

ON THE FEEDING ECOLOGY OF *PSAMMOMYS OBESUS*  
(RODENTIA, GERBILLIDAE) IN THE WADI SAOURA,  
ALGERIA

by

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*Psammomys* mange électivement les tiges et les feuilles salées et succulentes de plusieurs espèces de plantes de la famille des Chénopodiacées. Des données sur les préférences et les besoins alimentaires de l'animal sont présentées et notamment sur les quantités qu'il peut ingérer lorsqu'il mange exclusivement soit *Suaeda mollis*, soit *Traganum nudatum*, soit *Salsola foetida*.

Au laboratoire comme dans la nature les *Psammomys* préfèrent les plantes qu'ils peuvent exploiter avec le plus d'efficacité. L'ordre de préférence constaté au laboratoire ne dépend pas de l'espèce végétale à laquelle était inféodé l'animal au moment de sa capture ; cependant celle-ci détermine l'adresse avec laquelle le *Psammomys* peut manger, adresse que l'on mesure par le taux relatif d'ingestion.

Les auteurs font état de leurs observations sur le terrain, de l'étude des effets de la privation de nourriture à court terme, du développement du comportement alimentaire, du rôle des concurrents, et de comparaisons avec l'écologie et le comportement d'autres rongeurs.

The gerbils comprise the majority of rodent species in the old-world deserts. Most of the group subsist on a high-energy dry diet and practice a stringent water economy (Petter 1961 ; Schmidt-Nielsen, 1964). *Psammomys obesus*, the « sand rat », is a Saharan species which exhibits a different feeding specialization, eating the leaves and stems of succulent, salty plants of the family Chenopodiaceae found in Saharan wadis and in the alluvial plains of North Africa. Although the plant species differ, the very reliable association of *Psammomys* with succulent Chenopods has been described by various authors in Algeria, Tunisia, Libya, Egypt, and Israel and seems to be without exception.

*P. obesus* develops diabetes when maintained on the sort of high energy diets fed to most domestic rodents (Schmidt-Nielsen, Haines & Hackel, 1964) and, under certain conditions, on all-vegetable diets (Brohoff, Penhos, & Levine, 1967). For this reason, it has

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become an important laboratory species. It has been suggested that the diabetic response may be due to a metabolic adaptation to low-energy diets and periodic famine (Hackel, Mikat, Lebovitz & Schmidt-Nielsen, 1967). However, data on the natural diet are few (Petter, 1961 ; Frenkel, Shaham & Kraicer, 1972).

While conducting a field study of *Psammomys* behaviour in the Wadi Saoura in the North-West Sahara (Daly & Daly, 1974), we collected many observations on their feeding, and performed a series of experiments on captive animals concerning preferences, needs, feeding rates, hunger, and the development of feeding behaviour.

### FIELD OBSERVATIONS

The Wadi Saoura is a dry river valley varying in breadth from about 300 m to over a km, and separating the Grand Erg Occidental, a dune desert, from the Hamada du Guir, a flat pebbly desert. The habitats in and around the Saoura and the rodents that occupy them, have been described in some detail by Petter (1961).

The Saoura is typically flooded for a few days annually, but the combination of new dams in Morocco and Algeria, and a prolonged period of relative dryness have resulted in the wadi's failing to flow between 1967 and the time of the study (Dec. 1, 1972 to Apr. 30, 1973). The vegetation is thus contracted around the permanent sources of water provided by oases and the *Psammomys* population is sparser and in more isolated pockets than was the case when Petter worked in the same region.

*P. obesus* digs multi-entranced burrows directly under the plants which serve as its food. Where a large bush exists, a resident animal may never leave it for days or weeks on end. In the areas studied, it was more usual for an animal to simultaneously exploit several bushes, often of a single species, running between them on well-worn paths.

*Psammomys* has a conspicuous effect on the bushes being exploited for food, stripping them of fresh growth over a period of a week to a month or more, and then moving to a different burrow, usually before the food supply is completely exhausted. A detailed account of the moves of a marked population around the little oasis of Ouarourout is presented elsewhere (Daly & Daly, 1974). During the winter the depleted plants were again covered with fresh growth within one to two months and the same sand rat or another might move in again.

