daughter conceived and emigrated 3 wk later.

A litter might be moved by the mother at almost any age after about a wk. The only directly observed case involved a litter 35 days old. The 5 pups were transported one by one in the mouth across 21 m of bare sand in a hesitant and jerky run that took about 30 sec per pup. At that age, the pups each weighed about 30 gm, $\frac{1}{3}$ of the mother's weight. She made several abortive starts evidently trying to coax one pup to follow her, but he kept turning back when a m from the burrow, and she eventually carried him. Food supplies did not seem to necessitate the move, but the mother's next litter was due soon. In other cases, dwindling food obviously did provoke a move. The greatest obstacle surmounted was a dune about 4 m high over which a mother moved a 22-day-old litter of 3; all food was exhausted at the old burrow site except for a nonpreferred species that may be toxic (DALY and DALY 1973).

From the earliest age, pups went limp when picked up by the mother in the laboratory. From 19 days of age some resistance to retrieval was seen: turning on the side, cringing and attempting to deflect the mother with the forepaws. However once a grip was achieved, the pups immediately stopped moving. After 3 wk of age, the limp response began to decline a little in caged pups. The very large 5-wk-old pups we saw carried in the field still remained completely motionless in their mother's mouth.

In *P. obesus* the limp response is stronger and longer-lasting and the mother's grip and orientation are more stereotyped than in laboratory rats or

hamsters (personal observations). Because moving litters through open terrain is common, there must be considerable selection against dropping the young.

C. Growth and Age Estimation

Our main interest in collecting growth data was to estimate ages of young animals in the field. The only measure of growth considered here is tail length. This particular measure increases both most steeply and most prolongedly of external body dimensions among gerbils (see Figs. in PETTER 1961). It should therefore be most useful in estimating age. Furthermore, it was conveniently measured with good accuracy from unanaesthetized animals in the field.

There were large differences in growth rate even among laboratory litters raised in constant conditions (Fig. 4a). Litter size has often been found to influence growth in laboratory rodents and the exactly corresponding ranking of these 4 litters on number and growth is an instance of the usual effect (exact $p = 1/24$, directional hypothesis). The slow growing individuals in the 2 largest litters were weak in the hind legs and feet, possibly from a vitamin D deficit. Recapture data on field-caught animals also showed variable growth rates apparently similar to those of laboratory-raised sandrats (Fig. 4b). A single capture of a ♂ whose age could be placed at 40 days (by having observed the postpartum oestrus behaviour of his mother), yielded a measure exactly equal to the fastest growing laboratory litter; both litters numbered only 2 pups.

After extrapolating back along the growth curve to an approximate birth date, it was possible to check records from trapping and observing the mother. Nipples swelled late in pregnancy, and a bulging abdomen and blood in the vagina were signs of imminent delivery. Very recently parturient ♀♀ also had noticeably hollow flanks. ♀♀ tended to be infrequently seen and to leave few tracks for about 3 days around parturition, and observation of laboratory ♀♀ suggested that birth took place early in this quiet period. By combining these