The animals cut the terminal twigs of their food plants with the incisors, while holding the branch in the forepaws. Successive cuttings are often held in the back of the mouth, sticking out one side, as the animal continues to cut with the incisors. The rodents climb easily in the tangles of *Chenopod* branches (mostly to heights of less than 1 m) to perform this work. During long bouts of food-gathering, about 2 to 4 cuttings will be accumulated during a single climb. After each climb, the animal descends to the ground and places his cuttings in a little pile. After about 3 to 6 such climbs, the whole pile is bundled up in the mouth for a quick dash to deposit it in the home burrow.

As an example of food-gathering, a young male was observed on Dec. 9, 1972. He was working two bushes at distances of 2 and 4 m from his home burrow, climbing, cutting and piling, then bundling and hoarding. In 12 minute's steady work, he hoarded 5 loads from the farther and 4 loads from the nearer bush. These loads were estimated at about 3 g each.

Most food gathering is done in the early morning and at dusk, but such activity may be seen throughout the day, especially in the coldest months (Hussein, Boulos & Essa, 1969 ; Daly & Daly, 1974).

Three plant species sheltered almost all the *Psammomys* burrows observed, and made up a great majority of the diet. These were *Suaeda mollis*, *Traganum nudatum* and *Salsola foetida* (see Fig. 1). *S. mollis* grows in bushes of up to about 1.5 m in height and 4 m in diameter. It occurs mainly on the flat clayey soils near the wadi bottom and in the sands adjacent to such clay where the sand is well-watered, as at the oasis of Ouarourout. Here, along with *Zygophyllum album*, *Tamarix speciosa* and *Phoenix dactylifera* (the date palm) it comprises the dominant species. It is also found in the dampest, saltiest soils of the wadi bottom although individual plants are small there. It is rare in the higher tributary wadis along the edge of the Saoura.

*T. nudatum* is the dominant plant in the lesser wadis entering the Saoura where it is associated with *Pergularia tomentosa*, *Euphorbia guyoniana*, *Retama raetam*, *Gymnocarpos decander*, and *Aristida pungens*. It is also abundant where *S. mollis* is the dominant chenopod but is absent from the very bottom of the wadi.

*S. foetida* is most common in flat clayey areas just above the lowest parts of the wadi, and is dominant in slightly drier soils than are favoured by *S. mollis* and *T. nudatum*. It also occurs on the hamada, where *T. nudatum* and *S. mollis* were never found.

A few *Psammomys* burrows were also observed under two other *Chenopods*, *Atriplex halimus* and *Salicornia fruticosa*.

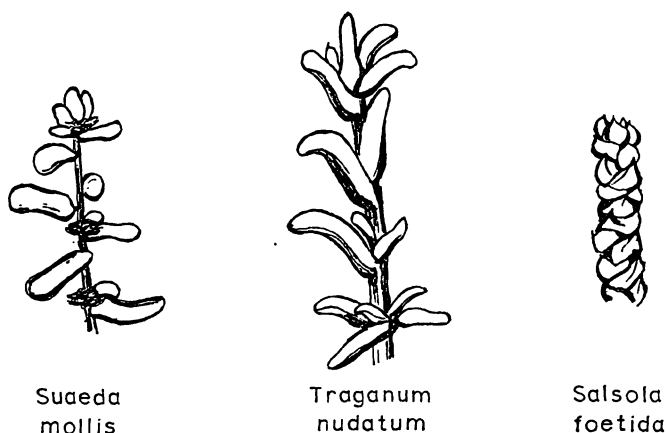


Fig. 1. — The 3 principal food plants of *Psammomys obesus* in the Wadi Saoura. Illustrated are the leaves and terminal stems of *S. mollis*, *T. nudatum* and *S. foetida* (Chenopodiaceae). About 1.5 × natural size.

Exploitation of other plant families is much less important. At Ouarourout many animals occasionally harvested small quantities of leaves of *Zygophyllum album* (Zygophyllaceae). In only one case did this evidently become a major part of the diet. In this case, a lactating female and her litter of three, isolated behind a large dune, virtually exhausted the available *S. mollis* and remained in the same burrow system exploiting nearby *Z. album* for a week before the mother moved her litter to a different area where *S. mollis* was abundant. Ozenda (1958) lists *Z. album* as a 'poisonous' species, presumably on the basis of some effects on domestic animals. However, *S. mollis* is also listed as poisonous, probably because of its high oxalic acid content, a substance which is not toxic for *P. obesus* (Schmidt-Nielsen, 1964). Burrows under *Z. album* were very rarely used, and never except in conjunction with nearby burrows under Chenopods.