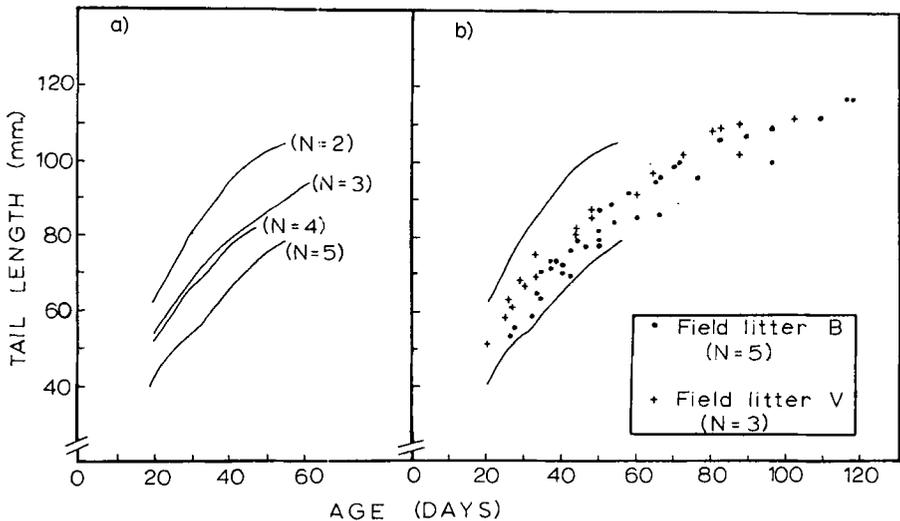


Fig. 4: Growth of tail length. a) Means for captive-born litters. b) Recapture data for 2 typical wild litters. The outer lines are the fastest and slowest-growing captive litters in a)

different sorts of evidence, birth dates were estimated with a maximum error of about 3 days.

According to these estimates, the pups first began to show themselves in burrow entrances at about 20 days of age, but were very wary, repeatedly dashing down and thumping in response to no obvious stimulus, "peekaboo" behaviour which appeared at the same age in cage reared animals.

D. Sexual Maturity

By the above methods, the birth dates of a ♀ and her first litter were estimable for 3 mothers. Assuming a 25-day gestation period, estimates of the age of first conception were 95, 106, and 92 days. Vaginal opening was noted as early as 53 days of age. Estimates of the age of sexual maturity in ♂♂ were not possible, but testicular descent occurred at about 3 mo of age.

IX. Dispersal of Littermates

A social-dwelling pup becomes a relatively solitary adult by a gradual process. First there is a waning of the attractiveness of littermates.

A. Waning Contact Behaviour in Laboratory Litters

Young pups crowd together in the nest and drag their food there to sit in a tight huddle. The attraction is not just to the nest, as the pups will crowd together outside it as well.

In laboratory litters, contact behaviour was scored in trials at 3 times of day: 1) shortly before dawn when lights were turned on, 2) mid-day, and 3) dusk, about 12 to 14 hr after the first trial before extinguishing artificial lights. At each trial, individual pups were observed in turn for 1 min each and the number of sec spent in bodily contact with one or more littermates was recorded.

Results are shown in Fig. 5. Litter differences are large but there was a declining trend within each litter ($p < .05$ in every case, using the Spearman rank correlation coefficient as a trend test: r 's correlating age and contact score = .66, .63, .31 and .40).

Litter differences reflect the growth differences in Fig. 4 a, with the slowest growing litters maintaining the greatest contact behaviour. These litter differences may depend directly on the numbers of pups, at least in part.

The decline in contact behaviour was not accompanied by any increasing antagonism. Playfighting, common in young litters, stopped after about 40 days, and no agonistic behaviour was ever observed between littermates. Pups continued to sleep in the same nest.

B. Waning Contact with Littermates in the Field

A similar change was observed in field litters. At weaning, mothers usually moved to a nearby burrow. The waning tendency of the pups to remain together could then be observed over days.

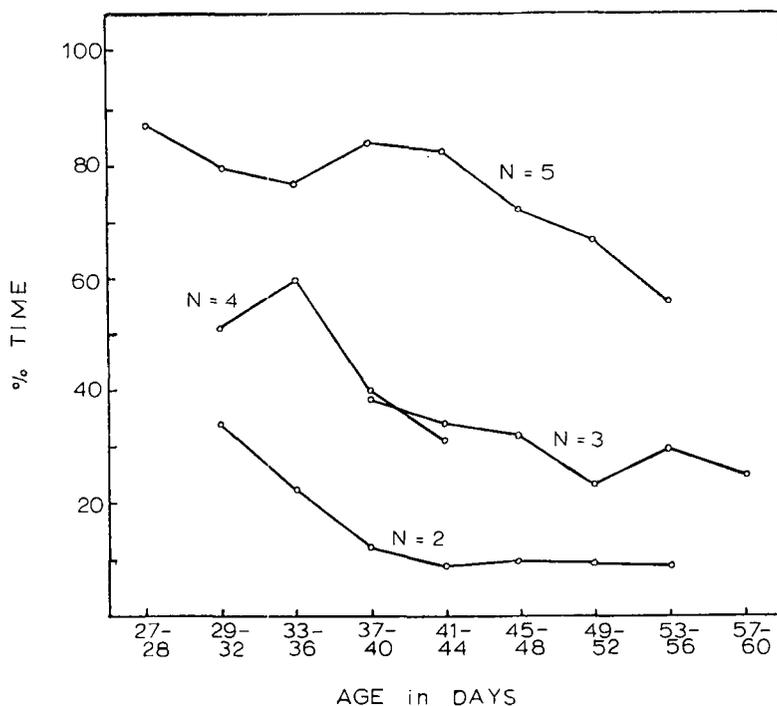


Fig. 5: Contact behaviour in captive litters.

The %age of total time individuals spent in bodily contact with littermates

Litter B (4 ♀♀ and 1 ♂), for example, were left by their mother at 39 days of age and did not leave the natal burrow until day 43. Then they began to visit nearby bushes and on day 50 each was at a different bush, although all were within the mother's former range. On day 58, an amicable contact between 2 ♀♀ was the last observed littermate interaction. By day 63 all 5 had left their mother's former range. 3 of the litter were known to survive to sexual maturity, with their adult ranges widely separated.

This case was in many ways typical of most of the litters observed. At first, pups stayed in a group. Then they began to move around within their mother's range or former range, and individuals became attached to different burrows a few m apart, continuing to visit one another. Longer dispersal might occur at about the time of sexual maturity or shortly before (see below), but a few individuals never moved far. Dispersal and mortality ended all littermate interaction by 2 to 3 mo of age. There was no evidence of aggression in this process, neither between littermates nor between mother and offspring, but the aggression of adult ♂♂ probably played a part in scattering young ♂♂.

C. A "Territorial" Phase

In one litter, a different progression of events from weaning to dispersal was observed. During a 3-day period of intensive observation (7 hr of behaviour recording) an opposite-sexed pair of littermates defended adjacent ranges of 3-4 bushes from each other. When the ♂ was working his food bushes, the ♀ frequently raided his home bush or food stores. Each time he caught her,

5 in all, he chased her back, usually causing her to drop any food she was carrying. Once home however, the ♀ was dominant. When the ♂ once chased her and actually entered her bush, she turned on him and chased him back. On another occasion, he approached her home while she was not there, and she dashed back and chased him out. The young ♂ also once chased away his mother, apparently nipping her, and both territorial animals followed a large ♂ and squeaked at him until he departed at a walk, whether thus "chased away" or not.

This territorial phase ended with a movement of the young ♀'s home burrow so that contact ceased. On a subsequent day, the 2 animals were observed together at a bush a few m from their former burrows. The 2 were mostly ignoring one another but occasional brief nose-to-nose "greetings" occurred. Eventually the 2 emigrated to establish adult ranges over 400 m apart. Before that time, the young ♂'s range and that of his mother drifted to overlap a bit, and no antagonism was evident.

The "territorial" phase was a brief one. It is of interest as our only observation of locus-dependent dominance, which has been proposed as a criterion for "territoriality" (e.g. WILLIS 1967).

D. Dispersal

Eventually pups, moving away from their home burrows and their littermates, established adult ranges, which usually did not overlap areas they knew as social-dwelling pups. This dispersal process clearly resulted in a scattering of siblings. Fig. 6 illustrates how sandrats, born to known mothers during the study period, and sexually mature by the end of it (Apr. 30), had become dispersed.