The only other food whose use was directly observed was the date; several instances of a sand rat taking home a fallen date were recorded at Ouarourout, but, whereas the sympatric *Meriones libycus* often burrows under date palms, *P. obesus* was only observed to do so when Chenopod shoots were present at the palm base. *Tamarix* trees and scrub were also occasionally burrowed under by sand rats, again only where Chenopod growth was very near the entrances.

Petter (1961) has recorded twigs of *Retama raetam*, *Chrysanthemum macrocarpum*, *Panicum turgidum* and cultivated barley in

burrows. Some caution is necessary in interpreting such finds ; we often observed *Meriones libycus* and *P. obesus* to inhabit the same burrows in direct succession (though never simultaneously), and *Gerbillus nanus* could also be responsible for accumulated plant debris.

*S. foetida* and *T. nudatum* (and, more rarely, *S. mollis*) can occur in virtually pure stands, and this sort of distribution in conjunction with observations of tracks and direct observation of the animals made it clear that many *Psammomys* live for long periods on a monospecific diet. Accordingly, it seemed interesting to investigate, by controlled laboratory testing, the relationship between preference and home species.

## EXPERIMENTATION

### *Laboratory maintenance.*

Wild-caught animals and captive-born litters were maintained in the laboratory in glass-and-metal terraria 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.

Chenopod plants were provided fresh daily, and were the only food, except in a few experimental tests, described below. *T. nudatum*, *S. foetida*, and *S. mollis*, the three main species of interest in the following experiments, were provided daily to all animals except where experiments involved restricting the diet. Other occasional foods were *Salsola longifolia*, *Salicornia fruticosa*, and *Atriplex halimus*. Twelve to 15 hr light a day were provided by natural and artificial lighting. All the experiments described were conducted in the late afternoon and evening.

## PREFERENCE EXPERIMENT

### *Method.*

Three adult *Psammomys* of each sex were live-trapped at their home burrows under each of *Suaeda mollis* and *Salsola foetida*. (Burrows under *T. nudatum* were too rare in the area then known to permit testing these). The 12 animals were then tested in 6 pairwise choice tests conducted on six different days, presenting each possible pair of the 3 plant species twice. In each test, an individual was placed in a fresh terrarium with two glass food

dishes and presented with 15 cuttings of each of the 2 species compared, a pair at a time, for 15 trials. The 15 cuttings of each species were of approximately equal size and weighed a total of 5 g. The time spent eating each food and the total quantity eaten were recorded. Each trial ended after 1 min, except that the animal was permitted to finish eating any cutting he was in the midst of. The intertrial interval was only as long as necessary to remove uneaten food bits and present new ones. The 15 trials of a single test required about 22 to 25 min to run. Animals were maintained on *ad lib* food up to the test, but were tested on fresh food while that in their cages was almost a day old ; this was enough to ensure that feeding always occurred.

### Results.

Briefly, although all animals ate some of all 3 species, *S. mollis* was preferred over *S. foetida* by all 12 animals regardless of which was their home plant. *T. nudatum* was intermediate. Home plant species and sex were without significant influence. Table 1 summarizes choice data.

Rates of ingestion of the different food species were computed from the weight and time measures, and are presented in Table 2. These rates stayed remarkably stable within animals, and the relative rates on different plant species are very similar from one animal to the next. Rates are not significantly related to capture species. However, a ratio measure of *S. mollis* rate / *S. foetida* rate indicates relatively greater speed on the home plant ( $U = 7$ , one-tailed  $p < .05$ ). This difference depends mainly on the females, who show no overlap (exact one-tailed  $p = .05$ ).

### A field survey of preference.

In discussing *P. obesus*' choice of burrow sites, Petter (1961) recorded that *T. nudatum* was « certainement la plante qui lui convient le mieux dans la région de Beni-Abbès. » Since *S. mollis* was clearly preferred in the laboratory, field data on the relative utilization of these two species were collected. On a clay plateau near the oasis of Igli, about 40 km from Beni-Abbes, the vegetation consisted entirely of *S. mollis*, *T. nudatum*, and a few small *Tamarix* trees. Within an area of about 1.5 ha, all bushes of greater than 1 m in diameter were surveyed for recent *Psammomys* use. (Burrows and tracks are very conspicuous except when blown over.) Table 3 shows the results of the survey. These data also affirm a preference for *S. mollis* over *T. nudatum*.

TABLE 1

Mean preference in pairwise choice tests, with preference expressed as percent of total eaten that was the preferred (first-named at left) plant.  
3 subjects per group.

	Captured under <i>S. foetida</i>		Captured under <i>S. mollis</i>	
	Males	Females	Males	Females
<i>S. mollis</i> over <i>S. foetida</i>	71	73	83	67
<i>S. mollis</i> over <i>T. nudatum</i>	61	64	68	62
<i>T. nudatum</i> over <i>S. foetida</i>	59	59	64	69

TABLE 2

Feeding rates (mg/sec) for each plant species during preference tests.

	Captured under <i>S. foetida</i>							Captured under <i>S. mollis</i>						
	♂ 1	♂ 5	♂ 6	♀ 3	♀ 4	♀ 6	Mean	♂ 2	♂ 3	♂ 4	♀ 2	♀ 7	♀ 8	Mean
<i>S. mollis</i>	10.2	10.9	11.9	11.1	9.3	12.9	11.1	7.2	13.4	11.8	11.5	12.7	16.1	12.1
<i>T. nudatum</i>	5.5	8.2	8.2	8.4	5.9	8.4	7.4	4.0	7.8	6.6	6.9	8.8	8.8	7.2
<i>S. foetida</i>	5.0	5.9	6.6	7.2	5.0	7.6	6.2	3.7	8.3	5.1	5.8	6.1	6.0	5.8

TABLE 3

*Psammomys* use of *Chenopod* bushes on a plateau near Igli.

	Signs of recent use	No signs
<i>Suaeda mollis</i>	18 (75 %)	6 (25 %)
<i>Traganum nudatum</i>	20 (28 %)	51 (72 %)
	$\chi^2_{df} = 16.4 \text{ } p < .001$	

### Discussion.

The preference ranking and the feeding rate ranking are the same : *S. mollis* over *T. nudatum* over *S. foetida*. It could thus be suggested that both quantity and rate are measures of the same motivational factor, such as « palatability ». This seems unlikely, since different quantities eaten do not correlate with rate differences within plant species. For example, in the preference tests, comparisons can be made between the performance of each single animal on each plant species within pairs of identical choice tests. In the 67 such pairs where a different quantity was eaten in the two trials, the faster rate accompanied the greater total eaten 35 times, and the lesser 32 times.

Instead, the rate differences appear to depend on small differences in the structure of the plants (Fig. 1) ; more refined measures of manipulatory behaviour or of time chewing per bite are needed to affirm this.

If rate differences are so caused, then they might reflect differences in plant-species-specific « skill ». The rate ratio measure may reflect this. Any effect of capture plant species would be expected to show up more strongly in females, who are much more sedentary than males (Daly & Daly, 1974), and for whom the capture plant species is thus a better indicator of experience in the wild. All the animals tested had at least a week's laboratory experience of feeding on both species.

Preferences were unrelated to capture plant species. They may instead reflect the efficiency with which *P. obesus* can exploit the different foods, a possibility that is suggested by the stable rate differences. Efficiency here refers to the time expenditure necessary for the animal to feed itself adequately. This raises the question of nutritive needs.

### ONE-DAY INGESTION EXPERIMENT

#### Method.

Three males and 3 females were each given a 24-hr ingestion test on each of the 3 plant species, in different orders. Test days



were alternated with days on which all 3 species were available in *ad lib* quantities.

In each test a weighed quantity of one food species was provided, and the remainder was weighed after 24 hr. A desiccation correction, based on the weight loss of a control quantity of food placed outside the animal's cage, was applied to the uneaten remainder to arrive at an estimate of ingestion expressed in weight of fresh plant.

### Results and Discussion.

Results are presented in Table 4.

Ingestion differences between species did not approach significance. The body weight change was significantly different between *S. foetida* and *S. mollis* ( $t = 3.1$ , 5 df,  $p < .05$ ) and between *S. foetida* and *T. nudatum* ( $t = 7.1$ , 5 df,  $p < .01$ ).

These results permit a loose specification of the total ingestion needed to maintain weight on the 3 species : i.e. more than 90 % of initial body weight on *S. foetida* compared to about 80 % or less on the other 2 species.