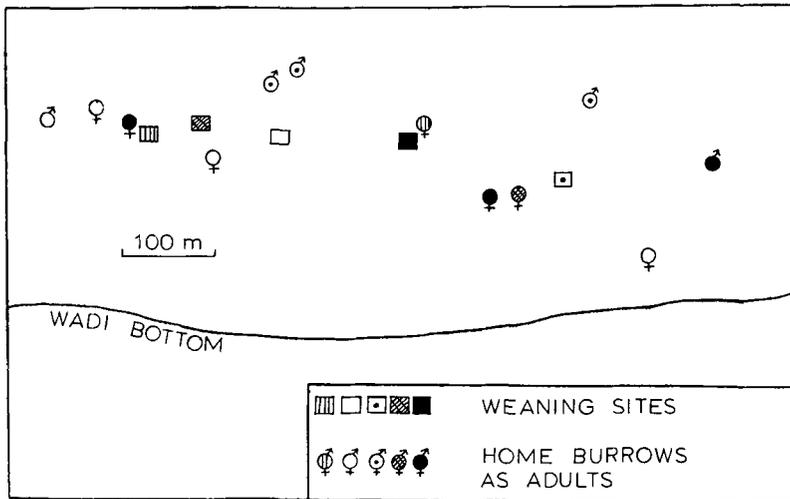


Fig. 6: The dispersal pattern by Apr. 30 of young adults weaned during the study period

1. A ♂ Example

In Fig. 7, the dispersal of a litter of 3 ♂♂ is portrayed. When the pups were about 50 days old, the mother moved to a new burrow 40 m away. One pup emigrated (V3), one

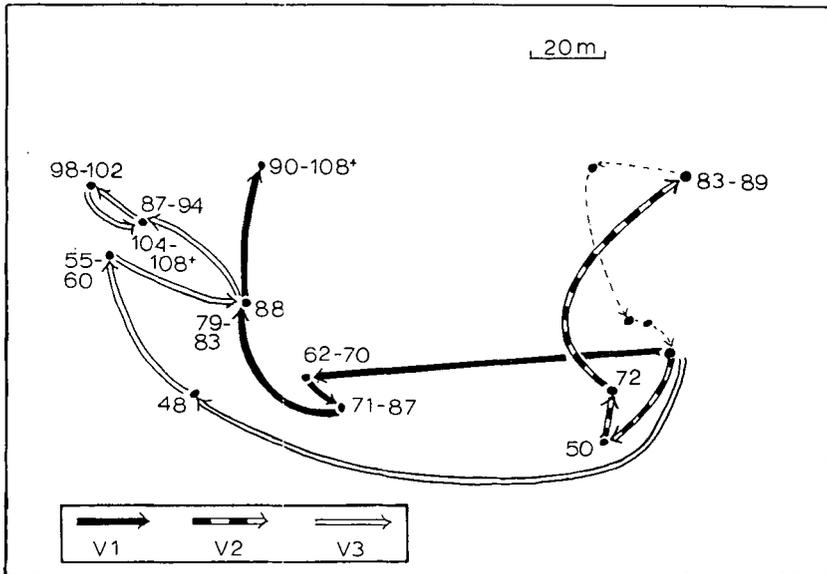


Fig. 7: Successive moves of a dispersing litter of 3 ♂♂. Arrows connect successive burrows where the animals were detected. Numbers represent the ages at which each burrow was occupied

moved to a new burrow within 20 m of his mother (V2) and the third (V1) emigrated soon after.

V2 moved shorter distances than his brothers. Perhaps by chance, his recorded movements were all within the range formerly known to his mother. When his final recorded move carried him over a large dune, this was a return to the burrow in which he had been born; there he reached sexual maturity. In this respect, V2's history was unique in our study, but one other young ♂'s successive moves doubled back to a point very near the natal burrow.

Apparently by chance, V1 and V3 emigrated in similar directions and at the end of the study, the 2 110-day-old, sexually mature, subordinate ♂♂ dwelt just 70 m apart.

2. A ♀ Example

2 of 4 ♀♀ in litter B (see section VIII. E. 2.) survived to sexual maturity. B1 made a number of moves between the cages of 50 and 80 days before settling in a burrow 62 m from her birth site; there she stayed for more than a month. She was ultimately evicted by an older adult ♀. B5 moved from the edge of her mother's former range more than 300 m between 70 and 80 days of age. Soon after, she moved a further 45 m and then stayed for more than 4 wk. The vaginas of both ♀♀ first opened while they were still within their mother's old range and while still encountering littermates, but both first conceived only when settled in a single burrow.

3. Can Juvenile Dispersal be Differentiated from Adult Ranging?

That some members of wild populations of rodents disperse or emigrate, usually at about puberty, has been noted in studies of many species. Rigorous differentiation of dispersal movements from lesser HR shifts, from HR drift, from normal activity within the HR, and from occasional "sorties" outside the HR is a formidable endeavour. To some extent, it may be a futile one, imposing an artificial categorization on the actual phenomena.