TABLE 4

Ingestion and body weight changes, expressed as % initial body weight, during 24-hr tests on monospecific diets.

	<i>Salsola foetida</i>		<i>Suaeda mollis</i>		<i>Traganum nudatum</i>	
	Ingestion	Wt. change	Ingestion	Wt. change	Ingestion	Wt. change
♂ 3	79.5	-7.3	76.4	5.8	84.5	4.2
♂ 5	84.4	-0.8	81.6	-1.1	85.6	2.2
♂ 6	77.3	-4.1	75.6	-2.2	77.1	5.3
♀ 2	95.8	-5.4	97.4	1.6	89.2	2.9
♀ 3	101.8	-8.1	59.4	-1.3	80.9	2.6
♀ 7	85.1	-4.7	96.0	3.5	95.5	4.7
Means	87.3	-5.1	81.1	1.1	85.5	3.7

It would obviously be preferable to maintain individuals for long periods on monospecific diets, but the laborious task of recovering and weighing uneaten food bits was deterring. However, in view of the weight losses incurred in 1-day tests on *S. foetida*, a longer experiment was conducted.

### 8-DAY INGESTION EXPERIMENT

#### Method.

Three males and 2 females were each fed *S. foetida* for 5 consecutive test days, and then switched to *T. nudatum* for 3 days. Daily ingestion was estimated as in the previous experiment.

### Results and Discussion.

Quantities eaten and body weight changes are presented in Fig. 2. The loss of body weight in the *S. foetida* phase, and the regaining of weight on a diet of *T. nudatum*, despite the generally decreased total ingestion, again show that greater quantities of the former are needed for sustenance.

The day 1 weight loss approached significance ( $t = 2.08$ , 4 df,  $p < .06$  on a directional hypothesis based on 1-day test data). For the day 2 loss,  $t = 3.47$ , 4 df,  $p < .05$ , and for the overall loss in the *S. foetida* phase,  $t = 2.80$ , 4 df,  $p < .05$ . The gain on the first *T. nudatum* day was highly significant ( $t = 14.8$ , 4 df,  $p < .001$ ), although ingestion was lowest on this day.

An initial weight loss on *S. foetida*, and its subsequent levelling off as ingestion increased, are similar results to the response of rats to diets made unpalatable by quinine adulteration (Mrosovsky, 1964). But palatability differences do not fully explain differential responses to plant species. Despite clear preferences (*S. mollis* over *T. nudatum* over *S. foetida*), quantities ingested in the 1-day experiment were not significantly different. In the 8-day experiment,

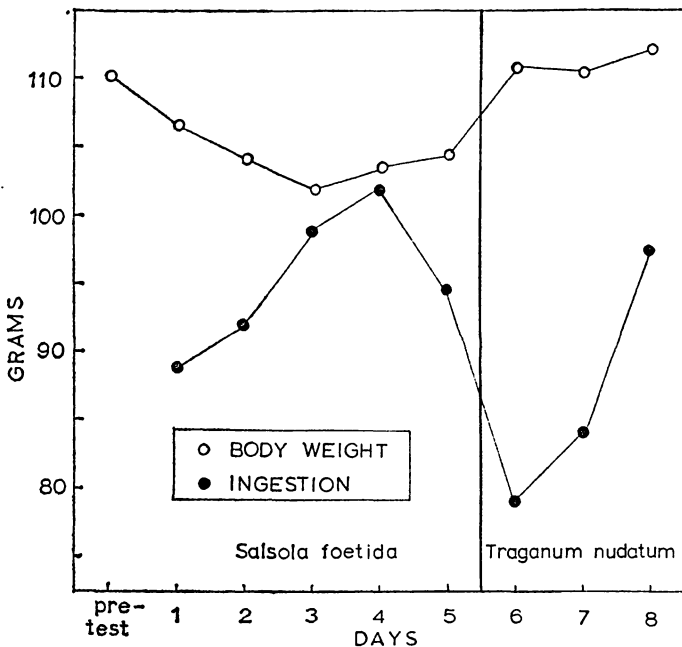


Fig. 2. — 8-day ingestion experiment : mean body weight and daily ingestion on monospecific diets.

when animals were switched to a preferred food, ingestion immediately decreased. Palatability (as reflected in choice test preference) is thus a poor predictor of ingestion behaviour, which evidently responds, even in the short term, to differences in the nutritive value of the foods.

#### TIME-BUDGETING ESTIMATES

A combination of feeding rates from the preference experiment and estimates of needs from the ingestion experiments affords the estimates in Table 5. The estimate of ingestion necessary for body weight maintenance is based on ingestion minus weight change from Table 4.

Although the estimates are rough ones, the species can clearly be ranked according to the efficiency with which the sand rats can exploit them, and this ranking is the same as the preference ranking.

TABLE 5

Parameters of feeding behaviour for a hypothetical average 110-g adult *P. obesus* feeding on monospecific diets.

	Daily ingestion	Feeding rate	Time spent eating daily
<i>Suaeda mollis</i>	88 g	11.6 mg/sec	2.1 hr
<i>Traganum nudatum</i>	90	7.3	3.4
<i>Salsola foetida</i>	102	6.0	4.7

The feeding rates, and thus the total time estimates in Table 5, are based on a narrow definition of feeding time. Pauses in chewing were not included, nor was any time after the last bite of a cutting disappeared into the mouth. Furthermore, the times spent eating are probably underestimates because animals eating in their nests evidently chew at a slower pace than in the preference test situation.

Exactly comparable data on other species are not available. Rats eat in « meals », and computations from data published by Kissileff (1970) give total daily meal-times on *ad lib* dry diets of about 45 min. This includes all pauses of less than 1 min. Wiepkema (1971) has observed that within such meals, mice spend only about 35 % of the time actually feeding. If this is true of rats, the feeding time estimate drops to a quarter of an hour per day. Thus the feeding time of a sand rat on its natural diet is about 10 to 20 times that of a laboratory rat.

*P. obesus* may become spontaneously obese when offered a diet of higher caloric value than the natural one (Haines, Hackel & Schmidt-Nielsen, 1965). This may represent a misfiring of the sand rat's adaptation to poor diets requiring long hours of feeding. This does not necessarily mean that the species lacks the ability for fine regulation of ingestion of its natural foods. Such regulation was investigated in the following experiment.

#### HUNGER EXPERIMENT

##### Method.

Five animals were tested in 9 trials run on 9 consecutive days. In each test trial, the subject was placed in a fresh terrarium. After a deprivation interval of 0, 40 or 120 min, he was offered 8 g of food divided into 24 cuttings. One cutting was presented at a time and the remainder was removed after 1 min or, if the subject was still eating at the trial's end, as soon as he stopped. Two males were run on *S. mollis* and 3 on *T. nudatum*. Each subject was given 3 trials at each deprivation level.

##### Results and Discussion.

Results are presented in Fig. 3. Although data with 40 min

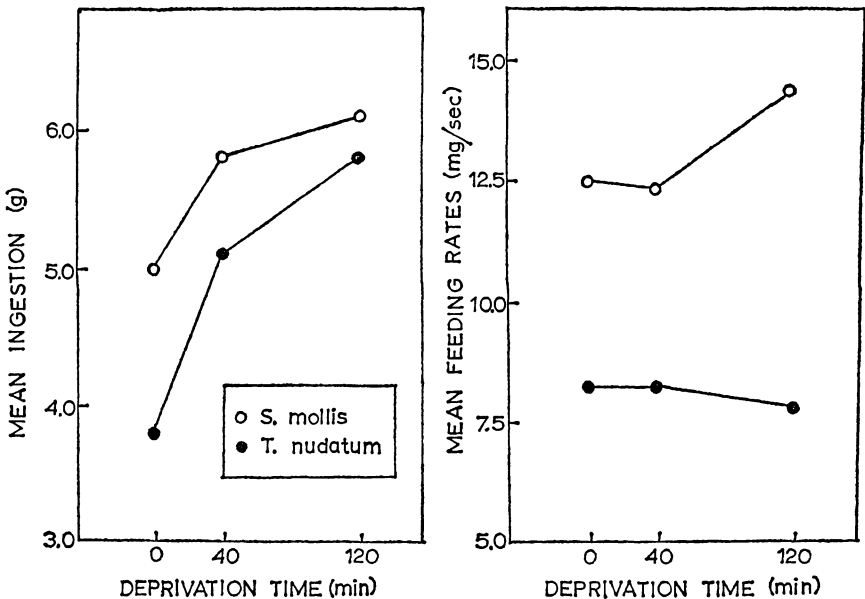


Fig. 3. — Hunger experiment : mean ingestion and feeding rate on *S. mollis* and *T. nudatum* as a function of deprivation time.

deprivation were very variable, 2-hr deprivation increased the amount eaten over no deprivation in all animals. 2-hr deprivation also produced faster eating in the animals tested on *S. mollis* (mixed model analysis of variance with deprivation level as the « fixed » variable :  $F = 35.8$  ;  $df = 2,2$  ;  $p < .05$ ). This was not true of *T. nudatum*, possibly because the hungrier animals usually ate the whole cutting, whereas when undeprived, they often left the stems, which take longer to chew up than the leaves.