Dispersal would be a clear phenomenon if a discrete emigration were followed by adult sedentariness. This is clearly not the case in *P. obesus*. In ♂♂, there seems to be no real turning point between dispersal behaviour and adult

ranging. Moves remain frequent among subordinate ♂♂ and are often not retraced. If "dispersal" implies movement into areas new to the animal, any move back to a burrow formerly occupied by the same animal could be called the end of dispersal. However, there is no evidence that different causal processes are involved in these moves, and such categorization seems unwarranted.

In adult ♀♀, long moves are rare, and prolonged residencies and short moves are usual. But moving into new areas continues. ♀ M2 (see section V. A. Fig. 2), for example, moved to a new bush in moving from A to F. Her later moves were each into bushes she had already visited for food from her previous burrow. New areas were constantly being added to her range. "Dispersing" juveniles often made very short moves, and adult ♀♀ occasionally made relatively long ones.

A second approach to defining dispersal is to seek directional perseverance. In the present study, with a narrow and elongated area of suitable habitat, moves between burrows were categorized as up-wadi or down-wadi. Counting as occupancy any instance of the animal's being seen on 2 successive days in the same bush, 2 successive occupancies define a move, and 2 successive moves can be in the same direction or in the opposite direction. We might expect that a dispersing animal is more likely to persevere in the same direction.

Table 3 tabulates such data; no differences are evident between age-sex classes. In both sexes, juveniles were slightly more likely than adults to continue in a uniform direction, but differences do not approach significance.

Table 3: Directional perseverance in successive moves

	♂♂		♀♀	
	Juvenile	Adult	Juvenile	Adult
Same Direction	7 (44 %)	12 (38 %)	6 (35 %)	8 (32 %)
Opposite Direction	9	20	11	17

Though neither exploitation of new areas nor directional perseverance differentiates juvenile dispersal from adult ranging, the question remains whether young are more likely to move long distances. A "Juvenile RL" (RL, see section V.) was measured for all those animals who were first captured when living with littermates in the maternal burrow and were last captured after sexual maturity. Table 4 shows that only in ♀♀ were the distances traversed by juveniles significantly greater than the areas ranged by adults. (A few long moves to areas outside the study area probably went unmeasured. We assume mortality accounted for most disappearances before adulthood.)

In ♀♀, dispersal may be terminated by the effects of reproductive maturity. In B1 and B5, described above, conception occurred early in the first prolonged adult residency, and this was the usual sequence of events. Pregnancy may have inhibited movements. Later, the direct attraction of pups may limit ♀ ranges.

Table 4: Comparison of Adult RL and Juvenile RL

	♂♂	♀♀	
Adult RL	189.6 m (N = 7)	75.8 m (N = 11)	U = 6 , p < .001
Juvenile RL	232.7 m (N = 6)	208.3 m (N = 7)	U = 19.5 , p = ns
	U = 15 , p = ns	U = 8.5 , p < .01	

In both sexes, longer moves by younger adults may result from the aggressive responses of older animals encountered along the way.

In *P. obesus*, there is no basis for defining dispersal as a particular behaviour or state of the animal, but a dispersed distribution does result from the movements of young animals, as illustrated in Fig. 6.

Summary

Psammomys obesus, the sandrat, an herbivorous, desert-dwelling, gerbil-line rodent, was studied in the Algerian Sahara. A 5-mo field study based on retrapping data and direct observation of marked animals was combined with observation of captive animals.

Adult sandrats are solitary animals which live in burrows directly under their food plants. Adult ♂♂ visit the burrows of ♀♀, but direct interactions are infrequently observed. Several behaviour patterns leave olfactory traces. Also of presumed communicative function is foot-thumping, but conspecifics proved surprisingly unresponsive to it.