Body weight losses ranged from 1.5 to 4.0 % during 40 min deprivation, 3.4 to 7.6 % during 120 min. After feeding, the average body weight change from the pre-deprivation value was a gain of less than 1 % at all 3 deprivation levels. There thus seems to be good regulation of ingestion in response to hunger. However, animals maintained on *ad lib* food occasionally lost or gained as much as 8 % in a day for no obvious reason.

## BIOLOGICAL OBSERVATIONS

### *Development*

The postnatal development of sand rats follows the typical Muroid pattern, but is accelerated compared to other Gerbillidae, especially in tooth eruption and exploitation of solid foods (Daly & Daly, 1974). Plant food begins to be eaten about day 11, but weaning is not complete until about 4 weeks of age. There is considerable variability in growth in both laboratory and wild litters, and food quantity or quality is not obviously responsible.

Three captive-born litters were given 24-hr total ingestion tests on a mixed diet at ages between 5 and 8 weeks. Ingestion dropped from about 140 % body weight at 5 weeks (individual weights : 30-50 g) to 115 % at 8 weeks (50-70 g), compared to about 85 % in adults (85-130 g). Quantities eaten showed the usual preference order : *S. mollis* over *T. nudatum* over *S. foetida*.

Feeding rate differences on the 3 species were clear and roughly proportionate to the adult rate differences from the earliest tests, as shown in Table 6.

TABLE 6

Feeding rates (mg/sec) on different plant species as a function of age.

	4 wks	5 wks	6 wks	7 wks	Adults
<i>Suaeda mollis</i>	4.3	5.5	6.3	6.7	11.6
<i>Traganum nudatum</i>	3.0	3.3	3.9	4.3	7.3
<i>Salsola foetida</i>	2.3	2.4	2.5	3.9	6.0

## OTHER FOODS

Two other Chenopods, *Atriplex halimus* and *Salicornia fruticosa* were used by *P. obesus* in the vicinity of Beni-Abbes, although very rarely and apparently never as the exclusive diet. However, *A. halimus* is the main food of Israeli populations (Frenkel, Shaham & Kraicer, 1972). and sand rats have been observed in monospecific stands of *S. fruticosa* (Petter, 1961).

Two males, experienced with both foods, were given a 1-day monospecific ingestion test on each of these plants. Both lost weight on both diets, a 10.4 % loss on *A. halimus* and a 12 % loss on *S. fruticosa*. Ingestion was only 35.8 % of body weight on *A. halimus*, and 33.1 % on *S. fruticosa*. Frenkel, Shaham & Kraicer (1972) recorded an ingestion of 38.4 % of body weight of *A. halimus* leaves in a larger subspecies of *P. obesus* during a 24-hr test, but whether the animals maintained their weight was not reported. Feeding rate tests on the 2 species gave mean rates of 4.7 mg/sec for *A. halimus* and 6.4 mg/sec for *S. fruticosa*.

*A. halimus* grows on the clayey plateaux near wadi bottoms in association with *S. mollis*, *T. nudatum*, and *S. foetida*, but there was little evidence of its exploitation by sand rats. The slow rate of feeding on it, evidently due to its broader leaves necessitating greater manipulation by the animal, suggests that it fits the preference-efficiency hypothesis, being both the least preferred and the least efficiently exploited of the 4 species. *S. fruticosa*, on the other hand, is evidently little used because it mainly occupies damper, saltier soils in the wadi bottom. Sand rats never burrow in these soils, and *S. fruticosa* is only available to them where it invades higher, drier ground.