Reproductive ♀♀ range a small domain corresponding to the bushes being exploited for food. This range "drifts" as old bushes are abandoned and new ones added. ♂♂ range more widely. Their use of the home range falls into one of two categories. Subordinate ♂♂ occupy a small domain like ♀♀, but tend to move more frequently and to shift the range over longer distances. Dominant ♂♂ actively range an area encompassing several ♀♀ and subordinate ♂♂.

The home range measure used was Range Length (RL). Mean total RLs for the study period were: ♂ 189.6 m; ♀ 75.8 m. Mean Weekly RLs were: ♂ 67.7 m; ♀ 11.7 m. These sex differences reflect the different patterns of home range use, but the RLs do not discriminate the 2 different ♂ patterns.

Most of the intraspecific encounters in the field involved one of the small number of dominant ♂♂. No interactions between adult ♀♀ were directly observed.

Sexual behaviour is described. The gestation period is 25 days. It is extended to about 36 days after postpartum matings, according to indirect evidence.

The early development of behaviour is described in detail. It follows the typical Cricetid pattern. Tooth eruption and the exploitation of solid food are accelerated relative to other gerbils; this is probably related to the sandrat's unusual dietary specialization.

Growth data are presented for captive and wild litters. These data were combined with observations on the mothers to estimate birth dates, and thus ages, of animals in the field. 3 ♀♀ born during the study period conceived their first litters at 3 to 3½ mo of age.

The process of littermate dispersal is a gradual one. Contact behaviour of captive-born litters wanes over time and chronologies of field litters reveal a similar decline in social contacts. The process does not usually involve overt antagonism, but one brother and sister underwent a phase of "territoriality" in the sense of locus-dependent dominance.

The dispersal of young is not achieved by any unique type of behaviour. Attempts to discriminate juvenile dispersal from adult movements by the magnitude of moves, by the penetration of areas new to the animal, and by directional perseverance, all failed. Nevertheless, at least in ♀♀, juvenile RLs

surpassed those of adults. The eventual scattering of the adult ranges of siblings was demonstrated.

Zusammenfassung

Psammomys obesus, eine pflanzenfressende Wüstenmaus, wurde in der Algerischen Sahara beobachtet. Ein fünfmonatiges Freilandstudium mit markierten Tieren wurde durch Gefangenschaftsbeobachtungen ergänzt.

Erwachsene Sandratten leben einzeln in Bauen direkt unter den Futterpflanzen. Erwachsene ♂♂ besuchen die Baue der ♀♀, aber selten kann man Sozialverhalten beobachten. Mehrere Verhaltensweisen hinterlassen Duftmarken. Auch das Fußstampfen hat vermutlich eine Sozialfunktion.

Geschlechtsreife ♀♀ bewohnen kleine Gebiete um die Futterbüsche. Diese Gebiete wandern mit der Auswahl neuer Büsche. ♂♂ bewegen sich weiter umher. Unterlegene ♂♂ bewohnen kleine Gebiete wie ♀♀, aber sie ziehen öfter und weiter um. Dominante ♂♂ durchstreifen ein größeres Gebiet, in dem es mehrere ♀♀ und unterlegene ♂♂ gibt. ♂♂ haben größere Streifgebiete als ♀♀.

An den meisten Begegnungen zwischen Artgenossen im Freiland war auch eines der wenigen dominanten ♂♂ beteiligt. Es wurden keine Begegnungen zwischen erwachsenen ♀♀ gesehen.

Das Paarungsverhalten ist beschrieben. Die Tragzeit dauert 25 Tage. Die Verhaltensentwicklung ist beschrieben. Sie ist typisch für Cricetidae. Der Durchbruch der Nagezähne und die Aufnahme fester Nahrung liegen früher als bei anderen Gerbillinae; das hängt wahrscheinlich mit der Nahrungsspezialisierung zusammen.

Das Wachstum wurde an gefangenen und freilebenden Würfen verfolgt. 3 ♀♀ wurden mit 3 und 3½ Monaten zum erstenmal trächtig. Die Geschwister zerstreuen sich allmählich. Meistens gibt es keinen offenen Streit, aber die Geschwister besetzten zeitweise getrennte Reviere.

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Authors' address: M. and S. DALY, Department of Psychology, University of California, Riverside, Calif., 92502, USA.