*Zygophyllum album* was much used as a supplementary food by the population at Ouarourout. In a single test with this species, terminated after 22 hr, an adult male ate only 31 % of his body weight and lost 11 %. His unsteady gait and other abnormal behaviour were tentatively attributed to a mild poisoning (see Ozenda, 1958). Only 3 faecal boluses were produced, compared to a normal daily total of over 150. Coprophagy, always frequent, must have greatly increased in this test, suggesting a nutritional inadequacy in the diet.

## COMPETITORS AND COMPARISONS

It has been suggested that in his Chenopod diet, *P. obesus* exploits a food resource not available to other animals (Schmidt-

Nielsen, 1964), but there are in fact many competitors. At Ouarourout, *Meriones libycus* was often observed climbing and feeding in *S. mollis* bushes. One resident sand rat repeatedly chased a larger raiding *M. libycus* from her home bush. Although *M. libycus* is mainly granivorous (Petter, 1961), captive animals ate large quantities of Chenopod leaves. A captive *Gerbillus nanus garamantis* likewise readily ate *T. nudatum* when offered, though it thrived on a diet of stale bread; this species is also common in the Wadi Saoura, and Kirchshofer (1958) found its diet to be mainly vegetable matter other than seeds. Other gerbil species in the Saoura (*G. gerbillus*, *G. pyramidum*, and occasionally *Meriones crassus*) may also compete with *P. obesus* to a lesser extent. Jerboas (*Jaculus jaculus*) were seen by their tracks and plant debris to browse on leaves of *S. mollis* and *T. nudatum* at Ouarourout.

Camels were serious competitors for all 3 of *P. obesus*' main foods. *T. nudatum* is their favourite food in the wadis (Gauthier-Pilters, 1965). Domestic goats and asses also occasionally fed on *S. mollis* at Ouarourout.

The sand rat differs from all its competitors in its narrow specialization on a single plant family. The high feeding-time-cost of this low-energy diet is compensated by its ready accessibility. The young male whose foraging was described above could collect a whole day's food supply in well under an hour. Most other gerbils are principally seed-eaters, « hunters » (see McNab, 1963) expending less feeding time but more search time than *P. obesus*.

Mothers with young work much harder. From data above, it can be estimated that a 5-wk-old litter will eat 3 to 4 times as much as the mother herself, yet they do not gather their own. Weanlings emerge from the burrows only to sit in the entrances and eat food the mother piles there. The largest litter size observed in the field was 7, and this mother worked the greatest area of food bushes of any individual, to distances of about 20 m from the home burrow. Since feeding is relatively slow and food-gathering relatively fast, the load on the mother is reduced by an earlier use of solid food by pups in comparison to granivorous species.

The same Chenopod specialization has evolved in 2 other Gerbillidae, *Rhombomys opimus* of Central Asia, and *Meriones hurrianae* of Iran, Pakistan, and India (Petter, 1961). The 3 species are also similar in their relatively dense populations and in their predominantly diurnal activity.

In North American deserts, a similar specialization is seen in a Heteromyid, *Dipodomys microps*, who feeds mainly on the Chenopod *Atriplex confertifolia* (Kenagy, 1972). *D. microps* shaves off

the hypersaline outer leaf tissue, and this behavioural adaptation to the diet was contrasted to *P. obesus*' physiological adaptations. However, sand rats often similarly remove and discard the outer layer of *T. nudatum* stems, and often shave off the outer leaves of *S. foetida*, letting them drop from the corners of their mouths without interrupting eating. How the composition of the discarded parts differs from that of the parts eaten is not yet investigated; Kenagy's findings suggest it should be.

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#### SUMMARY

A study of the feeding ecology and behaviour of *Psammomys obesus*, the sand rat, was conducted in the Algerian Sahara. *P. obesus* specializes in feeding on the succulent salty leaves and stems of plants of the family Chenopodiaceae. Data are presented on preferences, feeding rates, and nutritional needs on the 3 main food species, *Suaeda mollis*, *Traganum nudatum*, and *Salsola foetida*, any one of which may comprise the rodent's entire diet in the wild.

The food species differ in the time-cost to a sand rat exploiting them. Preferences parallel these differences, with the most efficiently exploited food being most preferred in both laboratory and field. The particular plant species occupied by an animal before capture does not predict laboratory preference behaviour, but is reflected in plant-species-specific feeding skill, measured by relative rates of ingestion.

Field observations, effects of short-term deprivation, the development of feeding behaviour, competitors, and comparisons with other rodents are also described.

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